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PREFACE

This number contains the papers read at a Symposium of the Society for Experimental Biology, which was held at Cambridge in July 1949. It is the fourth of an annual series of Symposium Reports. The Symposium for 1950 will be on 'The Fixation of Carbon Dioxide'.

The Society is deeply indebted to the Rockefeller Foundation and to the British Council for financial aid. We must also thank the British Council and the Foreign Office for assistance in making travelling arrangements for European visitors to the Symposium.

The editors wish to thank the members of the advisory committee which prepared the symposium programme; thanks in particular are due to Dr R. J. Pumphrey and Dr W. H. Thorpe. The Symposium was held in collaboration with the Institute for the Study of Animal Behaviour. We also wish to thank the Cambridge University Press for the kindness with which we have been assisted in producing this report.

J. F. DANIELLI
R. BROWN

Honorary Symposium Secretaries
Society for Experimental Biology

THE RANGE OF CAPABILITIES OF SENSE ORGANS

HEARING

BY R. J. PUMPHREY
Zoological Laboratory, Cambridge

I. INTRODUCTION

Everyone will be conscious that the senses of touch and hearing are quite different in man. In fact, the differences are so many and so obvious, that definitions of tactile and auditory senses based on them lead only to confusion unless a careful selection is first made.

If the term 'hearing' is to have any place at all in descriptions of the behaviour of any animal other than man, the definition of 'hearing' must be based on primitive and persistent attributes of the sense and not on structural or functional features peculiar to man or to primates or to terrestrial animals or to any other limited category of animals. Neglect of this obvious precaution has led different authorities to definitions of hearing which are unsatisfactory because they are arbitrary and exclusive and because, in consequence, a host of new terms with arbitrary and restricted meanings have to be invented to describe sensory responses which by definition are not 'hearing' but which are nevertheless obviously related to it. Thus, for example, 'hearing' has been defined as an attribute of animals possessing a cochlea, or a tympanic membrane or the capacity of frequency analysis or the capacity to respond to air-borne vibrations. None of these definitions is inclusive and none is free from ambiguity. Moreover, all must be complemented by other terms, Ferntastsinn, vibrational sensitivity, phonoreception, etc., to describe sensory responses excluded by the definition of 'hearing'.

It must be agreed that both touch and hearing belong to Parker's system of mechano-receptors. The end-organs of both senses are primarily sensitive to mechanical deformation. I want to suggest to you that an absolute distinction can nevertheless be made between tactile and auditory senses. The primitive function of touch is the location of moving objects in contact with the animal. The primitive function of hearing is the location of moving objects not in contact with the animal. So we can define hearing as follows. an animal *hears* when it *behaves as if* it has located a moving object (a sound source) not in contact with it. And *sound* can be defined as any mechanical disturbance whatever which is potentially referable to an external and localized source.

This definition of hearing has at least the merit of being objective.

Hearing is an attribute whose existence in a particular case can be checked by observation. Moreover, it is consistent with our knowledge of the evolution of hearing. It is true that man is degenerate compared with many other animals in his ability to locate a sound source, and in civilized life other functions of hearing are much more important. Probably this is the reason for the reluctance of physiologists to recognize directional sensitivity to sound as the fundamental and primitive property of hearing. But it is nevertheless true that when we both hear and feel a loud sound, we feel it at the stimulated point, we hear it outside ourselves, and though we may locate it incorrectly, we do locate it. A man's first response to an unexpected sound is to turn his eyes towards the source.

I cannot refrain from a slight digression at this point, because it occurred to me only recently that a very close analogy existed between the evolution of hearing in the mammalian line and the evolution of radar during the war.

Radar, as you know, is an electromagnetic device for (*a*) finding a target, (*b*) determining its position in polar co-ordinates, i.e. by determining its distance from and its direction from a datum point which is the position of the radar installation. The accuracy of range-finding depends on irrelevant considerations which we can ignore. The accuracy of direction-finding is directly proportional to the frequency and to the size of the aerial. And because the earliest radar employed only relatively low frequencies, the directional accuracy was rather low, although the installations were huge. The evolutionary pressure was at first wholly towards the employment of higher frequencies in order to increase the accuracy and reduce the size of the outfits. And at the same time subsidiary devices were employed to cheat the disabilities of low frequencies. One of these devices consists in principle of a nul comparison of the signals received on two directional aerials which could be rotated together through a wide angle and rotated through a small angle with respect to each other. Now the earliest mammals, we believe, were nocturnal creatures with indifferent eyes which must have depended on their ears for directional warning, much as man has learned to depend on radar in bad visibility. And we can note in mammals: (i) an extension of the range of frequency sensitivity upwards far above the reptile limit, (ii) the development of directional aerials, the pinnae, and (iii) the development of the necessary musculature and reflexes for directing the pinnae together but with some degree of independence. The nocturnal bats seem to represent the pinnacle of achievement in this line. Their upper limit of frequency sensitivity is said to be in the neighbourhood of 0·25 Mcyc./sec.

But there is a limit beyond which there is nothing to be gained by the employment of higher frequencies in a single radar installation, because as the directional accuracy increases, the time taken to find a target in the first instance also increases inconveniently. When extreme accuracy was required, as in the control of long-range artillery, this difficulty was circumvented by the use of two sets. The first could keep a continuous all-round watch and indicate immediately the approximate direction of an approaching target. The second, the fire-control set, could then search the indicated sector, single out the target from other objects and put the guns on to it with high directional accuracy.

Now consider the evolution of the primates. At first nocturnal, the higher primates are now diurnal and, alone among mammals, have developed foveate eyes and elaborated the oculo-motor reflexes for keeping the fovea on a moving target. Such an eye has precisely the properties which we were striving to give to fire-control radar, and it suffers from the same disadvantage, that it takes a long time to search a wide solid angle. The ear has taken over the functions of warning radar, it serves to put the eye on to the target; but great accuracy is no longer needed, and the devices associated with it, the large mobile external ears, the extrinsic muscles and associated reflexes, are in a fair way to disappear.

The parallel is curiously close and, I think, illuminating. It has, I hope, given point to my argument that the primitive function of the ear was direction-finding, and that our poor performance in this respect is directly related to our diurnal habits and our perfected eyes. It would be wrong therefore to judge the auditory powers of animals (except perhaps the higher apes) by our own standards.

Consider the following examples: a female cricket moves directly to a chirrupping male, an aquatic toad springs at a wriggling insect several centimetres away, an ichneumonid wasp lays eggs on a *Sirex* larva through an inch of bark and wood, a whirligig beetle detects and avoids sources of disturbance in the water-air interface, a scorpion turns towards and threatens a moving object on its substrate, a spider locates and identifies living prey in its web, a blinded fish in a water current maintains its position with respect to other fixed objects in the current, a bat avoids obstacles and catches moths in the dark. By my definition and provided stimulation in other modes can be excluded, as, in fact, it can, these are examples of hearing.

II. THE EVOLUTION OF HEARING

In any endeavour to trace the evolution of a highly specialized organ, a difficulty often arises in the application of what may be called the principle of continuity. It is repugnant to reason to suppose that eye or ear appeared suddenly in evolutionary history. Their evolution must have been a continuous process, and there must certainly have been antecedent organs which were potential eyes and ears and which, however crude and inadequate compared with their successors, were at every stage functional. But it is often not by any means self-evident what the functions were, and in consequence there may appear to be an awkward discontinuity. In such cases it is frequently illuminating to consider what functions are physically conceivable, and then to try to relate physical inference with evidence from other sources.

Although palaeontological evidence is of little direct assistance, a fairly clear plan of the evolutionary sequence can be constructed from the wide variety of auditory structures in living animals. This is particularly true of the vertebrates. The origin of the acoustico-lateralis system is lost, but it is clear on several grounds that the labyrinth is a specialized and structurally modified part of the lateral line and not conversely. The implications of this have not always been appreciated, and it will be useful to consider them from a physical point of view, for it will, I think, become apparent that the lateral line is functionally the missing link between the tactile sense and the ears proper of vertebrates.

An aquatic animal, since it is largely composed of water, has necessarily nearly the same compressibility and density as the medium it inhabits, at least so far as its soft tissues are concerned. As a consequence the mechanical discontinuity at its boundary is far less abrupt than it would be for an animal living in air. And a body moving close to the surface of an animal in water will deform that surface to an extent comparable with the deformation produced by bare contact.

If we assume that a tactile system capable of localizing contacts already existed, it is easy to see how hearing could have begun. Moving objects very close to the surface can be localized with sufficient accuracy, merely by determination of the point of maximum stimulation.

Now consider that some moving object, let us say a wriggling worm, is moved progressively away from the sensitive surface. A wriggling worm, considered as a source of sound, is physically equivalent to a doublet. It may be represented as a sphere oscillating about a mean position without change of volume. The frequency of this oscillation is unlikely to exceed 10 cyc./sec., equivalent to a wave-length of 140 m., so that all the dimensions of the system we are considering are small compared with a wave-length. At distances greater than a wave-length from a source of sound, the displacement amplitude of particles of the medium due to the sound is inversely proportional to the distance of the source, but at distances from a doublet much less than a wave-length the amplitude is inversely proportional to the *cube* of the distance. Fig. 1 illustrates the change of amplitude at a surface and the change of gradient along it as the distance of the source changes. It will be noted that both maximum amplitude at the point nearest to the source and the gradient along the surface fall rapidly with increasing distance. But the source can still be located accurately if three conditions are satisfied, namely, (1) the range of sensitivity at sensitive points is sufficiently increased, (2) the extent of surface over which simultaneous comparisons of amplitude can be made is sufficiently increased, (3) the sensitivity of the most sensitive elements is sufficiently increased.

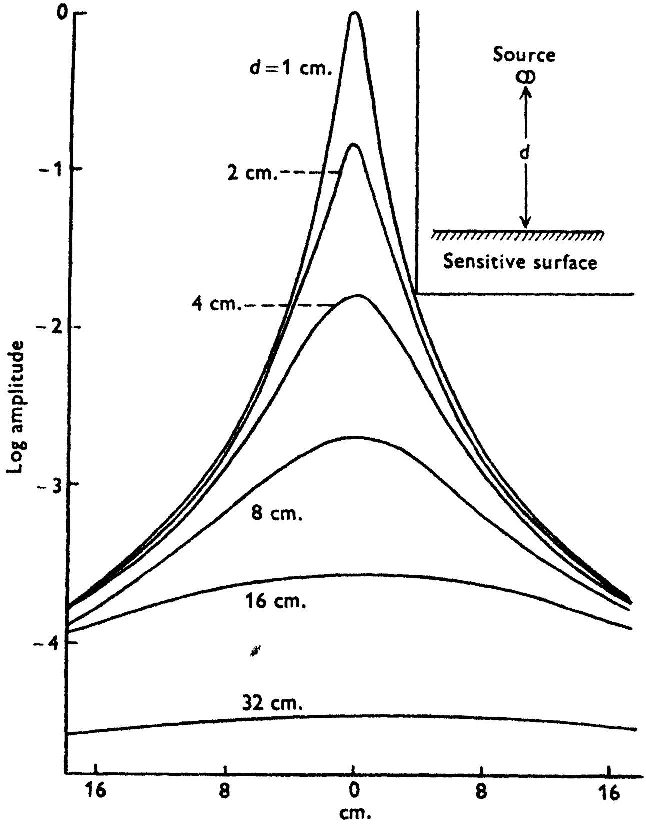


Fig. 1. The graph shows the change on the displacement amplitude along a surface for varying distances (d) between the surface and a doublet source of constant frequency and power ($d \ll \lambda$).

These three conditions seem to be fulfilled by the lateral line of fishes as far as is theoretically possible.

(1) The end-organs are grouped so that a considerable number of hair cells of widely different threshold are included in each group. This arrange-

ment is characteristic of *all* known auditory organs. Fig. 2 shows that in the optimum case, if there are *n* end-organs each of a working range *m*, the working range of the group is m^n. So that if a single end-organ has a working range of 30/1 in intensity, a group of six may have a working range of $10^9/1$.

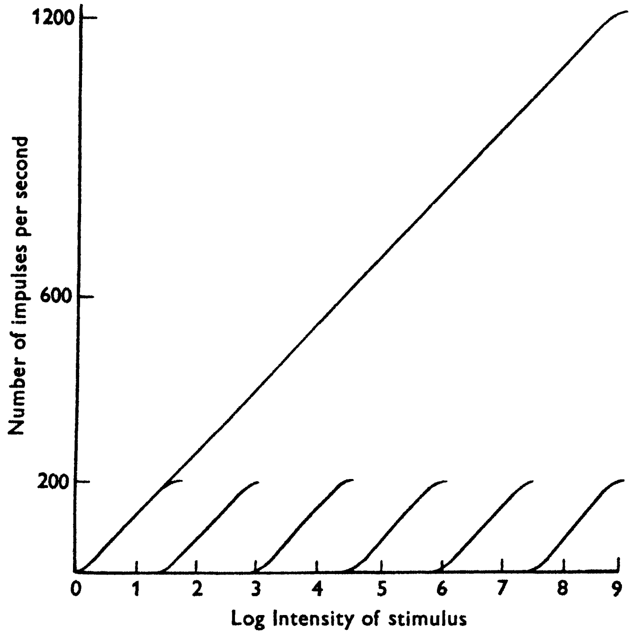


Fig. 2. Explanation in text. It is supposed that the six end-organs are independently innervated and that the afferent fibres reach a common centre in which the impulses from the group produce an additive effect. $10^9/_1$ is perhaps a fair average range for auditory organs. For the human ear in the middle of its frequency band the range is about $10^{12}/_1$.

(2) It is evident from inspection of a fish that the lateral-line system utilizes the whole length, height and breadth though the density of groups of hair cells varies. And unlike the tactile system which has segmental innervation, the lateralis fibres all enter the same nucleus in the medulla, so that simultaneous comparison of the degree of excitation over the whole surface is possible (Fig. 3).

(3) I have mentioned that the sensitivity of the most sensitive end-organs of the lateral-line system is extraordinarily high, so improbably high in fact, that doubt has always existed about the accuracy of estimates in the minds of those who have not actually worked on them. So a brief parenthesis summarizing recent indications about the origins of this sensitivity may not be out of place, although the story properly starts at the other end of the evolutionary scale. Gold & I (1948) have recently shown that the

selectivity of the resonant elements of the human cochlea is about two orders of magnitude higher than could reasonably be expected of a passive system. It has been known for about twenty years (Wever & Bray, 1930) that sounds impinging on the mammalian ear excite not only impulses in the auditory nerve but also an additional electrical effect arising apparently from the cochlear hair cells and nowadays generally referred to as the microphonic potential. Conversely, Gersuni & Volokhoff (1936) showed that direct stimulation of the cochlea by alternating electric currents caused an auditory sensation as if the current was equivalent to an acoustic stimulus of the same frequency. Gold (1948) has suggested that these observations are consistent with the action of the cochlear hair cells as regenerative amplifiers, an action which would provide a reasonable explanation not only of their selectivity in the cochlea but of their sensitivity. (The minimum audible energy for the human ear is about 10^{-12} erg, the minimum *visible* energy is about 10^{-10} erg.) If this view is correct, my own 10-year-old observation (1939) that the microphonic potential is not, in fish, confined to the auditory part of the labyrinth acquires a new significance, as does the recent claim by de Vries (1948) that a microphonic potential can be recorded from lateral-line organs. In default of evidence to the contrary, it is reasonable to suppose that *all* end-organs of the acoustico-lateralis system are regenerative, and that their maximum sensitivity is consequently only

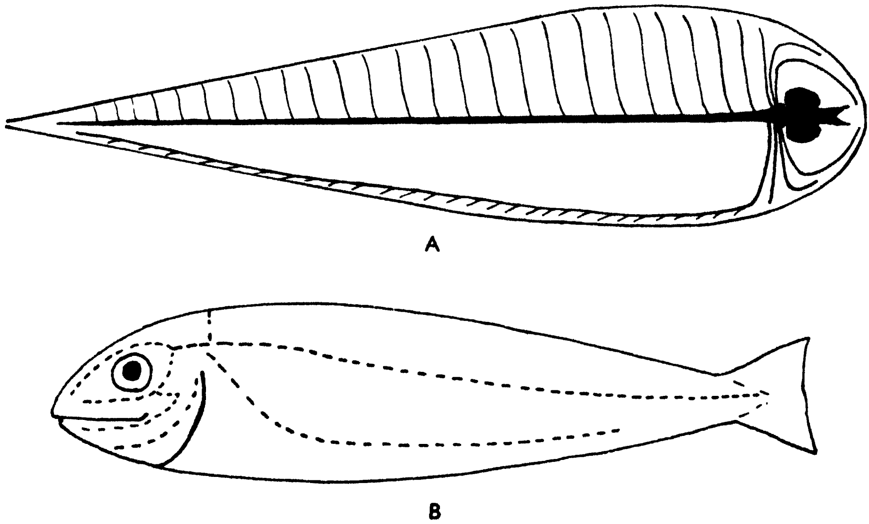


Fig. 3. Diagrams to show (A) that the lateralis system utilizes the whole available extent of the surface of a fish, (B) that, though the tactile innervation is segmental, the lateralis innervation has a common centre in the medulla, so that simultaneous central comparison of nerve signals from the whole extent of the surface is feasible.

limited by thermal noise and by considerations of internal stability. Such end-organs, if we judge by the activity in the afferent fibres supplying them, have no true threshold. Under conditions of zero stimulation, there is a continuous 'rest' discharge in the afferent fibres. This also we should expect is a regenerative system on the edge of instability; it suggests an analogy with the super-regenerative type of radio receiver. It may be significant therefore that a similar 'rest' discharge is found in the afferent fibres of all auditory organs, invertebrate as well as vertebrate, which have so far been investigated, and, indeed, in sense organs of very great sensitivity responsive to stimulation in other modes. Quite possibly regeneration plays a more extensive role in sensory mechanisms than has been suspected hitherto.

We have seen that so long as the source is a doublet and its distance is not too great, the lateralis system is physically competent to determine not only its direction but its position. That, in fact, it may do so has been demonstrated by Scharrer (1932), Kramer (1933), Dijkgraaf (1933) and others. The failure of v. Frisch to demonstrate lateral-line responses to sound by the training method is therefore not a proof that the lateral line is not an auditory organ, but an indication that the conditions of stimulation were inappropriate.

The direct experimental evidence comes naturally enough from small and easily handled animals from superficial waters. But it is natural to suppose that the lateral line would be most serviceable in deeper waters where the eyes are of little use. Muir Evans examined the nervous system of the scabbard fish, a large predator living on other fish and caught at considerable depths off the Canary Islands. He found no abnormal development of the olfactory or visual centres, but a disproportionate enlargement of the lateralis centres in the medulla.

It is worth noting therefore that Fig. 1 can be scaled up. Suppose that the source is a fish the size of a mackerel instead of a small worm. A hundredfold increase in length corresponds to a millionfold increase in volume and hence in power output. So the other linear dimensions in the figure can be increased one hundredfold (from centimetres to metres) for the same end-organ sensitivity. It is not impossible that the scabbard fish can detect and locate its prey in movement at distances up to 16–32 m. using the lateral line alone.

As the distance of the source is increased, the lateralis system must ultimately become inadequate. The gradient along the surface will become eventually so low that the differential threshold of the end-organs between extreme points on the animal's surface is not exceeded, so that no clue to direction and position of the source exists; and the peak displacement at an organ will become comparable with the effect of thermal agitation which sets an absolute limit to sensitivity. The lateralis system is essentially a short-range auditory system.

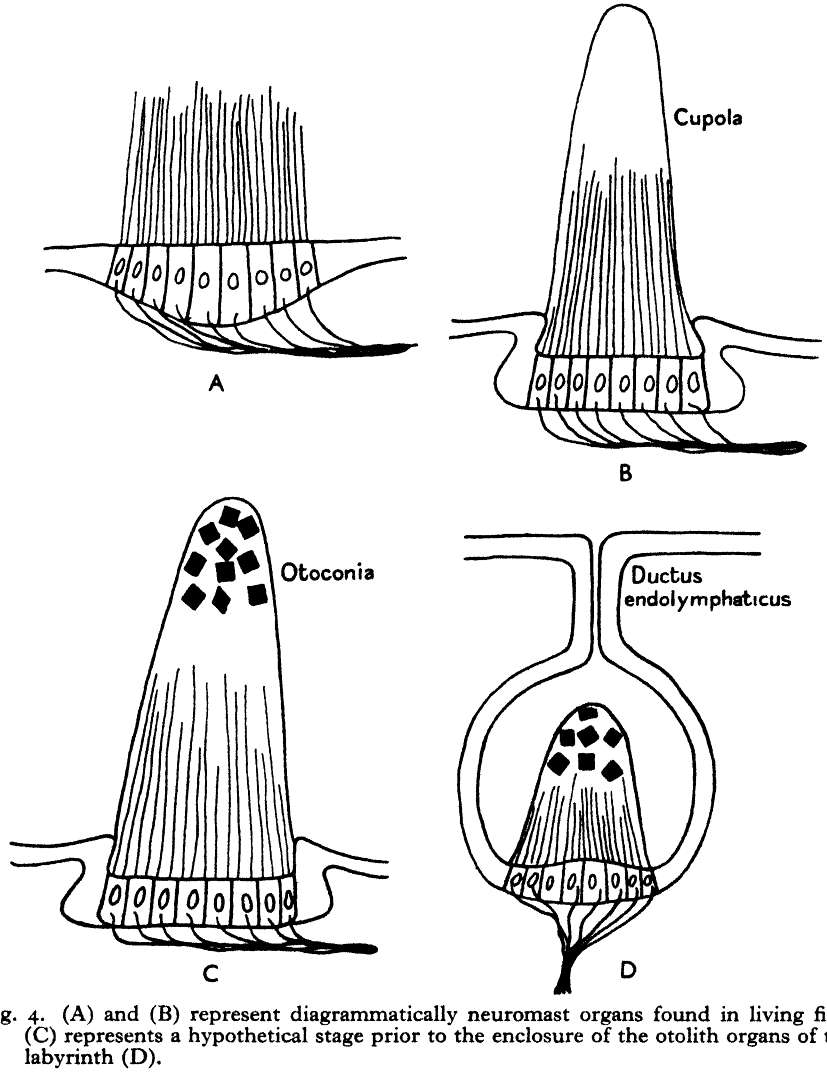


Fig. 4. (A) and (B) represent diagrammatically neuromast organs found in living fish. (C) represents a hypothetical stage prior to the enclosure of the otolith organs of the labyrinth (D).

If we consider the motion of a fish in the path of sound waves from a distant source, we see that it must correspond closely with that of the medium. The fish in a train of plane sound waves has no fixed co-ordinate system by which it can measure the displacement of particles of the medium, since its own particles are undergoing the same displacement. The fish as a whole is virtually transparent to sound and cannot readily utilize the energy of sound waves to excite its end-organs. In fact, the maximum deformation to which a single end-organ would be subject would be equal to the peak displacement amplitude of the medium multiplied by the ratio of the length of the end-organ to a quarter of a wave-length. The ratio is about 10^{-6} at the frequency we have been considering.

There are two ways out of this dilemma, both of which are utilized by fish. If one end of an end-organ is firmly anchored to a mass denser than water, its deformation is greatly increased. If the mass were infinitely dense, it is obvious that it would not move at all and consequently would supply the fish with the fixed reference point needed to register both the magnitude and the direction of the displacement of the medium.

It is not so easy to see intuitively what happens with a mass only slightly more dense than water, but by applying Stokes's law, it can be shown that the utilization of a mass two or three times as dense as water will allow increase in sensitivity approaching that which would be obtained with an infinitely dense mass.

Alternatively, if there is a bubble of a medium much more compressible than water, the displacement amplitude of water particles in its vicinity will be greatly increased and there will be a corresponding increase in the deformation of an end-organ close by. The utilization of this second device is confined to fish with air bladders. The utilization of the first began before the fossil record.

At first sight the utilization of a dense mass in association with the lateralis organs appears to require an awkward jump in the evolutionary process, but the difficulty is probably more apparent than real.

The immense quantities of chalk and limestone in the world are evidence enough that animals find it easy to precipitate calcium carbonate from a calcium-rich medium, and the formation of otoconia of calcite in the cupolae of the lateral-line organs is the sort of thing that might have happened by accident in an epoch when the calcium content of sea water was higher than it is now. The density of calcite is about 2·6, amply sufficient to raise the sensitivity by a factor of 10^8 for low-frequency plane sound waves.

Nevertheless, a lateral-line organ loaded with otoconia cannot have been an unmixed blessing. Such an organ must be susceptible not only to the stimuli which are adequate for the unloaded lateralis organs but, in addition, to deformation by gravity, and linear and angular acceleration. It is not surprising that no fish with external otoconia survives, for the enclosure of the labyrinth and the beginning of the process of sorting out these classes of stimuli must have been an immediate consequence of their development.

Enclosure of the labyrinth, save for a single external connexion, the *ductus endolymphaticus*, protects the end-organs completely from external streaming. We need not be concerned further with the end-organs of the semicircular canals which have lost or never had otoconia and which have successfully achieved a geometry that renders them sensitive only to angular acceleration. This arrangement is found in all living vertebrates. The other groups of end-organs in the labyrinth still have problems to solve. They can now be regarded as the *anlagen* of utricle, saccule and lagena. In such systems deformation of the hair cells must result from gravity and from linear and angular acceleration as well as from the effect of sound waves. The effect of angular acceleration is reduced though not eliminated by siting the end-organs near the centre of gravity of the animals. But separation of the effects of gravitation and acceleration from those of sound can only be on a temporal basis. The auditory end-organs or their centres must somehow reject signals resulting from slow deformations, the gravity organ (the utricle) or its centre must somehow reject signals resulting from fast deformations. It will be evident that the problem is a problem of frequency discrimination. v. Frisch and others have proved that many fish are capable of distinguishing the pitch of sounds over a wide range; in all probability they owe this faculty to the primitive necessity of distinguishing sound from gravitation. But it has generally been supposed that the sorting was central rather than peripheral, since the saccule and lagena resemble the utricle so closely that it was difficult to believe that their responses to deformation were very different. Lowenstein (1948), however, has pointed out the sensitivity to sound of the *macula neglecta*, most appropriately named in this connexion. The hair cells of this macula are unloaded, and it is situated in the cavity of the saccule. Reference to the diagram (Fig. 5) will indicate that movements of the saccular otolith, in addition to deforming the hair cells of its own macula, will be accompanied by compensatory movements of the endolymph which may deform the hair cells of the macula neglecta. In the first case the deformation will be proportional to the displacement, in the second case it is likely to be proportional to the velocity of streaming, i.e. displacement × frequency. In the limit for very slow displacements the macula neglecta will be unexcited. A comparison of the responses of macula neglecta and macula sacculi clearly could be a basis of frequency discrimination.

There is no time to carry this story further. I have gone so far only in order to emphasize the following points which seem to me very significant:

(1) In the vertebrate line, hearing organs antedated sense organs responsive to gravity. The response to gravity is, so to speak, a by-product of the improvement of hearing.

(2) The faculty of frequency analysis is, in its turn, a by-product of the necessity of discriminating between responses to sound and to gravity.

(3) There is no reason to suppose that the history of auditory structures in aquatic invertebrates differs in essentials from that of vertebrates.

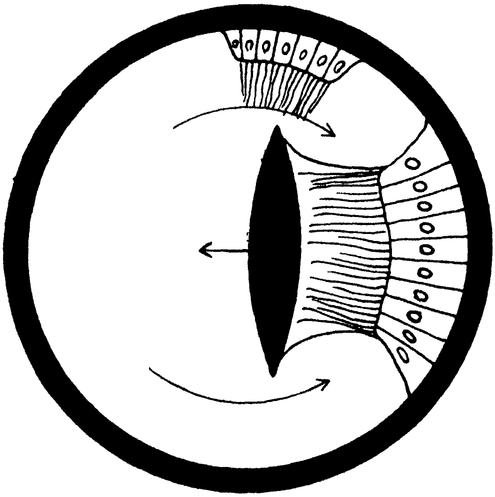


Fig. 5. Explanation in text.

If these conclusions seem trivial, I would like to remind you that the pendulum has swung far the other way. Although Hensen (1863) proved nearly a century ago that the otocysts of some Crustacea were auditory organs, he is rarely quoted. Otocysts are always now called statocysts, and it is impossible to read any modern book of comparative physiology without gaining the impression that while most aquatic invertebrates respond to gravity, most of them are deaf. I hope I have made it clear that the more reasonable conclusion is that an aquatic animal could not respond to gravity unless it heard.

III. HEARING AND COMMUNICATION

I would like to remind you also that 40 years ago it was fashionable to believe that the vast majority of animals were not only deaf but dumb. The exceptions admitted were birds and mammals and a few insects, and it was even doubted whether these insects could hear the racket they made.

Now the position is changed or at least changing. One can perhaps distinguish stages in the process. In the first stage Regen's papers (1912–26) gave a definitive proof that some, at least, of the insects which made noises could hear in the sense I have defined, i.e. that from the behaviour of one insect it could be established that it referred the noise made by another to a source external to itself in a particular direction. He also proved that such insects possessed considerable powers of discrimination; they recognized the noises of their own species and were not easily fooled by imitations. Later, Albrecht Faber (1929–32), in a detailed and invaluable study of the grasshopper genus *Chorthippus*, demonstrated not only that the noises of the different species were specifically different, but that within each species there is what must be regarded as a language. He discriminated up to twelve different songs or phrases, each evoked by a particular emotional situation. Of these the most important were:

(1) The wonted song (gewöhnliche Gesang) of males, alone or in company (no female present).

(2) The serenade (Werbegesang) of a single male in the presence of female which if uninterrupted ends in

(3) The shout of triumph (Paarungslaute).

(4) The rivals' duet (Rivalenlaute) initiated by the intrusion of another male upon the serenade.

(5) Song of the male during copulation.

(6) Various transitional passages and modifications of the above contingent on special circumstances.

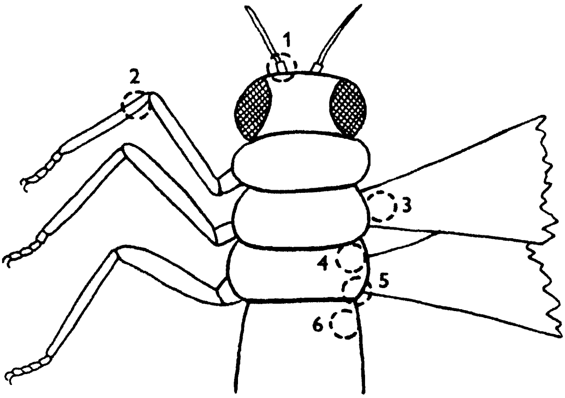
In some species the serenade may be missing altogether. In others it is of great length and elaboration, not simply repetitive but a continuous development of a theme in two parts. The bowing of the tegmina on the two sides is different and the phase relations of the left and right legs change during the performance. I have confirmed many of Faber's observations on the two species of his series which occur in England, and I have also observed a third which was not available to him but which has a love song equal in elaboration to any he describes. And, though I was originally sceptical, I am now perfectly satisfied with the general accuracy of his description. I conclude that we have here a symbolic emotional language, symbolic because the musical phrases appear to be both expressive of a particular emotional state in the singer and evocative of a complementary emotional state in the auditor. It is of a lower order of symbolism than human speech, but apparently quite comparable with the language of non-human mammals and birds.

Faber's observations were possible because these grasshoppers are common and easily observed, and because a large part of their sound output is in the human auditory range. But it would be very previous to assume that the complexity of their language is exceptional. It is becoming evident that it is the deaf and dumb insect which is exceptional, and that sounds used for communicative purposes have been overlooked either because they were inaudible to a human observer unassisted by special equipment or because they were supposed to be accidental. For example, although *Cicada* song has been known for millennia, it was only last year that Ossiannillson (1949) found that not only Cicadas but the whole of the great group of bugs called the Auchenorhynca were songsters. Within the last few years Pierce at Harvard (1948) and Pielemeyer (1946) at Philadelphia have shown that many supposedly dumb crickets and grasshoppers have a large supersonic output. And recently it has been confirmed, as Mayer long ago (1874) suggested, that the flight notes of gnats and mosquitoes are specific sexual recognition signals with a directional sign. The female is attracted by the flight noise of a male swarm, and the flight noise of the female attracts and elicits the clasping reflex from the nearest male. Quite evidently it is safer to assume that an insect can hear than to assume the contrary. It is probably legitimate to generalize this assumption for all truly terrestrial animals.

It must be remembered that the chordotonal system of insects which is in some respects the functional analogue of the lateralis system of the fishes consists of end-organs which primitively were probably segmentally arranged, though in all living insects there are concentrations of them at particular points. The figure shows the positions in which chordotonal organs associated with devices for matching to air are known. Such ears seem generally to be associated principally with sexual communication. But their absence does not mean deafness, for certainly many Hymenoptera, Orthoptera and Coleoptera, in which the tibial concentration is well developed, can hear, although there is no eardrum, and their sensitivity is probably much greater to displacements of the substrate than to displacements of the air (cf. also the Arachnida).

A complementary change in outlook towards aquatic animals is also being enforced. So far as vertebrates are concerned it has been shown that the lateral-line system, so long a mystery, is an auditory organ which functions in exactly the way which a physical analysis leads one to expect, and that it represents a necessary stage in the development of auditory organs of greater range and sensitivity. Just as for the insects, so for the fishes, it was once supposed that the ability to make noises was possessed by a few exceptional groups like the Sciaenidae which happen to make a great deal of noise in a band to which the human ear is sensitive. But more careful observation is showing that many fish have some noise output in the range audible to man and, of course, everything that moves must produce infrasonic noise.

It is also becoming apparent that the silence of deep waters is a myth. They are full of noises. Some are certainly due to Crustacea, but many types have been recorded which have not been identified. On the whole it would be surprising if it were otherwise. The important receptors for gathering information from a distance are the eyes, the nose and the ears. The visual field which for a terrestrial animal may be kilometres deep is reduced for fish to metres at the most and in turbid waters to centimetres. The nose of an aquatic animal is similarly handicapped, for the diffusion of volatile substances is enormously slower than in air and the currents which might aid their spread are also slower. On the other hand, conditions for sound transmission are better than in air.



1.	Diptera	Culicidae, Chironomidae, Cecidomyidae
2.	Orthoptera	Gryllidae, Tettigoniidae
3.	Lepidoptera	Nymphalidae
4.	Hemiptera	Corixidae
5.	Orthoptera	Acridiidae
	Lepidoptera	Noctuidae
6.	Lepidoptera	Geometridae, Pyralidae
	Hemiptera	Cicadidae

Fig. 6. Diagram of a generalized insect to show the positions in which groups of chordotonal sensilla associated with a tympanic membrane or other air-matching device have been found.

I think on balance the evidence justifies the conclusion that hearing is a well-nigh universal attribute of animals, that communication by sound, whether by simple specific and sexual recognition signs or by a more extensive vocabulary, is very widespread, and that in consequence some power of analysis in addition to directional sensitivity is equally widespread. So even if you prefer a definition of hearing which implies an analytic process, there is no justification for restricting it to mammals and birds which have a cochlea. The cochlea represents one method of analysis out of at least three possibilities and two other methods are certainly employed by animals.

The surface of the problem has hardly been scratched, but the result of excavation so far is clearly in the nature of a warning to students of behaviour not to ignore hearing when attempting to control an experimental situation, or, what is just as serious, to assume that a situation which appears silent to a human observer is silent to the experimental animal. Even when the latter is a mammal a small displacement of the band of maximum sensitivity may make a large difference. A rat's maximum sensitivity is probably two to three octaves higher than a man's. And if you go into a room where rats are kept and talk in an ordinary voice you can see the rats wincing in unison every time you come to a sibilant. As Rayleigh showed, the sound *sss* has most of its energy in the band between 8 and 12 kcyc./sec., to which the human ear is relatively insensitive, but which probably includes the peak of sensitivity for the rat. For him the hiss of a snake is likely to be louder and more shattering than the lion's roar is to us.

I have tried to select aspects of hearing which show that its problems are general problems which ought to be looked at in perspective, and which are of general interest to students of behaviour. Hearing has been my principal scientific interest for the past 15 years, and it may be thought that I have over-emphasized its importance. But even if this is true, it is certainly true also that the role of hearing in animal behaviour has been underestimated for many years and its study correspondingly neglected.

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VISION

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A very common misconception tends to arise when visual capacity is under discussion. I refer to the rather widespread idea that the eye has reached its highest developmental form in man and that the eyes of many of the 'lower' animals mark stepping stones in the evolution of the most useful and intricate one of all, the human eye. In so far as this idea has any foundation it applies only to mammals where, with the exception of the squirrels, whose whole retina apparently has as high a resolving power as the human fovea (Rochon-Duvigneaud, 1920), there does seem to be a steady increase in visual acuity, colour vision and probably binocular and stereoscopic vision as one ascends the evolutionary scale (Walls, 1942). If one takes the whole animal kingdom for comparison, the human eye does not show up so very well. Our visual acuity is definitely poor as compared with many birds, our colour vision does not cover as much of the spectrum as that of the honey bee, and the eyes of many insects recover more quickly from a stimulus so that they can more effectively distinguish rapidly moving objects (Autrum, 1948). The high visual capacity characteristic of man is due to the great development of the associated cerebral structures rather than to a very highly developed eye.

This paper will deal, in the main, with the vertebrate eye about whose structure and function there is a fair body of systematic knowledge. The general pattern of all vertebrate eyes is much the same; Pl. 1, fig. 1 is a diagrammatic representation of a section through the human eye. This consists, roughly, of a dioptric apparatus made up of the cornea, lens and vitreous body, which casts an inverted image of external objects on to the retina, where, through the mediation of one or more photochemical pigments, the light energy is transformed into something which can stimulate the fibres of the optic nerve so that a complicated pattern of nervous impulses is transmitted to the brain. The capacity of such an eye to distinguish different degrees of brightness (the intensity of the stimulus) depends fundamentally on the reactions of the photochemical pigments involved. These appear to be much the same for all vertebrate eyes and are based on a small group of substances of which visual purple (the pigment responsible for night vision in man) is the best known. It is probable that all the visual pigments of the vertebrate eye are chemically related to visual purple. Two of the invertebrate eyes which have been studied from this point of view, those of *Limulus*, the horseshoe crab, and *Loligo*, the squid, also possess a pigment which seems to be very closely related to visual purple (Hartline & McDonald, 1947; Bliss, 1948). The sensitivity of the retina in vertebrates (but not apparently in *Limulus* and *Loligo*) depends on the concentration of photochemical pigment present at any given moment. The exact relationship between the two is not really clear, but it does not seem to be as direct as Hecht (1919) believed and we have mostly been taught. The concentration of pigment, in its turn, depends on the state of adaptation of the eye and on the type of receptor cell predominant in its retina. Thus a power of dark adaptation comparable to our own is associated in all vertebrate eyes with rods in the retina (Schultze, 1866), and, in general, animals with predominantly rod retinas are found to be night feeders and to live in dark places (rat, owl, hedgehog), while those whose activity is diurnal (some snakes and lizards, many birds) have mainly cone retinas and rather poor dark adaptation.

It would be most inaccurate to think of the vertebrates as strictly divided into a diurnal and a nocturnal group. Various adaptations have been developed in many species to allow activity to be spread more evenly over the extremes of night and day illuminations. Such mechanisms are often designed to protect a sensitive retina during daytime activity, and include the pupil reaction of most mammals and many reptiles as well as the retinal photomechanical changes of fish, Amphibia and birds. A device for *increasing* the sensitivity of eyes which are either strictly nocturnal or adapted for 24 hr. activity is the tapetum, often found in the larger terrestrial mammals. These have a high rod to cone ratio to ensure sensitivity, large eyes with large retinal images to give a reasonable resolution in spite of relatively few cones, and a tapetum to compensate for the consequently lowered brightness of the image. In strictly nocturnal animals with pure rod retinas visual acuity is poor anyway, and a tapetum is helpful in allowing the maximum use to be made of any light which does reach the retina. We will return to this question of visual acuity in a moment.

Walls (1942) divided the vertebrates into five rough groups according to habit. There are the *diurnal* animals which are active chiefly by day and whose eyes are incapable of any considerable dark adaptation or of night vision. Such animals always have pure cone retinas and are largely independent of any of the protective mechanisms just described; they include the turtles with immobile pupils and a slight, slow retinal pigment migration, the diurnal lizards with little pupil movement and probably no pigment migration, and the diurnal snakes with neither mobile pupils nor retinal changes. Next there is the *crepuscular* group, members of which have retinas made more sensitive by the addition of some rods, but which show no adaptation to extremes and therefore tend to be dazzled at high and insensitive at low illuminations. This group includes such secretive snakes as *Chemophera* and the mud-loving rainbow snakes. It is doubtful whether their rods contain visual purple. Members of the third group probably possess the most generally useful eyes of all. These are the 24 hr. or *arhythmic* animals which are about equally active by both night and day. All the members of this group possess both rods and cones, have good dark adaptation and use some protective device, either a mobile pupil or retinal movements or both. Nearly all mammals fall into this group or the next (nocturnal), the larger species tending more towards 24 hr. activity. The group also includes many teleost fish, the slit-pupilled reptiles which tend to hunt at night but, being poikilothermic, enjoy basking in the sun, and frogs which rely on photomechanical changes to protect their retinas and have also developed protective intraocular filters in the form of yellow oil droplets. The *nocturnal* group contains most of the smaller mammals and tends to overlap the arhythmic group, having usually more rods and better protection against dazzle; where protection is due to the pupil only this is often slit-shaped when constricted, thereby ensuring more effective closure than is possible with a ring-shaped sphincter. The last group of *strictly nocturnal* animals possesses pure, or nearly pure, rod retinas and little or no protection from bright light. In addition, these animals usually have such poor visual acuity that they have become largely dependent on hearing and smell rather than on vision. This is the case in nearly all rodents which are so vulnerable at high illuminations that they never emerge from their holes by day.

While the sensitivity of an eye to light and to changes in light fundamentally depends on its photochemical mechanism, the acuteness of vision, or ability to distinguish shapes and details, is a property first of its dioptric apparatus and secondly of its retinal structure. These can usefully be compared with the lens and plate or film of a camera, the former determining the accuracy of the image and the 'grain' of the latter the fidelity with which it can be reproduced. In pure rod eyes the retinal structure is always the limiting factor for visual acuity, and in these eyes it is always poor. This is due to the fact that in such retinas the 'convergence' of visual cells on to individual fibres of the optic nerve is very great, in other words very many (often several hundred) rods tend to be attached to the same final common path—the optic nerve fibre. The difference between rod and cone retinas in this respect can be clearly seen by comparing Pl. 1, fig. 2 and Pl. 2, fig. 1. Pl. 1, fig. 2 is a section through the retina of the rat, an animal which belongs to Walls's group of nocturnal animals and which possesses too few (if any) cones to affect its visual capacity. The proportion of visual cells to the optic nerve fibres serving them can be judged by the relative thickness of the outer layer of rod nuclei and of the ganglion cell layer, each outer nucleus representing one visual cell and each ganglion cell one nerve fibre. In the rat an outer nuclear layer approximately 10 cells thick is associated with a ganglion cell layer never more than one cell thick and in which the nuclei are often quite widely separated horizontally. Let us compare this arrangement with one in which there is high visual acuity but poor dark adaptation. Pl. 2, fig. 1 shows a section through the human fovea centralis which is generally considered to be devoid of rods. Here the thicknesses of all the nuclear layers are much more nearly equal, although there is still some convergence on to the ganglion cells and optic nerve fibres. The development of a high visual acuity is, in the first instance, always at the expense of sensitivity, which appears to require the connexion of a large number of visual cells (which may be thin and closely packed as in the eel) to each optic nerve fibre and which must, therefore, be the result of a summation of responses as well as of a high concentration of photopigment. In the case of animals in the 24 hr. group the difficulty of combining the high sensitivity necessary for night vision with the acuity which makes day vision worth while is overcome by developing a mixed rod and cone retina. Where the eye can be large enough as in the larger mammals (e.g. horse), the relative coarseness of the retinal 'grain' (the retinal area served by one optic nerve fibre) does not matter so much, since the size of individual receptor cells is not increased while the size of the image is. Where such large eyes have not been developed, as in the primates and man, the solution has been by the differentiation of a special pure cone area with a high visual acuity (the fovea centralis) in the middle of a mixed retina dominated by rods, which is sensitive enough at low illuminations but whose visual acuity is much poorer than most people realize (Pl. 2, fig. 2).

On the whole, birds are diurnal in habit and possess a very high visual acuity. This is accomplished by a combination of both the methods just described. Birds' eyes are, relative to the size of the head, enormous, and the diurnal ones possess the most highly developed foveae we know, equalled, but not surpassed, in lizards. Some birds have two foveae, one central, used for monocular vision at right angles to the head, and one temporal which can combine with that of the other eye to give binocular vision straight forward. The squirrels are the only mammals with a visual acuity comparable to that of man and the higher primates; they are also the only mammals to possess a pure cone retina. This enables them to see clearly without the necessity for eye movements, for their whole retina is as efficient from this point of view as our fovea, but it also means that they have entirely sacrificed night vision. In Table 1 the visual acuities of the few animals for which it has been measured are compared.

Table 1. *Visual acuities (separation of two parallel lines) of different animals (from Walls)*

These figures come from various sources and were obtained under different conditions. They are, therefore, only very roughly comparable to one another.

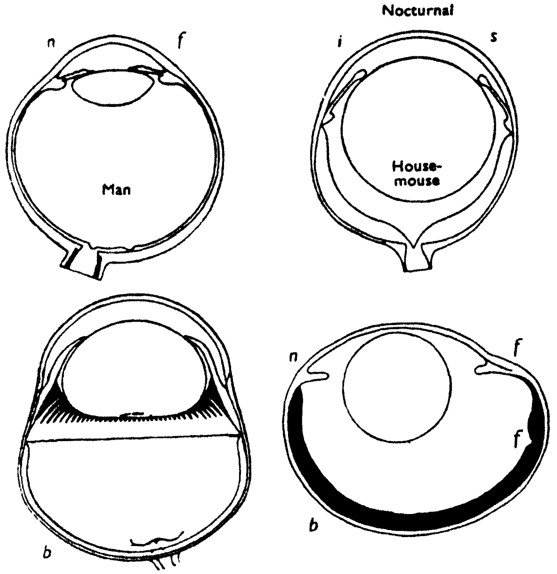
	Visual angle (min.)	Corresponding distance on retina (μ)
Diurnal animals:		
Man	0·64*	2·76
Chimpanzee	0·47†	1·86
Rhesus monkey	0·67	2·33
Cebus monkey	0·95	3·31
Pigeon	1·54	2·79
Gamecock (no fovea)	4·07	9·58
Nocturnal animals:		
Cat	5·5	—
Alligator	11·0	—
Opossum	11·0	—
Rat	26·0	23·8
Rat (albino)	52·0	47·7

* Mean of 7 figures from different sources.

† Mean of 2 figures from different sources.

Visual acuity is finally dependent on the retinal structure, but a retina as well developed in this respect as that of the squirrel would be wasted in an eye whose optical system could not produce a sharply focused image in the right place, as well as one as large as individual circumstances permit. Where, as in birds, a large image cannot be achieved by a marked increase in the size of the eye as a whole, the solution is usually to enlarge the *posterior segment* as much as possible. This, of course, entails an increase in the distance between the lens and the retina with a consequent flattening of the cornea and lens to increase the focal length of the optical system. This adaptation reaches its farthest point in man. The fish lens has an extremely high refractive index and can produce a large near image; in consequence the whole fish eye is often flattened (Text-fig. 1).

The large eyes of some nocturnal animals, so long as the pupil is enlarged in proportion, increase sensitivity by admitting more light. Unless the increase in pupil size is accompanied by an increase in the size of the lens there will be a troublesome increase in spherical aberration. Such an increase in the size of the lens will throw the optical centre of the eye backwards and the image behind the retina unless refractive power is also increased by increasing the curvature of lens and cornea. This, in turn, will increase the size of the image and still further depress visual acuity unless the animal has room in its head for an over-all enlargement of the eye to push the retina backwards. Thus, once again we recognize the antagonism between acuity and sensitivity. The eyes of nocturnal animals, then, always have a large and powerful optical system, large pupils and, where possible, very large eyes. Large eyes in which the posterior segment is increased in length but not in width (tubular eyes) are characteristic of nocturnal species which have retained better vision, such as the owls, lemurs and some deep-sea fish. The optical structures of a nocturnal animal with poor vision, the mouse, a nocturnal animal with relatively good vision, the lemur, and two diurnal types, man and a diurnal fish, are compared in Text-fig. 1.



Text-fig. 1. Variation of general ocular structure with habit. Diagrammatic horizontal sections through two diurnal eyes with good vision, man (top left-hand) and the teleost fish *Serranus scriba* (bottom right-hand), one nocturnal eye with good vision, the lemur (bottom left-hand) and one nocturnal eye with poor vision, the house mouse (top right-hand). (After Walls.)

For one reason or another many animals do not require and do not have any specific mechanism for accommodation. Eyes with poor visual acuity, either because they are very small or because they have a rod retina, will get little, if any, benefit from a mechanism for fine adjustment. In addition, since the absolute size of the visual cells changes so little throughout the vertebrates, these will be relatively long in a small eye, while at the same time the lens must have a short focal length and therefore a large depth of focus. Another type of eye which has no need of a separate focusing mechanism for objects at different distances is that with a pupil which contracts to a pinhole or slit in the light.

However, most vertebrates which depend on their eyes have some means of altering the focus of their optical system. This is done either by altering the distance between the lens and retina or by altering the shape, and so the focal length, of the lens. The first method is employed by fish and Amphibia, the second by reptiles and birds and by mammals. All these alterations are accomplished by the intraocular muscles.

Elasmobranch fish are hypermetropic (up to as much as 15 dioptres), and their accommodation is, like ours, for near vision; it is accomplished by moving the lens forwards towards the cornea. They may have as much as 20 dioptres of accommodation and so are able to focus on very near objects (Franz, 1931). Teleost fish, on the other hand, are myopic and accommodate for distant vision by moving the lens towards the retina and sideways so as to bring the image on to the fovea (if present), which is also the retinal area involved in binocular vision. For fish 'distant' objects will never be more than about 20 ft. away, since underwater visibility beyond this must be very poor indeed. In all fish the cornea is, of course, eliminated as a refractive structure, and this function of the lens becomes very much more important in consequence. Fish lenses, therefore, have to lie much farther forward in the eye—if possible to protrude beyond the head—and to have a high refractive index. They also tend to be very convex, in fact about spherical.

The effect of the change from under-water to air vision can be seen in the amphibious Amphibia, where the cornea is more curved and the lens flatter and farther back in the bulb. Amphibia have comparatively little or no accommodation, perhaps 5 dioptres (as against our 13·5 in childhood and 6 at the age of 40), and are not apparently able to compensate for the changes in refraction due to the change from air to water and vice versa. Newts are emmetropic under water and must, therefore, be highly myopic in air when the corneal refraction is added to that of the lens. Frogs, on the other hand, are emmetropic in air and therefore hypermetropic under water when they lose the use of the cornea.

The possessors of the highest degree, as well as the quickest, accommodation among the vertebrates are to be found in the lizards and birds, and all employ the same method. It is easy to see that swift-flying diurnal birds must have effective and rapid accommodation (cormorants are reported to have 40–50 dioptres), but not so clear why the relatively slow reptiles should. However, lizards feed on quickly moving insects which are caught by eye. Accommodation is always for near vision and is accomplished by the ciliary muscles. These exert direct pressure on the lens equator, causing its anterior part to bulge forward and so increasing its power. In birds and reptiles both ciliary and iris muscles are striated. In addition, some birds (notably the hawk) reinforce the lens change by an increase in corneal curvature. Accommodation is relatively poor in snakes and is accomplished by moving the lens forward as in elasmobranch fish and Amphibia. There is no ciliary body, but the muscles at the base of the iris contract, pressing on the vitreous and producing a rise of intraocular tension which pushes the lens towards the cornea.

Most mammals, except primates, have little or no accommodation. With the exception of the baboon, which is said to be myopic, mammals in their natural state are slightly hypermetropic. Zoo and domesticated species tend, for some reason, to become myopic, and one should, therefore, always show caution in accepting accommodation data obtained on such material. Table 2 shows the power of accommodation in some species.

With the exception of the bats, vertebrates can only judge distance by means of their eyes. There are, of course, a number of monocular clues which can be, and constantly are, used for this purpose, such as size and overlapping shadows, but, in man at least, the most accurate method of judging distance and solidity is by means of stereoscopic vision. This appears to depend on the simultaneous appreciation of the slightly, but not too widely, dissimilar images from corresponding points on the two retinas. For this to be possible it is obviously essential to have binocular vision, that is, the faculty of viewing an object with both eyes simultaneously and seeing one and not two images.

Of course, binocular vision can only develop where there is some overlapping of the two visual fields and, therefore, the more frontally the eyes are placed in the head the greater the part of the visual field which is potentially binocular. In mammals the degree of frontality of the eye is correlated with the extent of the partial decussation of the optic nerves in the chiasma; in man only about 50% of the fibres cross over, in the rabbit the figure is nearly 100%. This correlation has apparently been mainly responsible for the theory that binocular and, therefore, stereoscopic vision is only possible where there is partial decussation of the optic nerves, that is, where impulses from each retina are received on both sides in the brain. If this were true, it would mean that non-mammalian vertebrates could never have binocular vision even where, as in many birds of prey and some fish, the eyes are frontal with overlapping fields. When one considers the extreme accuracy with which such non-mammalian vertebrates can pounce on their food, it is hard to believe that they do not enjoy true binocular vision. In this connexion it is of interest that, where the position of their

Table 2. *Refractions and a power of accommodation in various animals*

Animal	Refraction (dioptres)	Maximum accommodation (dioptres)	Mechanism of accommodation
Fish:			
Lamprey	−8	>8	Lens moved towards retina
Elasmobranch	+10–15	15–20*	Lens moved away from retina
Teleost	−15	15	Lens moved towards retina
Cod	—	0	Do.
Amphibia:	0 in usual habitat	<5	Shape of lens changed by direct pressure
Reptiles:			
Crocodiles	0 in air	Slight	Do.
Turtles	0 in usual habitat	—	—
Lizards	0	Great	Do.
Snakes	+2–9	0–9	Lens moved away from retina
Birds:			
Owl	0	4–6	Shape of lens changed by direct pressure
Hen	0	8–12	Do.
Pigeon	0	8–12	Do.
Cormorant	0	40–50	Do.
Mammals:			
Sea-cow	−5 in air	0	Shape of lens changed by moulding by capsule after relaxation of zonule fibres
Mouse	+10	0	Do.
Horse	+1	0	Do.
Sheep	+1	0	Do.
Pig	+1	0	Do.
Rabbit	—	0†	Do.
Dog	0·5	1†	Do.
Squirrel	0·5	1·5	Do.
Cat	0	3·5‡ 1·75†	Do. Do.
Wolf	—	2·75†	Do.
Primates other than man	0 (baboon myopic)	10–12	Do.
Man (aged 21)	0	11·0	Do.

* Franz (1931).
† Hess & Heine (1898).
‡ Hartridge & Yamado (1922).

eyes allows, most animals use both together from choice. The factor which really appears to be correlated with frontality throughout the vertebrates is feeding habit. Thus hunting animals nearly all have some overlapping of their fields in front, while those which are normally hunted tend to have lateral eyes giving a maximum total field but little or no binocular overlap. Hunted animals must be able to spot danger coming from any direction, while predatory ones need the best possible vision of their prey and, not usually being in danger themselves, can dispense with a knowledge of what happens behind them. The total and binocular fields of a number of vertebrates, both predatory and hunted, are given in Table 3. Although the degree of frontality does, in the main, determine the extent of these two fields (which, of course, tend to vary inversely with one another), other factors also play a part; for instance, the degree of protuberance of the eyes and the relative sizes of cornea and retina. There are also many interesting variations in the *directions* of the fields depending on the particular habits of a species. Thus, the bittern, which when alarmed 'freezes' with its bill in the air among the reeds, has its eyes so placed that with the head in this position they can be turned downwards to give it binocular vision straight ahead *underneath* its bill. On the other hand, in aquatic mammals such as seals, the eyes are tilted upwards, so giving good vision above the water while swimming.

Table 3. *Total and binocular visual fields of various species, showing the larger binocular fields characteristic of predators*

Animal	Monocular field (degrees)	Total visual field (degrees)	Binocular field (degrees)
Fish:			
Most	—	—	20–30*
Gurnard	—	—	4*
Flatfish	—	—	> 30*
Fresh-water predators	—	—	30– > 40*
Bottom dwellers	—	—	25–40 (dorsal)
Reptiles:			
Crocodiles	152–156	—	25
Turtle (*Testudo*)	—	—	18
Turtle (snapping turtle)	—	—	38
Lizards	144–160	—	10–20
Monitors	—	—	14–32
Snakes	146–168	—	20–40
Birds:			
Graniverous	—	340–342 (pigeon)	6–25
Hawks	—	—	35–50
Owls	—	—	60–70
Mammals:			
Rodents	190	360	10–40
Ungulates	215 (horizontal pupils)	—	60–80
Dog	—	250	—
Cats	—	287	130
Apes and man	—	180	140

* Kahmann (1935).

One of the most vital and fundamental functions of an eye is the perception of movement. This capacity is necessary for any animal which itself moves (sea anemones and suchlike have no eyes), and particularly if it feeds on moving objects. The faster an animal normally moves and the faster its prey moves the more acute must its movement perception be. Now, the stimulus value of a moving object depends not only on the actual capacity of the eye to detect and evaluate movement, but also on such psychological factors as the general importance of moving objects to the owner of the eye and the amount of competition for attention provided by other simultaneous visual sensations. This last factor is probably the reason why *perception* of movement is usually better in the periphery although the physiological mechanisms for it are usually worse. The *attention value* of a movement seen peripherally is greater because, anyway in reasonably good lights, it is practically the only visual function of which the periphery is capable.

Physiologically, the two visual functions concerned in the perception of moving objects are visual acuity and the 'persistence time', the latter measured by determining the flicker fusion frequency. Where visual acuity is poor the retinal area served by a given nerve fibre is large, and it is only when fresh fibres are stimulated that an image is recognized to be moving on the retina. In a retina with poor visual acuity the details of an image will have to move much farther before they hit the sensory cells attached to new fibres than in a retina with good visual acuity. The 'persistence time' is the time for which a sensation persists after the stimulus has ceased, and obviously the shorter this period the more quickly is an eye ready to perceive a new object. It is the length of the persistence time which determines whether a moving object is seen as a blurred streak or as a discrete pattern moving across the visual field. The flicker fusion frequency (the lowest stimulation rate which gives a homogeneous sensation) varies for different types of retina and according to the state of adaptation, and the perception of movement will vary in the same way; the higher the fusion frequency the better is movement perceived. Fusion frequency is higher at high illuminations, and also higher for cone than for rod vision except during dark adaptation, when the frequency for rod vision rises and for cone vision falls (Lythgoe & Tansley, 1929). This means that in any given eye perception of movement will tend to be best under the conditions in which the eye is generally most efficient. In general, animals which move swiftly themselves or which feed on quickly moving prey have high fusion frequencies. The highest figures so far recorded are those obtained by Autrum (1948) for the fly *Calliphora erythrocephala*, where the fusion frequency is at 100 per sec. under conditions where it is only 40 per sec. in man. Table 4 gives the fusion frequencies measured by various means on a selection of animals.

We now come to the question of colour vision in animals—a question which always seems to arouse more interest and to which our answers

Table 4. *Fusion frequencies in different animals under conditions of light (L.A.) and dark adaptation (D.A.)*

Animal	Type of retina	Fusion frequency (flashes per sec.) L.A.	D.A.	Method of recording
Insect (*Calliphora erythrocephala*)	Compound eye	250	—	Electroretinogram*
Snail	—	4–5	—	Sensory response
Cephalopod (*Eledone*)	—	90	—	Electroretinogram†
Fish (*Betta splendens*)	Cone	110	—	Sensory response‡
Fish (*Conger vulgaris*)	Rod	14	—	Optic nerve§
Frog	Mixed	13	7	Electroretinogram‖
Pigeon	Cone dominated	45	40	Electroretinogram‖
Hen	Cone dominated	—	35	Electroretinogram¶
Buzzard	Cone dominated	—	40	Electroretinogram¶
Owl	Rod	34	21	Electroretinogram‖
Cat	Rod dominated	27	26	Electroretinogram‖
Rabbit	Rod dominated	32	30	Electroretinogram‖
Monkey	Cone dominated	—	17	Electroretinogram¶
Man	Mixed	20	—	Electroretinogram**
		50	14	Sensory at 0°††
			15·5	Sensory at 90°††

* Autrum (1948).
† Fröhlich (1913).
‡ Beniuc (1933).
§ Adrian & Matthews (1928).
‖ Granit (1947).
¶ Piper (1911).
** Bernhard (1940).
†† Lythgoe & Tansley (1929).

are usually more unsatisfactory than is the case in any other branch of the subject. One reason for the unsatisfactory answers is the difficulty of demonstrating the presence or absence of colour vision in animals. Colour is only one of the attributes of an object which make it visually recognizable, and an animal which seems to be choosing an object because it is, say, yellow, may really be attracted because it is moving, or of a certain shape or seems bright.

In order to be able to say for certain that a given species possesses or does not possess colour vision one must perform rigorously controlled training experiments—a tedious and lengthy undertaking and one which is often not practicable. However, a considerable number of such investigations have, in fact, been undertaken with the result that we can now say with fair certainty that colour vision is possessed by certain insects—notably the honey bee— by diurnal fish and birds and, among the reptiles, by turtles and diurnal lizards. We have no information about snakes, and the frog is the only amphibian which has been tested; it seems not to have colour vision. The only mammals proved to have colour vision are the higher primates, and it is certain that many definitely have not; all the nocturnal species tested, cat, rat, mouse, rabbit, etc., having given negative results when the experiments were properly controlled. The results on the more diurnal mammals are doubtful, but there is evidence that both the dog (Samoiloff & Pheophilaktova, 1907; Smith, 1912) and some species of squirrel (Locher, 1933; Kolosváry, 1934) may have a rudimentary colour sense.

During the last ten years a great deal of information has been gathered by Granit and his co-workers (1947) about the actual sensitivity of the retinas of different animals to different wave-lengths. All the reputable (and some not so reputable) theories of colour vision agree that the fundamental discrimination between wave-lengths must take place in the retina, colour vision being based on differences of sensitivity between the retinal end-organs linked to a cerebral ability to recognize which end-organs are responding and to what extent. It is, therefore, not to be expected that an animal whose end-organs responded identically to all wave-lengths should have colour vision. The converse, however, seems not to be true—that all animals in which differential retinal sensitivities to wave-length can be demonstrated necessarily have colour vision. Granit has found some indication of differential sensitivity in all the retinas he has examined so long as they were in the light-adapted state, and these include the rat, guinea-pig and cat, all of which have been pretty conclusively shown to possess no colour vision at all. It seems very likely that all vertebrate retinas possess at least a rudimentary mechanism for wave-length discrimination which may only be functional during light adaptation, but that true colour vision—the central *recognition* of wave-length differences—only develops in certain instances. It has been suggested that colour vision will develop where it is required, but it must be remembered that although Granit obtained evidence of some wave-length discrimination even in the pure rod retina of the guinea-pig, it was very much less definite and much harder to demonstrate than in pure cone or cone-rich retinas such as those of the frog, grass snake and turtle. In the case of the frog, which probaby has no colour vision and yet appears to have a well-developed retinal mechanism for wave-length discrimination, it is easy to imagine the possibility of its developing full colour vision through the elaboration of the necessary cerebral machinery. In the case of the rat and guinea-pig any such elaboration would apparently have to be accompanied by profound retinal changes.

The classical association of colour vision with cones and daylight vision is confirmed by Granit's results. He was never able to demonstrate any differential sensitivity to wave-length in a dark-adapted eye, and although the pure rod retina of the guinea-pig and the almost pure rod retina of the rat occasionally gave evidence of some differential sensitivity on the part of rare groups of end-organs, all the most striking and best-defined results were obtained from retinas with high cone densities. If one had no evidence other than Granit's to connect colour vision with cones and high illuminations, one would make the same rough generalizations about their relationship as were made over fifty years ago by the authors of the duplicity theory, although one would, perhaps, fill in the details rather differently.

In this paper I have tried to give a general idea of how visual capacity in general can be expected to vary among the vertebrates, in the hope that it may be helpful to people planning animal experiments involving vision. I hope that I have said enough to persuade people that an animal such as the rat, which, from what one might perhaps call a purely visual point of view, would be admirably suited to give results on factors affecting dark adaptation, might, nevertheless, be a poor choice for experiments on visual acuity or colour vision.

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PLATE 1

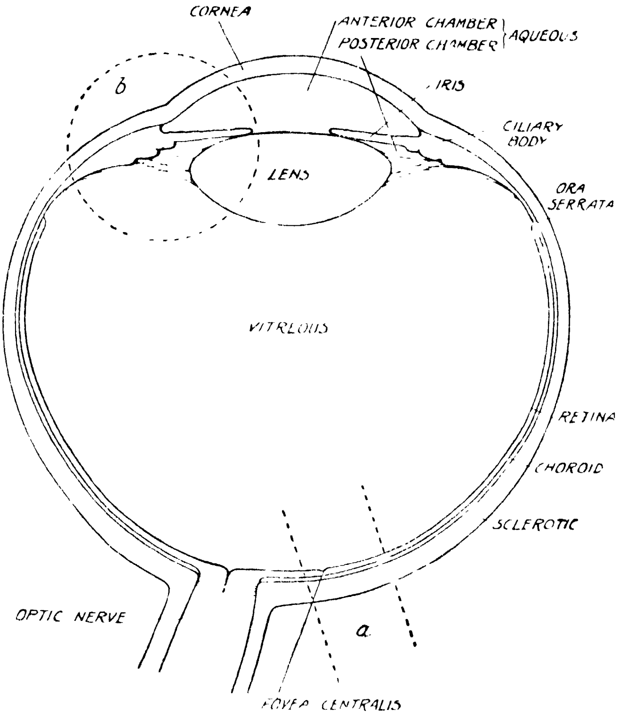

Fig. 1

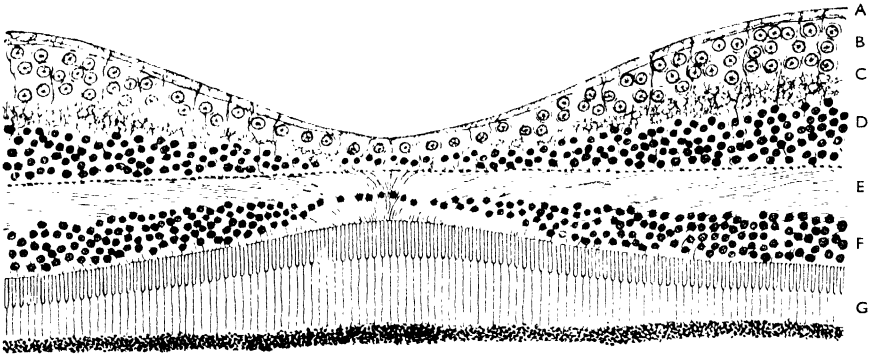

Fig. 2

For explanation see p. 33

PLATE 2

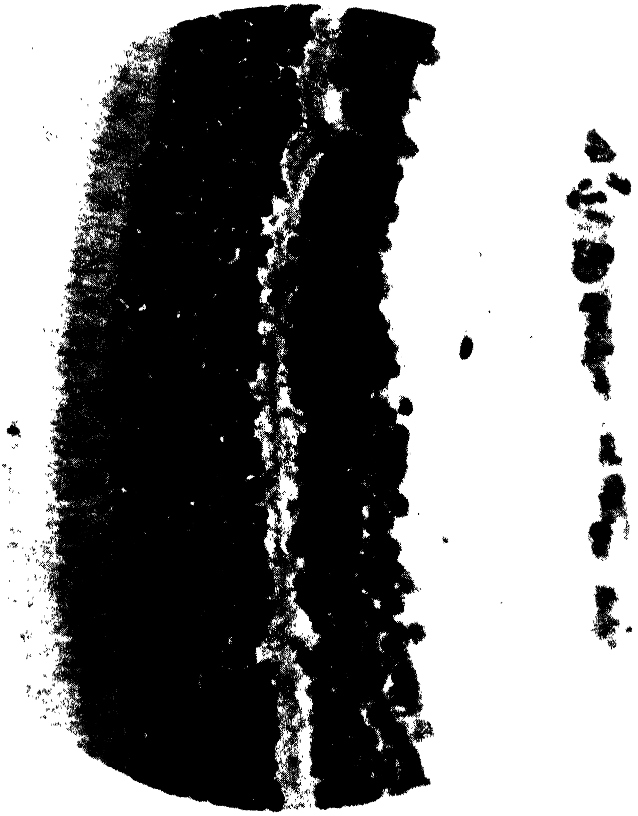

Fig. 1

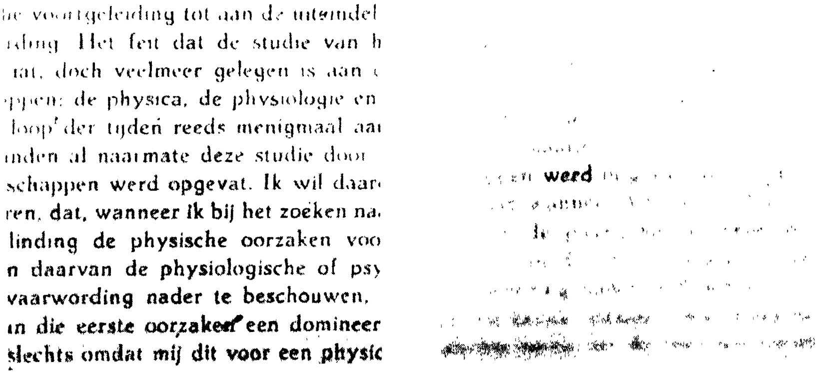

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Fig. 2

For explanation see p. 33

EXPLANATION OF PLATES

PLATE 1

Fig. 1 Diagrammatic horizontal section of the human eye (Parsons).

Fig. 2. Transverse section through the rat retina. The outer surface of the retina with the rods is at the bottom. Note the thick layer of rod nuclei and the very thin ganglion cell layer near the inner surface. *A*, nerve fibre layer; *B*, ganglion cell layer; *C*, inner molecular layer; *D*, inner nuclear layer; *E*, outer molecular layer; *F*, outer nuclear layer; *G*, rod and cone layer. Cf. Pl. 2, fig. 1.

PLATE 2

Fig. 1. Diagrammatic cross-section of the human retina in the region of the fovea (after Sobotta). In the parafoveal region the three nuclear layers (cone nuclei, bipolar and ganglion cell layers) are of nearly equal thickness. Cf. Pl. 1, fig. 2.

Fig. 2. Visual acuity around the fovea. The right-hand picture illustrates how badly the left-hand picture is seen when the eye is fixated on the word 'werd' at a distance of about 1 ft. (After Schouten.)

PROPRIOCEPTORS

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If we try to account for the behaviour of an animal in terms of cause and effect, we are soon faced with the question: 'What came first, was it a sensation from the environment or was it an activation of the motor neurones from within?' One school of thought claims that if we subtract all behaviour reactions which are clearly caused by sensory stimulation we will still be left with a residue of inherent reactivity which is independent of incoming impulses. On the other hand, attempts are also being made to resolve behaviour into reflex arcs so that each phase of movement is related to a stimulus or to a set of stimuli. In many instances such external stimuli, their receptors and the reactions which they evoke are fairly obvious. Whichever of these two views we may favour we cannot afford to overlook a sensory mechanism which is not so obvious and which is not exclusively concerned with stimuli arising out of the environment, i.e. the proprioceptive system. To the student of animal behaviour the proprioceptor is often the wallflower amongst sense organs. Such compact sense organs as eye and ear, and such striking stimuli as light and sound with their associated reactions, have attracted many more observers than have occupied themselves with the exploration of the diffuse proprioceptive system. This system registers less apparent stimuli, and it is usually held responsible for a rather vaguely defined muscle sense or a kinaesthetic sense. Yet, if we grant that there is some degree of logic and economy in the morphological plan, the significance of the sensory equipment of the muscle can be visualized in proportion by considering the number of nerve fibres which supply it. For instance, it is well known that almost half the fibres of a nerve to a skeletal muscle in a vertebrate are sensory and that they carry impulses to the central nervous system from proprioceptors and other deep structures. If all the sensory fibres of the somatic musculature were gathered together into two nerve trunks, as happens in the case of the eye and ear, a tract of such impressive dimensions would be obtained that no student of biology could possibly ignore it. On the physiological side, we have good reasons to believe that many profound defects in behaviour which attend section of these sensory nerves are due to the inability of the proprioceptors to exercise their normal influence.

According to Sherrington's (1906) definition, proprioceptors are somatic sensory end-organs which are stimulated by 'actions of the body itself', and, he adds carefully, that they are so stimulated in much greater measure than are the sense organs of the surface field of the organism. To Sherrington we owe much of the early information about the physiology of the proprioceptors in vertebrates, but the definition does not appear quite adequate, because, clearly, there are few types of sense organs which cannot be stimulated by actions of the body itself. For the purpose of this discussion, I should like to define proprioceptors as sense organs capable of registering continuously deformations (changes in length) and stresses (tensions, compressions) in the body. These can arise from the animal's own movements, or may be due to its weight, or to other external mechanical forces. Through their activity the proprioceptors help to establish the relationship of each part of the body to the rest, and of the body as a whole to the outside world.

The detection of such sense organs in the animal's body is not always an easy matter, and we can be quite confident that a large number have yet to be discovered. Before Sherrington's physiological discoveries were known, however, histologists had already revealed a variety of sense organs which appeared eminently suited for the perception of posture and postural changes. Behaviour can be analysed in such terms of changing posture. From this, then, the question arises, how far can behaviour be correlated with the sensation of behaviour? The question whether we would (or the central nervous system could) behave at all, if we did not know we were behaving, should not only be of interest to the moralist but also to the behaviourist and the physiologist.

Subjectively, one might take the view that whereas the higher sense organs convey to us the impression of an outside world, these lower sense organs convince us of the reality of our bodily existence—to which we have got used to such an extent that it is taken very much for granted. Nevertheless, this seems to be an experience from which no recluse and no philosopher can escape, however detached they may consider themselves from outside events.

Objectively, two types of effects have been ascribed to proprioceptors, (i) specific reflexes; (ii) a stimulatory action (in the sense of Wolsky (1933)); this by itself may not evoke any visible responses but may keep the central nervous system in a state of readiness to act in definite ways. The central nervous system is, of course, such a complicated part of the animal's anatomy and physiology—no doubt for good reasons—that it has also become a convenient store-cupboard for any phenomena in behaviour which we cannot unravel at first glance. A scrutiny of the role of the proprioceptive system may help to drag out into the open some of the mysteries which have been put into this hiding place, and may thus reduce the chance of misinterpretation of animal behaviour. By subtracting all effects which are known to be of proprioceptive origin it should be possible to gain some insight into behaviour reactions which are either caused by other receptors or by any purely central mechanism.

In the normal sequence of events the proprioceptive messages received by the nervous centres lead to excitation and inhibition of individual muscles or muscle groups, thus producing smooth, finely adjusted and effective movements. These movements can only be effective if the centres which send out the motor impulses take into account prevailing environmental conditions. In a changing environment this is inconceivable in the absence of guidance from the periphery. The degree of guidance is obviously limited to the perceptive range of the sense organs and must be considered first.

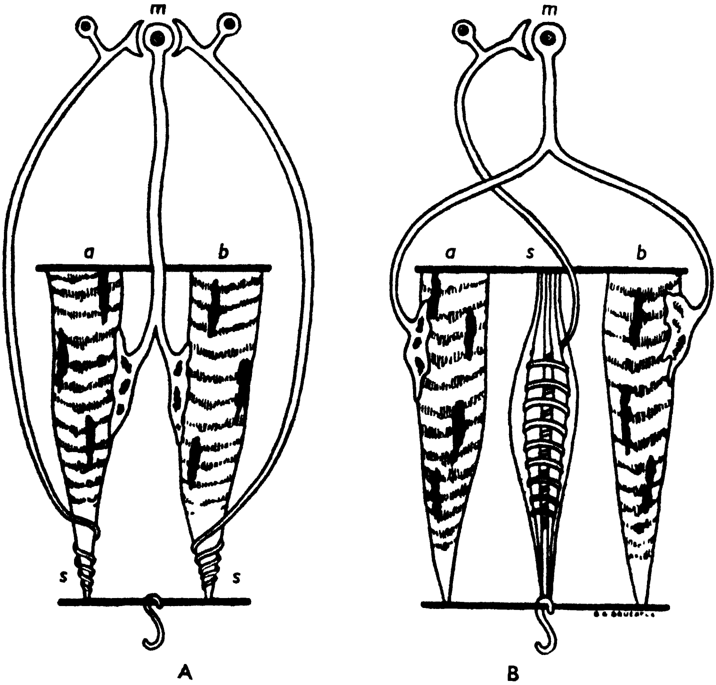
Vertebrates. Viewed superficially, the problem of proprioceptive function in vertebrates appears simple and logical. A somatic body or limb muscle has two main types of function: (*a*) to execute movements; (*b*) to carry loads. During these activities two types of mechanical effects are produced: (*a*) changes in length of tissues; (*b*) the development of tensions. To register these effects, two types of receptors would appear necessary, stretch receptors and tension receptors; and two types of receptors have been found in close association with the musculature: (*a*) the muscle spindle; (*b*) the tendon organ (see Pl. 1). As is well known from classical physiology, the influence from proprioceptive organs on the motor apparatus can be twofold: (*a*) excitation; (*b*) inhibition.

Finally, two opposing theories have been put forward which link causes and effects in a substantially different manner as is shown below:

Theory of Fulton & Pi-Suñer (1928)		Theory of Denny-Brown (1928)	
tension	stretch	tension, stretch	muscular action potential
↓	↓	↓	↓
tendon organ	muscle spindle	tendon organ	muscle spindle
↓	↓	↓	↓
inhibition	excitation	excitation	inhibition

Both theories try to derive support from histological details of the sensory endings. While Fulton & Pi-Suñer stress the 'in series' and 'in parallel' arrangement of tendon organ and muscle spindle respectively (Text-fig. 1), Denny-Brown points to the close association of the sensory termination of the muscle spindle with a contractile element, since he had recognized the motor innervation of the intrafusal fibres of the muscle spindle (Pl. 1). However, unless rather unconventional assumptions are made neither theory is entirely satisfactory, although Fulton & Pi-Suñer's scheme has gained more general acceptance. The difficulties become obvious as soon as one tries to apply either theory to certain well-known physiological observations.

(1) If the hindleg of a spinal frog or toad is passively extended, it offers no appreciable resistance, but at a certain point it responds by flexion. According to Fulton & Pi-Suñer the muscle spindles are activated by stretch, and this leads to an excitation of the stretched muscles, while in Denny-Brown's view the pull on the tendon organ would be held responsible for the flexion.



Text-fig. 1. Diagram showing two types of sensory ending in a skeletal muscle. In A the tendon organs are disposed 'in series' with the tension supporting elements. *a*, *b*, skeletal muscle fibres; *m*, motor-horn cell; *s*, sensory ending. In B a diagram of a muscle spindle is showing the condition of 'in-parallel' arrangement with the tension supporting elements. When the muscle fibres *a* and *b* contract, they take up any tension which may previously have been exerted upon *s*, the muscle spindle. (From Fulton & Pi-Suñer, 1928.)

(2) If, during active movement, the limb of a tetrapod or the trunk musculature of a fish or snake encounters an obstacle, the tension in the contracting muscles is greatly increased and is maintained for a considerable period. This additional excitation of the contracting muscles could be accounted for in Denny-Brown's scheme, but in this case the tension on the tendon organ, assumed to lead to excitation, would be counteracted by the simultaneous inhibitory effect from the muscle spindles which, it is suggested, are capable of appreciating the onset of the electrical wave which precedes contraction. According to Fulton & Pi-Suñer's view one would have expected inhibition of a muscle which develops tension under isometric conditions.

(3) In a preparation showing decerebrate rigidity any attempt to stretch the contracting muscles is met with increased resistance. This may be similar to the resistance reflex described under (2). If, however, the attempt to lengthen the contracting muscles is continued with increasing force, there comes a point at which the muscles suddenly 'give' and can be stretched to any desired length (lengthening reaction). Tension, therefore, can produce either excitation or inhibition. The observation of this effect of tension cannot be fitted into either theory.

Thus, it appears that the work on the proprioceptive system in vertebrates has reached that tiresome adolescent state at which it is no longer possible to skip over certain facts of life with either of these simple diagrams, and, clearly, the whole question requires revision in the light of more recent investigations. The first problem to be solved is the adequacy of stimuli for each proprioceptor.

A detailed examination of the structure of proprioceptors, of their mode of distribution within the body of each animal and a knowledge of their occurrence in the animal kingdom helps to piece together the information at present available about the adequate type of stimulation of different proprioceptors, although the inadequacy of our knowledge is very apparent and leaves many perplexing problems unsolved.

Only through the vertebrates can we trace a thin dotted line of the evolution of some proprioceptors. Muscle spindles occur in vertebrates in the fleshy part of the musculature. They are provided with a complicated system of sensory and motor innervation, and have been found in mammals, birds, reptiles, anurans and in the limb muscles of one urodele; none have been discovered in fish or in the trunk muscles of urodeles. This may lead one to the rash conclusion that the occurrence of muscle spindles in all true land-living vertebrates may be taken as a sign of their unobtrusive service in an ever-present, homogeneous gravitational field which acts upon a body heavier than its surrounding medium. This belief is, however, somewhat shaken by two observations.

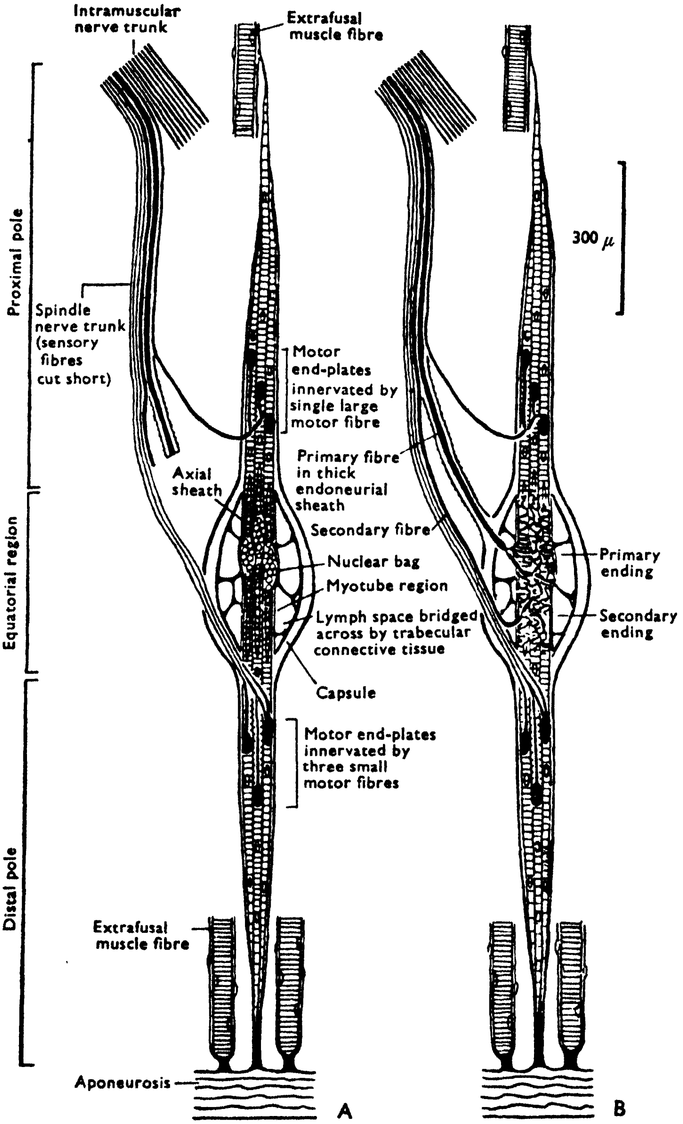
(1) It is true that these muscle spindles occur in greater numbers in the muscles of the limb than in the trunk, and the structure of the spindle seems to increase in complexity from the proximal to the distal muscles, but it cannot be claimed that they are confined to muscles which fulfil an anti-gravity function, for they have been found in the diaphragm, the tongue, the extrinsic muscles of the larynx, in the eye muscles, etc. On the other hand, as far as I know, they have not been found in some facial muscles, the intrinsic laryngeal, etc. (Reviews by Hines (1927); Hinsey 1934).)

(2) Allen (1917) has reported and figured the presence of muscle

spindles in a cyclostome. Any notions of explaining this fact away by reference to the heavily armoured, bottom-living silurian relatives of lampreys is prejudiced by the fact that these muscle spindles have only been observed in the m. cordis caudalis, the muscle for the pulsating caudal heart which receives its innervation from certain spinal nerves. From Allen's brief account, it would appear that in structure the muscle spindles of this cyclostome correspond more closely to the general pattern of those of higher rather than lower vertebrates.

A minimum of histological detail cannot be avoided if we are to understand those principles and peculiarities of the sensory mechanism of the spindle which have a bearing on the reactions they evoke. Barker's (1948) diagram of the rabbit's muscle spindle (Text-fig. 2) may serve as an illustration of the general arrangement from which, by abstraction, simpler types can probably be derived. The spindle consists of a small bundle of 'intrafusal' muscle fibres (1–12) which are enclosed in a capsule of fibrous tissue. In mammals this capsule is filled with lymph, so that the spindle appears well cushioned and protected against lateral mechanical distortions. This perilymphatic space is said to be absent in other groups of vertebrates, and in the urodele there is no trace of the connective tissue surrounding the intrafusal fibres (Mather & Hines, 1934). In the equatorial region these fibres appear to be completely filled with nuclei (nuclear bag), and in this region, according to some observers, the intrafusal fibres are devoid of the cross-striations which are characteristic of the two extremities. This has been taken to mean that the two polar regions are contractile and are separated by the non-contractile nuclear bag. The whole spindle is surrounded by the much larger 'extrafusal' fibres which constitute the muscle (Pl. 1).

The innervation of the intrafusal fibre as pictured by Barker differs somewhat from Denny-Brown's diagram (Pl. 1). Each intrafusal fibre has a double somatic motor innervation, and a motor end-plate is found at each polar region. The fibres to each pole may be of different diameter, and from this it was concluded that each of the two halves of an intrafusal fibre may be an independent contractile unit. The sensory innervation is highly complicated. Ruffini (1892) had already described in the mammal the so-called primary or 'annulo-spiral' and the secondary or 'flower-spray' termination. The primary ending ramifies and spirals round the equator of the intrafusal fibres, and it is supplied by a large nerve fibre ($8–12\mu$ in the rabbit). The secondary ending shows a certain degree of variation in different species of mammals; it does not ramify to the same extent as the primary ending and is supplied by a nerve fibre of medium size ($6–9\mu$). If more than one intrafusal fibre is present, both the primary and secondary nerve fibres divide so as to innervate each intrafusal fibre of the muscle spindle. In mammals there is always one primary ending present; in addition, there may be one or two secondary endings. In lower vertebrates only one type of termination is found.



Text-fig. 2. Barker's (1948) diagram of a rabbit's muscle spindle consisting of three intrafusal muscle fibres. In A only the motor innervation is shown; B shows in addition the sensory innervation of one primary (annulo-spiral) and one secondary (flower-spray) ending.

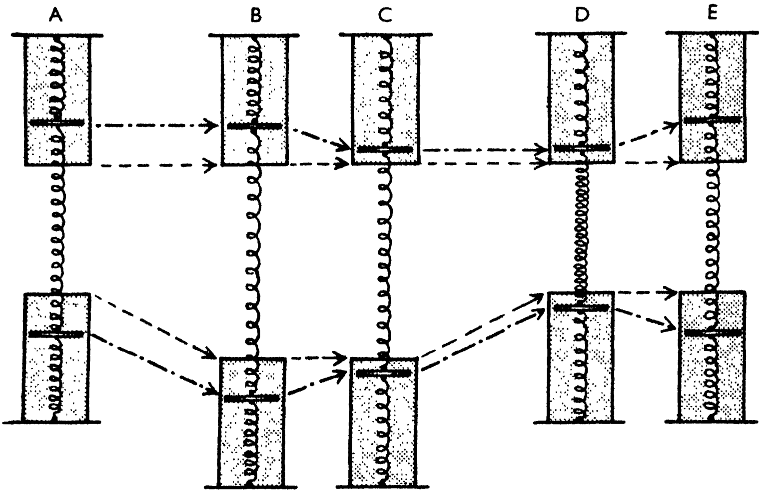
Taking advantage of the presence of a single end-organ in the muscle spindle of lower vertebrates, Matthews (1931 *a*, *b*) made the first important step forward in the investigation of its sensory mechanism. To reduce complications further Matthews selected the small muscle on the upper outer side of the middle toe of the frog (m. ext. brev. prof. dig. III) which typically contains a single muscle spindle. The sensory discharges from this spindle were recorded under different conditions of passive stretch and active contraction of the whole muscle.

As soon as the muscle is stretched, impulses at the rate of up to 250 per sec. are recorded in the sensory nerve, the frequency gradually declining to about 20 per sec. The rhythm then remains steady often for 20–30 sec., after which it loses its regularity. Under small extensions the random discharge goes on for some minutes. Indeed, Matthews has observed a discharge of impulses in the absence of any external stretch or tension, thus confirming Adrian & Zotterman's (1926) earlier findings of a resting discharge in the end-organs of the frog's muscle.

There are two possibly related phenomena which seem to be general attributes of muscle spindles and similar stretch receptors and which are likely to be of functional significance. (i) When a muscle is rapidly stretched the characteristic response does not show the gradual decline in the rate of impulse discharge, instead, after an initial high frequency, there is a sudden drop to a lower frequency. (ii) When a muscle spindle which is exhibiting a slow rate of discharge, either spontaneously or under a small extension, is temporarily loaded, it remains inactive for a period after the load has been removed; it then starts again to discharge impulses at the original rate.

Both these effects, therefore, tend to produce a contrast by exaggerating in their sensory messages the physical change which has taken place. This observation may have its parallels in other sense organs and in the central nervous system, but in the case of the proprioceptors it is of special interest because it is clearly a purely peripheral contrast phenomenon observable in the sensory nerves. This may not have been sufficiently taken into account in the interpretation of what has been described as central or spinal contrast, which may lead to a rebound reaction. Whether in the case of the spindle this physiological peculiarity can be interpreted as the result of a difference in the visco-elastic properties between the equatorial and the polar regions of the intrafusal fibre, as illustrated in Text-fig. 3, is still a matter of speculation, but this view has received further support by the behaviour of the sense organ while the muscle was made to undergo active contraction.

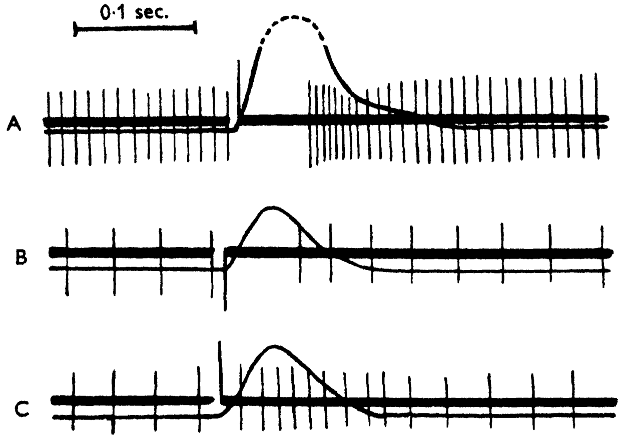
When the muscle is under slight initial extension, and is made to contract by electrical stimulation of the motor fibres, the initial sensory response ceases during the contracting phase but emerges again at considerable frequency during relaxation (Text-fig. 4 A, B). Matthews claimed that this applied to both isotonic and isometric conditions. However, more recently Katz (personal communication), working on the spindle of another muscle of the frog, has shown that during strictly isometric conditions the sensory discharge is boosted. This had only been observed by Matthews during supramaximal stimulation of the motor nerve (Text-fig. 4C).



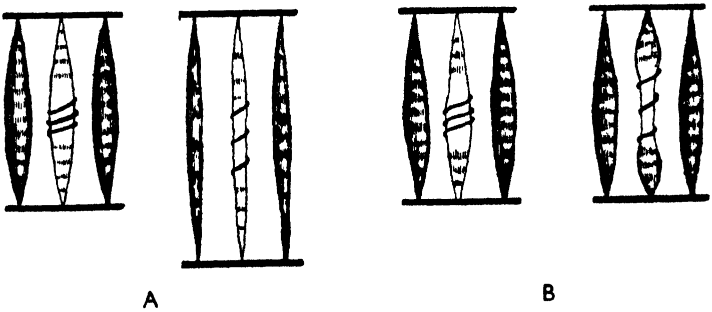
Text-fig. 3. Model to illustrate the contrast effect of the muscle spindle. A. The polar regions of the intrafusal fibre are represented as two cylinders filled with oil. A spring extends from one polar region to the other and is provided within each oil chamber with a damping plate. The spring between the plates corresponds to the sensory termination of an intrafusal fibre; its degree of extension determines the frequency of impulse discharge. B. During sudden stretch the extension of the spring in the equatorial region will be greater than at the polar ends. C. After a short interval the tension of the spring in the equatorial region will overcome the damping effect of the plate, and equilibrium of tension will be re-established between equatorial and polar regions. D. During sudden shortening the spring in the equatorial region is slackened while tension at the polar ends persists. E. The original equilibrium is re-established after an interval.

The picture which emerges from these experiments indicates that during passive stretch of the muscle there is an uncomplicated sensory discharge. During active contraction the afferent firing depends upon a balance of two forces: (*a*) release by extrafusal shortening, and (*b*) the extra pull by intrafusal contraction. In all cases the afferent discharges seem to depend on stretch of those parts of the intrafusal fibre which bear the sensory terminations, as shown in Text-fig. 5.

It is interesting to note that Katz has found in the frog that the intrafusal muscle fibres and the rest of the muscle receive a common motor innervation, but that the intrafusal motor junctions are less susceptible to fatigue. Now the occurrence of apparent inconsistencies under identical external conditions, either in intact animals or in reflex preparations, has been a constant source of irritation to the tidy mind. Reflex reversal, particularly (Sherrington, 1912; Graham Brown, 1911; Verzár, 1920, 1923; Beritoff, 1923), has often been attributed to autonomous conditions in the central nervous system. In some instances central fatigue has been quoted as the cause of reflex reversal, because it could not be imagined that a series of



Text-fig. 4. Discharges recorded in the sensory nerve of the frog's muscle spindle during isotonic twitch. A. Initial load 2g. Note the cessation of impulses during the contracting phase and their reappearance at considerable frequency during relaxation. B. Initial load 1g. Stimulus applied to motor nerve only just maximal. C. The same preparation as B discharging at higher frequency during contraction after supramaximal stimulation. (From Matthews, 1931*b*.)



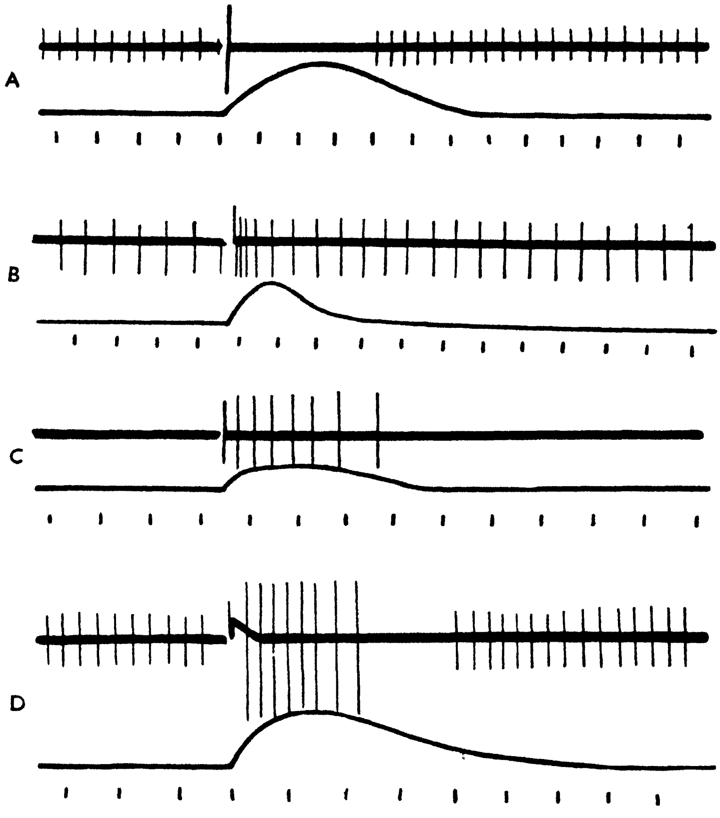
Text-fig. 5. Diagram of the conditions of activation of a sensory termination of a muscle spindle. A shows an intrafusal fibre with its sensory ending flanked by two extrafusal fibres. The sensory termination is stretched during passive extension of the whole muscle and responds with afferent discharges. B shows the same structures under isometric conditions. When the motor nerve is stimulated all three fibres contract, but the contraction of the intrafusal fibre is limited to the polar regions. Since the isometric conditions do not allow the muscle to shorten, the equatorial region of the intrafusal fibre with its sensory termination is extended and responds with afferent impulses.

constant stimuli applied to a motor nerve could generate anything but a correspondingly consistent volley of proprioceptive impulses varying merely in frequency. In the absence of any direct evidence it can only be suggested that the behaviour of the muscle spindle opens new possibilities, and may, in part at least, provide peripheral reasons for reflex reversal. If a fresh muscle is stimulated, the afferent discharge ceases during the shortening phase because of extrafusal release; once the muscle is fatigued, only the intrafusal fibres would contract causing an afferent volley during stimulation, thus giving under identical conditions a complete reversal of the afferent inflow. Whether this picture can be applied in the case of an intact animal which gets tired of trying to do something and changes its mind to try something else is more difficult to decide at the moment.

These speculations are based on the behaviour of the frog's muscle spindle. The sensory endings in the mammalian muscle spindle are both more numerous and more complex, but Matthews (1933) was able to explore their responses by less direct methods. By cutting down the nerve trunk until single-fibre discharges were obtained, the different types of responses were compared on a statistical basis with the proportional occurrence of different endings in the cat's muscle. It was found that 50% of the responses were very similar in behaviour to the frog's muscle spindle (Text-fig. 6A). 25% were similar, but had a higher threshold, showed a tendency to discharge during twitch and tetanic contraction, and the impulses appeared to be conducted in fibres of larger diameter (Text-fig. 6B). Histological examination had shown that the ratio of secondary to primary endings was approximately 2 : 1. Hence the responses were associated with the secondary or 'flower-spray' and primary or 'annulo-spiral' endings respectively.

The majority of the remaining 25% of Matthews's single-fibre preparations showed a type of response which was altogether different from that of the muscle spindle. During rapid stretch they did not give the initial high-frequency response of the muscle spindle receptors and they had a much higher threshold. On the other hand, they responded to tension whether this was produced by active contraction or by passive stretch (Text-fig. 6D). In other words, they behaved as if they were arranged 'in series' with the muscle fibres. In most cases the endings were traced to a position in the muscle towards the tendinous end, and in two cases they were clearly located in the tendon. By a process of exclusion Matthews attributed this response to the tendon organ, which has been known to histologists since Golgi (1880); on purely structural grounds a function had been assigned to this organ similar to that demonstrated by Matthews.

The structure and nerve supply of the tendon organ are simple compared with the muscle spindle (see Pl. 1). The sensory ending lies within an encapsulated bundle of tendon fasciculi which are often attached at one end to a small group of muscle fibres, so that anatomically it is really 'in series' with the rest of the muscle. The nerve supply is usually from a large nerve fibre which may be the branch of a fibre innervating several of these organs. Such neurotendinous organs have been described for all groups of vertebrates, including a teleost (*Hippocampus*) and an elasmobranch (*Torpedo*) (cf. Pansini, 1889; Huber & de Witt, 1900).



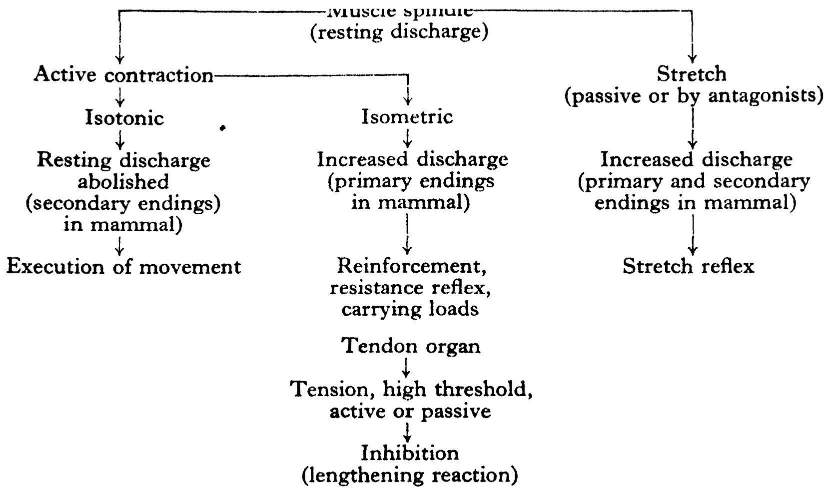
Text-fig. 6. Responses of nerve endings in mammalian muscle. A. Response a of flower-spray (secondary) ending during isotonic twitch (tension 40 g.). Note cessation of impulses during contraction. B. Responses from an annulo-spiral (primary) ending during twitch evoked by maximal stimulation. Initial tension 40 g. Note that the frequency of discharge is increased during twitch. C. Responses of a tendon organ during isometric twitch; initial tension 130 g. Note the appearance of sensory discharges during contraction. D. Two-fibre preparation containing one flower-spray (secondary) ending and one tendon organ. During isometric twitch the flower-spray ending ceases to discharge while at the same time the impulses from the tendon organ appear. Time marker $\frac{1}{50}$ sec. (From Matthews, 1933.)

The mode of the interaction in a reflex response of the three types of mammalian receptors, viz. primary and secondary endings of the spindle and tendon organ, is still a debatable issue. The secondary (flower-spray) endings have the lowest threshold and thus may be assumed to evoke the stretch reflex. However, the stretch reflex in physiological experiments is a very quick response. Measurements have shown (Lloyd, 1943) that it must be conducted in the largest fibres, and these are not connected with the secondary endings. Tension of high threshold clearly seems to have an inhibitory effect as demonstrated by the lengthening reaction. This is attributed to tendon organs. The primary (annulo-spiral) endings appear to be the most doubtful part of the mechanism. The increased discharge during contraction suggested to Matthews that they may be inhibitory simply on the grounds that a contracting muscle would always tend to inhibit its own contraction. Moreover, since the impulses are conducted in large fibres, the time relation with the tendon organ would be very similar. Therefore, though the evidence was admittedly slight, Matthews favoured the view of an inhibitory effect of both tendon organ and primary (annulo-spiral) ending. If this is accepted, then the stretch reflex would be considered as the balance of the excitatory effect of the more numerous secondary (flower-spray) endings and the inhibitory effect of the primary (annulo-spiral) endings; both discharge during passive stretch, but the latter have a higher threshold. This suggested interpretation is not convincing, because (i) it offers no explanation for the resistance reflex; (ii) the stretch reflex in physiological experiments is too quick to be evoked by anything but the largest sensory fibres; (iii) if the primary (annulo-spiral) and secondary (flower-spray) endings in mammals are differentiations of an unspecialized muscle spindle as seen in the frog, it would be difficult to visualize how an originally excitatory organ can evolve into a partly excitatory and partly inhibitory organ.

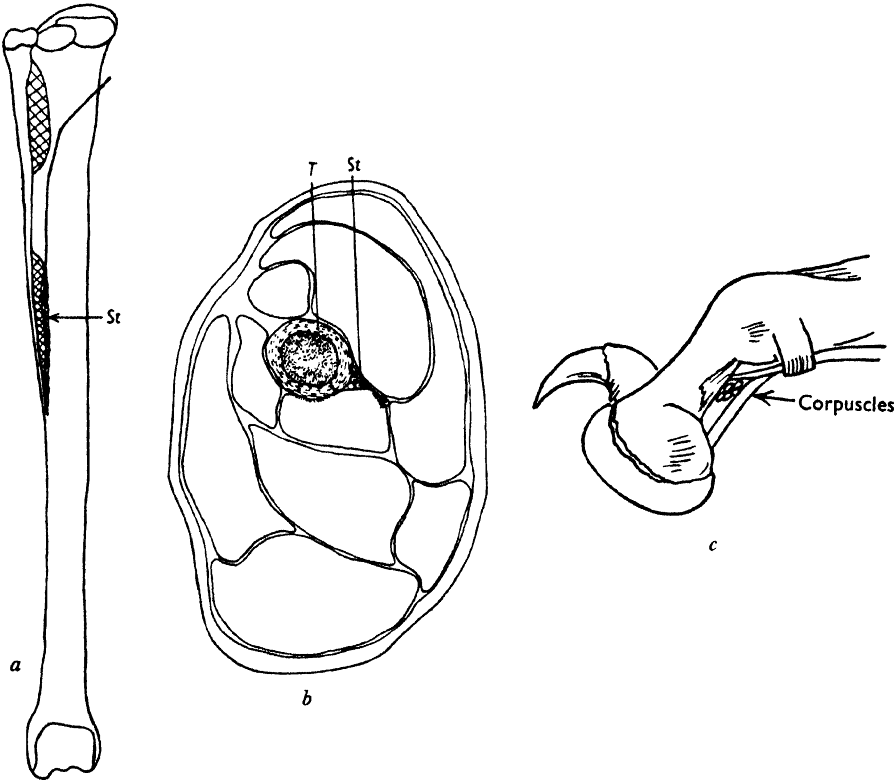
On the other hand, if we assume that the primary (annulo-spiral) endings are exciting the muscle with which they are connected, the whole picture seems to gain more coherence. (i) The stretch reflex can be evoked by both types of ending in the muscle spindle. If the rate of stretch exceeds a certain point, the rapid conduction in the large nerve fibres of the annulo-spiral endings would be sufficient to account for the quickness of the stretch reflex. (ii) If the muscle during contraction encounters a resistance, it would be excited still further by the primary (annulo-spiral) endings until the resistance is overcome. This would provide a mechanism for fine adjustment of tensions in the muscles depending on environmental conditions such as occur when walking up or down a slope. (iii) The primary (annulo-spiral) endings can also be held responsible for the increased tension with which a limb in a decerebrate preparation resists passive flexion. If the force is further increased, tendon organs are brought into play, and this presumably inhibits both intrafusal and extrafusal contraction, so that the tension of the muscle suddenly 'melts'. The threshold difference to tension between tendon organ and primary (annulo-spiral) ending appears more significant (approximately 100 times) than the threshold difference to rate of stretch between primary and secondary endings of the muscle spindle. (iv) It must be realized that tension receptors and stretch receptors within an animal are subject to the same limitations as our mechanical recording devices, such as isotonic and isometric levers. We cannot register tension unless we allow a certain amount of movement, and we cannot record changes in length unless mass is accelerated, and this, in some measure, is the expression of a force acting through a certain distance. It is therefore easy to imagine that in the course of evolution a sense organ could undergo specialization in one or other direction while retaining its nervous connexions and effects. In this respect the difference in behaviour of the frog's muscle spindle in two different muscles, as described by Matthews and by Katz, may be significant, and the difference in threshold to stretch between primary and secondary endings may be due to specialization.

With only a single sensory termination in the spindles, as found in the frog, the muscle does not seem to possess any means to signal to the central nervous system the difference between passive stretch and isometric contraction (see Text-fig. 5). This discrimination could be achieved by correlating the sensory messages from antagonistic muscles; e.g. during passive extension of a frog's limb only the flexor stretch receptors would respond. On the other hand, if the leg extends actively against a resistance, additional impulses will arise in the spindles of the extensor muscles. A single muscle would be capable of distinguishing between these two conditions only if it had two types of specialized sensory endings in the spindle as in fact occur in the mammal. The flower-spray (secondary) ending sends out messages relating the passive elongation of the muscle; since it ceases to respond during contraction it may be assumed to be located on the contractile region of the intrafusal fibre. The annulo-spiral (primary) ending, on the other hand, with its separate sensory innervation signals both passive elongation and isometric contraction. The combined effect in different proportion of these two types of sensory response makes it more intelligible that a muscle should be capable of carrying the same load at varying lengths, and that it can carry different loads at the same length. At the same time it must be borne in mind that as yet we do not seem to possess a sufficiently clear picture of the role of the double motor innervation of each intrafusal fibre to come to any final conclusion about gradation of responses obtainable from a muscle spindle. Recent work on the small motor fibre activity has stressed the significance of this system in the maintenance of posture. It is conceivable that the small motor nerves to the intrafusal fibres are involved in this process, and that the large motor fibres are reserved for special reflexes.

If these observations about the vertebrate proprioceptive system are added up, the following scheme of their mode of operation may be tentatively suggested:



Although a relatively complete theoretical picture of proprioceptive responses could be derived by reference to these two types of antagonistic sets of proprioceptors in vertebrates, it must be remembered that there are in and around muscles and tendons, apart from free nerve-endings, other well-differentiated encapsulated sense organs which have hardly been explored. There are reasons to believe that, in some instances at least, they may fulfil the role of proprioceptors. In their typical form they are found only in the higher vertebrates, e.g. Herbst's corpuscles in birds on the surface of the pectoral muscles and at the base of the tail feathers and primary feathers of the wing, with the notable exception in the case of the penguin. In most birds there is a conspicuous strand, containing hundreds of such corpuscles, which runs along the tibia and is completely covered by overlying muscles (Text-fig. 7*a*, *b*). It has been shown that stimulation of the sensory nerve supplying this strand causes relaxation of the flexor muscles and contraction of the extensors (Schildmacher, 1931). On the other hand, these corpuscles also occur in places where they are not in close association with muscles, e.g. in the beak (in great numbers in the case of the woodpecker) and at other places where pressure receptors may be expected to serve a useful purpose. Correspondingly, in mammals the well-known Pacinian corpuscles are found, sometimes in large aggregations in the neighbourhood of tendons and joints, particularly on the flexor aspect. But they are also found in the abdomen, mesenteries, pancreas, etc. Adrian & Umrath (1929) have given us some information about the sensory mechanism of a group of such corpuscles beneath the flexor tendons of the cat's toe (Text-fig. 7*c*). Both passive flexion and extension produce a discharge of much the same character in the sensory nerve, as does also pressure on the tendon above this group of corpuscles. A single corpuscle responds to steady pressure with a fine glass rod with frequencies from 5 to 100 per sec., and the duration of the discharge makes it appear likely that these sense organs are more closely related to proprioceptors than to touch.



Text-fig. 7. (*a*) (*b*) Strand with Herbst's corpuscles (*St*) on the tibia (*T*) of a finch. This strand is completely covered by the overlying muscles. (From Schildmacher, 1931.) (*c*) Vater and Pacinian corpuscles beneath the flexor tendons of the cat's toe. (Adrian & Umrath, 1929.)

However, sensations of joint movement are probably derived from more than one or two types of sense organs. In the frog, which has no Pacinian corpuscles, movement of the knee joint produces a discharge of impulses even after all branches of nerves to the muscles have been cut. This raises the question of proprioceptive function in those vertebrates, such as fish, which do not appear to be endowed with any of these complicated receptors. In the limb muscles of the urodele *Triturus*, Mather & Hines (1934) had found two types of sensory innervation. In the first, the termination of the nerve was upon the belly of the muscle fibre (this was called the primitive muscle spindle), in the second the terminations of the nerve were in the vicinity of the attachments of the muscle fibre to a tendon. Earlier histologists (Giacomini, 1898; Perronchito, 1902; Ceccherelli, 1904) have described similar conditions in selachians, teleosts, urodeles, and larval anurans and in the back muscles of adult frogs and toads. In the fibrous tissue of the myocommata, which separate the myomeres of the lateral muscle masses of these lower vertebrates, there is a rich plexus of myelinated nerve fibres, which, after branching, give rise to unmyelinated fibrils. These, in one type of innervation, finally surround the tips of the muscle fibres, and from the mode of termination they have derived the name 'basket-like endings' (*terminazione nervosa a paniere*). A second type of sensory ending ('reticelles') is found upon the equatorial region of muscle fibres. In this case the sensory ending does not spiral round the muscle fibre, but, as in the frog, runs along it and sends out excrescences which in turn embrace the muscle fibre. It may be that these two types of sensory terminations are the primitive precursors of the tendon organ and the muscle spindle.

Whatever may be the correct picture of the evolutionary unfolding of the vertebrate proprioceptive system, there is strong physiological evidence that in fish there is a proprioceptive mechanism at work, which is analogous, if not homologous, to that of tetrapods. The only direct piece of evidence which is available comes from an investigation by Fessard & Sand (1937) on the stretch receptors in fish. Records of afferent impulses evoked by passive stretch of different muscles of the ray and dogfish revealed that all of them contain some sort of stretch receptor. Observation of the behaviour of single, morphologically undetermined end-organs showed a close similarity with the frog's muscle spindle. The differences are mainly quantitative. The range of frequency discharge appears to be lower in fish than in Amphibia and mammals, the respective maximal values being 100, 250 and 500 per sec.; the slowest regular rhythm was slower in the ray (1·5 per second) than in the other two animals. On the other hand, the ray maintained the discharge under slight extension for longer periods than the cat or the frog. Discharges of about 10 per sec. have been observed for over an hour before the records were discontinued. Matthews had found that under constant stimulation the discharge from the frog's toe muscle usually continues for some minutes, but in the cat he noticed a resting discharge from a muscle before its tendons were divided; this indicates that, as in the ray, there may be no limit to the duration of a discharge from a muscle stretch receptor under the slight extension of its normal attachment in the intact animal. It must be added that preliminary tests with teleost muscles and observations of responses during active contraction have not yielded positive results so far. This, however, does not imply that further investigations in that direction should be discouraged.

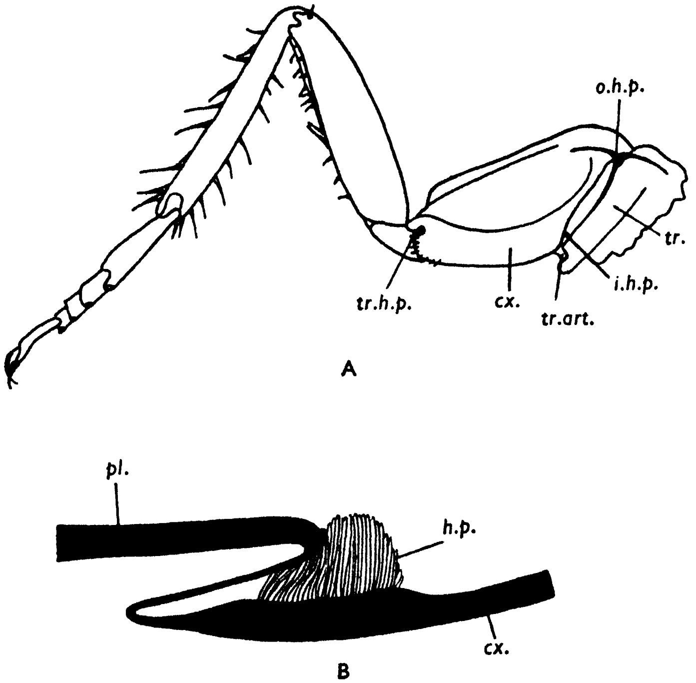
Invertebrates. The same state of affairs as is found in fish, where our information of proprioceptive impulses cannot be related with certainty to any definite sensory terminations, prevails, with one exception, in invertebrates. Sensory discharges have been recorded in worms after passive stretch (Gray, Lissmann & Pumphrey, 1938) and during active movement (Prosser, 1935). In arthropods different types of myo-chordatonal organs have been described (e.g. Barth, 1934); these seem to be well suited to register the state of the muscles, and bending of the limbs produces a burst of sensory discharge (Barnes, 1932). In the majority of cases, however, there is no conclusive evidence to show in which of the numerous sensory structures which have been described these impulses might arise, and the results therefore admit a certain latitude of interpretation.

The one exception mentioned above is Pringle's (1938, 1948) valuable contribution dealing with the proprioceptive system in insects. Apart from the internal myo-chordatonal organs, about whose function little definite information is available, insects possess cuticular sense organs which undoubtedly act as proprioceptors. Two different types have been examined in some detail:

(i) Distributed in the joints of the body and limbs are found hair sensilla, often arranged in the form of 'hair plates' (Text-fig. 8). They are excited by folds of intersegmental membrane, which bend the hair to a greater or lesser degree, according to the relative angle of adjoining segments. In this manner they act as 'position sense organs' whose sensory discharges remain independent of muscular tensions.

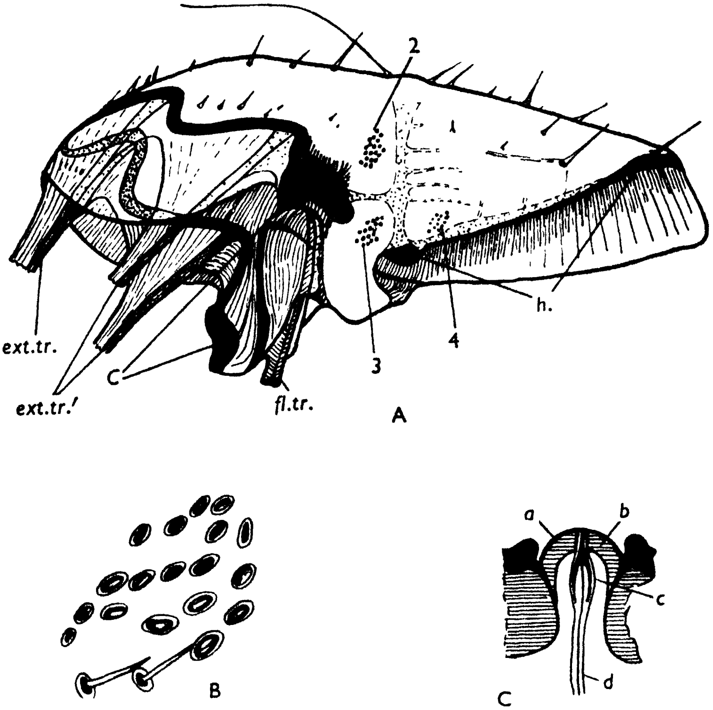
(ii) A second type of receptor found on the joints of insects are the campaniform sensillae. These respond to stresses and strains in the cuticular skeleton and may be compared with tension receptors in vertebrates (Text-fig. 9). Pringle comes to the conclusion, after examining the structure of campaniform sensillae, their arrangement and distribution on the legs and the nature of their response, that they are particularly suited to register the forces which act on the various joints of the limbs when the animal is standing on the ground, while the campaniform sensillae at the base of the halteres are activated by this gyroscopic mechanism and have a significance in directional control during flight.

General considerations. If we try to assess the significance of proprioceptive messages in the behaviour of a living animal, it must be conceded that there are many more sense organs apart from the ones already mentioned which play the rôle of 'proprioceptors' in Sherrington's wider definition of the term. The labyrinth of vertebrates and touch receptors have certainly a very close functional connexion with stretch and tension receptors. If all these receptors are stimulated by actions of the body itself the proprioceptive messages will trail behind each act of behaviour, and it may seem that they can evoke nothing but secondary reflexes. On the other hand, the responses from proprioceptors, both in vertebrates and invertebrates, have certain features in common which distinguish them from responses from other, similar receptors. The most striking of these are the resting discharge and the slow, often incomplete adaptation to a constant stimulus, well expressed in Adrian's comparative diagram of vertebrate



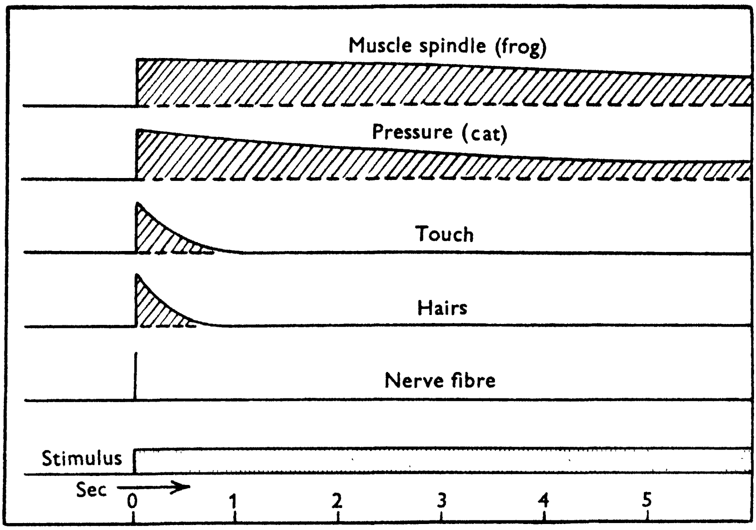
Text-fig. 8. A. Distribution of hair sensilla on the second leg of *Periplaneta*. *cx.* coxa; *i.h.p.* inner coxal hair plate; *o.h.p.* outer coxal hair plate; *tr.* trochantin; *tr. art.* trochantinal articulation of coxa; *tr.h.p.* trochanteral hair plate. B. Diagram to show the method of excitation of the inner coxal hair plate by a fold of the intersegmental membrane. *cx.* coxa; *h.p.* hair plate; *pl.* pleuron. (From Pringle, 1938.)

receptors (Text-fig. 10). In insects also the impulses from single sensory hair often show a rapid rate of adaptation, whereas the initial high frequency of discharge from 'hair plates' falls off slowly to a steady level at which it is maintained for a long time. It is well to remember this type of behaviour of proprioceptors if one tries to assess the relative merits of proprioceptors and touch receptors, because it is difficult to achieve their complete separation in an experiment. To say that proprioceptive reflexes are 'grafted' on to other behaviour reactions probably conveys a wrong impression of the true state of affairs. If in an intact animal the proprioceptors are signalling their messages continuously, these messages will not only be integrated with more short-lived signals from other receptors, but the proprioceptors may well determine the disposition and the state of activity of the central nervous system more permanently than is often assumed. Phenomena like slow adaptation and resting discharge must be essential attributes of



Text-fig. 9. A. Trochanter of the third right leg of *Periplaneta* (ventral view) showing the distribution of groups (2, 3, 4) of campaniform sensilla. *ext.tr.* extensor trochanteris; *ext.tr'.* accessory apodemes of extensor trochanteris; *fl.tr.* flexor trochanteris; *h.* trochantero-femoral hinge joint. B. Details of the orientation of a group of campaniform sensilla. C. Diagram of sensillum. *a*, *b*, outer and inner lamellae of cap membrane; *c*, cuticular connexion of *d*, the distal process of the sense cell. (From Pringle, 1938.)

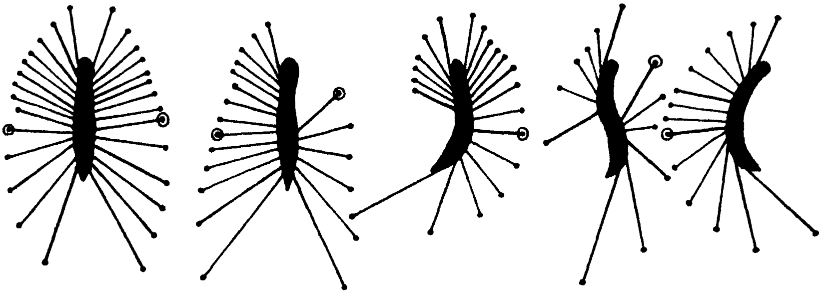
position sense organs if they are to contribute to the maintenance of a static posture. There is ample evidence to show the dependence of characteristic resting postures in animals on sensory activity. If in a frog or toad a hindleg is desensitized, leaving the motor nerves intact, this leg can be placed passively into any position, and it stays there as long as the rest of the body is not moved. In this condition the proprioceptive influences from the intact limbs and the body do not affect visibly the posture of the individual desensitized limb. This indicates that in the resting posture the proprioceptors of each limb are continuously active and determine its posture.



Text-fig. 10. Diagram showing the differences in rate of adaptation of sense organs to a continued stimulus. Note that adaptation is slowest in the sense organs of the muscle (Adrian, 1928.)

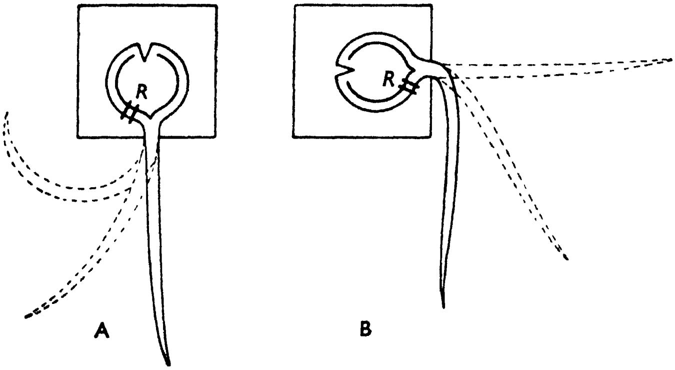
The long-lasting effect of proprioceptors during static posture is also illustrated by preparations showing decerebrate rigidity, which typically in a tetrapod involves the extensor muscles, but atypically, as in the sloth, may be transferred to the flexor muscles, or, in the case of the pigeon, to the depressor muscles of the wing, i.e. in all cases it affects the anti-gravity muscles of these animals. This sustained activity in the muscles can be abolished either by cutting the dorsal roots or by severing one of the tendinous attachments of the muscle. Since the sustained activity of a muscle is made to disappear completely, either by preventing the sensory impulses from reaching the cord, or by avoiding stimulation of the sensory endings, it follows that whatever the central influence may be, by itself it does not affect the events in the muscle.

The normal posture of a typical land-living animal seems designed to fit the prevalent condition of standing on a horizontal level, but any deviation from this normal condition, even if it affects a single limb, shows a quick appreciation of this change and it affects the posture as a whole. For instance, Pi-Suñer & Fulton (1928) have shown that the lengthening reaction in the cat, i.e. the enforced flexion of a hindlimb, causes also flexion of the diagonal forelimb, and extension of the ipsilateral fore- and contralateral hindlimb. Gray (1944), in an analysis of mechanical conditions which prevail during standing or movement, has discussed the profound significance of reactions of this type, and has shown the degree in which they contribute to the maintenance of balance. In many animals the weight of the body tends to flex the limb joints and to stretch the extensor muscles. The reflex contraction which is thus evoked counteracts gravity and helps to maintain the standing posture. Very often the stretch reflex is a localized response, and this allows a fine adjustment of the posture when the centre of gravity of the animal is slightly shifted, and thereby the distribution of stretch and tension of the various muscles is changed. Analogous responses can be seen in invertebrates, e.g. in a centipede which has lost a number of legs and which has to redistribute its weight to the remaining legs in such a way as to retain a standing posture (Text-fig. 11). Many similar reactions have been classified under the name 'geotaxis'. Whether we would gain a deeper understanding of such responses by calling them 'geotactic' seems a rather formal side issue, but it must be remembered that the gravitational force is not the only one affecting proprioceptors, and such a classification would cut across the concept of the proprioceptor as a functional unit.



Text-fig. 11. Postures of limbs and body of the centipede *Scutigera* after autotomy of a number of legs. The weight of the body is redistributed to the remaining legs in such a way that the standing posture is safeguarded. The ninth leg is marked in the successive postures. (Lissmann, 1935.)

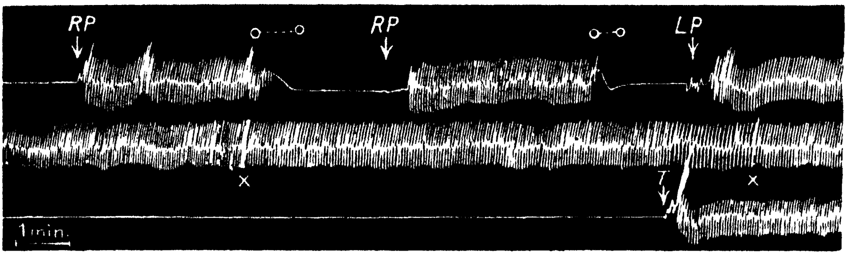
The nature of the physiological activity which will occur at the instant of change from resting posture to movement is also determined to a considerable extent by the activity of proprioceptors. Examples of this kind are usually summarized under the heading of 'Uexküll's law of stretched muscles' and illustrate the significance of a pre-existing posture on the subsequent performance. The very general phenomenon that proprioceptive reflexes may not only appear as superimposed on other reflexes, but that they are capable of reversing these reflexes has been shown in many instances. First discovered in the brittle starfish, *Ophioglypha* (Text-fig. 12; v. Uexküll, 1904), it has been found to apply equally to the cat's tail (Magnus, 1924), the trunk musculature of the dogfish (ten Cate, 1933), etc. An exteroceptive stimulus which would normally cause contraction of a group of muscles leading to a specific response is modified to such an extent that the antagonists of these muscles, if initially stretched, undergo contraction. Magnus (1924) has shown that this reaction need not be considered as part of a phasic response. The crossed extensor reflex in a dog is reversed into a crossed flexor response if the responding leg is initially extended. However, if the leg is only partially extended, the response does not start by completing the extension but flexes at once on application of the stimulus. Even more spectacular is the influence of a stretched muscle if it is far removed from the responding muscle. Thus bending the neck can modify or reverse the response of the hindlegs in a mammal.



Text-fig. 12. von Uexküll's experiment on *Ophioglypha*. As long as the antagonistic muscles of the arm are stretched symmetrically a stimulus at *R* causes the arm to beat to the left (A). When the muscles on one side are stretched the same stimulus excites the stretched muscles (B).

In rhythmic actions of the musculature, such as in locomotion, it is obvious that proprioceptors send to the centres a pattern of impulses which must be assumed to correspond to the pattern of muscular contraction at any one moment. The work of Fessard & Sand (1937) has shown that in elasmobranchs stretch receptors can respond during passive imitation of swimming movements in two ways: either by increased discharge during stretch of one set of muscles or by decrease or even complete abolition of the resting discharge during stretch of the antagonists. It has been suggested that this mechanism could provide an accurate control of timing for the undulatory rhythm (Pl. 2).

The view, which has largely been held about the significance of these patterns of proprioceptive messages since Graham Brown's (1914) work in this field, is expressed in the words of Creed *et al.* (1932): 'The phasing of these alternating reflexes can be affected by the proprioceptive and other stimuli which they generate...but their phasing is not caused by peripheral stimuli. The self-generated proprioceptive stimuli of the muscles which take part in progression can regulate the act, but are not essential to its rhythm.' On a general acceptance or rejection of this view depend to a large measure some fundamental interpretations of normal animal behaviour.



Text-fig. 13. The persistent locomotory rhythm of a spinal dogfish (*Acanthias*) can be inhibited by contact of the ventral surface. When the contact stimulus is removed the swimming movements do not reappear, but they can be evoked again by any unspecific stimulus. The tracing shows the initiation of persistent swimming movements through touch of the tail and of the right or left pectoral fin and their inhibition through ventral contact with a glass plate. At ↓ the fins or tail were stimulated; at o - - - o the ventral surface was in contact with a glass plate. The recording drum was stopped at ×.

An experiment which is designed to cast some doubt on this categorical statement can be performed on the dogfish (Lissmann, 1946). After spinal transection the dogfish maintains a state of continuous locomotory activity. This can last for days or even weeks. However, this activity can be inhibited by touch applied to certain areas of the body. When the inhibitory stimulus is removed the preparation remains inactive and may retain this state of inactivity for many hours. On the other hand, any brief and unspecific stimulus, such as a strong pinch or a gentle touch with a camel-hair brush, can act as a releasing stimulus and can again evoke the uninterrupted swimming movements (Text-fig. 13). Since the releasing stimulus is of short duration and presumably of a quick-adapting nature, it is difficult to see what, apart from self-generated proprioceptive stimulation, can 'keep the animal ticking'. That it cannot be a central phenomenon has been shown by deafferentation experiments.

If posture, if change of posture and if locomotory movements are so closely supervised by and dependent on proprioceptors, one would naturally like to know what the capabilities of the proprioceptors might be with regard to more complex acts of behaviour. It seems to be generally agreed that many complex instinctive acts contain elements of chain reflexes. All instinctive acts are executed in the medium in which the animal lives, and unless it can deal effectively with the conditions imposed by this medium—in which process we may presume the proprioceptors to play an important part—it is difficult to visualize what any instinctive impulses, wherever they may arise, could produce in the way of instinctive acts denuded of this adjustable coat of reflexes. I am aware that definite opinions have been expressed on this point, but at the present time I know of no experimental evidence which would settle the question in a decisive manner.

The object of this review has been to discuss the range and capabilities of proprioceptors. The physiological groundwork has given us some indication about what proprioceptors can be expected to do. It is unfortunate that it should be more difficult to decide what they actually do in the life of an animal. A muscle which contracts after stimulation of its motor nerve does not do quite the same thing as it does in an intact animal, and passive imitation of locomotory movements is unlikely to produce the natural type of proprioceptive response. The influence which the proprioceptors exert on the central nervous system is even more difficult to assess, but with modern methods these difficulties do not appear insuperable. Incomplete as the results may be, they should serve as a reminder that in an analysis of animal behaviour it might be worth while to focus part of one's attention on this system of sense organs, which is so easily overlooked.

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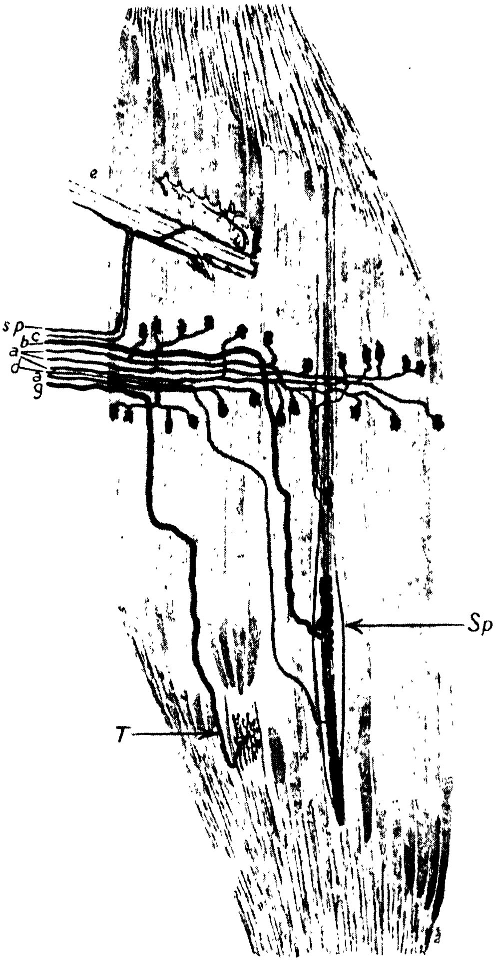
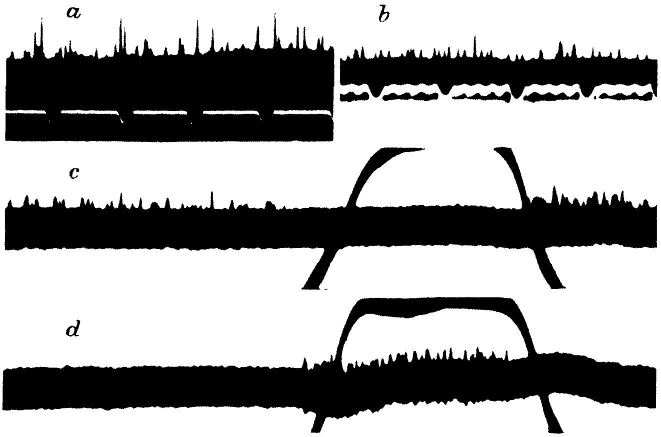
PLATE 1



For explanation see p. 59

PLATE 2



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EXPLANATION OF PLATES

PLATE 1

Diagram illustrating the position and innervation of proprioceptors in a mammalian muscle. The muscle spindle (*Sp*) consists of three intrafusal fibres, each one innervated by branches of motor nerve fibres (*a*) which also supply the surrounding, extrafusal fibres. The spindle has one large annulo-spiral (primary) ending innervated by the large sensory nerve (*b*) and one flower-spray (secondary) ending connected with the nervous system by a smaller fibre (*d*). The Golgi tendon organ (*T*) is supplied by a large sensory fibre (*g*). (From Denny-Brown in Creed *et al.* 1932.)

PLATE 2

Top records, sensory resting discharges from radial muscles of *a*, pelvic fin; *b*, pectoral fin of *Raja*, when the fish lies flat and muscle attachments are intact; *c*, record from dorsal branch of pectoral fin nerve; *d*, record from ventral branch of pectoral fin nerve. In both *c* and *d* the fin was initially drooping down, and the signal marks the raising and lowering of the fin. Note the disappearance of sensory discharges from the dorsal muscles and their appearance in the ventral muscles during elevation of the fin. Time marker 0·2 sec. (From Fessard & Sand, 1937.)

LABYRINTH AND EQUILIBRIUM

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I. INTRODUCTION

The present Symposium is fittingly opened by a survey of the range and capabilities of sense organs, for they constitute the peripheral physiological mechanisms responsible often for the initiation and generally for the running control of the various patterns of effector behaviour. The biological principle of double and even multiple safeguard of function finds its convincing expression in the fact that the topic of this communication, the maintenance of equilibrium, is found to be within the range of capabilities of all the types of sense organs under review. My task will be confined to a re-examination of the mode of function of the vertebrate labyrinth in the light of new experimental evidence and theoretical analysis made known since the great summing up carried out by a number of authors after the subject had reached its centenary in the middle twenties (Maxwell, 1923; Magnus, 1924; Magnus & de Kleijn, 1926*a,b*; Fischer, 1926; Camis & Creed, 1930; Lorente de Nó, 1931; Lowenstein, 1936). It will be my endeavour also, when dealing with the various aspects of vestibular function, to attempt to direct attention to problems concerning the control of equilibrium by analogous sensory structures in the invertebrates, although our knowledge of the functional mechanism of these organs has made no appreciable advance after the appearance of the excellent reviews of the subject by Kolmer (1926), Jordan (1929), and v. Buddenbrock (1937).

The subdivision of the labyrinth into semicircular canals and otolith organs is phylogenetically fundamental. It is found in the Cyclostomata, and according to Stensiö (1927) in the fossil Ostracoderm *Kiaeraspis*. In addition, the labyrinth of *Petromyzon* is equipped with two large cavities which are lined with a ciliated epithelium. Two counterrunning endolymph vortices are constantly maintained in each cavity by vigorous ciliary activity. The ensuing endolymph movements do not, however, appear to spread to other parts of the labyrinth, although the ciliary cavities are in open communication both with the ampullae and with the space containing the maculae (de Burlet & Versteegh, 1930). In the absence of any additional sensorium specially related to the ciliary sacs, de Burlet & Versteegh declined to elaborate a hypothesis about their function. Such a hypothesis has recently been formulated by Mygind (1948), who assumes that the endolymph vortices can be gyroscopically affected by movements of the animal in a horizontal plane. When thus made to deviate from their usual direction they are held to bring about pressure changes in the neighbouring vertical ampullae in such a way that motoric compensatory reactions are elicited. Thus the ciliary sacs are said to act as a substitute for the horizontal semicircular canals wanting in these animals. It is difficult to judge the merits of this hypothesis. The fact that *Petromyzon* does show reflex reactions to angular accelerations about the dorso-ventral axis in the absence of horizontal canals does not in itself necessitate the assumption of an additional receptor mechanism, as it has been shown that vertical canals can be directly stimulated by horizontal rotations (Lowenstein & Sand, 1940*a*).

II. THE SEMICIRCULAR CANALS

The semicircular canals are fluid-filled canals which widen at one end into an ampulla and make open connexion at the opposite end with the vestibular cavity. The ampullae, too, open into the vestibulum, and complete continuity of the endolymph system is thus established. The receptor structure of the canals is found in the ampullae in the form of a sensory crista with a neuro-epithelium composed of neuromast cells, the hairs of which are ensheathed in a gelatinous cupula terminalis. Owing to the fact that in life the cupula has about the same refractive index as the endolymph, and that it shrinks drastically on fixation, its size was grossly underestimated until Steinhausen (1931, 1933, 1935) showed that it extends to the opposite wall of the ampullary dome, and during its deflexions glides in swing-door fashion along it with a minimum of endolymph leakage. It was thus established that cupula and endolymph form a rigidly coupled system, and that the elastic cupula is to be defined as a highly damped torsion pendulum with a period, in the case of the pike (*Esox lucius*) in the neighbourhood of 20 sec. Deflexions of the cupula under the impact of angular accelerations in the appropriate plane of space represent the stimulus to which the animal reacts by the well-known dynamic effector reflexes in the form of compensatory movements of eyes and limbs.

In the elucidation of the mode of function of the semicircular canals as such, and the interaction of the six canals in the maintenance of dynamic equilibrium, elimination experiments and experiments with artificial mechanical and caloric stimulation have served to establish a fair amount of information. There was, however, left a hard core of controversial problems the solution of which did not come within reach until it became possible, by the application of Adrian's technique of the oscillographic analysis of sensory action potentials, to approach the various sense endings directly and to record their electrical responses under conditions of natural stimulation.

Since the publication of Ewald's theory of the 'Tonus Labyrinth' (1892), in which he based the tonus production by the labyrinth on a constant ciliary activity of the hair cells of the semicircular canals, a number of workers contributed experimental evidence in favour of canal tonus (Maxwell (1919, 1920*a*, *b*) on Elasmobranchs; Lowenstein (1937) on a bony fish; Tait & McNally (1934) on the frog; Huizinga (1932, 1935) on birds; Magnus & de Kleijn (1922) and Lorente de Nó (1926) on mammals). These results were often considered surprising, even by their authors, in view of the fact that under the impact of the work by Magnus & de Kleijn and their school on the influence of position on the tonus of the various muscle groups in mammals, it had become generally accepted that the otolith organs were chiefly, if not exclusively, concerned with the maintenance of tonus. The

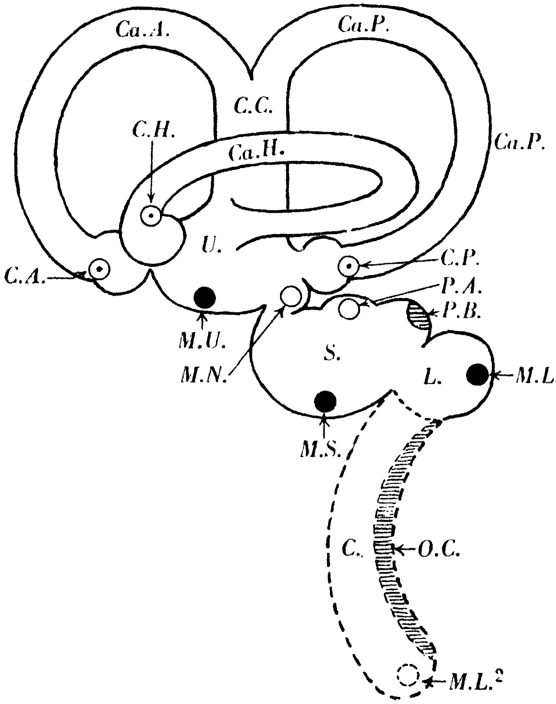

Fig. 1. Diagrammatic combination of the characters of the membranous labyrinth in all vertebrate classes. *C.* cochlea; *C.A.* crista anterior; *C.H.* crista horizontalis; *C.P.* crista posterior; *C.C.* crus commune; *Ca.A.* canalis anterior; *Ca.H.* canalis horizontalis; *Ca.P.* canalis posterior; *L.* lagena; *M.L.*^{1} macula lagenae in fishes and Amphibia; *M.L.*^{2} macula lagenae in reptiles and birds; *M.N.* macula neglecta = papilla neglecta; *M.S.* macula sacculi; *M.U.* macula utriculi; *O.C.* organ of Corti; *P.A.* papilla amphibiorum; *P.B.* papilla basilaris; *S.* sacculus; *U.* utriculus. The ductus endolymphaticus is omitted for the sake of clarity. (From O. Lowenstein, 1936.)

lasting effect of the otolith weight on the associated sensory macula suggests itself as a source of continuous stimulation responsible for maintained tonic states in the postural effectors. The semicircular canals, however, which became recognized to be delicately designed for the rapid perception of rotational changes from and the restoration of the resting position, could not with the same obviousness be regarded as sources of continuous tonus-producing activity, once Ewald's erroneous assumption of ciliary endolymph currents had been discarded.

In experiments on the ampullae of the horizontal semicircular canal of the dogfish (*Scyllium canicula*), and all three semicircular canals of the ray (*Raja clavata*) (Lowenstein & Sand, 1936, 1940*a*, *b*), in which the activity of the neuromast cells of the canal cristae was oscillographically recorded before, during, and after rotary displacement in various planes of space, it was shown that the sense organ in the canal ampulla is in a constant state of excitation. This manifests itself in the existence of a continuous discharge of action potentials in the resting animal in the absence of any obvious external stimulus. From records obtained from single neuromasts (single-fibre preparations) it was seen that the resting frequency varies considerably. At room temperature a range from 5 to 25 impulses per second was observed. Similar electrophysiological observations of 'spontaneously firing' neuromast cells had previously been made by Hoagland (1933) on the lateral line of trout and catfish and by Ross (1936) on the frog. Hoagland, in a way reminiscent of Ewald, explained it on the assumption of a ciliary activity of the neuromasts in the lateral line, and, comparing the neuromast cells with the Purkinjé cells of the mammalian cerebellum, thought their continuous activity might be responsible for a central inhibitory influence. Ross did not attribute any normal physiological function to the resting discharge which he observed to 'keep appearing for no very good or obvious reason'.

The constancy of the appearance of such a resting discharge in the preparations from the semicircular canals of the Elasmobranchs led to their interpretation by Lowenstein & Sand as an integral part of the normal functional behaviour of the labyrinthine neuromasts and to the assumption that it represents the substrate for a tonic function of the semicircular canals. Experiments on the pike (*Esox lucius*), in which it was possible by isolated nerve transection to eliminate one or both horizontal canals, yielded convincing evidence for this tonic function (Lowenstein, 1937). The operation, carried out unilaterally, leads to a lasting tonus asymmetry of the horizontal eye muscles manifesting itself in the resting animal and is to be correlated with the influx into the central nervous system of the resting discharge from the intact canal. Zotterman (1943), recording from the posterior vertical canal of the pike and burbot (*Lota vulgaris*), found a resting discharge in some but not all preparations. His preparations also differed in their response to rotatory stimulation from the behaviour of the canals of the elasmobranch labyrinth. Resting discharges from receptors responding to angular accelerations were also recorded from the brain of the cat by Adrian (1943), who found the behaviour of such receptors to agree with the discharge picture obtained from the elasmobranch labyrinth.

A tonus-producing activity of the canals may thus be considered to be well documented. But what is the mechanism responsible for the continuous resting discharge from the neuromast organs? In order to discuss this problem it is important to take into account the behaviour of the ampullary sense endings on rotatory stimulation. In the case of the horizontal canal of the elasmobranch labyrinth it was found that the frequency of the resting discharge is either increased or decreased by angular accelerations in a horizontal plane. An increase in frequency is obtained at the onset of ipsilateral rotations (ampulla trailing) and decreased by contralateral rotatory acceleration (ampulla leading). Deceleration at the end of prolonged rotation produces correspondingly reversed effects. We shall consider later the significance of this behaviour for the control of the compensatory reflexes in responses to rotation. Here we are interested in the fact that deformation of the cupula pendulum in one way encourages and in the opposite way counteracts or even abolishes the resting activity. It could be assumed that in the resting position the cupula structure imposes a certain mechanical strain on the hair processes of the neuromast cells which is intensified by one and alleviated or abolished by the opposite deformation of the cupula jelly. In this case the neuromast cells have to be considered to be very slowly or non-adapting receptors, responding to a lasting stimulus with continuous discharge activity (Ross, 1936; Adrian, 1943). On the other hand, the view cannot be excluded that the agency responsible for the rhythmical depolarization leading to the resting discharge is intrinsically localized in the neuromast cell, but subject to the stimulatory and inhibitory effect of opposite deformations of the hair processes. In view of our complete ignorance as to the intimate processes immediately preceding the production of action potentials in sensory cells, it is quite impossible to give theoretical preference to one or the other of these mechanisms. It is, however, quite clear that the term 'spontaneous' discharge, where it is used to describe the resting discharge, should only be understood to refer to the absence of external stimulation.

The functional mechanism of the ampullae, as shown up by the electrophysiological method, furnishes the answer to yet another old controversy in labyrinth physiology, viz. to the question as to whether a semicircular canal is a uni- or bi-directional receptor. Ewald's theory of canal function was based on the assumption that both ampulla-leading and ampulla-trailing rotations stimulate the ampullary end-organs, and he stated that in the case of the horizontal canal the stronger effect was brought about by ampulla-trailing rotations, the opposite holding for the vertical canals. This view was never seriously challenged by any worker experimenting on birds and mammals, as it was found that after unilateral labyrinth extirpation in these animals compensatory head and eye reactions can still be called forth by rotations in the horizontal plane in either direction, especially after a certain degree of central compensation of the post-operative tonus asymmetry has taken place. Moreover, mechanical and thermal stimulation experiments yielded similar results for the vertical semicircular canals. In the case of man it has even been suggested, on the basis of clinical evidence, that the unilateral preponderance postulated in Ewald's law does not hold at all, i.e. that both ampulla-trailing and ampulla-leading rotations are equally effective (Lorente de Nó, 1931; Cawthorne, Fitzgerald & Hallpike, 1942). Finally, the oscillographic analysis of vestibular responses from the brain stem of the cat (Adrian, 1943) definitely confirms the bi-directionality of the mammalian semicircular canals.

The mechanism of this bi-directionality was first established in experiments on the elasmobranch labyrinth (Lowenstein & Sand, 1936, 1940*a*, *b*). Angular accelerations in opposite directions were found to have opposite effects on the resting discharge. In the case of the horizontal semicircular canals the activity of the ampullary end-organ is increased by ampulla-trailing and decreased by ampulla-leading acceleration. The vertical canals behave in the opposite way. Provided the central nervous system is capable of utilizing a decrease in discharge frequency as a directional signal, the mechanism for a bi-directional response of the canal is clearly given.

A uni-directional canal response has, however, been postulated in work on the following lower vertebrates: Elasmobranchs (Maxwell, 1923), bony fish (Steinhausen, 1935; Zotterman, 1943), Amphibia (McNally & Tait, 1925, 1933; Main, 1931; Ross, 1936), reptiles (Trendelenburg & Kühn, 1908). Steinhausen's results in the pike are based on experiments in which endolymph movements in opposite directions could be induced by means of a cannula tied into the exposed semicircular canal. Simultaneous observation of the reflex eye movements under local anaesthesia showed the absence of compensatory eye reflexes during utriculo-fugal deviation of the horizontal and utriculo-petal deviation of the vertical canal cupula. These are the cupula deviations which would cause a decrease in the discharge frequency in the ampullary nerves of an Elasmobranch. In contradiction to this it was found by Lowenstein (1937) that after unilateral elimination of the horizontal canal of the pike ampulla-trailing rotation does give rise to reflex responses of the eyes which become increasingly more normal as the post-operative tonus asymmetry of the horizontal eye muscles is gradually abolished by central compensation. A similar recovery process has also been described in the minnow (*Phoxinus laevis*) after unilateral labyrinth extirpation (Lowenstein, 1932). It is possible that the discrepancy in the results gained in the same animal (pike) is due to the difference in technique, viz. artificial stimulation under anaesthesia in the one case and natural rotary stimulation in the unanaesthetized animal in the other, or to the fact that in Steinhausen's experiment the unstimulated state of the intact horizontal canal opposite led to a suppression of the reflex response to utriculo-fugal cupula deviation. For the sake of completeness it must, however, be added that Zotterman (1943), in a cursory study of the electrical responses from the posterior vertical ampulla of the burbot (*Lota vulgaris*), failed to see a reduction in discharge frequency on ampulla-trailing rotation in the few cases where he observed the existence of a resting discharge.

For the frog, McNally & Tait (1925) emphatically adhere to the unidirectional action of the canals as postulated by Crum Brown (1874), one of the co-founders of the classical theory of labyrinth function. Ross (1936, p. 129), in his paper on the electrophysiological study of the activity of the frog labyrinth, makes the statement that the resting discharge, where it was observed, could in fact be as a rule 'momentarily suspended by a movement in the direction opposite to that which stimulates the end-organ'. As Ross did not consider the resting discharge to be part of the normal behaviour of the neuromast organ, he did not attach any importance to this finding, and consequently supported the theory of a unidirectional function of the semicircular canals. Ledoux (1947) repeated Ross's experiments recording from the nerve branches of individual canal-ampullae of the frog and found, in full agreement with the results on the elasmobranch labyrinth, a clear bi-directional response against the background of a resting discharge.

In my opinion it is very likely that the mechanism of a bi-directional modulation of a resting discharge is characteristic for the neuromast organs in all vertebrates, but that there may be a considerable variation in the degree to which this peripheral reflex substrate is centrally utilized in the various vertebrate types, and that there may be a certain correlation between this utilization and the particular mode of locomotion. This might explain the absence of reflex bi-directionality in the squatting Amphibia and reptiles.

When a single-fibre preparation from the horizontal ampulla of the elasmobranch labyrinth is subjected to prolonged ampulla-trailing rotation with constant speed, the discharge frequency is increased at the onset of rotation during the period of acceleration. This is followed during the period of constant-speed rotation by a gradual return to the frequency of the resting discharge. The question arises whether this is to be interpreted as the result of a process of adaptation in the neuromast cells, or whether it is strictly correlated with the elastic cupula's gradual return to its resting position. On this point the observations of Steinhausen (1933) appear decisive. He observed the elastic return of the cupula and gives a graph of the time constants of the behaviour of the cupula which is in excellent agreement with the electrophysiological findings.

In a recent publication on the semicircular canal responses in man, van Egmond, Groen & Jongkees (1949) comment on the remarkably close agreement between the time constants found by them and those of the elasmobranch labyrinth.

The occurrence of a cupula deviation has been altogether denied by Wittmaack (1929), who put forward a hypothesis of labyrinth function in which changes in the hydrostatic pressure in response to rotational stimuli are made responsible for deformations both in the cupula and in the underlying neuro-epithelium of the crista. These were demonstrated histologically in animals rapidly killed during the application of rotational and artificial stimulation. Wittmaack's hypothesis led to a prolonged controversy with Steinhausen (for references see Steinhausen, 1935), which would lead too far to deal with here.

For the assessment of the way in which the six semicircular canals collaborate in the control of the reflex responses of eyes and limbs to angular acceleration it is necessary to have a clear picture of the range of response of individual canals to rotations in various planes in space. It may be considered safe to state that maximum reaction is produced by positive and negative accelerations in the plane of the canal. Sensitivity to acceleration in other planes, including those perpendicular to the plane of the canal, is theoretically possible and actually observed in the case of the vertical semicircular canals (Tait & McNally, 1934; Lowenstein & Sand, 1940*a*). It is interesting, however, that this wide range of receptivity is not shared by the horizontal semicircular canals which were found to be restricted in their responses to rotations in their own plane within fairly narrow limits. This may be due to a fundamental difference between the cristae of the two types of canals. The cristae of the phylogenetically older vertical canals make contact with the ampullary wall by the formation of two plana semilunata and are often subdivided by a septum cruciatum, whereas the cristae of the phylogenetically more recent horizontal canals are of a somewhat asymmetrical and simpler design (de Burlet, 1935*a*; Mygind, 1948).

The functional significance of the sensitivity of the vertical canals to horizontal rotation appears at first sight obscure, especially as it could be shown that the bilateral elimination of the horizontal canals by the interruption of their nerve supply in the pike abolishes the compensatory eye reflexes to horizontal rotation (Lowenstein, 1937). Thus the perception by the vertical canals of angular accelerations in a horizontal plane does not affect the reflex activity of the inner and outer straight eye muscles. Only the upper and lower straight and upper and lower oblique muscles are governed by the vertical canals. When stimulated by horizontal rotations the left anterior vertical canal and the right posterior canal collaborate, and vice versa (diagonal synergy). The result of this synergy is striking. It leads to a simultaneous contraction during horizontal rotation of the last-named four eye muscles, a reaction which has actually been kymographically recorded in the rabbit by Lorente de Nó (1931), who assigned to it the function of providing a firm pivot for the phasic eye responses executed by the inner and outer straight eye muscles under the control of the horizontal canals. Lorente de Nó assumed this response pattern to be of central origin, an assumption which is made unnecessary by the existence of a possible peripheral mechanism (Lowenstein & Sand, 1940*a*).

A sharp division of opinion still exists as to whether or not the semicircular canals can be stimulated by linear acceleration (de Kleijn & Magnus, 1921). The results of experiments on the guinea-pig, in which typical reactions to linear acceleration were unaffected by the destruction of the otolith organs by prolonged centrifugation, led to the adoption of the view that the semicircular canals have at least a share in the perception of such accelerations. As this would mean an extension of their range also to the perception of stimulation by gravity and centrifugal force, the acceptance or rejection of this view is of great theoretical and practical consequence. De Kleijn & Magnus were forced to their conclusions by what they regarded as incontrovertible evidence obtained from reflex tests and from a histological study of the effects of centrifugation. A working model constructed by Orenstein & Burger (Magnus, 1924, p. 463), which included a representation of the connexion between the canal system and the saccus endolymphaticus, showed clear cupula responses to linear acceleration, which were considered by the authors as further crucial evidence in favour of their assumption. When Hasegawa (1931) found by means of a similar method and in the same animal that all reactions to linear acceleration disappeared after centrifugation, he came to the conclusion that they were localized in the otolith organs, as previously postulated by

Fleisch (1922). De Kleijn & Versteegh (1933) reaffirmed the persistence of reactions to linear accelerations after destruction of the otolith membranes and rejected Hasegawa's contrary findings as based on negative results. The severance of the otolith membranes from their maculae by centrifugation brought to light yet another puzzling result. Hasegawa and de Kleijn & Versteegh report that positional reflexes persist after this operation, and come to the conclusion that these must be elicited by gravity responses from the otolithless maculae. It is not clear why the latter authors did not attribute the persistence of the reactions to other linear accelerations to the same mechanism instead of attributing them to the semicircular canals, which on theoretical grounds appear to be designed exclusively for the reaction to angular accelerations (Quix, 1925; Jongkees & Groen, 1946; Mygind, 1948). If the cupulae of the semicircular canals were in fact designed to respond delicately to linear accelerations, it is difficult to see how they could escape damage during centrifugation which must necessarily represent considerable over-stimulation. The possibility of the elicitation of gravity responses from maculae without otoliths would, if further confirmed, explain Maxwell's claim of a static function of the semicircular canals, which he based on experiments in which he washed out the calcareous otolith from the utriculus of the elasmobranch labyrinth without consequent abolition of positional responses. Their preservation might in this case be attributed to the activity of the macula itself. This whole complex of open questions clearly calls for an electrophysiological analysis. In our experiments on the elasmobranch labyrinth we have not found the semicircular canals to respond to gravitational stimuli, and have therefore considered it unnecessary, so far, to study their reactions to other linear accelerations.

In summing up it may be said that the semicircular canals have a considerable share in the production of labyrinthine tonus and elicit and control the compensatory reflex movements of eye, limb and body muscles which are designed to counteract the effect of positive and negative angular accelerations. During the normal activities of an animal an acceleration is almost immediately followed by the corresponding deceleration at the end of the short and limited turning movements. The inertia effect on the cupula is reversed, and the organ is pushed back into its resting position by a force equal and opposite to that responsible for its deformation. Prolonged accelerations or rotations with constant speed are not usually encountered except under experimental conditions or during the execution of the pirouette in ballet dancing. In the latter case the appearance of post-rotatory after-effects (after-nystagmus, vertigo) are prevented by skilled rapid head movements in a horizontal plane, dividing the spin into short equilibrated to-and-fro movements, with the effect that the cupula is prevented from executing the slow elastic drifts which are responsible for the creation of rotary illusions and vertigo.

No sense organs closely corresponding in design and function to the semicircular canals are known to exist in the Invertebrata. Functionally, however, the halteres of the Diptera represent a certain parallel despite the divergence in the underlying mechanical principle. The interpretation of their functional significance has a varied history (Fraenkel, 1939). After their role as gyroscoping balancing organs had been put on a sound observational basis (Fraenkel & Pringle, 1938), it was left to the successful application of the oscillographic technique to furnish incontrovertible proof that during flight the halteres are acting as sense organs for the signalling of rotations around the dorso-ventral axis (in the yawing plane (Pringle, 1948)). A hypothesis for the explanation of their mode of function was elaborated, according to which the perception of right and left turns depends on the central analysis of the time relationships of the impulses from a group of campaniform proprioceptor organs in the stalk of the actively oscillating haltere and from a large chordotonal organ in its basal region. The rate of rotation, apart from affecting the timing, is also gauged from the total effect (number of sensillae affected). For a given direction the two halteres are oppositely excited, but with additive central effect. There is no evidence that rotation about the longitudinal and transverse axes (rolling and pitching) can produce distinctive signals from the halteres. The organs thus represent a functional analogue to the horizontal and not to the vertical semicircular canals of the vertebrate labyrinth. A significant difference between the gyroscopic mechanism of the haltere and the torsion pendulum mechanism of the cupula is, that the halteres respond to constant speed rotations as well as to angular accelerations, in view of which they show a resemblance to the invertebrate and vertebrate statolith organs (*vide infra*).

III. THE OTOLITH ORGANS

Sensitivity to mechanical deformation under the influence of gravity is universal among living organisms. The regulatory mechanisms involved in the maintenance of the intimate structural organization and coherence of living cytoplasm is sure to depend in part on the reaction against the gravitational pull of cell inclusions of a density differing from that of the surrounding protoplasm, reactions in the absence of which a considerable degree of unmixing and polar separation of the cell constituents would be unavoidable. Electrostatic forces and reversible gel-sol readjustments are probably chiefly involved in this regulation.

In plant cells and in the cell body of Protozoa specifically heavier cell inclusions have been held responsible for the elicitation of geotropic and geotactic responses. The statolith theory of geotropism in plants makes movable starch grains responsible for the transmission of the gravitational stimulus to the cytoplasmic lining. After the part played by auxin in plant tropisms had become known, it was suggested (Cholodny, 1926, 1927) that the movement of auxin was due to an electromotive force caused by the direct action of gravity. Brauner (1927) found in horizontally placed plant organs a potential difference across them of 5–10 mV., with the upper part negative to the lower. This was called the geoelectric effect. There is, however, so far no experimental evidence that auxin is in fact transported along such gradients of electric charge. In connexion with the problem of geotropic perception in plants it is of interest to recall that Loeb (1918) postulated the accumulation of growth-regulating substances in the lowermost parts of the cells of hydroid polyps (Antennularia), which also show the familiar phenomena of geotropic growth reactions.

Among the Protozoa there is some experimental evidence that in the negative geotactic responses shown by *Paramecium* in a medium rich in carbon dioxide, the contents of the food vacuoles may have a statolith function. Koehler (1922) fed Paramecia on iron particles and found that the negative geotactic response can be enhanced or counteracted by the directional influence of a magnetic field. The movement of the animals is in every case directed away from the magnet, which excludes the interpretation of the effect as due to direct magnetic attraction.

Dogiel (1929) studied the so-called concrement vacuoles in symbiotic, holotrichous Ciliates (Bütschliidae and Paraisotrichidae) from the intestine of the horse and the stomach of ruminants. He came to the conclusion that they may act as intracellular statocysts. The organelle found near the anterior pole consists of a vacuole with an internal pore but no external opening. The vacuole contains concretions of crystalline granules which are probably identical with similar structures found diffusely distributed in the cytoplasm, whence they can be sometimes observed to enter the vacuole through the internal pore. Its boundary membrane is thickened into a cuticular cap at the outer end and equipped with a system of argentophil plasmatic fibrillae. A centripetal fibril often connects the internal pore with the endoplasm of the cell. A connexion between the fibrillae of the vacuole wall and the 'motorium' of the cell on the one hand and with the base of the cilia on the other suggests, according to Dogiel, a controlling influence of the organ on the locomotory activity of the animal. It is regrettable that Dogiel's arguments against an excretory and for a statocyst function of the concrement vacuoles are not supported by an attempt to ascertain whether these Ciliates do in fact exhibit geotactic responses.

The prototype of the otolith organs may thus be fully elaborated in the Protozoa. The imposing array of statocysts among invertebrate Metazoa of all major phyla (Kolmer, 1926; Jordan, 1929; v. Buddenbrock, 1937) bears witness to the fundamental importance of gravity perception. It is interesting, however, that an auditory function was originally attributed to all so-called otocysts. Eimer (1878), Romanes (1885) and Delage (1887) were the first to apply the newly discovered equilibrium function of the vertebrate ear to the lithocysts of Medusae, attributing to them, in addition to their assumed auditory function, the regulation of locomotory movements. This led in the following years to a general renaming of invertebrate otocysts into statocysts, in many cases at first without any attempt to justify the change by argument or experiment. Numerous elimination experiments (reviewed by v. Buddenbrock, 1937) and the classical experiment of Kreidl (1892) on the influence of a magnetic field on the posture of *Palaemon*, in which the statolith was replaced by iron particles, firmly established the invertebrate statocyst as a gravity receptor.

In the vertebrates the detailed study of the mode and function of the otolith organs has all along been handicapped by their inaccessibility to separate elimination or stimulation. The operative interruption of the nerve supply of individual otolith organs is generally made almost impossible by the shortness of the nerve branches, and the removal of the otoliths usually involves wide openings in the vestibular space with considerable endolymph loss and spread of the damage to all other parts of the labyrinth. It is therefore not surprising that until recently the functional analysis of the otolith organs was mainly based on the interpretation of the spatial arrangement and the anatomic relationships of the otoliths and their sensory epithelia, supplemented by rather contradictory results of experiments with artificial mechanical and other stimulations (Kubo, 1906; Maxwell, 1923; Ulrich, 1935), or the equally contradictory results gained in mammals by means of the centrifugation method (see p. 73).

The operative interruption of the nerve supply to isolated parts of the otolith apparatus did, however, succeed in the frog (McNally & Tait, 1933; Tait & McNally, 1934), and has contributed a good deal to the clarification of the position. The general conclusions drawn from these experiments were that in the frog the utriculi are the only source of all responses to gravity, centrifugal force, and linear translation. The elimination of the pars inferior of the labyrinth containing the sacculus and lagena among other sensoria was shown to be without noticeable effect on known equilibrium reflexes. Similar findings were reported by a number of workers in experiments on Elasmobranchs (Maxwell, 1923), on the minnow (*Phoxinus laevis*), among the bony fishes (Lowenstein, 1932), on reptiles (Tait, 1932), with certain reservations on birds (Benjamins & Huizinga, 1927, 1928*a*, *b*), and finally on mammals (Versteegh, 1927). Benjamins & Huizinga were not quite sure, however, whether the rotary eye responses were not, after all, interfered with by the elimination of the sacculus.

Oscillographic recordings from the sacculus nerve of the frog (Ashcroft & Hallpike, 1934) showed an absence of tilting responses but a high sensitivity to vibration. Ross (1936), however, recording from the posterior ramus of the eighth nerve of the frog, found evidence for the presence in the posterior part of the labyrinth (pars inferior minus sacculus) of at least one type of gravity receptor. MacNaughton & McNally (1946) succeeded in the isolated elimination, by nerve cutting, of the lagena. The unilateral operation resulted in a slight upward tilt of the head on the ipsilateral side, whereas the effect of bilateral elimination was a slight unsteadiness of the head on the cessation of movement. The possession of two lagenae in absence of all other equilibrial end-organs left the frog with a capacity for righting distinctly better than that of a completely de-labyrinthized animal. From this the authors concluded that the lagena has an equilibrium function, sharing with the vertical canals the task of antagonizing the activity of the utriculus. Adrian (1943), recording from the vestibular nucleus in the brain stem of the cat, described gravity-controlled responses to lateral and fore-and-aft tilting. The gravity receptors showed a resting discharge (about 6 per sec.) when the head was level, and were increasingly stimulated when the head was tilted through a small angle (20°) out of its normal position, becoming very slowly adapted to the stimulus. Out-of-level tilting in the opposite direction reduced or abolished the resting discharge. It is of theoretical importance that some of the gravity receptor units controlled by lateral tilt also responded to linear fore-and-aft acceleration and to fore-and-aft tilting of the head, a dual function characteristic also for the gravity receptors in the elasmobranch labyrinth.

The accessibility of the various labyrinthine end-organs in the cartilaginous cranium of the ray (*Raja clavata*), and the fact that their activity can be studied in a surviving isolated preparation of the otic capsule, made possible a point by point oscillographic analysis of the sensoria contained in the utriculus, sacculus and lagena (Lowenstein, 1948; Lowenstein & Roberts, 1948, 1950*a*,*b*). The results of this analysis can be summarized as follows: Receptors responding to gravitational stimuli and to linear acceleration in general are in the elasmobranch labyrinth found in all three otolith organs. The widest range of receptivity is found in the utriculus, which can be considered potentially capable of controlling all the known gravity responses, a task which it may well have to perform in a number of vertebrate types (see p. 76). The sacculus, in which only the posterior part of the macula contains gravity receptors (the rest being highly vibration sensitive), doubles some but not all of the utricular functions, whereas the lagena is in a way to be considered antagonistic to the other two. Before describing the individual gravity responses from typical sensory units of the three otolith organs with respect to the theoretical significance of their behaviour, it will be necessary to recall some of the outstanding problems concerning the functional mechanism of the otolith organs.

The original assumption that the gravitational stimulus is transferred to the macula by the gliding of the otolith in certain directions relatively narrowly prescribed by the morphological characteristics of the organ (Breuer, 1891) was generally rejected by later workers (Maxwell, 1923). It was replaced by two rival hypotheses, viz. the theory of Magnus & de Kleijn (1926*b*), who held that the maximum of the tonus effect is produced by an otolith organ when the otolith is hanging from the macula, tension or pull on the sensory hairs or sense cells being the effective stimulus, and the theory of Quix (1925), who conversely held the pressure of the otolith on the macula to produce a maximum of stimulation. In a recent treatise on the static function of the labyrinth, Mygind (1948) makes changes in otolith pressure on morphologically discrete dominant and subordinate areas of the macula responsible for the integrated control of the various compensatory reflexes of limbs and eyes. Apart from the direct otolith action Mygind also operates with the concept of a hydrostatic endolymph pressure responsible for the generation of labyrinthine tonus in areas of the sensoria not specifically exposed to the changing influences of otolith pressure or pull.

Much confusion exists in this field, and this is not surprising, as the little physiological evidence there is depends on observations of reflex behaviour, i.e. reactions which have gone through the clearing house of the central nervous system. Far-reaching interference by automatic central mechanisms in the elaboration of vestibular reflexes are postulated by Lorente de Nó (1933), who suggests that lesions in any part of the vestibular system are likely to affect all equilibrium reflexes simultaneously.

It may be useful at this point to consider the results of the analysis of the electrical responses from the elasmobranch otolith organs (Lowenstein & Roberts, 1950*a*). The majority of the sense endings in the maculae of the utriculus, sacculus and lagena were found to be in a state of continuous activity. In the normal position in space the sensory units situated in the lateral aspect of the utriculus macula (the only part of it readily accessible for electrical recording) would fire a continuous stream of impulses at a moderate frequency of 5–20 per sec. at 20° C. This discharge frequency can be either increased or decreased when the preparation's spatial orientation is altered by tilting about a horizontal axis. As a rule one and the same ending responds both to lateral and to fore-and-aft tilting from the normal in such a way that its discharge frequency reaches a maximum when the preparation is approaching a position in which the labyrinth under observation lies uppermost (lateral tilt) or in which the nose is tilted vertically up or down (fore-and-aft tilt). Preparations responding with an increase in discharge frequency to a lateral lowering of the labyrinth were rarely encountered on recording from the outer part of the macula. Whether such sense endings exist in significant numbers in the inaccessible basal and innermost parts of the utriculus macula remains an open question. Provisionally ignoring the latter type of organ, it can be stated that the outer part of the utriculus macula contains at least two types of sense endings, which can be classified into organs responding with an increase in discharge to side-up and nose-up or to side-up and nose-down displacements. Nerve fibres from these two types can be found side by side in one and the same small nerve twig. This does not, however, mean that they are necessarily derived from neighbouring neuromasts, as a considerable amount of fanning out is characteristic of the end-ramifications of the nerve strands. It is thus difficult to localize the exact position of the sense endings under observation with sufficient confidence to base upon such a localization far-reaching theoretical deductions. From the fact, however, that the lateral parts of the utriculus macula yield preponderantly preparations whose discharge frequency increases on side-up tilting, it may be tentatively suggested that either a gliding away of the otolith producing a medial deflexion of the sense hairs of the neuromasts or a relief of the vertical pressure of the otolith on the macula may represent the appropriate stimulus, with the reverse hair deformation or pressure change producing a reduction in the discharge frequency. If this were correct, then the side-up and nose-up organs ought to be located in the antero-lateral, the side-up and nose-down organs in the postero-lateral part of the utriculus macula. This localization would be in full agreement with the stimulation experiments on the dogfish (Maxwell, 1923), where it was found that pressure on the otolith applied laterally, so as to move the otolith slightly inwards, produced eye responses corresponding to those occurring on the lateral up-tilting of the stimulated labyrinth. Pressure on the anterior side of the otolith produced the effect of nose-up tilting and pressure on the posterior end the opposite. From this Maxwell concluded that the effective stimulus is a displacement of the otolith. This satisfactory agreement based on two entirely different methods is not supported by the results of similar stimulation experiments on the pike (Ulrich, 1935). Here the effects of delicately apportioned pressures on the utriculus otolith are directly opposed to those described by Maxwell. Furthermore, eye responses to artificial pressures could only be evoked uni-directionally, a finding which, if further substantiated, would point to fundamental differences in the mode of function of the labyrinthine end-organs in the bony fishes and Elasmobranchs (compare also Steinhausen's results on semicircular canals, p. 65). Before coming to such a conclusion, it must be borne in mind that the electrical behaviour of single sensory units could only be taken as representative of the activity of the macula as a whole if they were uniformly active in all parts of the sensorium. It is certain, however, that far from showing such uniformity the frequency changes in the sense endings differ widely at any given moment during a tilting movement or in various spatial positions. Direct evidence for this can be derived from the records from the elasmobranch utriculus. There are two extreme types of sense endings. In one a complete rotation about a horizontal axis yields a continuous change in the discharge frequency with a maximum and minimum of activity in certain characteristic positions in space. When the rotation is arrested in any given position, only slight adaptive changes take place, and the discharge frequency stays at a level significantly different from that characteristic for the normal position. On rotation in the opposite direction the frequency changes are faithfully reproduced in a reverse sequence, and the spatial positions for maximum and minimum activity are uninfluenced by the direction from which they are reached. Such end-organs are ideal position receptors capable of indicating spatial positions by the absolute level of their activity. At the other extreme we find organs which on the reversal of the direction of displacement show their maxima (and minima) of activity in diametrically opposite positions, having, for example, a minimum in the nose-up position when this is reached on the shortest way from normal by a nose-up tilt, whereas a nose-down tilt produces the minimum activity near the nose-down position. All grades of intermediate types of organs with various degrees of divergence in the position of the maxima and minima have been found. It is not surprising that organs with an appreciable shift of their maxima and minima on displacement in opposite directions do not show fixed frequency values for certain positions in space and tend to return to a basic level of activity when the tilting movement of the head is stopped. They are, however, sensitive out-of-position receptors apparently delicately poised to signal the departure from critical positions, answering such departure by the same change in activity irrespective of the tilting direction.

There are also organs whose basic activity remains largely unaffected by positional changes, and others which are completely inactive in certain positions. The former type was encountered in the so-called lacinia process of the utriculus macula and in the greater part of the macula of the sacculus and was shown to be extremely sensitive to vibration. The latter type was not by any means uncommon and appeared to have a relatively limited spatial range of activity. It occurs especially frequently in the position-sensitive posterior part of the sacculus macula which preponderantly responds by an increased discharge activity to side-up and nose-down tilting. The greatest uniformity of response was found in the lagena where the majority of sense endings sampled from all parts of the macula showed their maximum activity in the normal position, their activity being strongly reduced in all other positions. Such receptors can best be described as 'into-level' receptors, and their discovery agrees well with the function of the frog's lagena as postulated by McNaughton & McNally (1946).

Thus a variety of differently responding sense endings may be assumed, especially in the utriculus, to collaborate in signalling individually to the central nervous system local mechanical changes brought about during displacement from the normal by the spatial shift or deformation of the otolith membrane. Mygind (1948), in his hypothesis dealing with the mode of function of vestibular end-organs, recalls that the labyrinth is developmentally a specially transformed cutaneous sense organ for which the adequate stimulus is pressure change. The effector responses of the animal to spatial displacement are such as to maintain contact between otolith and macula in the manner characteristic for thigmotactic (contact-seeking) responses. Opposite parts of the neuro-epithelium lying in the same plane of its curvature elicit 'oppositely curved' reactions. Mygind distinguishes between opposing dominant and subordinate parts of the various maculae, the dominant parts always lying at the distal end of the nerve fan and being composed in many cases of higher neuromast cells. They are more sensitive and elicit the stronger reactions. In a sketch of the hypothetical central link-up of the utriculus macula, Mygind postulates the dominant parts to control the ipsilateral anti-gravity muscles, collaborating during lateral displacement with the subordinate part in the opposite labyrinth by crossed innervation. There arises a discrepancy between Mygind's hypothesis and the behaviour of the elasmobranch utricular sense endings which, showing maximum stimulation on side-up tilting, must evoke maximum contraction in the contralateral anti-gravity muscles. The interpretation, in these terms, of the well-known tonus asymmetry found in all vertebrates after total unilateral labyrinthectomy meets with a similar difficulty. The asymmetry arising after this operation always consists in the preponderance of the anti-gravity muscles of the intact side which must be correlated with a continuous tonus-producing activity of the intact labyrinth which, in turn, must therefore be assumed to be predominantly responsible for the maintenance of the tonus in the ipsilateral anti-gravity muscles. And yet, in the elasmobranch labyrinth, the majority of the utricular sense endings so far recorded from behave as if they were linked with the anti-gravity muscles opposite. Every difficulty of this kind can, of course, be discussed away by *ad hoc* hypotheses. One such hypothesis would be to absolve the otolith organs of a significant share in the production of general labyrinth tonus, assigning this task to the semicircular canals. On this basis an integrated scheme can be elaborated which would account for all the known consequences of unilateral total labyrinthectomy (Lowenstein & Roberts, 1950*a*). It must be pointed out, however, that the observations reported by Tait & McNally (1934) in what they call the uni-soli-utricular frogs, in which all labyrinthine sensoria except one utriculus were eliminated by nerve cutting, also point in the direction of ipsilateral preponderance of the anti-gravity muscles under the influence of the intact vestibular end-organ. In agreement with this all records obtained from the vestibular nucleus of the mammalian brain stem (Adrian, 1943) showed increased impulse discharge on side-down tilting. This was tentatively attributed to the activity of the ipsilateral sacculus. In view of the striking regularity with which side-up tilting produces an increased discharge activity in the neuromasts of the lateral (according to Mygind dominant) region of the elasmobranch utriculus macula, and the fact that the gravity responses of the sacculus, too, behave in the same way, we are faced here with a contradiction which cannot be removed without further electrophysiological experiments on as many different vertebrates as possible.

A significant indication of the complexity of this problem is further provided by the results of Tait & McNally (1934), who postulate the existence in the utriculus macula of two types of responses resulting in diametrically opposite compensatory and anti-compensatory reactions to slow and rapid displacement in the same direction. As a graded continuity was found to exist between these opposite reactions the authors concluded that they are due to the activity of the same sense endings under different conditions of stimulation. They found themselves forced to abandon the prevailing idea that the otolith acts like 'the sand grains' in the statocyst of *Palaemon*, i.e. by a simple and uniform sliding descent from a higher to a lower level, and came to the conclusion that a hypothesis of a point-to-point independence of the elements composing the otolith organ is unavoidable.

Full agreement exists among all workers that the otolith organs respond not only to gravitational stimuli but also to all other linear accelerations. Such responses were recorded by Ross (1936), Adrian (1943) and Lowenstein & Roberts (1950*a*). A valuable contribution to the theoretical aspect of the responses to horizontal linear translation was made by Adrian, who pointed out that pressure changes cannot be considered the sole conditions for stimulation, as the otolith organ can respond to otolith displacement in the plane of the utriculus macula (Adrian, 1943, p. 395). Stimulation of the otolith organs is generally brought about in a direction opposite to the direction of displacement during tilting, e.g. an organ which responds by increased activity to side-down tilting will show a similar response to contralateral horizontal linear acceleration. It is obvious that organs responding to linear accelerations must necessarily be affected by centrifugal forces and give rise to the notorious false horizon sensations experienced during banking in fast-flying aircraft.

The chief difference in receptivity between semicircular canals and otolith organs is the generally assumed restriction of the former by their morphological peculiarities and spatial arrangement to the reception of angular acceleration. By being as it were shielded from the action of gravitational and other linear accelerations, they are set aside for the signalling of onset and cessation of curved movements and provide a mechanism for the gauging of the magnitude of the rotary 'impulse' and its direction. In comparison, the otolith organs have a wider range of capabilities. Sensitive as they are to all forms of constant and changing linear acceleration, they are fundamentally not precluded from responding to any type of movement, straight or curved, as long as it entails a change of momentum. The old distinction between dynamic receptors (semicircular canals) and static receptors (otolith organs) is thus meaningless (Jongkees & Groen, 1946). The potential functional range of the otolith organs is wider still. Their sensitivity to changes in linear acceleration must of necessity make them respond to mechanical vibrations which are nothing but alternating linear acceleration phenomena (see also Mygind, 1948). Whether a given otolith organ does in fact act as a vibration receptor depends on the manner and degree of its exposure. In a very important essay on this question de Burlet (1935*b*) drew attention to the existence in various vertebrate types of what he called 'perilymphatic' labyrinthine end-organs. This rather unfortunate but nevertheless descriptive term refers to those among the labyrinthine sensoria which lack a protective padding in the form of perilymphatic connective tissue trabeculae and which are by their topography selectively exposed to extraneous mechanical influences reaching them through perilymphatic pathways. De Burlet applies this term to the sacculus of the Ostariophysi, the utriculus of the Clupeoidea among the fishes, the papilla amphibiorum and the papilla basilaris in the Amphibia, the papilla basilaris and the cochlea in the

Sauropsida and mammals. The localization of sound perception in the sacculus of ostariophysean bony fish (v. Frisch, 1936) and the fact that vibration-sensitive sense endings have been found in the labyrinths of a number of vertebrate types lacking a cochlea (Ashcroft & Hallpike, 1934; Ross, 1936; Zotterman, 1943; Lowenstein & Roberts, 1948, 1950*b*) add weight to de Burlet's morphological analysis.

The wide range of potential function of the vertebrate otolith organs makes it more than likely that the receptive range of the invertebrate 'lithocysts' may well be found in certain cases to transcend the field of gravity reception pure and simple. This problem is awaiting renewed exploration with modern experimental methods. One of the questions of fundamental importance arises from the fact that stimulus reception in the invertebrate lithocysts is entrusted to primary sensory cells whose adaptive behaviour and general mode of response may well radically differ from the corresponding physiological characteristics of the vertebrate neuromast cells. For this reason alone it would be inadmissible to attempt far-reaching theoretical deductions with respect to the mode of function of these organs on the basis of our knowledge of the functional mechanism of the sensory structures of the vertebrate labyrinth.

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CENTRAL AND PERIPHERAL CONTROL OF BEHAVIOUR PATTERNS

THE CONTROL OF NERVE-CELL ACTIVITY

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In the higher levels of the mammalian nervous system many of the nerve cells are in constant electrical activity as long as the animal is awake. The activity often takes the form of a regular beat, the frequency ranging from 10 per sec. in the cerebral cortex to 200 per sec. in the cerebellum, and the magnitude of the potential changes showing that there must be extensive synchronization of the different cell units.

Much of this activity is to be regarded as a background state which must be modified locally when the animal is engaged in movement or in recording sensory impressions. In fact it is in steady undisturbed conditions that we find the most widespread synchronization and therefore the most striking electrical rhythms. But there is every reason for thinking that the background plays an important part in the whole picture, that the instability of the brain cells is related to what the brain can do, i.e. to the variety and apparent spontaneity of normal behaviour. At all events the background fades when the animal goes to sleep; as Bremer has said, the α rhythm seems to express a degree of cortical tonus proper to the waking state, a certain 'vigilance', to use Henry Head's expressive term.

This background activity can be reduced or suppressed altogether by anaesthetics, to return again when the effects of the anaesthetic have worn off. During the stage of recovery a single sensory stimulus will often produce the sudden return of persistent activity in large numbers of the nerve cells, just as a single stimulus may rouse a sleeper, and it is often possible to correlate the return of nerve-cell activity in the brain with increased tone in the muscles and increased responsiveness to stimulation. By changing the level of anaesthesia, therefore, we can change the level of basic activity in the hope of finding out how this will modify the flow of impulses in the central nervous system.

Some recent work on the olfactory system has given a good illustration of what may happen in a sensory pathway. It is not possible to record impulses in the individual nerve fibres from the olfactory receptors, for they are non-medullated and difficult to reach, but in the rabbit a wire electrode can be thrust into the olfactory bulb so as to pick up the action potentials in the medullated fibres of the mitral cells. These are the fibres which go to form the olfactory tract; they are comparable to the optic nerve fibres in that they are in touch with the receptors through synaptic connexions, but the olfactory bulb differs from the retina in having large numbers of nerve cells which are not on the direct pathway from the receptors to the brain. These accessory cells are usually in constant activity.

In very deep anaesthesia with urethane or one of the barbiturates the continued activity of the nerve cells can be suppressed, and this occurs with little alteration, if any, in the sensitivity of the olfactory receptors. There is also little sign of interference with the synaptic mechanism of the glomeruli, where the receptor fibres meet the dendrites of the mitral cells. Thus the mitral cells will respond whenever the olfactory receptors are stimulated, and the discharge of impulses in the olfactory tract will be entirely controlled by them. The discharge occurs at each inspiration when the air contains an olfactory stimulant, and it varies in magnitude in the usual way with the intensity of the stimulus. In deep anaesthesia therefore the discharge in the olfactory tract fibres can be used to study the receptor mechanism of the nose and the way in which smells are distinguished from one another. As in the optic nerve the discharge will not be an exact copy of the receptor signals, but it will be completely dependent on them.

In anaesthesia of moderate depth the whole picture changes. The accessory cells are in constant activity, sometimes with independent rhythms and sometimes in large groups beating synchronously at a rate between 60 and 90 per sec. There is a constant and usually irregular succession of impulses in the olfactory tract fibres; an intense olfactory stimulus may produce an appreciable increase in the discharge, but with so much activity it is usually impossible to detect any change in it from moderate stimulation. There is no doubt that the sensitivity of the olfactory organ is as great as before—it is possible to estimate this from records taken to show pre-synaptic as well as post-synaptic activity—but at this stage of anaesthesia most of the mitral cells are dominated by the constant activity in the bulb and they are scarcely affected by the messages from the olfactory organ.

As the anaesthesia wears off the olfactory organ resumes control, though to an extent which varies from one animal, or from one group of nerve fibres, to another. There is still considerable activity in the cells of the bulb, whether the nose is stimulated or not, but the high-frequency beating is rare, and if the inspired air contains an olfactory stimulant (as it usually does) the discharges in the tract occur mainly at each inspiration, as in very deep anaesthesia. If allowance is made for changes in the depth of breathing, the sensitivity and general behaviour of the olfactory organ seems to agree with what is found in deep anaesthesia, and the main difference is that in the olfactory tract the discharges at each period of stimulation no longer appear on a quiet base-line.

The effects of different depths of anaesthesia suggest that the mitral cells can be influenced both by the olfactory receptors and by the accessory cells of the bulb. The latter are highly unstable, but when the anaesthesia is very light their activity is controlled to some extent by the olfactory discharge. In very light anaesthesia, therefore, and presumably in the normal state, the discharges which pass to the brain will be mainly determined by the olfactory stimuli. In medium anaesthesia the accessory cells are if anything more active and they are much less influenced by the olfactory impulses; they dominate the mitral cell discharge, and the olfactory signals make little impression on it. In deep anaesthesia, however, the accessory cells are inactive, and the discharge in the olfactory tract is then entirely governed by what is sent in from the olfactory organ.

It is interesting to compare these three stages in the response of the olfactory bulb with the similar three stages in the response of the cerebral cortex. In the receiving areas the synaptic connexion between the afferent fibres and the cortical cells is more diffuse than that afforded by the glomerular structures of the olfactory bulb, and we can scarcely distinguish between accessory cells and cells on the direct pathway. But in deep barbiturate anaesthesia which has reduced the cortical cells to inactivity an afferent discharge will usually produce a few electrical oscillations showing that the nerve cells have responded. In medium anaesthesia, when the cells are in continuous activity, the afferent discharges have little or no effect, whilst in very light anaesthesia the cortical activity is again controlled by the afferent discharge, though there is now the background of rhythmic disturbance to be harmonized with the induced responses (Adrian, 1941). In this case we have no emergent pathway to investigate like the olfactory tract and no synapses which are likely to be specially resistant to the anaesthetic; thus the most that we can expect in deep anaesthesia is a feeble response of some of the cortical cells, a response not great enough to lead to further effects elsewhere. But by using chloralose as an anaesthetic instead of a barbiturate we can suppress the continued activity without much interference with synaptic conduction. The afferent signals are then so much in control that a slight touch may produce a convulsive jerk of the whole of a limb (Adrian & Moruzzi, 1939).

It is natural to inquire how far the continuous activity of the nerve cells is dependent on stimuli from the environment and how far on the properties of the nerve cells themselves. We have seen that a single afferent signal will often arouse the cells after an inactive period, and although the activity seems to persist without further stimulation it is, of course, impossible to secure a complete absence of incoming signals from all of the sense organs. Even with isolated preparations of nerve cells we cannot be sure that the environment is not partly responsible for whatever excitation is present. We can say, however, that the particular rhythms which are developed by the cells are not imposed on them by a corresponding rhythm in the sensory inflow. As with a stretched muscle spindle the rhythm of discharge expresses a particular level of excitation, and in the nerve cells of the brain that level seems to be decided by a number of factors, the general physical and chemical state of the cells as well as the number of afferent impulses reaching them (cf. Bremer, 1941*a*). It has been the fashion to regard the continued rhythms of nerve cells as a consequence of their organization in a close network through which waves of excitation might circulate endlessly. This reverberating circuit idea has histological backing, but there are so many instances of single isolated units, nerve cells or sensory endings, discharging rhythmically for long periods that it seems unnecessary to postulate a mechanism which has never been demonstrated in action. No doubt circulating activity may help to maintain the level of excitation, but there is no reason to think of it as the sole factor involved.

For one reason or another, then, the sheets of nerve cells which receive the sensory messages are so constituted that they tend to remain in continuous activity. The reasons for this instability need not be considered till there is more evidence, but there is at least some evidence relating to the changes which can occur when a message arrives.

It is well known that the α rhythm of the human brain is suppressed by opening the eyes, and that similar electrical oscillations in the brains of different animals are suppressed by touch, sound or smell. The suppression might be due to an interference with the synchronization of the different nerve cells. If the synchronous beat implies a uniform level of excitation or of instability throughout the beating area, then the disturbance produced by an afferent message would break up the rhythm by abolishing the uniformity. An explanation on these lines has been put forward by the writer to cover various examples of the suppression of a rhythmic beat, and it has usually been possible to show that the suppression of the waves is accompanied by increased activity in some of the neurones. But the explanation needs recasting, for it is based on an assumption which is scarcely justified, i.e. the assumption that all the cells are equally ready to beat.

The clearest evidence comes from the high-frequency rhythm which appears in the olfactory bulb in fairly light anaesthesia. Electrical records from the bulb show this to be a widespread synchronous beat with a frequency ranging from 60 to 90 per sec. After a strong olfactory stimulus the rhythm is abolished and it is built up again gradually, but its absence is associated with a reduction in the activity of the olfactory tract and its return with an increase in activity. In this case therefore the break up of the rhythm seems to involve a decrease in the activity of the cells, and it is not merely that their activity is no longer synchronized.

Since we are dealing with a high-frequency rhythm implying a high level of excitation in the nerve cells, the fall in activity might be a consequence of fatigue, but the gradual return of the beat with increasing amplitude suggests a different explanation. In this as in the other systems which give a rhythmic beat we are dealing with a mass of nerve cells which are influenced by one another as well as by afferent discharges. A few cells beating at a high rate may therefore excite their neighbours, and these in their turn would excite others until the rhythm has spread throughout the mass. But a disturbance of the pacemaking cells, a change of frequency in some of them for instance, would disorganize the rhythm, and the cells which had been drawn into it would cease to respond or would revert to lower levels of activity. In the same way a low-frequency rhythm might be maintained by a group of cells acting as pacemaker, but the majority of the cells taking part in the beat might well become inactive if the pacemaker failed and they were left to themselves. In fact, a synchronous beat need not imply a uniform level of excitation, and the suppression of the beat by an afferent discharge may well involve a considerable fall in activity in many of the nerve cells. The suppression of the beat would still be due to the disturbance of synchronization rather than to some kind of direct inhibition, but we should expect to find that most of the units would become less rather than more active.

The point may be of some interest, for it involves the idea that many of the continuously active cells are not in fact inherently unstable, but are driven by the fewer cells that are, and that the former sort can be drawn in to reinforce whatever may be the dominant rhythm in their neighbourhood. It also involves the idea that numbers may be important, since a large mass of nerve cells will be more effective than a small. A rhythmically active cell may influence its neighbours by means of the impulses which it sends to them or conceivably by the electrical or chemical fields engendered by its activity. Whatever the means, a group of cells beating in unison will have a greater effect than a single cell because the group will produce a more massive excitation, there will be more impulses sent out and the electrical and chemical fields will be more concentrated. Thus a few active cells may draw more and more units into the group, and the larger it becomes the more the rhythm will tend to spread into regions previously inactive. The process will be stopped when the beat invades the territory dominated by another rhythm, but in a large sheet of cells it would be possible for several beating systems to co-exist as more or less stable units. There is as yet no direct evidence to show that this snowball effect is an important factor in the building up of rhythms, but there are a good many indications of it. When a beat begins, the magnitude of the oscillations will usually increase slowly at first and then more and more rapidly, and Bremer's observations on the strychnine waves in the spinal cord show the dominant effect of massive discharges (Bremer, 1941*b*).

At all events it is clear that a system which contains large numbers of unstable cells with diffuse connexions will give a much greater variety of response to an incoming message than a system with definite through routes and few accessory cells. In the retina there are relatively few, and the message in the optic nerve is closely related to the receptor excitations; in the olfactory bulb there are more, and they have to be put out of action before the olfactory tract discharge can show us clearly what is happening in the nose; in the cerebral cortex there are no through routes, and here the incoming signals lose their identity as soon as they have left the receiving areas. They are dispersed among the crowd of active units which form the bulk of the brain, and the larger the bulk the more complex will be their effects in the various cell groups which have come to beat in unison.

SUMMARY

The cells of the central nervous system are often in continuous activity. Various stages can be recognized in the control of this activity by afferent signals. For instance, in the mammalian olfactory bulb deep anaesthesia stabilizes the cells, abolishing the continued discharge but leaving some which give a direct response to afferent impulses. In lighter anaesthesia many of the cells are in constant activity and are no longer affected by an afferent discharge, but as the effects of the anaesthetic subside the afferent control is re-established. The cells are no longer passive as they are in deep anaesthesia, and are now liable to discharge spontaneously if they are not subjected to afferent control. Similar changes in the stability of the cells and in their response to afferent signals are found in the cerebral cortex.

As the cells can influence their neighbours they tend to discharge in unison, forming large or small groups which beat synchronously. Afferent signals break up these groups, causing a concentration of activity into particular channels. The stability of the groups probably increases with its size, for the simultaneous discharge of the cells will have a massive effect which will increase with the number in action. It is suggested that the mass effect of cell aggregates may play an important part in determining the patterns of activity which can be formed in the central nervous system.

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EXPERIMENTAL ANALYSIS OF CO-ORDINATION BY THE DISARRANGEMENT OF CENTRAL-PERIPHERAL RELATIONS

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INTRODUCTION

Science owes many of its most spectacular advances to improvements in methodology and the introduction of new techniques. This being the case, I need hardly apologize for giving as much emphasis in my talk to a method which has proved profitable as to the results thus far obtained with it. The method in question is not new, but it has not yet been properly exploited. The examples to be presented will indicate its potentialities. It consists of testing the role of neural connexions not merely by the negative test of severance but by the positive test of systematically altered reconnexions. Although the story has been reviewed on several earlier occasions (Weiss, 1936, 1941), it bears repetition in view of the fact that additional pertinent information has been gathered in the meantime and because its content is quite germane to the objective of this conference, which is to bridge the gap between our concepts of overt behaviour and the underlying neural mechanisms.

Our method is a logical extension to physiology of some standard procedures of experimental embryology. In this latter field, it has long been customary to subject an unknown relation to a triple test of the following kind. If we wish to establish the kinds of interactions that exist among the component parts of a complex organic system, we single out each component, one at a time, and study its relation to the remaining system. After severing the connexion between a given part and the system, we can determine the behaviour of the isolated part on the one hand, and of the correspondingly defective system on the other. In a way, these tests of defect and isolation are complementary. Yet their instructiveness is limited. Severance often reveals no more than the fact that some relation has been destroyed, while leaving the nature of the dependency undisclosed. This is because severance disrupts all relations, specific as well as general ones, those peculiar to the particular part as well as those common to all parts, significant and trivial ones alike. To determine the character of a relation, the defect and isolation experiments are therefore supplemented by a third intervention, the recombination experiment, in which a removed part is reincorporated in the system, but in a modified form, which may mean altered position, orientation, or connexion. In this manner, the common and general influences between system and part are restored, while those specifically depending on position, orientation and connexion will reveal themselves by correspondingly altered behaviour.

Several lines of biological research have profited from the use of such recombination techniques. We may point to the extensive use of transplantation in the analysis of embryonic development, in the study of endocrine functions and in tumour research. I shall now outline how this method can be used to good advantage in the analysis of those functions of the nervous system in which the relations between the parts and the whole, between the elements and the collective, are at issue. The orderly group behaviour of neural elements is commonly referred to as 'co-ordination'. Such co-ordination, in turn, is generally, if vaguely, thought to be predicated on systematic patterns of structural connexions among the constituent members of the group. This is precisely the sort of thesis that cannot be conclusively tested by the defect and isolation techniques alone—both widely used in neurology—but can be crucially decided by recombination experiments. The study of neural elements in isolation, however invaluable in itself, has taught us little about their group relations, and the defect experiments of severing connexions—nerve fibres, in this instance—have only confirmed that neural connexions of *some* sort are indispensable for neural conduction, but have in no way proven that the particular and precise distribution of these connexions is responsible for the orderliness and precision of a given neural response. It is evident that to be conclusive, the test would have to be made after the severed connexions have been restored, but in a pattern different from the original one. If this alteration of the connexion pattern results in a corresponding distortion of the response pattern, the functional relevance of the former would be demonstrated; otherwise, merely the necessity of connexions of some kind.

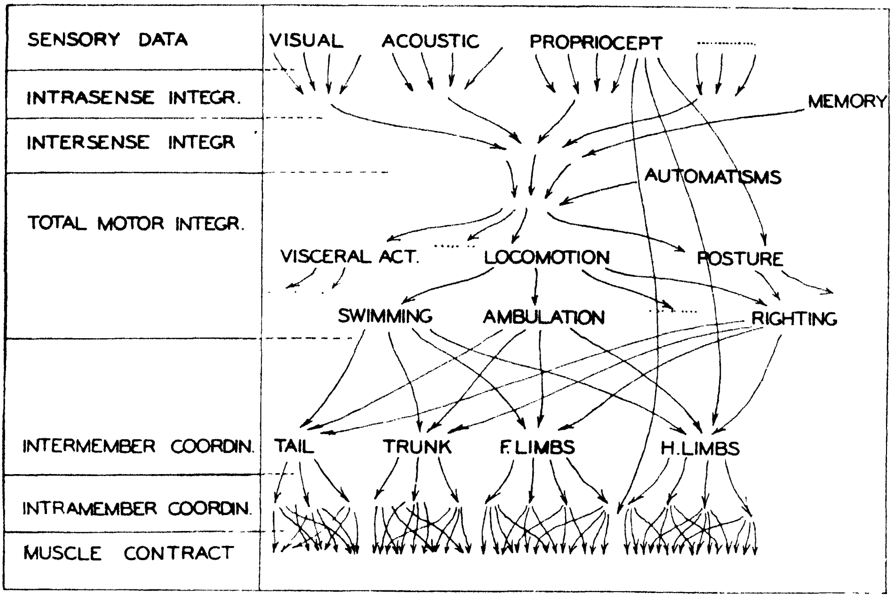
Any ordinary nerve regeneration after transection actually furnishes us with a recombination experiment, inasmuch as the new connexions do not precisely duplicate the original ones. The attempts to find out more about co-ordination by deliberately changing and crossing nerve connexions, repeated for nearly a century, are likewise in the recombination class. If they have not brought the desired clarification, the blame goes to the incomplete analysis and insufficient precision in the description of the observed facts, and to the vagueness and ambiguity of the concept of co-ordination. Instead of an objective record of just what happened after a given interference, one usually is presented with a subjective summary appraisal according to which there either had or had not occurred 'recuperation of function', 'restoration of co-ordination', 're-education', 'regulation', and the like. 'Restored function' to some meant recovered conductivity, to others (e.g. orthopaedic clinicians) the return of some semblance of normal usefulness of a member. Lacking standard criteria of assessment, the experimental and clinical literature dealing with this subject contains a great number of confusing, contradictory and misleading statements (see Sperry, 1945*b*). To avoid ambiguity, we shall deal here not with the problem of co-ordination in its traditional indefiniteness, but rather with a specific example.

AN EXAMPLE OF CO-ORDINATION

Co-ordination is the orderly relation between parts engaged in a given act. Ultimate effectors are the individual muscles and glands. We shall concentrate on the muscles. Operating *en masse* or in indiscriminate combinations, they produce a disorderly and ineffectual convulsion. By contrast, co-ordination is meant to signify their activation in such orderly groupings in space and time that the resulting movement or posture will be effective and useful. It is a basic fact of nervous function that these groupings follow a hierarchical principle. For example, the organized patterns of muscle combinations producing the movement of a joint are relatively stable elements in the various types of limb movements. The latter, in turn, are entities of unitary character in motor performances involving the whole body, such as swimming, walking or righting. These latter activities, finally, are organized parts of more complex behavioural sequences of still higher order, such as hunting, feeding, nest building, etc. I have outlined this hierarchical concept back in 1925 and later reiterated its implications for a theory of the neural foundations of behaviour (1941). It has received renewed and independent emphasis by the work and ideas of Tinbergen. The crux of the matter is that since the phenomenological study of behaviour has revealed the existence of such a hierarchical principle beyond all doubt, we must infer that it has a neurophysiological counterpart, and that co-ordination, therefore, may involve quite different mechanisms depending on the level of integration which we are considering.

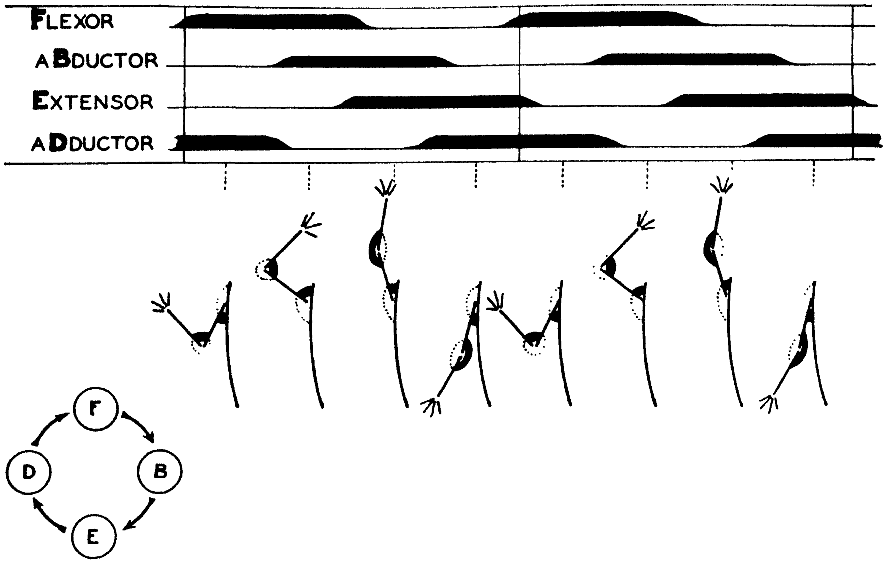
The following diagram (Text-fig. 1) is meant to represent in simplified form the hierarchical structure of vertebrate co-ordination. Each item stands for an organized activity of some degree of stability which functions by setting into operation similarly organized activities of a lower order in the sense of the arrows. While the variety of possible interrelations is even greater than indicated in this profusion of arrows, it is important to keep in mind that the activities on any one level are strictly limited by the number and kind of effector mechanisms of lower levels at its disposal.

Our further discussion will centre on the lowest level of integration, labelled here as 'intramember co-ordination', that is, the orderly plan of muscles in executing a limb movement. Specifically, let us consider the activity cycle of the forelimb of a urodele amphibian in ambulation on solid ground. Text-fig. 2 shows diagrammatically the time sequence in which four representative muscles, an abductor (*B*) and an adductor (*D*) of the humerus, and a flexor (*F*) and an extensor (*E*) of the forearm, enter into action. The lower part of the figure shows successive positions of the limb, with solid arcs representing the contracting muscles, and stippled arcs their relaxed antagonists. The upper part gives the time score ('myochronogram') for the various muscles. As can be seen from the insert at the lower left, the activity spreads from *F* to *B* to *E* to *D* and back to *F*; or, if we take these letters as symbols for the motor neurons connected with the respective muscles, the train of arrows symbolizes the orderly chain of events in the corresponding nerve centres. The illustrated sequence is stereotyped for progression, but is not the sole sequence in which these muscles can be linked. The movement of retreat, for instance, involves a sequence *FDEB*. In righting, still another pattern is utilized. Of such patterns, the animal possesses a definite limited assortment.

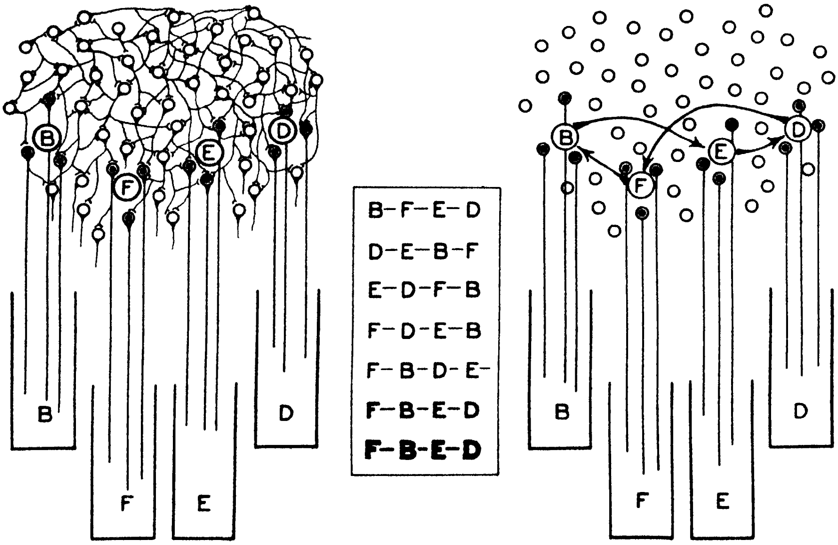


Text-fig. 1. Diagram of hierarchical organization of central nervous functions.

The problem of co-ordination on this 'intramember' level then resolves itself essentially into the specific question of why the motoneurons are activated in just these particular orders and sequences, as *FBED* for advance, *FDEB* for retreat, etc. Past answers to this question have followed essentially two lines of argument corresponding to the two alternative views of co-ordination as either innate or acquired. The former assumed that the orderly sequence of excitation is based on regular and stereotyped structural



Text-fig. 2. Sequence of muscle contractions (myochronogram) and cycle of movements of left fore limb in ambulation.



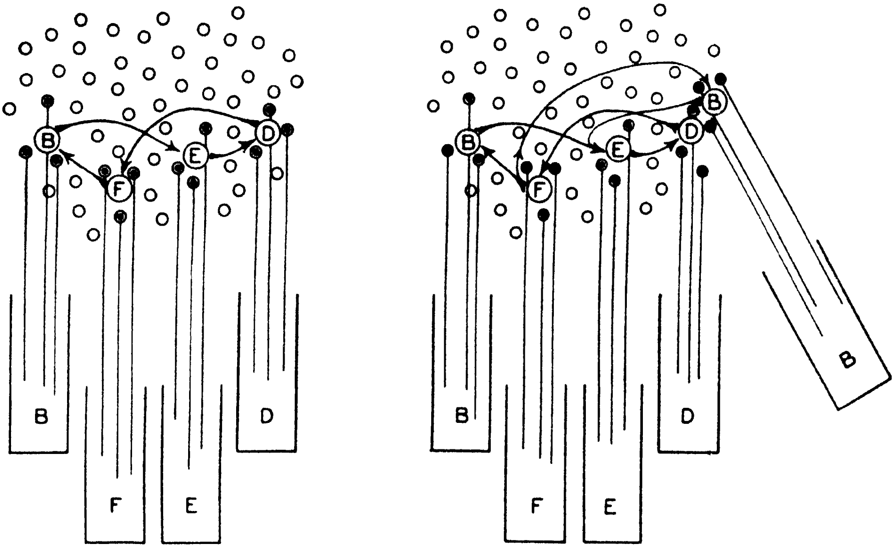
Text-fig. 3. Development of muscle co-ordination *FBED* in a diffuse neuron net (see text).

interconnexions among neurons, reproduced in each member of a species by a rigid and precise developmental mechanism. The latter assumed a secondary origin of co-ordination by trial and error or some related procedures, in which the success of the resulting performance is the decisive factor. The former view presupposes a minutely predesigned system of interneuronal pathways, while the latter view implies a rather indeterminate neuronal network amenable to patterning under the guidance of experience. How this would apply to our specific example is illustrated in the left part of Text-fig. 3. Starting with random excitation of a network with a very large number of possible interconnexions among its elements, including reverberating circuits, varying sequences and combinations of muscles *B*, *D*, *E*, *F* would be tried, as indicated in the middle of the figure, and discarded again until the right sequence leading to the desired effect is discovered. Once assured of its success, this sequence would then be somehow grooved so that from then on, excitation would routinely follow the course of the arrows outlined in the right half of the illustration. Obviously, this right diagram holds for any current concept of co-ordination, irrespective of whether learned or innate. Both these concepts imply that functional effectiveness is definitely assured, and this primacy of functional adequacy of the arrangement has always been taken for granted.

MYOTYPIC RESPONSE

These premises were put to the test in a series of recombination experiments, in which (*a*) the supposedly crucial prearrangement of connexions was disarranged and (*b*) the supposedly decisive functional adequacy of the peripheral effects was ruled out. This can be achieved by removing a muscle or muscle group from its normal position and nerve connexions and transplanting it to a position where (*a*) its nerve supply is secured from a foreign source, and (*b*) its anatomical relations, as well as its motile effects for the body, are abnormal. In practice this is done by transplanting supernumerary limbs (Weiss, 1924, 1937), limb parts (Weiss, 1923, 1937) or muscles (Weiss, 1931) into a new site and letting them become innervated by some other limb nerves, either at random or chosen from a known source. Since these experiments have been reported in detail previously, it may suffice here to summarize the results. They are symbolized in the diagram (Text-fig. 4).

A supernumerary muscle *B* is shown grafted to the vicinity of *D* and innervated by nerve fibres of that locality. The question was how and when such a heterotopic muscle would be activated by the central nervous system. The answer was surprising, and no one could have deduced it from current concepts. The following general rule was found to hold true under a very wide variety of conditions. Any supernumerary muscle contracts always synchronously and with the corresponding strength as the normal muscle of the *same name* of the limb whose plexus the transplant shares. This phenomenon, originally described as 'homologous' function, was later more appropriately relabelled as 'myotypic' (i.e. muscle-specific) response (Weiss, 1941). Since the contraction of the muscle merely serves as a signal indicating activity in its motoneurons, one could conclude that the ganglion cells newly connected with the graft *B* have become functionally linked with those innervating the regular muscle *B*, resulting in a flow of excitation as indicated by the arrows in the right half of Text-fig. 4. With a full complement of muscles, as in a transplanted limb, and with each one of them becoming engaged strictly at the proper time, as here described, this would call for an immensely complicated rearrangement of central connexions, if, indeed, co-ordination depended on the minute order of neuronal connexions. Yet, all of this serves no useful purpose, as far as the individual is concerned. For due to their myotypic responses, the transplants execute movements which deviate from those that would be useful to the animal by as much as their anatomical arrangement relative to the body deviates from normal. It is best to bear in mind the extreme condition of disharmony, namely, the case of limb pairs of opposite asymmetry, for instance, a right limb transplanted horizontally near a left limb (Pl. 1, fig. 1). Synonymous muscles being in mirror-image positions, the synchronous movements of



Text-fig. 4. Functional association between a supernumerary muscle *B* and the co-ordination pattern *FBED* of Text-fig. 3 (see text).

these twin limbs occur in exactly opposite directions and therefore counteract each other. Three or four limbs supplied from a common plexus merely triplicate or quadruplicate the myochronograms of each other, regardless of the wholly absurd functional effects resulting therefrom. Never has there been any sign of an adaptive remedial change.

The supernumerary mirror-image limbs continue to function in reverse even after their normal partners have been removed. In fact, if instead of grafting supernumerary limbs, one merely replaces the normal limbs by limbs of opposite symmetry in correct dorso-ventral orientation, the function of the grafts is also reversed from the standpoint of the body, so that whenever the animal intends to move forward, the reversed transplants move it backwards, and vice versa (Weiss, 1937). If this experiment is carried out in the early larva prior to the onset of limb function, the function appears in reverse from the very start. Pl. 1, fig. 2 shows such an animal at the left, with its normal control at the right (Weiss, 1941). The forelimbs of the left animal moved in perfect co-ordination, but so as if the head of the animal were where its tail is. Pl. 1, fig. 3, shows both the dorsal and ventral aspects of a similar freak, a frog in which the hindlimb buds had been inverted dorso-ventrally in the tadpole stage. When the legs grew and began to function, they showed perfect 'jumping' co-ordination, but the kick was upward into the air instead of downward against the ground, and thus produced no locomotion.

These few examples may suffice to put the significant features of these experiments into relief. They have conclusively disproved both contentions, according to which either stereotyped connexions or functional adequacy are relevant factors of co-ordination. In our example, the regular discharge pattern *FBED* arises and continues in the limb segments of the cord despite arbitrary connexions and functional irrelevance. On the positive side, it must be inferred from this that the mechanism responsible for such a discharge pattern as *FBED*, whatever its nature, is of intracentral origin, very stable and independent of peripheral control. A second equally important conclusion is that the individual muscles possess some means by which they put themselves into the proper response relation with that intracentral mechanism. The muscle *B* secures response to the *B*-element in *FBED*—or any other central score with a *B*-element—the muscle *D* to the *D*-element, and so forth. How the muscles 'tune themselves in' on the central effector mechanisms is a matter for speculation. That they do not do it by way of afferent nerves has been proven by the fact that myotypic response appears and persists in limbs devoid of all sensory innervation. It has been suggested tentatively that each individual muscle 'modulates' its nerve fibres biochemically in accordance with its own biochemical characteristics, comparable to an antigen-antibody effect, and thereby impresses its character on the motor ganglion cells and their further proximal ramifications. It must be stressed, however, that this process of 'modulation' on no account furnishes an explanation for the central patterns of co-ordination themselves, but merely explains why a central impulse reaches precisely the particular muscle for which it is destined.

The origin of the central scores as such remains obscure, except for a few clues contained in the experiments, as follows:

(1) All levels higher than 'intramember' co-ordination (Text-fig. 1) operate through the activation of partial mechanisms of lower order in definite and set patterns. Animals with reversed forelimbs and normal hindlimbs are most instructive in this regard. In order to walk properly, they would only have had to make the forelimb centres discharge the 'retreat' pattern *FDEB* in combination with the 'advance' pattern *FBED* of the hindlimb centres. Yet, this never occurred. It was either all four spinal centres set on 'advance' (*FBED*) or all four on 'retreat' (*FDEB*). Thus, even on the 'intermember' level, the central nervous system is unable to isolate parts of one score and combine them with parts of another score into a more adequate performance.

(2) Each animal is endowed with an inherited set of such definitely patterned 'scores', which constitute its motor repertory. In subprimate forms, the capacity to 'learn' does not include the capacity to develop novel 'scores', but is confined to varying the occasions, force and timing of the activation of existing 'scores'. In these forms, co-ordination patterns can only be facilitated, retarded, perfected or suppressed, but can be neither remodelled nor designed *de novo* even in the face of most urgent biological needs. The remarkable instances of central 'plasticity' described by Bethe and his school for many invertebrates merely demonstrate latitude in the activation of pre-existing, though often latent, mechanisms, rather than the on-the-spot invention of new ones, as claimed. When a beetle (or a fly), which commonly uses only one pair of legs for a given act of swimming (or grooming), upon amputation of this pair immediately uses another one vicariously, this fact merely shows that the 'scores' to execute the particular movements are preformed in all limb segments alike, but are activated only in accordance with an intracentral dominance-inhibition pattern, which varies with the constellation of limbs actually present. This means plasticity on the 'intermember', but not on the 'intramember' level. One may expect that if one of the vicariating limbs were of the opposite asymmetry, as in our *Salamander* cases with limb reversal, the 'plastic' substitution would still occur, but the effective movements would be in reverse, hence, contrary to the adaptive needs of the animal. These remarks are not to minimize the

importance of plasticity on higher than 'intramember' levels, but merely to put that plasticity in its right place.

(3) It has been contended that the co-ordination of ambulation is not effected by an intracentral discharge pattern, but is an orderly sequence of proprioceptive reflexes, each activated by the passive stretching of one group of muscles as a result of the displacement of the body during the active phase of other muscles. Such a contention is clearly ruled out by our observations on reversed limbs. In a normal animal, the abductor of the forelimb (*B*) lies in front. As the body is being moved forward (by the other extremities), this abductor is being stretched, which could automatically initiate the reflex abduction necessary to bring the limb forward for the next step. This concept hinges on the coincidence between the anatomical forward position of the abductor muscle and the forward locomotion of the body. By eliminating this coincidence, the recombination experiment has again proved its value. In the reversed limbs, the forward position was occupied by the adductor (*D*) instead of the abductor (*B*) muscle. If the phase of action were determined by passive stretch, the adductor of the transplant should now have worked when normally the abductor, whose place it occupies, would have come in. Yet, the opposite happened. The limbs were thrust backward during this phase instead of forward. This very fact, that the transplanted muscles contracted in accordance with their names, rather than in accordance with their positions, proves that co-ordination patterns are determined centrally, and that the central patterns, though normally reinforced by proprioceptive reflexes, take precedence over the latter under conflicting circumstances. The well-established fact that completely deafferented limbs continue to function without essential impairment of their co-ordination likewise proves that intramember co-ordination, such as *FBED*, cannot possibly be the result of chain reflexes. This in no way detracts from the importance of proprioceptive reflexes as subsidiary reinforcement mechanisms.

PROPRIOCEPTIVE SPECIFICITY

The sensory side of nervous activity presents the thoughtful inquirer with similar puzzles to the motor side. The problem of how a given afferent excitation is centrally identified as to its modality and point of origin so that it may initiate the right kind of response, is akin to the problem of how a given motor response can be made to reach the muscles for which it is destined. Technically, the sensory side offers greater difficulties. While a motor discharge is signalled by the subsequent contraction of the muscle, equally unequivocal indicators for the central response to an afferent discharge exist only in those kinds of reflexes that are rigidly discriminatory for the type of end-organ stimulated. Such responses can then be used as a sort of language in which the central nervous system expresses how a given afferent impulse has registered.

The myotatic reflex ('Eigenreflex') is our first example. Afferent impulses set up by stretching certain muscles have the property of producing a discharge of the motor centres of the very same muscles. For the normal animal, this has been explained by the direct synaptic linkage of the afferent and efferent neurons of the given muscle (Lloyd, 1944), although there has been no further suggestion as to how to visualize the origin of such unfailingly matched connexions without conceding to the two branches of the arc means of mutual recognition. But how the afferent impulses from abnormally connected muscles would register centrally was wholly unpredictable prior to the appropriate recombination experiment. When a given muscle of a supernumerary limb is stretched, there follows immediately a reflex contraction of this same muscle, as well as of the synonymous muscle in the normal fellow limb. For example, in the diagram (Text-fig. 4, right), stretch of either muscle *B* would entail contractions of both muscles *B*. By this method it was possible to demonstrate that the centres can correctly identify the afferent excitation from any single muscle as to its exact origin, even with disordered nerve connexions. One had to conclude, therefore, that, much as on the motor side, each muscle impressed on its afferent fibres a specific discriminative mark enabling them to establish in the centres discharge relations characteristic of the particular muscle. Specificity thus rules both in the afferent and efferent branches.

CORNEAL SPECIFICITY

A second similar example was found in the case of the corneal or lid-closure reflex. Present in amphibians after metamorphosis, it consists of a retraction of the bulb, effected through the abducens nerve, upon touch to the cornea. If a supernumerary eye is transplanted anywhere within the sensory field of the trigeminal nerve, either forward in the region of the nose or backward in the place of the ear (Pl. 1, fig. 4), tactile stimulation of the cornea of the graft promptly yields retraction of the normal eye on that side. Since the trigeminal fibres newly connected with the grafted cornea had in their erstwhile connexions with the local skin only given rise to head flexure, they must be assumed to have undergone cornea-specific remodulation so that their discharge now actuates the abducens nucleus (Weiss, 1942).

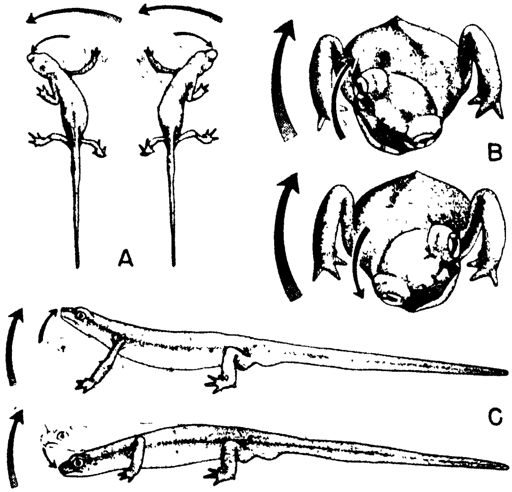
On the basis of these results, it becomes necessary to subdivide the recognized sensory modalities into submodalities, each endowed with its own specificity on top of the general characters of the class. Thus, we must assume not simply one single proprioceptive modality, but a separate one for each individual muscle. Within the tactile field, we find such specializations as the corneal sense. How far this parcellation will have to be carried is an empirical question. At any rate, the basic fact to emerge from our experiments is that the sensory periphery consists of patches of specifically different constitution, which by 'modulating' the afferent neurons accordingly, project their specific differentials into the central nervous system, in which by virtue of these specific clues correspondingly specific response relations are effected.

The same type of operation lent itself to the actual execution of a famous imaginary recombination experiment proposed by Du Bois-Reymond. If optic nerves were connected with acoustic centres, would we hear lightning through our eye? Some of the optic nerves of the above eye grafts were oriented so as to regenerate into olfactory or acoustic channels, while the normal eyes of the host animals were removed. Thus far, no visual reactions of any kind have been observed that would indicate resumption of effective functional relations by the grafted eyes. Histological evidence shows the presence of some optic connexions in the new channels, but perhaps insufficient in amount. If a more comprehensive repetition of the experiments were to substantiate this negative result, one would have to answer Du Bois-Reymond's question in the negative and conclude that none but the regular visual centres can properly evaluate and respond to optic impulses.

SPECIFICITY WITHIN THE OPTIC SENSE

The described observations on sensory specificity have been greatly extended by the systematic studies on transplanted eyes carried out by Sperry (1943, 1944). He found that even the retina is further subdivided into sectors possessing different specificities instrumental in the establishment of functional correspondence with the respective optic brain centres. The proof was possible because of the clear-cut differences in the response of amphibians to optic stimuli falling on dorsal, ventral, temporal or mesial quadrants of the retina, respectively. The normal animal bends and strikes upward toward food presented from above (image in the ventral retinal field), downward toward food presented from below. Movement of the visual field in horizontal direction evokes a compensatory lateral flexure of the body tending to keep the orientation of the animal fixed relative to visual objects. In diagrammatic simplification, we may say that a visual image projecting on the ventral half of the retina leads to contractions of the dorsal musculature, while one that sweeps over the retina in mesio-lateral direction leads to contraction of the lateral body muscles of the opposite side (other associated contractions being here ignored).

With these tests reliably established, it was possible to examine whether the sensory cues 'dorso-ventral' or 'mesio-lateral' took effect in terms of the axes of the animal as a whole, as usually supposed, or rather in terms of intrinsic properties of the excited retinal sectors. Amphibians with cut and successfully regenerated optic nerves, whose central connexions could be assumed to be aberrant, had been found to have undisturbed vision (Koppanyi, 1923; Matthey, 1926). However, this could still be ascribed to some sort of functional adjustment restoring normal adaptive behaviour by a learning process. To exclude this possibility, Sperry worked with animals whose eyes had been rotated in their sockets by 180° (for other variations of the experiments, see the original papers). Thus, the originally dorsal half of the retina came to lie ventrally relative to the body, the originally ventral half dorsally, the originally mesial half laterally, and the originally lateral half mesially. As a result, all visuo-motor reactions of such animals were reversed, and remained so throughout life. When food was presented from above, the animals struck downward; food from below was responded to by dorsal bending (Text-fig. 5 C). In either case, the animal missed the food. One notes that flexion of the dorsal musculature was still elicited by images falling on the originally ventral half of the retina, in spite of its actual dorsal position with regard to the animal and its effector apparatus. Similarly, horizontal movements of the visual field had to sweep over the retina in what used to be its old mesio-lateral direction in order to call forth lateral bending on the opposite side (Text-fig. 5 A, B). Since this happened when-



Text-fig. 5. Visuo-motor reactions of animals with normally oriented and inverted eyes. Concurrent arrows indicate normal reactions; arrows in opposite directions, reversed reactions. (From Sperry, 1950.)

ever the visual field was actually shifting in mesio-lateral (instead of latero-mesial) direction, one realizes that the animals, instead of following the stimulus, turned away from it. This led to the very curious phenomenon that whenever one of these animals turned its head sideways, thus initiating an apparent rotation of the visual field, it set itself off on a prolonged tour of circus movements, 'compensating' the optical shift in the wrong direction.

By their consistency and absurdity, these responses were suitable as tests for non-adaptive specific relations between periphery and centres, in the same sense as were the previous cases of reversed limbs. It remained to superimpose upon the functional distortion random confusion of nerve connexions. This was done by cutting the optic nerves of the inverted eyes and letting the fibres regenerate at random. The animals thereafter responded again in reverse, as before. Clearly, therefore, stimulation of a given retinal quadrant, irrespective of its actual orientation in the body, evoked the very same central response that it had evoked prior to the inversion of the eye, as well as after the inversion, but prior to the cutting of the nerve. The results of Sperry have been fully confirmed by Stone, who, moreover, extended them into the embryonic phase to determine the period in which retinal specificity was first established.

Sperry could drive the analysis yet one step farther. By placing lesions in different parts of the midbrain and determining the location of corresponding scotomas in the optic field (by the absence of motor response), the functional projection of the various quadrants of the normal retina upon the optic tectum could be roughly plotted. When, then, in an animal with inverted eye and regenerated optic nerve a lesion was made, for instance, in the projection area of the dorsal retina, the animal proved to be blind for light from above, that is, falling on the natively dorsal half of the retina. This proves that, notwithstanding the abnormal anatomical position and notwithstanding the confusion of the regenerated optic fibres in their course from eye to brain, excitations from the various retinal sectors still are received in the very same central stations in which they would, and formerly did, register under normal conditions.

Less extensive, but equally compelling, evidence was obtained with regard to the labyrinth after regeneration of the vestibular nerve (Sperry, 1945). In this case, too, the various functionally differentiated parts of the peripheral organ proved capable of modulating their nerve fibres in such specific manner as to enable them to discharge into the corresponding central stations of matching specificity regardless of the detailed fibre course.

All the reported experiments, involving disarrangement of nerve fibre connexions between limbs, cornea, retina and labyrinth on the one hand,

and the central nervous system on the other, have conclusively demonstrated the basic principle through which the peripheral organs establish proper correspondence of response with the centres—a dual system of matching specificities, one in the centres and the other in the periphery, the latter capable of projecting itself into the nerve fibres and their central ramifications and effecting selective relations with the central counterparts. How this selectivity of relations is to be conceived and the manner in which it is established, is still purely conjectural. I have described it under the figurative, but otherwise non-committal, term of 'resonance', and while at present I am inclined to assume that some sort of selective impulse conduction depending on sterically matching molecule systems is involved (Weiss, 1947), this is sheer speculation and not to be dealt with in this paper. Nor can we discuss the equally speculative hypothesis of Sperry, who prefers to view the specificities involved as operating through the linking together of neuron chains into fixed morphological compounds, a view which glosses over some of the basic difficulties inherent in the problem of central activity with its many unknowns. There are still fundamental gaps in our knowledge of the central nervous system, which it seems to me wiser to acknowledge than to conceal, and the experiments reported here have contributed more to showing them up than to closing them. Surprising as the results have been, we may expect still further surprises to come and had better be prepared for them with an unbiased mind.

EXCEPTIONS AND LIMITATIONS

Together with the new phenomena, the experiments have brought out certain limitations of their validity. These deserve additional mention here because they further demonstrate what precise information can be obtained by the recombination method.

In our amphibian experiments, different nerves of the limb plexus have proved to be fully interchangeable. That is, any combination of nerve fibres can mediate co-ordinated forelimb function as long as the fibres originate within the normal forelimb segments of the cord (segments 3–5 in urodeles). However, when the nerve supply of a limb is derived from any other central region, limb function remains rudimentary. These facts, first established by Detwiler & Carpenter (1929) with heterotopically grafted embryonic limb buds, have been fully confirmed for larval limbs transplanted in the developed stage. Although limbs grafted into the orbit of the eye were once reported to show motility associated with eye movements (Nicholas, 1933), these turned out to be movements not in the grafts, but of the grafts, produced by residual ocular muscles which had become attached to them (Piatt, 1941). All evidence thus far obtained indicates that the 'scores' specific for limb muscles, and hence, capable of activating efferent fibres modulated by limb muscles, operate solely within the limb levels of the spinal cord. A similar localization may be assumed to exist in other functional districts.

Thus, an analogous situation was encountered in our experiments on corneal specificity. In order to obtain a specific response from a transplant, the latter had to be located within the distribution of the trigeminal nerve. Beyond this area, the response ended abruptly, sometimes with a sharp demarcation line running through an individual cornea. Evidently, the specific relation to the efferent abducens nucleus can be effected only within the regular neuropilic field serving this activity.

In conclusion, the same experiments that revealed the lack of detailed neuronal prelocalization within given functional districts speak strongly in favour of a rigid topographical localization of these districts themselves. In this regard, our results bear close resemblance to those obtained by Lashley (1942) in the visual cortex of the rat.

It is probable that further insight into the nature and origin of the different regional, particularly segmental, mechanisms can be found by recombination experiments consisting of the reciprocal exchange and other disarrangement of central districts. Such attempts, successfully initiated by Detwiler, are at present being continued in my laboratory and may bring some elucidation of the rather obscure origin of the central 'scores' of co-ordination.

There also seems to be an age limit up to which nerves switched to new terminations can be remodulated. While in urodele amphibians no such limitation has been observed, there are definite indications that in anurans, the motor nerves lose their faculty for remodulation with increasing post-metamorphic age. When such a nerve is then made to innervate a new muscle, the response will no longer be myotypic, or rather will remain myotypic in the sense of the muscle in which the nerve had formerly resided during its plastic period. Further data on this loss of reversibility are urgently needed.

If confirmed, this progressive fixation of nerves with age could account for the fact that myotypic response after post-natal nerve crossing has not yet been observed in forms other than amphibians. In rats, the motor nerves have been shown to be fixed in their functional relations as early as 15 days post-partum (Sperry, 1941). One would have to go back to a still earlier, presumably foetal, stage in order to prove their faculty for remodulation. That such an earlier period exists, in which mammals and amphibians react alike, is indicated by the fact that even in man, supernumerary muscles resulting from embryonic reduplications comply strictly with the principle of myotypic function (Weiss & Ruch, 1936).

NERVE AND TENDON CROSSES

Mammals have generally been conceded to possess a much wider 'plasticity' and 'adaptability' of co-ordination than do amphibians. One could view this as compensation for the early loss of remodulability. However, critical experiments have shown the scope of co-ordinative readjustments in sub-primate forms to be rather narrow. The crucial experiments are nerve crosses and tendon crosses, the former gaining in conclusiveness by the absence of the complicating factor of remodulation. These two operations convert, each in its way, an orderly central co-ordination pattern into a disordered peripheral effect; nerve crosses, by leading excitation into the wrong muscles, and tendon crosses, by causing the right muscles to move the skeleton in the wrong directions. Contrary to earlier claims, it was proven that rats cannot meet the resulting functional disorder by appropriate corrections of the central co-ordination patterns on the intramember level (Sperry, 1940). The dysfunction in the experimental animals remains permanent even under optimal training conditions to induce corrective changes. Reports to the contrary have been largely due to erroneous interpretations (Sperry, 1945*b*). In monkeys, a faint trace of adaptive adjustments has been noted in arms with crossed nerves (Sperry, 1947).

In man, finally, considerable reparative ability has been demonstrated at least after tendon crossing (so-called muscle transplantation), but even these cases call for a considerable modification of the interpretation formerly given to them. To explain this, let us assume that *FBED* represent the sequence of muscle actions in a single step during walking. Let us now cross the tendons of the extensors (*E*) and flexors (*F*) of the knee. At first, the knee movements are reversed. Then an adjustment occurs so that the flexors are excited in the former extensor phase, and the extensors in the former flexor phase; in brief, the sequence *FBED* is changed to *EBFD*. In poliomyelitis patients with transplanted tendons, this change could be actually followed and recorded electromyographically (Weiss & Brown, 1941). At the same time it was discovered, however, that the adjusted patients would frequently relapse into the old incongruous pattern *FBED*, even after years of practice. It must be concluded, therefore, that there had been no remodelling of the old pattern itself, but that a wholly new pattern *EBFD* had been set up on a higher level to substitute functionally for the inadequate one. The latter remained latent but retained its integrity and reappeared periodically whenever the higher replacement went into recess.

CONCLUSIONS

It is evident that the described recombination experiments have greatly helped to clarify the formerly confused issue of 'reco-ordination' after peripheral interventions. They have defined and delimited the scope of 'modulation' and central adjustments on the various levels of co-ordination. They have confirmed and elaborated the hierarchical order of neural function. Above all, they have broken up problems, which in their generality proved untractable, into smaller tangible issues amenable to precise formulations and to profitable experimental attack. The reported results are only a beginning. If they have not yet given us any consistent concept of just how central co-ordination works, they have at least shown definitely how it does not work, narrowing thereby our field of search and eliminating some past misconceptions. They have also led us into a realm of biological specificity into which no other techniques have as yet been able to penetrate. No doubt, to become fully effective, the recombination methods ought to be carried on in closest association with standard physiological techniques. In that combination, great advances can be predicted. Yet, even by themselves, these methods seem to have proved their value sufficiently to justify further application on a large scale.

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PLATE 1

Fig. 1

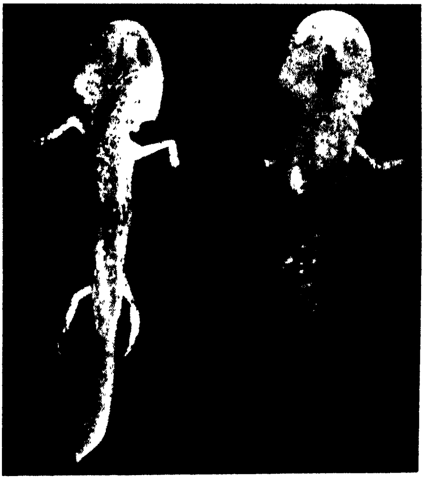

Fig. 2

For explanation see p. 111

PLATE 2

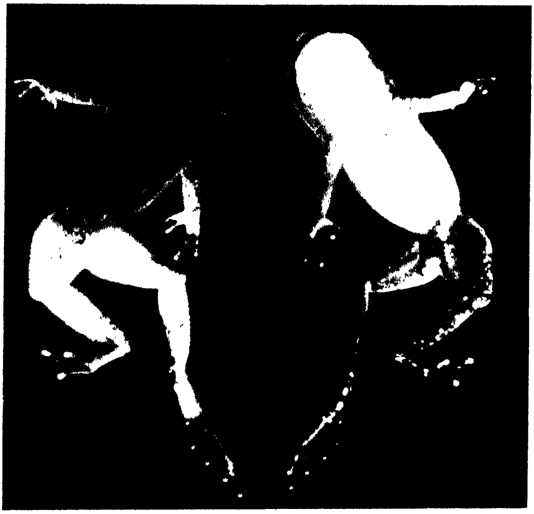

Fig. 3

Fig. 4

For explanation see p. 111

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EXPLANATION OF PLATES

PLATE 1

Fig. 1. Successive phases of a single movement of a symmetrical limb pair consisting of a normal left limb (upper) and a transplanted right limb (lower), innervated from a common nerve plexus. The pictures represent individual frames of a motion picture film. (From Weiss, 1937.)

Fig. 2. Left: Salamander larva with reversed forelimbs (right limb on left side and left limb on right side) developed from limb rudiments transplanted in a pre-functional stage. Right: Normal control animal. (From Weiss, 1941.)

PLATE 2

Fig. 3. Dorsal and ventral aspects of metamorphosed frog developed from tadpole in which limb buds had been exchanged and dorso-ventrally inverted in a pre-functional stage.

Fig. 4. Newt with supernumerary eyes transplanted to the ear capsules.

THE ROLE OF PERIPHERAL SENSE ORGANS DURING LOCOMOTION IN THE VERTEBRATES

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From a physiological standpoint, one of the central problems of animal behaviour can be expressed in the form of a question: 'Can an animal initiate and maintain patterns of co-ordinated muscular movement without reference to the outside world?' If we are prepared to accept such a possibility, part, at least, of an animal's normal behaviour can be regarded as an expression of the intrinsic powers of the central nervous system to evolve along lines which may have had no fundamental relationship to changes in the external environment, whilst patterns of behaviour originally dependent on signals from the outside world might acquire executive independence at a later stage in ontogeny and phylogeny. In the realm of human behaviour, the concept of central control is not without its subjective attractions; in the field of animal behaviour, it liberates discussion from the limitations imposed by the more rigid picture of inevitable and automatic reflex responses to external events. In order to approach this problem by analytical methods, it is essential to concentrate on types of behaviour which are highly characteristic of a particular species of animal, and which can be elicited with relative ease. Patterns of this type are usually associated with respiration or locomotion; the present paper deals solely with terrestrial aspects of the latter.

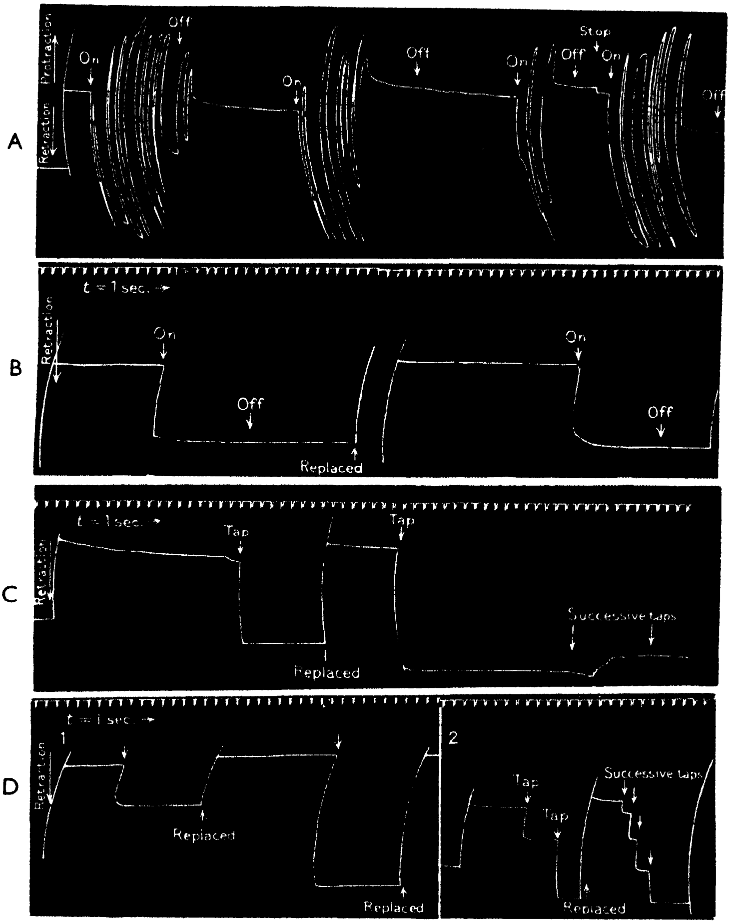
If a toad (*Bufo bufo*) or frog is freely immersed in water, it invariably swims, both hindlimbs extending and flexing synchronously; if the animal is allowed to engage a forelimb with a relatively rigid object, these movements cease, and the two hindlimbs remain passively extended. If, on the other hand, the animal is on land, the whole pattern of locomotory activity changes, each limb leaving the ground and swinging forward in an orderly ambulatory sequence—right fore, left hind, left fore, right hind. This highly characteristic diagonal sequence is of fundamental functional significance. It is the only sequence of limb movements whereby the body of the animal can be balanced on a tripod of support during the whole locomotory cycle (Gray, 1944); any other sequence involves phases of mechanical instability. The diagonal pattern is, in fact, an expression of the fact that a limb is not lifted from the ground unless the weight of the body can be effectively carried on the other three feet. Since the ability to grade the muscular response to the external forces acting on the limb can, in the resting animal, be traced to local proprioceptor activity, and since well-defined responses can frequently be elicited when muscles are subjected to passive stretch, it is tolerably certain that each phase of the ambulatory cycle initiates a complex but highly characteristic pattern of exteroceptive and proprioceptive excitation of the central nervous system. It is on this basis that the 'chain reflex' theory of ambulation largely rests.

The first attempt to present a reflex picture of ambulation appears to be that of Philippson (1905), who analysed the cycle of limb movements of an intact dog into a series of successive phases. He suggested that the backward thrust of a limb was induced by a stimulus arising automatically when the limb came into contact with the ground, this action being reinforced by a crossed extension reflex associated with active flexion of the opposite limb. Similarly, the onset of the protraction phase was attributed, at least in part, to the stretched skin of the inguinal region of a contralateral limb. These conceptions, however, were quickly found to be inadequate. Sherrington (1910) showed that a cat can walk quite effectively when all sensory nerves distal to the wrists and ankles have been severed; neither contact of the foot with the ground, nor the activity of pressure receptors in the plantar region can therefore be regarded as essential for the maintenance of the normal rhythm. Nor could Sherrington find any support for the suggestion that impulses from stretched areas of skin played a decisive, or even important role. A very careful investigation of the 'mark time' or stepping reflex in the spinal dog led Sherrington to the conclusion that the ability to maintain a rhythmical and alternating series of movements in the hindlimbs depended on the proprioceptors in the muscles of the upper regions of the limbs themselves; no stepping occurred if the limbs were de-afferentated. Sherrington's work clearly showed the inadequacy of at least part of Philippson's picture; further difficulties were in store for the chain reflex theory.

If a locomotory rhythm is dependent upon rhythmical excitation of proprioceptor end-organs, it should cease when the appropriate sensory nerves have been cut. In 1912 Graham Brown de-afferentated the tibialis anticus and gastrocnemius muscles of a decerebrate cat, and was able to elicit from them a well-defined and alternating rhythm of contraction and relaxation in response to sudden transection of the nerve cord. Unless, therefore, we regard this rhythm as fundamentally different from that of normal ambulation it is difficult to deny the legitimacy of Graham Brown's conclusion that however much proprioceptor activity may grade the normal rhythm and adjust its mechanical power to the forces exerted by the outside world, they do not initiate it. Proprioceptors may be the regulators of ambulation; they are not the initiators. Shortly after the publication of these important results, Sherrington (1913) described the effect of continuous and simultaneous reflex stimulation of the right and left peroneal nerves on the activity of the de-afferentated extensor muscles of both knees of a decerebrate cat. This preparation displayed a rhythmical response in both muscles, contraction in one muscle synchronizing with relaxation in the other. The existence of a rhythmical muscular response in the absence of any rhythm in peripheral sense organs was therefore no longer open to doubt, and the concept of ambulation as a chain reflex appeared to fade still farther into the background; the central theory seemed to rest on a firm foundation of experimental facts. Nevertheless, difficulties remain.

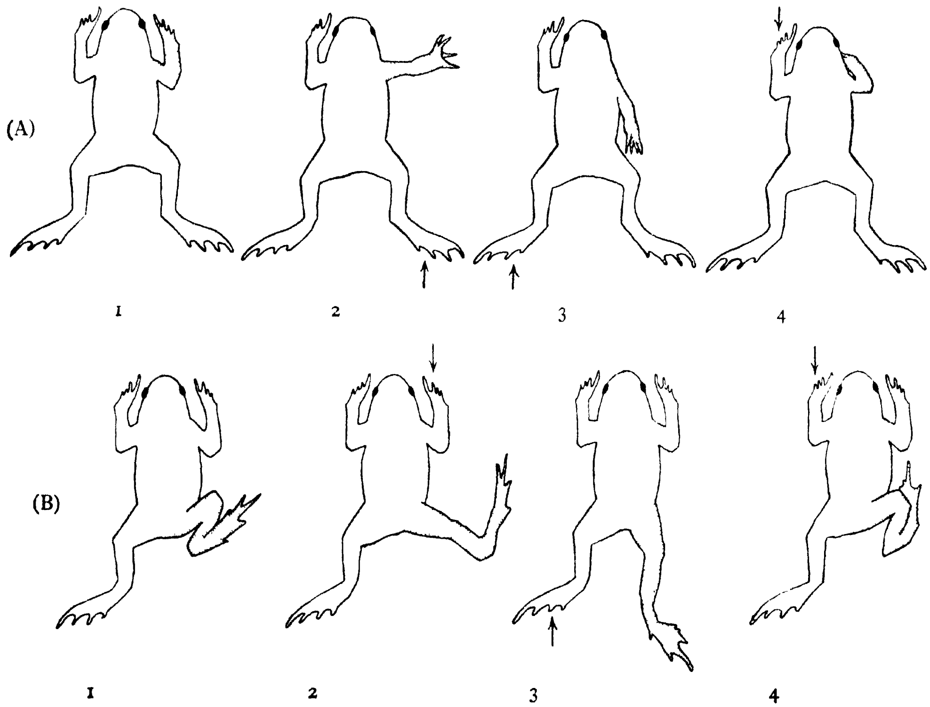
If the ambulatory rhythm of a mammal is of central origin, it might be expected to display itself in its most characteristic form when the limbs are freed from all proprioceptor control. In fact, however, even a single de-afferentated limb of a mammal usually fails to exhibit locomotory activity although the other limbs are functioning normally (Ranson, 1931). Again, although Smith, Mettler & Culler (1940) were able to elicit, by stimulation of the cerebral cortex, ambulatory movements in intact limbs, they only obtained monophasic responses from de-afferentated limbs. There thus remains some element of doubt concerning the precise relationship of the rhythms observed by Graham Brown and Sherrington to the true ambulatory rhythm of an intact animal (see also Laughton, 1924). Before considering this possibility in further detail, it is convenient to review the evidence derived from Amphibia.

If the sensory roots of either one or two limbs of a frog or toad are cut, the operated limbs lose all postural tone and, so long as the animal is at rest, can be placed passively in any position without eliciting any response from the animal; as soon as the toad begins to walk, however, the insensitive limbs take their normal part in the diagonal pattern of ambulatory movements. This striking fact has been known for many years; both Hering (1893) and Bickel (1897) showed that de-afferentation of two limbs did not seriously affect the general pattern of walking, swimming or jumping in the frog. On the other hand, if de-afferentation be applied to all four limbs, the animal becomes markedly lethargic and all types of locomotory activity are reduced to a relatively low level. All these observations have been fully confirmed by subsequent work (Weiss, 1936; Gray & Lissmann, 1940*a*). There is, in fact, general agreement concerning the functional effects of de-afferentation in Amphibia except with respect to one highly important point. According to Weiss (1936) there is no fundamental difference in the behaviour of a toad in which *all* spinal nerves have been cut from that of one in which de-afferentation has been restricted to the four limbs. 'However serious the effect of de-afferentation may be with respect to the total



Text-fig. 1. Records showing the response of a right posterior limb of a toad before and after de-afferentation. Stimulation was applied to the de-efferentated left posterior limb, all other spinal nerves (motor and sensory) being cut. (A) Rhythmical response to condenser discharges applied to the plantar surface of the left posterior limb, the sensory supply to the right posterior limb being intact. (B) Response to an identical stimulus after de-afferentation of the right posterior limb: note the monophasic extension. (C) Monophasic response to mechanical stimulus after de-afferentation. (D) Monophasic response to electrical stimulation of the dorsal roots of the left posterior limb.

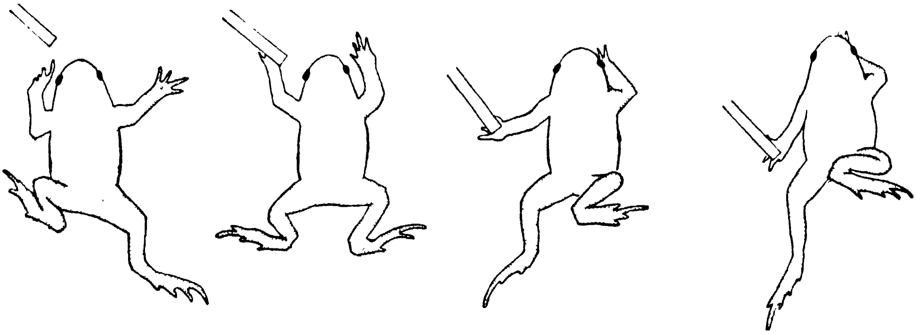
behaviour of the animals, it certainly cannot be said to involve a disintegration of the basic patterns of motor co-ordination as such, since, once made to appear, these manifest themselves in—qualitatively speaking—full integrity' (Weiss, 1936, p. 469). This conclusion is, clearly, of fundamental importance, and since it appears to be based on the behaviour of a single animal, its experimental background must be considered with considerable care. In 1940, and again in 1946*a*, Dr Lissmann and I reported the effect of progressive de-afferentation on the ambulatory activity of the toad (*Bufo bufo*). In common with previous observers we observed the relatively slight effect of de-afferentating two hindlegs, and we observed distinct traces of a diagonal ambulatory rhythm after de-afferentating four legs (Pl. 1), but we did not observe any sign of ambulatory co-ordination in animals in which the whole of the spinal nerves (II–XI) had been de-afferentated. The detailed examination of a large number of animals revealed the remarkable fact that the diagonal pattern of limb movements could be elicited from or displayed by any animal in which one spinal segment was allowed to retain its motor and sensory nerve supply intact. The site of the intact segment is relatively immaterial; animals walked after all spinal nerves were de-afferentated with the exception of those supplying the muscles of the back or even the small nerve (XI), which sometimes supplies the region of the pelvis. No trace of diagonal activity was observed in animals wherein substantial regions of the body remained sensitive but rendered immobile by severance of their motor roots, whereas other regions retained their motor supply but were rendered insensitive by de-afferentation. At least one *intact* spinal nerve was an essential feature of all animals exhibiting ambulatory movements. From these results only two conclusions seem possible, either (i) the normal ambulatory rhythm is dependent on rhythmical excitation of peripheral sense organs or (ii) a massed, but not necessarily rhythmical, discharge from peripheral sense organs is required in order that the central nervous system should exhibit an intrinsic rhythmicity. To distinguish between these two interpretations, use has been made of preparations in which three of the limbs, together with all the dorsal musculature, have been immobilized by severance of their motor roots, whilst the fourth limb was, at first, intact, although its nerve supply had been exposed. As soon as the effect of the anaesthetic has ceased, the application of a relatively weak stimulus to any of the de-efferentated limbs elicited clearly defined ambulatory movements in the intact limb (Text-fig. 1); the excitability was not substantially lower than that of an intact animal, and the movements of the responding limb were well co-ordinated and vigorous. There is therefore no evidence that a cessation of the peripheral stimuli, normally reaching the central nervous system from at least three-quarters of the total ambulatory musculature, has involved a general lowering of excitability either in the central nervous system or in the muscles of the intact limb. If, at this stage, the dorsal roots of the intact limb were severed, all rhythmic response disappeared—nor could it be elicited by increasing the intensity of the stimulus to any of the other limbs; after de-afferentation, the response of the previously intact limb was specific but invariably monophasic (Text-figs. 1 and 2). It is difficult to draw any conclusion other than that when proprioceptor impulses from other limbs are effectively excluded, the impulses arising in the proprioceptor endings of the intact limb are essential for the maintenance of the ambulatory rhythm. This conclusion is supported by the behaviour of a preparation in which three limbs and the body were de-afferentated whilst the fourth limb remained intact; this animal walked in response to a stimulus applied to the fourth intact limb, all four limbs taking part; if, subsequently, the motor roots of the fourth limb are severed—all rhythmical response is permanently abolished—a stimulus applied to the sensitive limb evoking a well-defined but monophasic response from the other three (Text-fig. 3).



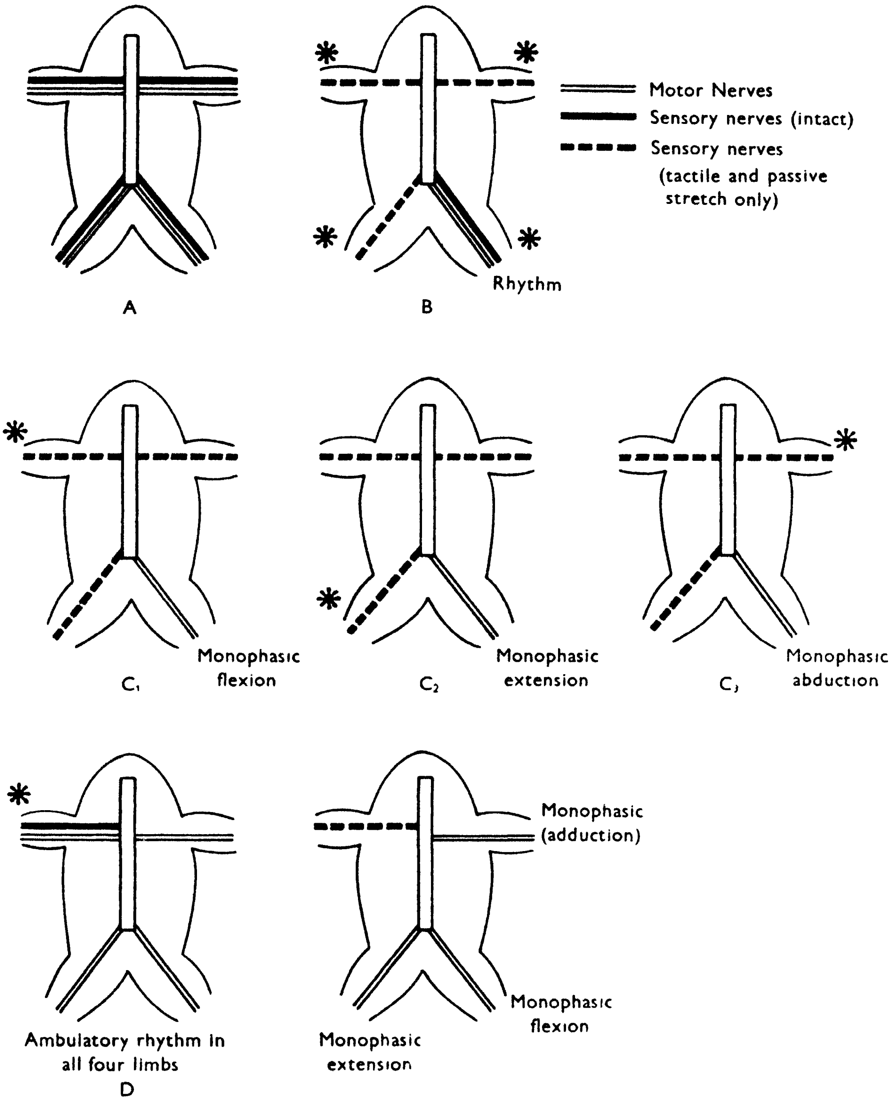
Text-fig. 2. Reflex posture of de-afferentated limbs. The shaded areas are de-afferentated; the white areas represent regions with only the sensory nerves intact. The arrows indicate the site of stimulation; prior to the stimulus the de-afferentated limb was passively placed in the posture shown on the left of each series (i.e. A1 and B1). The response is invariably monophasic and the posture adopted by the limb depends on the site of the stimulus. (See Fig. 4.)

One of the most striking features of the ambulatory mechanism of a toad is the extent of somatic musculature over which the impulses arising in the proprioceptor endings of a single spinal segment can exert their influence. It is therefore important to know the precise nature of the responses which arise in response to the specific pattern of proprioceptor activity which exists during normal ambulation.

The proprioceptor organs of an amphibian appear to be of two kinds: those which respond when the muscle is under tension, and those which respond when the muscle is passively stretched. If a normal toad be suspended in air or in water and gently stimulated when its plantar surfaces are in contact with a rigid but moist glass plate, the resistance of the plate is sufficient to enable the stimulus to elicit a co-ordinated and sustained ambulatory rhythm although the feet slip on the surface of the glass. If, under these conditions, one of the limbs (A) be allowed to come into contact with an isometric lever when the limb is approaching the end of a retractor-extensor phase of its movement, all rhythmical movements in this limb cease; the limb remains at rest exerting a sustained but variable pressure against the lever (Text-fig. 5A). Meanwhile the other three limbs continue their normal rhythmical movements. As soon as limb A is released from contact with the lever, it resumes its rhythmical movements in correct phase relationship with the other three limbs. Under such conditions any central rhythm must be entirely masked by the local proprioceptor reflex, for the power to exert the sustained thrust is completely abolished by de-afferentation of the limb (Text-fig. 5B). The pressure exerted by the restrained limb appears to have no effect on the stepping rhythm of the others, but it is possible to show that its proprioceptor action does, in fact exert its influence over practically the whole of the somatic musculature. This fact emerges if one or more of the other limbs are de-afferentated; for example, a retractor-extensor thrust exerted by a forelimb elicits (i) protraction in the contralateral forelimb, (ii) retraction of the contralateral



Text-fig. 3. Monophasic responses of three de-afferentated limbs to pressure and passive retraction applied to a left de-efferentated fore limb. The shaded limbs are de-afferentated, the white areas indicate regions in which the sensory nerves alone are intact.



Text-fig. 4. Diagram illustrating the dependence of an ambulatory rhythm on an intact nerve supply to one or more spinal segments. (Motor nerves; sensory nerves, together with sensory supply from passive stretch receptors; sensory nerves from tension receptors). The site of an external stimulus is shown by an asterisk. In all cases, the back has been completely denervated.

(A) The nerve supply to all four limbs is intact and the animal walks normally.

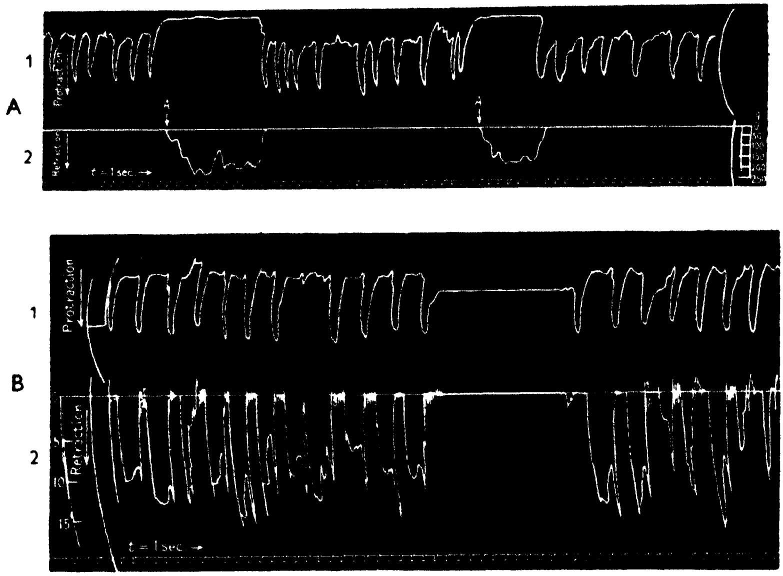
(B) Only the right hindlimb has an intact supply; the motor nerves to the other three limbs have been cut. A stimulus applied to any limb elicits an ambulatory rhythm in the right hindlimb.

(C) As in (B), but the right hindlimb has been de-afferentated. The response of the right hindlimb to a stimulus is then monophasic—and its nature depends on the site of the stimulus.

(D) The left forelimb is intact, the remaining three limbs being de-afferentated. A stimulus applied to the left forelimb elicits a co-ordinated ambulatory rhythm in all four limbs.

(E) As in (D), but the motor nerves of the left forelimb have been cut. A stimulus applied to the left forelimb elicits a characteristic but monophasic response in each of the others.

hindlimb, and (iii) partial protraction of the ipsilateral hindlimb. These responses together constitute a postural picture highly characteristic of one phase of normal ambulation (Text-fig. 6). The reflex picture is entirely dependent on the integrity of the proprioceptors which respond when a group of extensor muscles contract against an external resistance.



Text-fig. 5. A. Record showing the retractor-extensor thrust in an intact left posterior limb of an intact toad in response to an external resistance. The ambulatory movements are shown by means of an isometric lever in the upper tracing; at *A* the limb was allowed to press against an isometric lever whose tension is recorded in the lower tracing. Note the cessation of the ambulatory rhythm during the period in which the limb was engaged with the isometric lever, and the resumption of the rhythm as soon as the external resistance was removed. B. Record showing the absence of a retractor-extensor thrust in a de-afferentated left posterior limb. The lower tracing is from an isometric lever acting as in Fig. A—note the absence of a sustained thrust. The upper tracing is from an isometric lever; note that the rhythmical movements continue although the extension of the limb is in contact with the isometric lever.

There are equally striking responses from the proprioceptors which respond when a limb is passively stretched. Here, again, the range of muscular response is best revealed by observing the effect of stretching one limb when the other three limbs have been de-afferentated. If the left forelimb is de-efferentated and gently placed in the protracted position, the right hindlimb can be placed passively in a state of full extension and the left hindlimb in full flexion. If the left forelimb is now passively retracted, the left hindlimb extends, the right hindlimb flexes, and the right forelimb is protracted (Text-fig. 3). Once again, the whole picture yields a characteristic phase of the normal ambulatory cycle (Text-fig. 6); it is, in fact, the mirror image of that elicited by a local extensor thrust from the left forelimb.

The most striking pictures of responses due to passive stretch are obtained from spinal preparations. When the spinal cord is cut, the limbs of a frog or toad usually fail to exhibit clearly defined reflexes until a period of shock has elapsed—from then onwards reflexes can be readily elicited from the flexor muscles; the loss of reflex response to tension receptors in the extensor muscles appears to be permanent, no extensor thrusts having been observed in spinal preparations. If a spinal toad is suspended with its hindlimbs resting on a moving drum, both limbs are at first passively extended—but as extension proceeds one or other of the limbs flexes whilst the other continues its extension; as soon as the first limb has flexed and begins to undergo passive extension, the second limb flexes—and, from then onwards, the limbs 'step' alternately as long as the drum is in motion. Even more striking is the diagonal pattern of limb movements seen when a high spinal preparation of a newt is towed passively by means of a string (Gray & Lissmann, 1940*b*). It is difficult to resist the impression that were it not for the absence of extensor reflexes, a spinal toad could walk.

From all these observations four facts appear to emerge:

(i) The ability of a toad to exhibit a diagonal pattern of ambulatory movements depends on the effective contact between animal and the ground and on the integrity of the sensory and motor supply to at least one spinal segment.

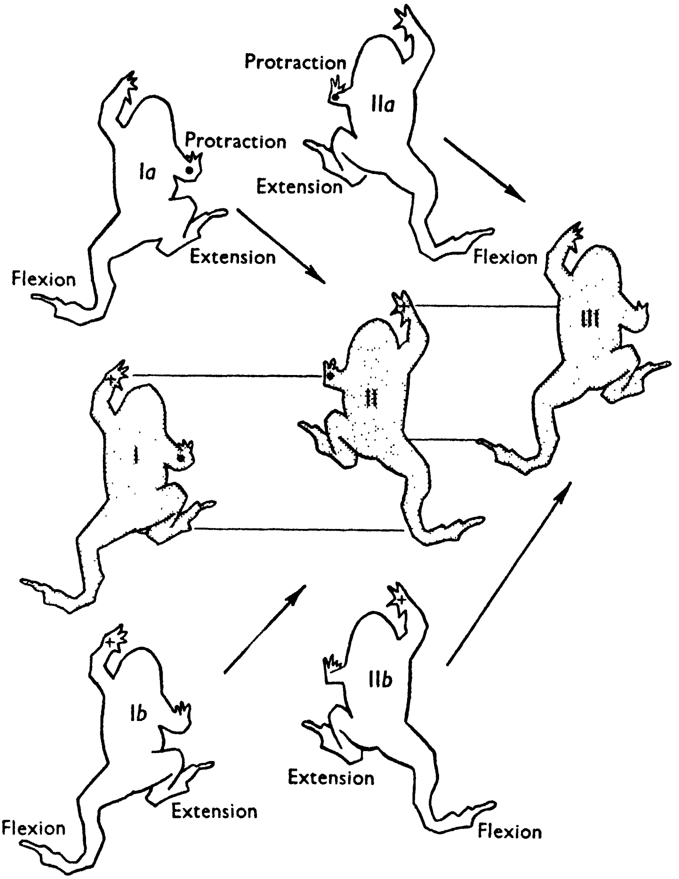
(ii) The ability to exert a sustained pressure against the ground depends on the integrity of the sensory nerve supply from the proprioceptors in the extensor muscles which respond when these muscles develop tension.

(iii) When a limb is freed from reflex activity arising in its extensor muscles, the limb flexes if the flexor muscles are adequately stretched.

(iv) The impulses arising in the proprioceptors of the extensors and flexor muscles of one limb have an influence on each of the remaining limbs. When these effects are summated they yield patterns of co-ordinated posture characteristic of the ambulatory rhythm of the intact animal.

In the light of these facts, it is difficult to avoid the conclusion that proprioceptor reflexes yield a relatively comprehensive picture of normal ambulatory activity in the toad. It is therefore necessary to consider, once again, how far the concept of central control is either essential or justified.

If it could be established that a diagonal rhythm can emerge after *all* sensory supply from the ambulatory musculature has been severed, clear evidence of a centrally determined rhythm would be available. After examining, with great care, more than thirty totally de-afferentated toads, Dr Lissmann and I have failed to find any evidence to support such a conclusion. All attempts to elicit 'stepping' in de-afferentated toads by methods comparable to those employed by Graham Brown and Sherrington in



Text-fig. 6. Diagram illustrating the relationship between the reflex effect of proprioceptor activity in the forelimbs to two of the main characteristic phases of normal ambulation. In phase I two types of proprioceptor responses are initiated by the forelimbs. (i) The protractor muscles of the right forelimb are passively stretched (I*a*) and the limb responds by protraction (II*a*); at the same time, extension is induced in the right hindlimb and flexion in the left hindlimb—thus yielding position II*a*. (ii) The retractor muscles of the left forelimb are exerting a retractor thrust (I*b*) and thus induce extension of the right hindlimb and flexion of the left hindlimb—this yields posture II*b*. In position II the protractor muscles of the left forelimb are passively stretched, whilst the retractors of the right forelimb are exerting a retractor thrust—both yield position III which is the same as position I. Note the synergic effect of a passively retracted right forelimb and of a thrust exerted by the right forelimb and vice versa.

mammals have, so far, proved unsuccessful and we are therefore in a quandary. Either the mechanism of ambulation in Amphibia is fundamentally different to that in mammals, or the rhythmical movements exhibited by the de-afferentated limbs of mammals are of artificial rather than of functional significance (see p. 113 and Gray & Lissmann, 1946*b*).

Since the evidence in support of a central ambulating rhythm in the toad must be regarded as inadequate, it is relevant to consider the somewhat wider question: 'To what extent is there decisive proof of a central locomotory muscular rhythm in any of the lower vertebrates?' A fully de-afferentated toad swims actively provided its membranous labyrinths are intact; no swimming movements have ever been observed after complete de-afferentation and bilateral labyrinthectomy. Until a great deal more is known concerning the action of the labyrinths, it is impossible to say whether swimming is dependent upon a rhythm in the sense organs or upon one of central origin. In the case of fish v. Holst (1935) showed that a tench can exhibit rhythmical swimming movements after severance of all dorsal spinal roots posterior to those supplying the pectoral fins, but in the light of the results obtained with the toad it is difficult to accept this as a decisive demonstration of centralized control. In this connexion Dr Lissmann's (1947) observations on the dogfish are highly suggestive, for he has shown that although the persistent rhythm, so characteristic of the spinal animal, can be sustained after severance of a surprisingly large number of sensory nerves, it is, nevertheless, abolished when de-afferentation extends beyond a critical number of spinal segments. For the time being, therefore, the degree of dependence of swimming rhythms on peripheral sense organs must be regarded as *sub judice*.

The evidence on which the present discussion is based is restricted to an observation of the mechanical responses of muscles. This restriction is unfortunate, since highly significant results could hardly fail to follow any successful attempt to relate an ambulatory rhythm of limb movement to a rhythm of electrical activity in the central nervous system. In the case of respiratory movements this potent line of approach was opened up by Adrian & Brytendijk (1931), who demonstrated in the excised brain stem of a goldfish a rhythm of changing electrical potential of the same order of frequency as the normal respiratory movements of an intact animal. An analogous discovery in relation to locomotory movements would be of extreme interest. At the same time it is necessary to be quite certain that the electrical changes observed in the excised brain are present when the latter is maintaining the activity of the respiratory or ambulatory muscles and are not the result of operative disturbance. Electrical exploration of the excised nerve cord of an earthworm yields evidence of spontaneous rhythmical activity, but the phenomena cannot readily be related to any natural function in the intact animal. Further, although the whole nerve cord of a leech exhibits a very well-defined electrical rhythm, so long as it is in contact with a region of the body exhibiting active swimming movements, the electrical rhythm ceases at once as soon as this connexion is severed (Gray, Lissmann & Pumphrey, 1938).

The whole problem of central versus peripheral control of muscular activity is obviously extremely complex, and for any particular observer there must nearly always be some element of bias in favour of the view which provides the more satisfactory picture of the particular material with which he is most familiar. To my mind, the role of the proprioceptors in amphibian ambulation seems to be sufficiently clear to doubt the necessity of introducing conceptions of central control for which there is at present no direct experimental evidence. How far we are justified in attempting to extend this picture to mammals is more doubtful. For present purposes, however, the main conclusion must be that the existence of centrally controlled patterns of locomotion should be regarded as non-proven. So far as the reflex picture is concerned, the data derived from a study of the Amphibia indicate that the pattern of peripheral excitation arising in a single limb does not necessarily result in a fixed or predetermined pattern of muscular response in any of the others, it only contributes to a general pattern of excitation coming from sense organs located throughout all the rest of the ambulatory musculature and elsewhere (see Gray & Lissmann, 1946*b*). This integrated pattern of stimulation elicits a pattern of response from the musculature as a whole. An application of these principles to wider fields of animal behaviour suggests that particular patterns of behaviour are not so much due to the activity of specific sense organs or to the intrinsic properties of the central nervous system, but to the whole pattern of peripheral stimulation and to the ability of the central nervous system to direct this excitation along pathways which involve the whole of the animal's musculature.

It is perhaps convenient to consider the simplest neuromuscular mechanism which would enable us to present a relatively comprehensive picture of the ambulatory cycle (see Gray & Lissmann, 1946*b*). Such procedure is admittedly speculative, but is possibly useful as a basis for further inquiry. Following the suggestion first advocated by Graham Brown for the mammal, each limb of a toad can be regarded as having two motor centres in the spinal cord, one concerned with the retractor and extensor muscles and the other with the protractors and flexors; these two centres are assumed to be incapable (by mutual inhibition or similar mechanism) of simultaneous activity. If one of these centres is to excite its associated musculature, it must be exposed to a greater balance of excitatory over inhibitory influences than is the case of the other centre. Starting with a limb at rest in a protracted posture, an extraneous stimulus

(=Sherrington's 'primary' stimulus) applied to the retractor centre will cause the limb to retract. As this movement approaches completion the tension of the retractor-extensor muscles decreases whilst the flexor-protractor muscles are stretched and the resultant proprioceptive activity raises the level of excitation of the protractor motor centres, but decreases that of the retractor centres. The relative excess balance of excitation of the retractor centres is thereby reduced and eventually the balance of excitation over inhibition moves in favour of the protractor centres; the limb then protracts and the cycle is repeated. If, during its phase of retraction, the limb encounters an external resistance, the excitatory balance of the retractor centres is reinforced by the proprioceptor activity of the retractro-extensor thrust, and the balance is thereby maintained in favour of the retractor centres until such time as the resistance is overcome. The excitatory balance in one limb is, however, influenced by events occurring in other limbs, and the effect of proprioceptor impulses arising in these other limbs will depend on the state of excitatory balance existing at the moment in the centres of the fourth limb itself; if the balance in a left hindlimb is only slightly in favour of the protractor centre, a stream of impulses arising in a right forelimb owing to the action of an external resistance will swing the balance of the left hindlimb in favour of the retractor centre and protraction is delayed; on the other hand, if the excitatory balance of the hindlimb is in favour of retraction, the action of the forelimb will be to prolong the period of retraction. In this way it is not difficult to reconstruct at least some of the main features of normal ambulation.

Granted the existence of two mutually inhibiting motor centres for each limb driven by rhythmic proprioceptive impulses to each in turn, it does not seem unreasonable to assume some form of rhythmical activity in the centres if the rhythmical stream of proprioceptor impulses is cut off and replaced by a non-rhythmical stream from elsewhere. Provided the mechanism whereby an active centre inhibits its opposite number is sufficiently powerful, only one centre can be active at a time, and if (i) a state of inhibition induces a state of enhanced excitability as soon as the inhibition is past, and if (ii) an active centre undergoes a process of fatigue, then it is possible to rationalize the results obtained by Graham Brown and Sherrington with the possibility that the normal ambulatory rhythm of a mammal, like that of a toad, may be dependent on proprioceptor control.

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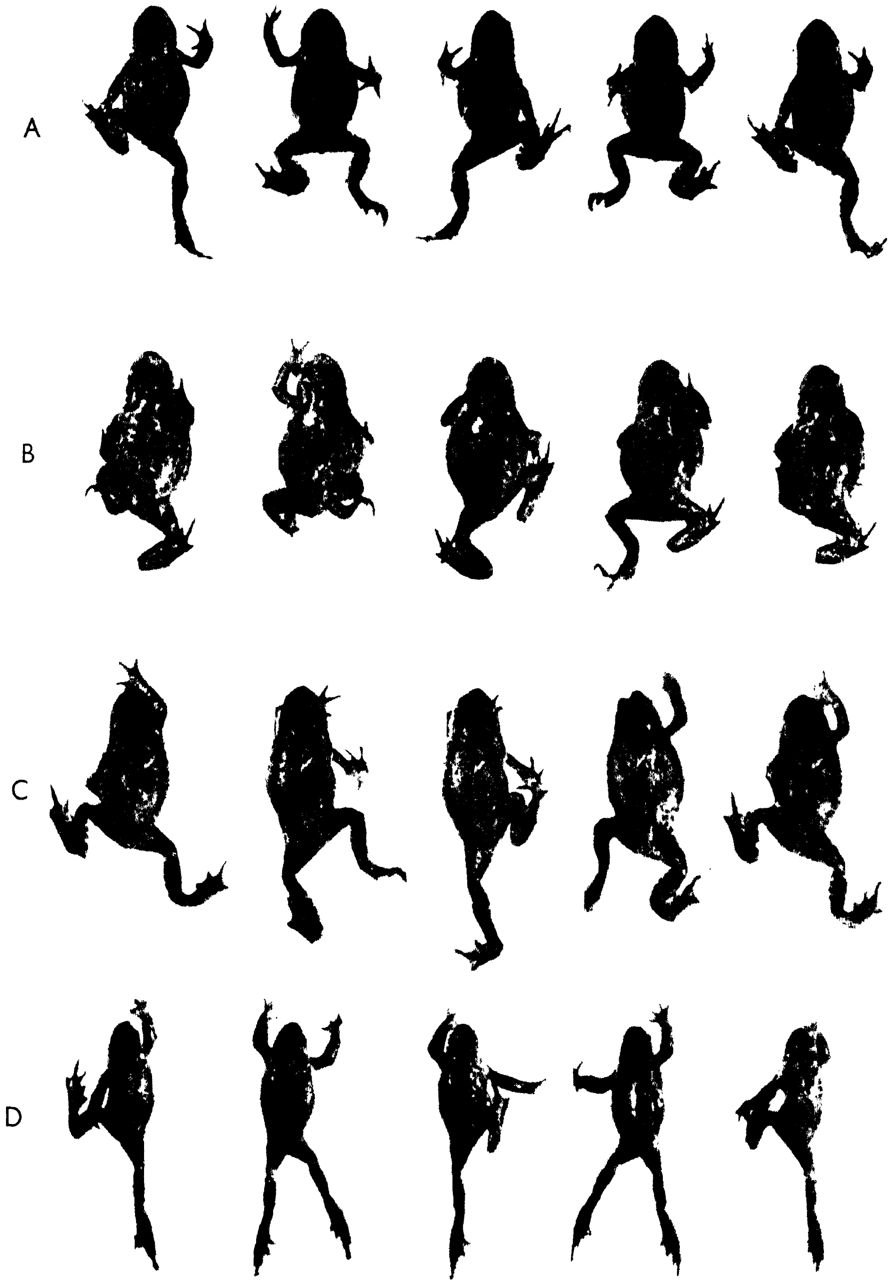
EXPLANATION OF PLATE

Plate 1. Corresponding phases in the step of A, intact toad; B, after de-afferentation of both hindlimbs; C, after de-afferentation of both forelimbs; D, after de-afferentation of all four limbs, the spinal nerves of the back being intact. Note the ungainly movements in D and the tendency in C for the body to roll from side to side.

PLATE 1



For explanation see p. 126

SPONTANEOUS ACTIVITY CYCLES IN POLYCHAETE WORMS

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In ambulation or swimming, the motor units undergo a continuously rhythmic alternation of phases, in which each phase is rapidly followed by the next. Such rhythms could conceivably be due either to spontaneous periodic discharges from pacemaker centres or to chain reflex systems in which each phase appears in response to the effects of the preceding one. Other contributors to this symposium are better qualified to decide this question than myself. The behaviour patterns now to be discussed are of a different type. They consist of bursts of activity alternating with periods of rest; the latter may, in certain circumstances, be of half an hour's duration. The rhythmic activity during the outbursts is continuous, like the rhythm of a crawling or swimming vertebrate; it might be spontaneously or reflexly produced; but the pattern—the very regular periodic release, or periodic suppression, of the rhythm—must necessarily depend on a pacemaker, presumably of the nature of a relaxation oscillator, since the systems may be absolutely motionless between outbursts. To emphasize this distinction, the behaviour patterns will be termed 'activity cycles'. It will be shown that two distinct patterns of this kind—both emanating from localized pacemakers in different parts of the body—play a dominating part in the ordinary, day-to-day behaviour of a common polychaete worm, even when it is living, apparently perfectly normally, in conditions as like those of the field as the experimenter can make them. They determine the incidence of certain specific and functionally important acts that one would expect, by analogy with ourselves, to be under direct reflex control. The suggestion will be made, in conclusion, that this kind of thing may have a widespread application to animals of many kinds.

I. THE MODE OF LIFE OF THE LUGWORM

Most of the experiments to be described were carried out on the lugworm, *Arenicola marina* L., which lives in great numbers in muddy sand flats between tide marks. It makes itself a burrow, and having done so, if the conditions are favourable, it lives in the same burrow for months (Thamdrup, 1935; Linke, 1939), feeding by passing sand through its gut. The behaviour physiology of the worm can be properly understood only if the mode of life, and especially the nature of the burrow—the worm's self-made environment—are taken into account.

The burrow as a whole has an asymmetrical U-configuration, and, as the worm moves to and fro in it, always facing one way, one can distinguish between a head end and a tail end of the burrow (Fig. 1). The tail end is marked by a pile of sand cylinders, the faeces or castings; below this is a 'tail shaft' (*T*) which has smooth walls and houses the worm's tail at the moment of defaecation. The 'gallery' (*G*) is a generally L-shaped tube, whose walls are often marked with the impress of the worm's segments and are impregnated and made firm by its secretions (Osler, 1826; Häntzschel, 1938; Linke, 1939). From the lower end of the gallery, the 'head shaft' (*H*) rises to the surface of the sand. The form of this part of the burrow varies greatly with the mechanical nature of the beach (Bohn, 1903; Thamdrup, 1935; Linke, 1939; Wells, 1945). Perhaps the most typical form of head shaft is that shown in the drawing—a cylinder of yellowish surface sand, with no lumen, ending above at a saucer-shaped depression of the surface. The head shaft is set up and maintained by the following forces: (i) the

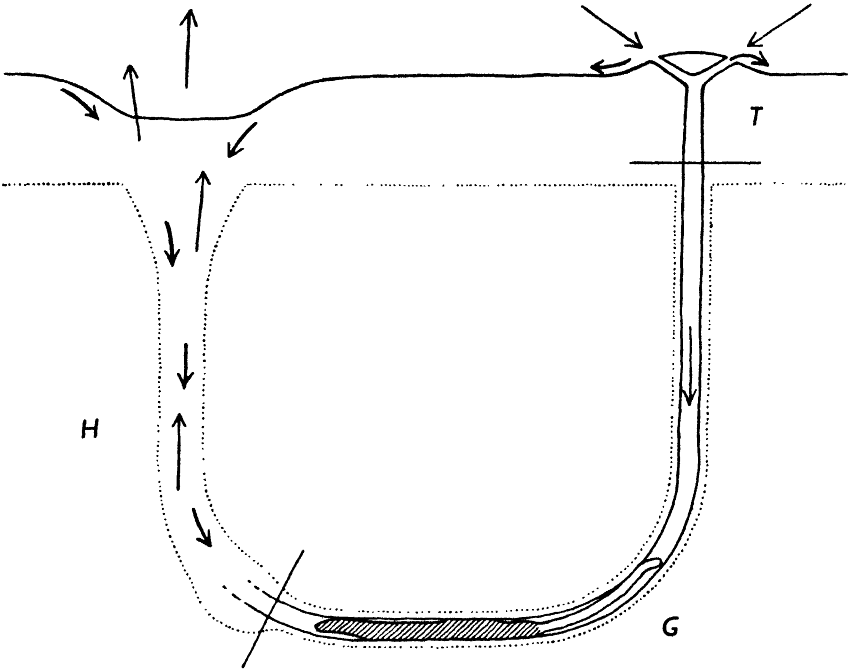


Fig. 1. Generalized diagram of a lugworm burrow, with the worm lying quietly in the gallery. The cross lines are drawn at the boundaries between head shaft (*H*), gallery (*G*) and tail shaft (*T*). The dotted line is the boundary between yellow and black sand. The long, thin arrows show the movement of water, and the short, thick ones that of sand.

worm feeds from its lower end, so that its substance constantly descends; it is renewed by sedimentation above; (ii) the worm drives water through the burrow, chiefly in a headward direction ('irrigation'), and this water escapes up the head shaft and helps to keep it soft; (iii) the worm occasionally makes 'working' excursions up the head shaft (Wells, 1945).

The animal's environment is clearly very uniform; it is sheltered from predators and (at least at high tide) it can feed whenever it chooses. One would therefore expect the pattern of its life to depend more on internal drives than on responses to external events, once it has set up a favourably situated burrow.

II. THE MOVEMENTS OF THE LUGWORM

Several authors have described the movements of which the worm is capable (Bohn, 1902; von Buddenbrock, 1912, 1913; Just, 1924; van Dam, 1937, 1938; Wells, 1944*a*, 1944*b*, 1945, 1948). The behaviour patterns to be analysed involve only those movements which it uses while living in a well-established burrow.

The motor apparatus consists mainly of the circular and longitudinal muscles of the body wall; these contract tonically and keep the fluid in the spacious coelome under a pressure which fluctuates with the worm's activity (Chapman & Newell, 1947). The phasic acts now to be described are brought about by local contractions and relaxations of this musculature, determining local constrictions and swellings of the body. The body is divisible into three regions: an anterior head, in which the prostomiun and two segments are welded together into a single functional unit; a middle region, or trunk, of nineteen chaetigerous segments, of which the hinder thirteen bear tufted gills; and a rather narrowed, posterior tail, consisting of many distinct segments which lack chaetae or gills.

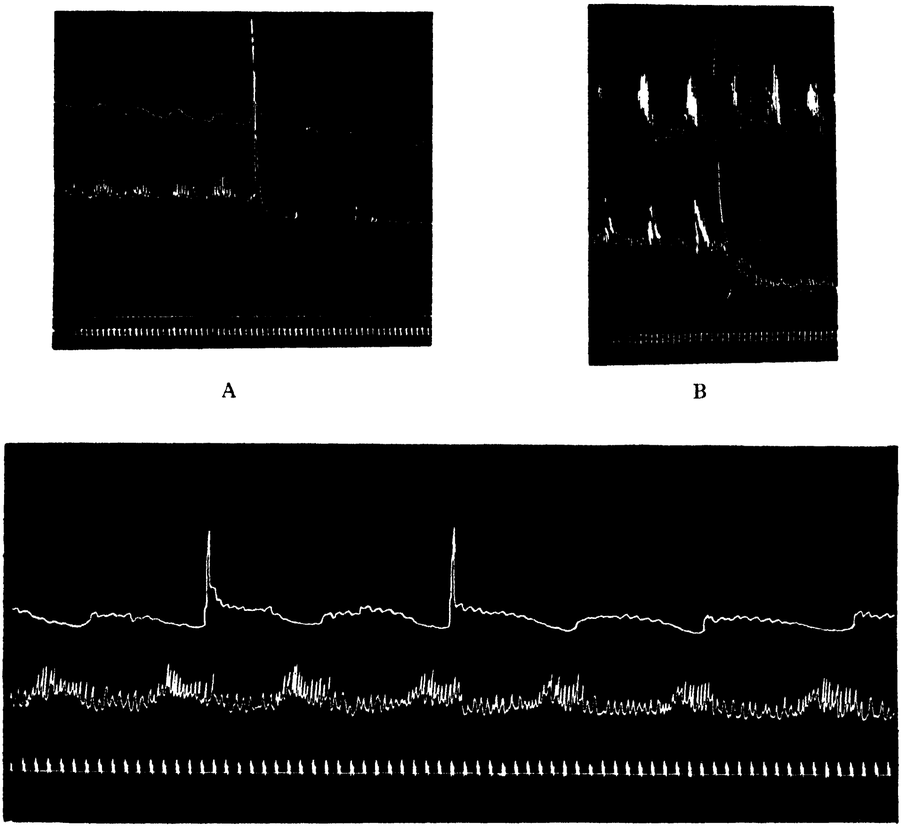
Locomotion and irrigation of the burrow are due to wave movements travelling along the hinder sixteen of the nineteen trunk segments. The waves (of swelling and narrowing) may travel in either direction, headward or tailward, and their effect depends on the attitude of the worm as a whole. In irrigation, the worm has its latero-ventral surface pressed against the tube, but a space (containing the gills) between its dorsal surface and the tube; waves of swelling travel along the body, occluding this space and pumping water through the tube. Locomotion may occur in either of two ways. In the first (*antikinetic locomotion*), the worm travels in the direction opposite to that in which the waves traverse the body; the body as a whole is narrowed and elongated, and waves of swelling (which grip the tube on all sides) traverse it and act as fixed points, thus driving the worm along. This movement—which can be very rapid—causes a displacement of the water in the tube in the direction of creeping. In the second (*synkinetic locomotion*) the direction of locomotion and wave travel coincide; the worm irrigates vigorously as described above, and at the same time creeps gently along in the direction of the water stream. The first three trunk segments play no part in creeping or in irrigation, as a rule.

Feeding is accomplished by means of the eversible proboscis; this leads into an oesophagus extending through several segments and opening behind into the stomach. Proboscis extrusion and withdrawal are brought about by the integrated action of the first three trunk segments, of the head, and of the proboscis itself.

III. THE FEEDING CYCLE

If one excises the proboscis with some of the oesophagus attached (but without the brain or nerve ring) and suspends the 'isolated extrovert' as a longitudinal preparation, either in sea water or in the worm's body fluid, one gets a very characteristic intermittent rhythm; periods of vigorous rhythmic contraction alternate with periods of rest; the whole cycle occupies about 7 min. (Wells, 1937*a*). This experiment can be modified by simultaneously recording from the two ends of the preparation, using the junction of proboscis and oesophagus as a fixed point, and so mounting it that the junction of the two structures can be severed without interrupting the record. In this case, the oesophagus traces a series of waves of low amplitude, on which one can occasionally detect much smaller oscillations, while the proboscis gives a rhythmic outburst at each of the oesophageal waves; when the junction is severed, the oesophageal waves continue, while the proboscis outbursts stop (Fig. 2A). Evidently, the oesophagus is driving the proboscis. If one divides the oesophagus into anterior and posterior halves, both show the wave rhythm, and if one divides an isolated extrovert longitudinally into four strips, all of them show the typical outbursts; so the pacemaker appears to be a diffuse structure, probably a nerve plexus, in the oesophageal wall.

Rather more elaborate preparations can be made by dissecting out the extrovert, but leaving its anterior end attached at the mouth, and by simultaneously recording from the extrovert and from the circular muscles of the body wall. Provided that care was taken to avoid injury to the ventral cord and nerve ring, a spread of the oesophageal rhythm to the body-wall muscles can be detected, but the effects vary according to the segment whose movements are recorded (Wells, 1937*a*, 1949*b*). The body wall of the first three segments (i.e. of those which participate directly in proboscis activity) is thrown into vigorous rhythmical contraction at each outburst of the extrovert; the movements of the two levers correspond stroke for stroke; and on dividing the nerve cord between the strips, the outbursts of the body-wall strip cease (Fig. 2B). The body wall farther back (i.e. from the segments responsible for irrigation and locomotion) is generally inhibited at each oesophageal outburst, though occasionally it shows a strong contraction as the outburst passes off (Fig. 2C).



A

B

C

Fig. 2. Experiments on the pacemaker action of the oesophagus. Read all records from left to right; upstroke of lever means contraction of preparation; time marker in minutes. A, Isolated extrovert, with separate recording of the oesophagus (above) and proboscis (below). The junction between the two is severed half-way across the record. B, Simultaneous recording from the extrovert (above) and the circular muscle of an anterior body segment (below). The nerve cord is divided between them, half-way across the record. C, Simultaneous recording of the extrovert (below) and the circular muscle of a posterior trunk segment (above).

If the entire worm is watched in a glass tube, a periodicity of anterior-end activity can usually be traced. In active worms, outbursts of proboscis extrusion and withdrawal alternate with periods of rest. In quieter ones, the outbursts are of gulping, swaying of the head and perhaps partial extrusion. The average period of these outbursts is about the same as that of the waves of the isolated oesophagus (Wells, 1937*a*). It is reasonable to conclude from all this that the two cycles are the same, and the suggestion arises that the worm in the field feeds periodically, under the influence of its oesophageal pacemaker. This point will be returned to in a later section.

Confirmation of the view that the movements of the dissected preparations correspond to proboscis movements in the intact worms is given by the response to adrenaline. Injected into whole worms, adrenaline induces a prolonged spell (of 30 min. or more) of regular proboscis extrusion and withdrawal. Applied to the isolated oesophagus it causes a sustained contracture. It throws the muscles of the proboscis and anterior body wall into continuous rhythmic activity if they are still connected with the oesophagus, but inhibits such movements as they may show after the conduction path has been severed. The continuous burrowing activity of the whole worm, evoked by adrenaline, seems therefore to be due to an exciting action of the drug on the oesophageal pacemaker (Wells, 1937*a*).

The oesophageal wall is, of course, a complicated structure and may contain reflex arcs; nevertheless, it seems to the writer that the activity cycles must originate in a spontaneously cyclic pacemaker. The extrovert in sea water often gives a considerable amount of background activity between outbursts, as the illustrations show. If, however, one raises the external magnesium concentration, the outbursts themselves are somewhat shortened, the intervals between them are lengthened, and the intervening activity is diminished or altogether abolished. With double magnesium, for example, an extrovert may show outbursts separated by half an hour of complete quiescence, but nevertheless following one another very regularly (Wells & Ledingham, 1940*a*). It is hardly conceivable that a pattern of this kind could depend on a reflex chain.

Occasionally, under abnormal conditions, a vertebrate or crustacean heart shows grouped beats very like the intermittent pattern of an isolated *Arenicola* extrovert, and the latter may perhaps be regarded as fixed in the condition which appears as an occasional freak in other preparations. The extrovert gives its pattern either in sea water or in the worm's body fluid, and whether suspended, and therefore lightly stretched by an isotonic lever, or lying freely in a Petri dish. The extrovert is very sensitive to potassium deficit, if the other ions remain at the sea-water concentrations; it loses its intermittent pattern and becomes continuously active; the same thing happens with magnesium deficit or potassium excess. The mechanism of intermittence is therefore more sensitive to changes in the ion balance than is the mechanism of rhythmic contraction (Wells & Ledingham, 1940*a* 1942). The pattern is, however, resistant to dilution of the bathing medium if the ion ratios are kept constant. The extrovert gives its characteristic cycles even in sea water diluted to 20% with M/400-$NaHCO_3$, if the transfer from sea water is made very slowly, though the amplitude of the individual contractions is greatly reduced at that salinity (Wells & Ledingham, 1940*b*). This resistance of the pattern may be biologically important, as the species occurs in nature down to about 20-25% of sea water (Krogh, 1939) and has no powers of osmoregulation (Schlieper, 1929).

IV. THE IRRIGATION CYCLE

In glass tubes, lugworms (once they have settled down) propel the water headwards through the tube in a series of very regular outbursts (van Dam, 1937, 1938). This irrigation cycle has a period which—although somewhat variable from worm to worm, and from day to day—is much longer than that of the feeding cycle; it is commonly about 40 min. Closer investigation shows that the headward irrigation is the second, and most prominent, phase of a three-phase outburst; the first is tailward creeping and the third is tailward irrigation (Wells, 1949*a*).

The three extracts of Fig. 3 illustrate the point. They were obtained by putting the worm in a U-tube of sea water, whose diameter approximated to that of the burrow; the upper ends of the limbs of the U opened into wide cylinders, one of which contained an aeration jet and the other a float connected with a writing lever; the cylinders were also connected by a fairly wide capillary. The pumping movements of the worm circulated the water in the whole system, and owing to the slight resistance of the capillary, caused fluctuations of level of the float which appear, much magnified, on the tracing. In each case, the worm's head was towards the float, so that a headward movement of water causes a downward movement of the writing point.

The three phases of the cycle can be seen to vary in relative prominence. The worm of extract A rested between outbursts at the bottom of the U; as each outburst began, it crept vigorously tailwards into one of the vertical limbs (upstroke of the lever); this then passed into headward irrigation (downstroke) during which it crept gently (synkinetically) back to the starting point; the third phase was vestigial. The worm of extract B gave only slight tailward creeps, but very well-marked third phases (tailward irrigation) except in one of the outbursts. The same worm, on another occasion, traced extract C; here the first and third phases are both vestigial, though they could just be seen when the worm was watched. Whatever the particular form of the outbursts at the time, they often continue, with almost clock-like regularity, for many hours on end.

The onset of an outburst involves a change in the whole attitude of the

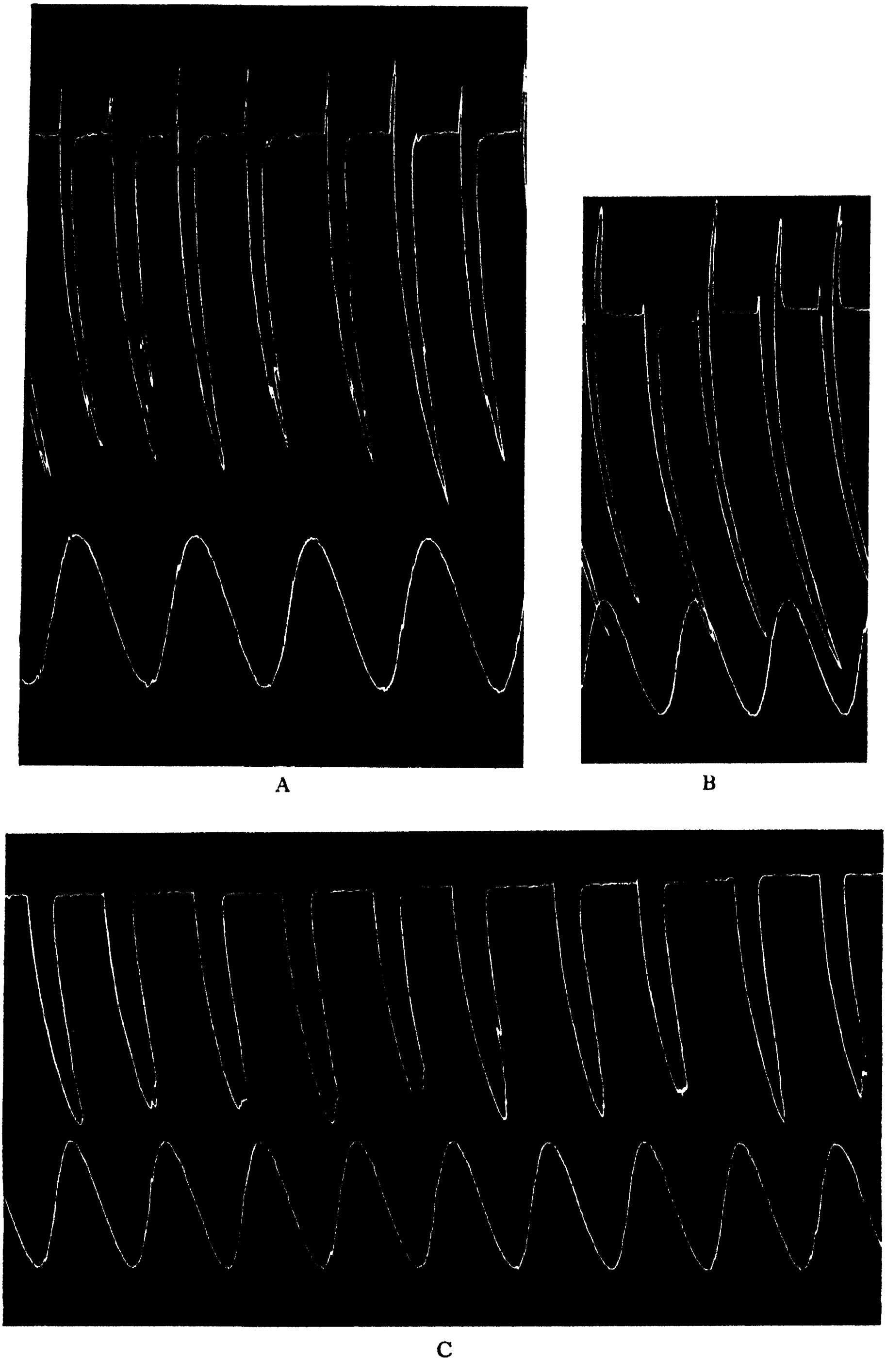


Fig. 3. Records of the water circulation produced by worms in glass U-tubes. Read from left to right; downstroke of lever means a headward propulsion of water; time trace at one cycle per hour.

worm. During the pauses, its body is shortened and generally presses on all sides against the tube. During the outbursts, the body is lengthened and narrowed. The appearances rather suggest, as one watches, a periodic awakening of the worm.

One might assume that the basis of intermittent irrigation is reflex; the appearance of an outburst being stimulated by oxygen lack or carbon dioxide accumulation in the tube. In this case, the outbursts would become more frequent and prolonged if for any reason the pumping movements failed to bring aerated water. In fact, however, if the recording U-tube system is modified so that the worm can circulate a small amount of water (about 35 c.c.) without thereby getting access to an air supply, the bursts appear at about the same intervals as before, but considerably less water is now pumped at each burst. On admitting aerated water again, after a few hours under 'no-air' conditions, the worm responds by pumping vigorously and continuously for a long time (e.g. 40 min.), and thereafter the outbursts are temporarily accelerated (Wells, 1949*a*; see also van Dam, 1937, 1938). These results show that the intermittence is due to an internal pacemaker whose action can be modified, much as the heart beat can, according to circumstances.

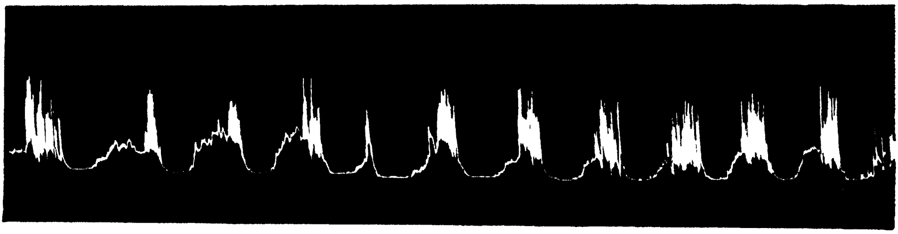


Fig. 4. Tracing of the movements of a worm pinned at both ends to a weighted sheet of cork in a dish of aerated and stirred sea water. The lever was connected to a hook passing under the middle of the worm. Read from left to right; duration of record 7 hr.

The existence of a pacemaker of suitable frequency can be demonstrated by two other methods.

(i) An intact worm is pinned to a cork sheet with two pairs of pins, one anteriorly and one at the base of the tail; the whole is immersed in a dish of aerated and stirred sea water; the worm's movements are simply recorded by means of a glass hook passing under the middle of the body and connected to a light lever. Worms so treated often trace bursts of activity, following each other with great regularity for hours, and corresponding in timing with the irrigation cycles (Fig. 4).

(ii) Longitudinal body-wall strips containing the ventral nerve cord, suspended in sea water, trace a complicated pattern in which conspicuously vigorous outbursts, of about the same timing as the irrigation cycles, can often be seen (Wells, 1949*a*). The presence of the brain is unnecessary. As body-wall strips are motionless in the absence of the ventral cord (Wu, 1939), the pacemaker may tentatively be placed in the cord.

De-afferentation of the cord is unfortunately impossible; it may be that a steady feed-in from peripheral sense organs is necessary to keep the cord active; but it seems clear, from the length of the intervals between outbursts, that the form of the cycle must depend on a spontaneously cyclic pacemaker.

V. ACTIVITY CYCLES UNDER NATURAL CONDITIONS

The appearance of regular activity cycles in worms in glass tubes might be due to the artificial conditions of the experiments. To test this, experiments were made on worms living as naturally as possible in their own burrows in sand. The animals were allowed to burrow in vivaria made of two glass plates, 18 cm. square, held apart by a rubber U about 1 cm. thick. The lower part of the vivarium was filled with sand from the beach. The upper part, containing sea water, was divided into two by a vertical rubber strip in the middle, penetrating for several centimetres into the sand. The two compartments were connected by a capillary siphon; one contained an air jet, and the other a float. Each vivarium contained a single worm. The dimensions were such that it usually made a burrow with the feeding funnel on one side of the centre partition and the faecal pile on the other. Thus the water movements in the burrow could be recorded by a lever connected to the float. The worms lived fairly normally under these conditions; by using a drum which turned once a day, their behaviour could be recorded for weeks on end (Wells, 1949*b*).

Taking all of the worms together (six worms, giving a recorded aggregate of seventy-two 'worm days'), about 45% of their total time was spent in feeding from a gradually subsiding funnel and piling up heaps of faecal cylinders, very much as they do on the beach. When this behaviour began, it usually continued for many hours at a stretch, and was invariably accompanied by very regular tracings of the type shown in Fig. 5. The worm shoots out a faecal cylinder at the tip of each of the sharp downward peaks. Under good conditions, the worms in the field defaecate about once every 45 min. (D. M. Kermack, unpublished observations), which agrees well with the timing of these tracings. It is fairly safe to assume that every saucer and pile of faeces on the beach is the outcome of a behaviour pattern like that of Fig. 5.

On comparing Fig. 5 with Fig. 3A (remembering that the worms are oriented in opposite senses relative to the float), it will be seen at once that the two cycles are identical. We may infer that the worm in sand creeps tailward into the defaecating position on the sharp peak, then creeps gently back during the irrigation phase. Now the worm of Fig. 3A had been fasting for days, and its rectum was empty. Evidently, the excursion which brings *Arenicola* into position for defaecation is not, as one might suppose, a reflex response to a full rectum, but an expression of one of the three phases of the irrigation cycle. The latter is well adjusted to the worm's normal mode of life.

Fig. 5. Records of the water circulation in burrows made by the worms in sand. Read from left to right; upstroke of lever means headward propulsion of water; duration of A, 7 hr.; of B, 6 hr.

The records got from worms in sand generally show a considerable amount of background activity between the irrigation outbursts. This often has an obvious periodicity, at one cycle every 7 or 8 min., as in Fig. 5B. This is about the frequency of the oesophageal pacemaker, and as the latter can influence the segments responsible for producing water movements (Fig. 2C), these minor oscillations probably indicate periodic feeding. Unfortunately, they were not traced by the worms in glass U-tubes, so a detailed confirmation of this suggestion is not available.

The above experiments were done with the burrow submerged, i.e. under high-tide conditions. If the surface sand is left dry at low tide, but the burrow is still partly full of water, a shortage of oxygen might arise, as circulation of the water in the tube is now impossible. Experiments were made with worms in glass U-tubes half-full of sea water, to see what they would do in the circumstances (Wells, 1945, 1949*a*). Most of the worms crept tailwards to the water surface and drew air down over the gills by means of headward waves of the irrigation type. This was periodic and corresponded in timing with the irrigation cycles, of which the whole performance was obviously an adaptation. By these means, a worm can live in excellent condition for several days, in a U-tube containing only some 15 c.c. of sea water. Once again, one cannot fail to be impressed by the fitness of the three-phase cycle to the worm's conditions of life.

One might suppose that the integration of a lugworm's life pattern could best be achieved by means of a hierarchy of reflexes, with appropriate responses to oxygen lack, to a full rectum, and so on. Can any advantage be attributed to the pacemaker type of organization which, in fact, it displays? With regard to the feeding cycles, it will be necessary to have more information, especially about the physiology of digestion, before the point can profitably be discussed. With regard to the irrigation cycles, the following suggestion may be made. The flat beaches frequented by these worms are often covered with puddles and sheets of surface water at low tide. On a sunny summer day, this water may be several degrees hotter than the underlying sand, and well above the optimum temperature for the worms (Thamdrup, 1935; Linke, 1939). A sharp frost, or a heavy downpour of rain, could also make the surface water unfavourable to the worms. Under such conditions, it would tend towards survival for the *Arenicola* to cease irrigating its burrow; a reflex hyperpnoea in response to oxygen lack might be disastrous; and we may guess that the worm would behave much as it does in the U-tube experiments described above, from which aeration was excluded. Under the influence of the irrigation pacemaker, it would make occasional tailward excursions towards the surface followed by short bursts of irrigation; these would serve to test the surface water; after the rising tide had covered the burrow again, irrigation would be seriously resumed at the next outburst and would then be very vigorous to make up for previous oxygen lack.

This suggestion assumes that the worms can survive oxygen deprivation for most or all of the low-tide exposure period. According to Hecht (1932), they can live with practically no oxygen and high concentrations of hydrogen sulphide in the water for days. Haemoglobin is present in the blood, and has been estimated to hold sufficient oxygen to support the worm for rather over an hour (Barcroft & Barcroft, 1924; Borden, 1931; see also Wolvekamp & Vreede, 1941). These estimates are based on comparisons of the total oxygen capacity of the blood with the oxygen usage measured under conditions of abundant oxygen supply, and they assume that usage will continue at the same rate if the external oxygen tension falls. The behaviour of the worms in the experiments with a non-aerated circulation, described above, suggests that activity is greatly reduced under such conditions (Wells, 1949*a*). *Arenicola* has recently been shown to have haemoglobin in its muscles, besides that in its blood (Fox, 1949), and this again will increase the time for which the stored oxygen can last. In any event, it seems clear that the worm is not immediately dependent, as we are, on an external oxygen supply, and the difference between its response to conditions of oxygen shortage and ours is the less surprising.

VI. COMPARISON WITH OTHER POLYCHAETE WORMS

As there is no 7 or 40 min. periodicity in the environment, the activity cycles of *Arenicola* are clearly not related to those cases in which a tidal, diurnal or other environmental rhythm is impressed on an animal. They are perhaps more comparable to the 2 hr. and 4-day activity cycles in the rat (Richter, 1927) or to the roughly cyclic variations in activity level of snails kept under constant conditions (Howes & Wells, 1934; Wells, 1944*c*). But the *Arenicola* cycles consist, not of diffuse changes in the general level of activity, but of the periodic evocation of highly specific and functionally important acts. It may be that pacemakers will be found to govern the behaviour of many animals, even in cases where, from an anthropomorphic standpoint, one would expect to find direct reflex control.

Gut preparations, or body-wall strips, from many polychaete species exhibit intermittent activity (Hogben & Hobson, 1924; Wells, 1937*b*, 1939), but unfortunately little is known about the functional significance of the resulting patterns. Various *Nereis* species live in burrows on muddy sand flats; they have an eversible, jawed proboscis of more complicated structure than that of *Arenicola*, and they feed, partly on dead animals and plant fragments, and partly by ingesting the surface sand (Thamdrup, 1935; Linke, 1939). The isolated extrovert is spontaneously active with a pattern more variable than that of *Arenicola* (Wells, 1937*b*). The worms show intermittent irrigation in glass tubes, and isolated body-wall strips give intermittent rhythms; as, however, such experiments as have been made on the effect of low oxygen tensions on irrigation gave inconclusive results, one cannot safely decide whether their intermittence is determined reflexly or by a pacemaker (van Dam, 1937, 1938). The *Glycera* species live in much the same way as *Nereis* and exhibit intermittent irrigation (Stolte, 1928, 1932). The isolated extrovert of *Glycera dibranchiata* is spontaneously active, and there is evidence that its rhythm is normally inhibited by the central nervous system (Wells, 1937*b*). In neither genus has a detailed comparison been made between the laboratory behaviour of the animals, or of isolated preparations, with the behaviour patterns under field conditions. Information along these lines, on these and other types, would be interesting.

Note

The following citation from *Natural History of Marine Animals*, by G. E. MacGinitie and Nettie MacGinitie (McGraw Hill, 1949) confirms the idea that the oesophageal rhythm determines intermittent feeding:

'When *Arenicola* is actively feeding, the process of everting and inverting the proboscis and then swallowing occurs about every 5 sec. Also, after a certain number of swallows, ranging from 8 to 15, the worm takes a rest period of a few minutes, then begins feeding again.'

This passage refers to *A. cristata*, which is closely similar to *A. marina*.

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QUANTITATIVE MESSUNG VON STIMMUNGEN IM VERHALTEN DER FISCHE

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I. EINLEITUNG

Wie macht man an frei beweglichen Tieren solche zentralnervösen Vorgänge sichtbar, die sich nicht als motorische Bewegungen äußern? Diese Frage wird einem Vertreter der 'klassischen' Nervenphysiologie sinnlos erscheinen, denn für ihn setzt sich jegliches Verhalten aus motorischen Reflexen zusammen, und Vorgänge der genannten Art kennt sein Begriffsschatz nicht. Für den Verhaltensphysiologen von heute dagegen ist diese Frage wichtig geworden, denn die Koordinationsforschung, die Elektrophysiologie des Zentralnervensystems und vor allem die neuere Verhaltensforschung selbst haben gezeigt, daß nur ein Teil der Abläufe im Zentrum als motorische Impulse wieder nach außen gelangt, während andere Vorgänge das Organ nur irgendwie umstimmen, d.h. die *Reaktionsnorm* des Nervensystems ändern. Wie also kann man solche Umstimmungen sichtbar und meßbar machen, ohne das Tier in seinem Verhalten zu stören? So lautet mein Thema.

II. STIMMUNGSÄNDERUNG MIT ÄNDERUNG DER GLEICHGEWICHTSLAGE

Erlauben Sie mir, Ihnen zwei Experimente zu schildern, die ich Ihnen lieber vorführen würde (was hier leider nicht möglich ist).

In einem zunächst verdunkelten Glasbecken befinden sich verschiedene Fische in einem Ruhezustand, den wir als 'Schlaf' bezeichnen dürfen. Der Boden des Beckens wird jetzt von unten her gleichmäßig erhellt. Die Fische erwachen und beginnen umherzuschwimmen. Nach einigen Minuten fängt ein Fisch, z.B. eine Barbe (*Barbus*) an, zu taumeln und nach kurzem Schwanken sich auf den Rücken zu legen; zie schwimmt weiterhin in dieser um 180° verkehrten Lage umher (Abb. 1). Bald danach geschieht das Gleiche etwa mit einem Tetra (*Gymnocorymbus*) und mit einigen anderen Fischen. Die übrigen bleiben unverändert in ihrer Normallage.

Ein zweiter Versuch: In einem Aquarium—der Lichteinfall ist hier gleichgültig—befindet sich ein männlicher Stichling im Hochzeitskleid, dem Anschein nach ein normales Tier, das in seinem Herrschaftsbereich umherschwimmt. Ein zweites kräftiges Männchen wird dazugesetzt.

Zunächst geschieht nichts, die Fische schwimmen umher, ohne Notiz voneinander zu nehmen. Jetzt hält der Neuankömmling in kurzem Abstand von dem anderen Fisch still, fixiert ihn mit den Augen, richtet ein wenig die Rückenstachel auf und wird vermutlich im nächsten Augenblick angreifen. Da plötzlich beginnt der bedrohte Fisch wie ein aufgezogener Kreisel um seine Längsachse auf der Stelle zu rotieren, mit einer Frequenz von etwa 80–100 Umdrehungen in der Minute (Abb. 2). Sobald der (offensichtlich etwas verwunderte) Gegner sich zurückzieht, hört dieses Manöver schnell auf, beide Fische schwimmen wieder normal umher. Bei jeder neuen beginnenden Attacke wiederholt sich aber prompt das gleiche Schauspiel.

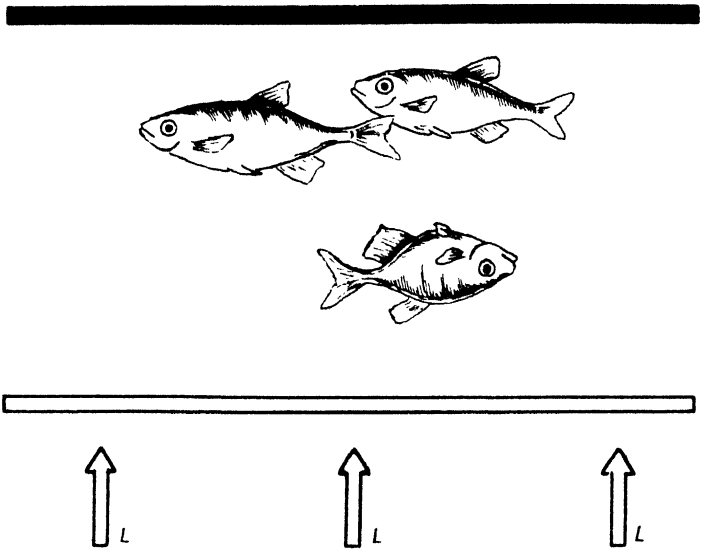

Abb. 1. Gleichgewichtslage verschiedener Fische bei Lichteinfall von unten (L); oberseits eine nicht reflektierende schwarze Fläche (Sammet).

In diesen zwei Beispielen sind zentrale Stimmungsänderungen sichtbar gemacht, die uns sonst verborgen bleiben, und die sich hier in einer *Änderung der Gleichgewichtslage* manifestieren. Um was es sich, genau gesehen, handelt, kann ich Ihnen jetzt noch nicht verraten. Ich habe diese Versuche nur erwähnt, um Sie selbst ein wenig auf mein Thema umzustimmen. Ich brauche nämlich für das Folgende Ihre Geduld, denn wir müssen einen Umweg machen. Ehe ich über zentrale Stimmungen Genaueres mitteilen kann, müssen wir zuerst das *Meßgerät* kennen, mit dessen Hilfe wir diese Stimmungen untersuchen. Es ist das Organ der Gleichgewichtsorientierung, also der *Statolithenapparat* im *Utriculus*. Sie sehen die beiden Utriculusstatolithen hier (Tafel 1) in ihrer natürlichen Lage im Kopf (den mein Mitarbeiter Dr. Ahrens ganz durchsichtig zu machen versteht).

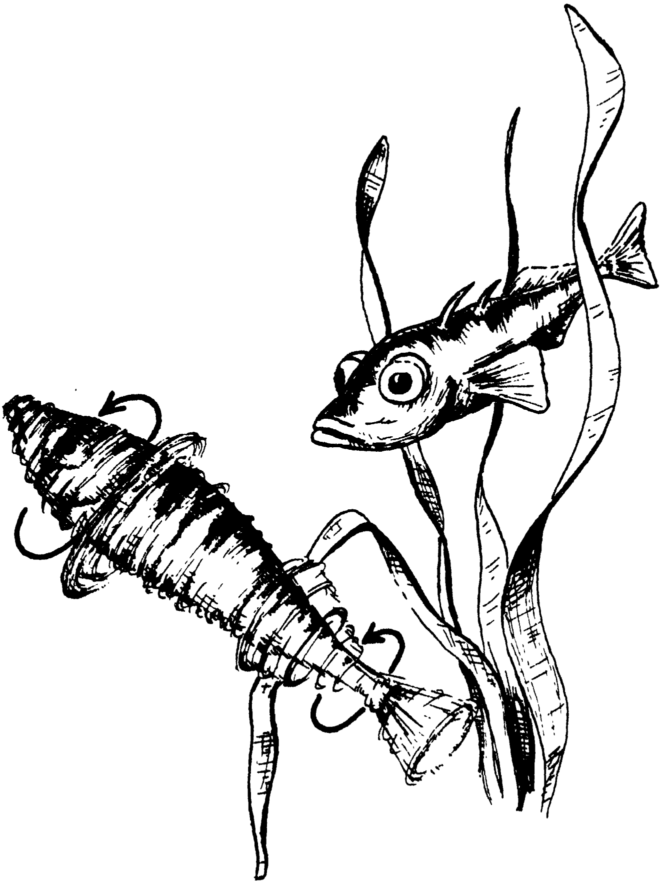

Abb. 2. Bei Bedrohung durch den Rivalen rotiert das linke Stichlings-♂ um die Längsachse. (Erläuterung im Text.)

III. DER MECHANISMUS DER GLEICHGEWICHTS-ORIENTIERUNG

Was geschieht in diesem statischen Apparat, wenn ein Tier seine Lage ändert? Diese Frage muß exakt beantwortet sein, ehe quantitative Angaben zur Physiologie dieser Umstimmungen möglich sind. Das Kapitel der *Lageorientierung* wird seit vielen Jahrzehnten eifrig bearbeitet, wobei man leider feststellen muß, daß die Theorien im Lauf der Zeit immer komplizierter und schwerer verständlich geworden sind. Trotz vieler schöner Befunde, über die Herr Löwenstein Ihnen berichtet hat, sind doch die drei Hauptfragen, die wir stellen müssen, wenn wir diesen Apparat verstehen wollen, noch immer nicht eindeutig beantwortet.

Erstens: Welches ist der adäquate Reiz der Statolithen auf das Sinnesepithel? Druck, Zug, Scherung (= Verbiegung der Sinneshaare durch seitliche Verschiebung des Steines) und hydrostatischer Druck stehen zur Diskussion.

Zweitens: Wie arbeiten der rechte und der linke statische Apparat zusammen? Setzen sie sich tropotaktisch gegeneinander ins Gleichgewicht oder summiert sich telotaktisch ihre Wirkung?

Drittens: Welche quantitativen Beziehungen bestehen zwischen dem adäquaten Statolithenreiz und seiner physiologischen Wirkung im Gleichgewichtszentrum?

(1) *Die Messung des adäquaten Reizes der Statolithen auf das Sinnesepithel*

Um diese Fragen zu beantworten, müssen wir (1), den Statolithenreiz quantitativ variieren und (2), seine Wirkung im Gleichgewichtszentrum quantitativ messen, was beides wohl bisher noch nicht geschehen ist. Was die Reizwirkung anlangt, so kann die Registrierung von Impulsen in afferenten Fasern oder umgrenzten Hirnpartien nicht zum Ziele führen, da wir nicht wissen, welche Beziehung zwischen Entladungsfrequenz und physiologischer Wirkung der Entladung besteht, und ob es zulässig ist, von einzelnen Elementen auf alle übrigen zu verallgemeinern. Und zur Messung der Reizgröße ist das verbreitete Verfahren, Reflexbewegungen selbst, also Stellungsänderungen der Gliedmaßen oder des Augapfels zu quantifizieren, ebenfalls unbrauchbar. Denn da bei jeder Bewegung gewisse Muskeln sich verkürzen und ihre Antagonisten gleichzeitig erschlaffen, so bleibt es willkürlich, ob man die Streckung oder Beugung eines Gliedes als Indikator für eine Reizzunahme im statischen Apparat verwenden will. Der verdiente Labyrinthforscher Magnus (1924) ist mit seiner, wie wir sehen werden verfehlten, Zugtheorie der Statolithenreizung Opfer einer solchen willkürlichen Festlegung geworden.

Fehler dieser Art werden vermieden, wenn wir uns an eine definierbare Gleichgewichtslage halten, nämlich die *Normallage*, in der keinerlei Gleichgewichtsreaktionen auftreten. Wir dürfen annehmen, daß hier auch im Zentrum ein physiologischer 'Gleichgewichtszustand' bestehen muß. Mit Hilfe der Normallage lassen sich quantitative Aussagen gewinnen, wenn man die Versuchsanordnung so einrichtet, daß diese Lage sich mit der Größe der mechanischen Kraft, die am Statolithen angreift, gesetzmäßig ändert. Das ist möglich, wenn man die *optische* Gleichgewichtskomponente zu Hilfe nimmt, deren Vorhandensein ich (1935, 1938) bei den meisten Knochenfischen feststellen konnte. Ein in der Wasserströmung stehender seitlich beleuchteter Fisch weicht von der Senkrechten um einen bestimmten Winkel α ab (Abb. 3 A), der mit der Helligkeit des Seitenlichts zunimmt; mit β sei der Winkel zwischen Lichteinfall und Dorsoventralachse bezeichnet, $\beta = 90° - \alpha$. Entfernt man operativ beide Utriculi, so stellt der Fisch seinen Rücken genau zum Schwerpunkt der Helligkeitsverteilung; α wird in diesem Falle $= 90°$, $\beta = 0°$ (Abb. 3 B). Da also die Augen den Fisch mit dem Rücken zum Licht, die Utriculi ihm mit dem Bauch zur Erde um seine Längsachse zu drehen suchen, so müssen wir erwarten, daß eine Erhöhung der mechanischen Kraft der Statolithen beim intakten, seitlich beleuchteten Tier den Neigungswinkel α verringern wird. Aus der Messung dieses Vorganges könnte sich die Antwort auf die Frage nach dem adäquaten Statolithenreiz ergeben.

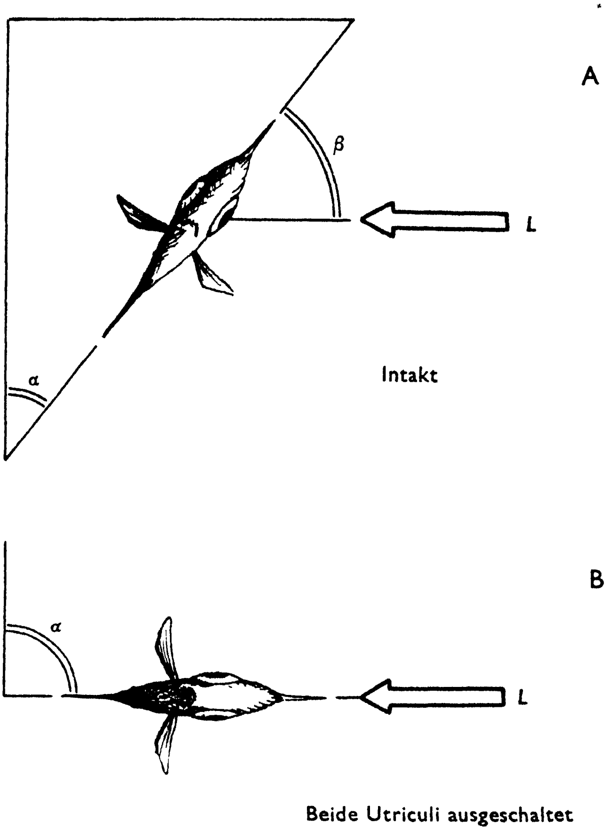

Abb. 3. Normaleinstellung eines in horizontaler Wasserströmung bei seitlichem (horizontalem) Lichteinfall *L* schwimmenden Fisches (z.B. Tetra, Barbe, Scalare u.a.).

Die mechanische Kraft, durch die der Statolith sein Sinnesepithel belastet, läßt sich durch ein zusätzliches Zentrifugalfeld quantitativ beliebig steigern (Abb. 4). Der Fisch schwimmt in einem kleinen Käfig *K* aus schwarzem Frauenhaar in einem Versuchsgefäß *g* gegen eine Wasserströmung. Das Gefäß ist auf einem Zentrifugenarm *H* so montiert, daß es

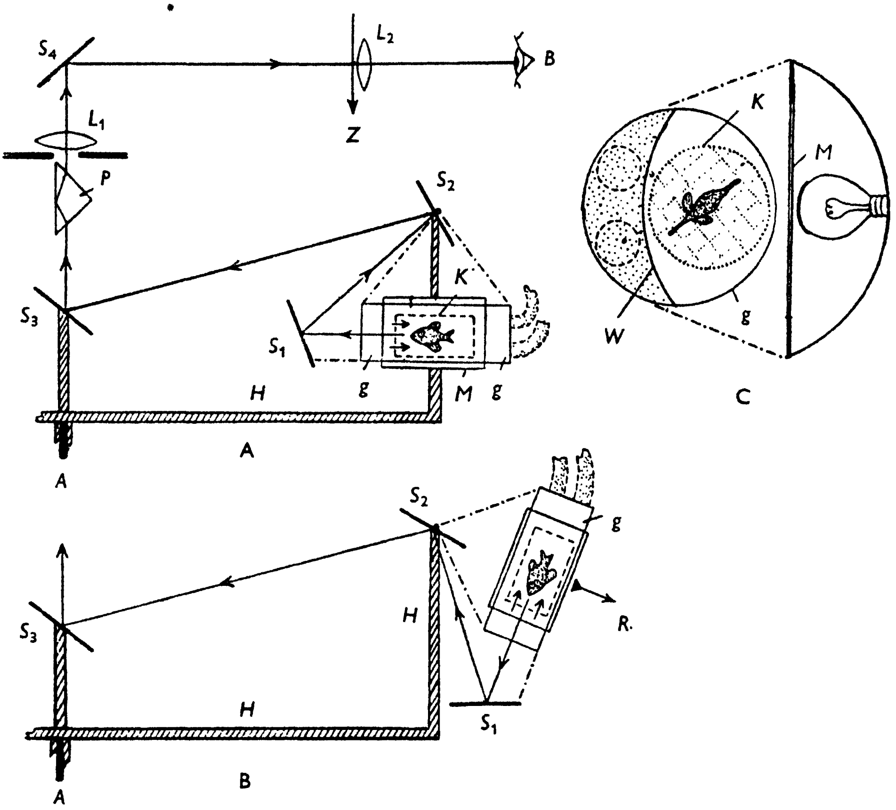

Abb. 4. Skizze des Zentrifugierversuchs. A, Gesamtansicht; B, Unterer rotierender Teil während des Umlaufs; C, Ansicht des Fischgefäßes von vorn. Es bedeuten: A = Drehachse der Zentrifuge, B = Auge des Beobachters, L_1 = Linse zur Abbildung des Fisches, L_2 = Feldlinse zur Abbildung der Öffnungsblende von L_1 auf die Augenpupille, M = beleuchtete Milchglasscheibe, W = nicht reflektierende schwarze Wand, Z = einstellbarer Zeiger zur Ablesung des Neigungswinkels α.—Der Pfeil R bezeichnet die Richtung der Resultante aus Schwerefeld und Zentrifugalfeld. Die beiden parallelen Pfeile im Gefäß g bezeichnen die Richtung der Wasserströmung. Die mit Richtungspfeilen versehene Verbindungslinie zwischen Fisch und Beobachterauge deutet den Weg der Lichtstrahlen an. Weitere Erläuterung im Text.

beim Umlauf der Zentrifuge frei auspendeln kann. Das Gefäß und ebenso auch der Fisch stellen ihre Längsachse stets in eine Ebene senkrecht zur Resultierenden von Schwerkraft und Zentrifugalkraft. Seitlich wird dem Fisch eine leuchtende Fläche geboten, sodaß er um einen bestimmten Winkel von der Richtung der mechanischen Feldwirkung abweicht (Abb. 4C). Durch ein System von gekoppelten beweglichen Spiegeln

S_1—S_4 und einem in halber Umlauffrequenz mitdrehenden Umkehrprisma P wird der Fisch vom Beobachter immer genau von vorne in Richtung seiner Längsachse betrachtet (Abb. 4C). Unsere Versuchstiere, hauptsächlich Tetra (*Gymnocorymbus*) und Scalare (*Pterophyllum*), sind schmal wie lebende Zeiger und stehen im strömenden Wasser so ruhig, daß die Ablesung des Neigungswinkels α bis auf ein Grad genau leicht möglich ist.

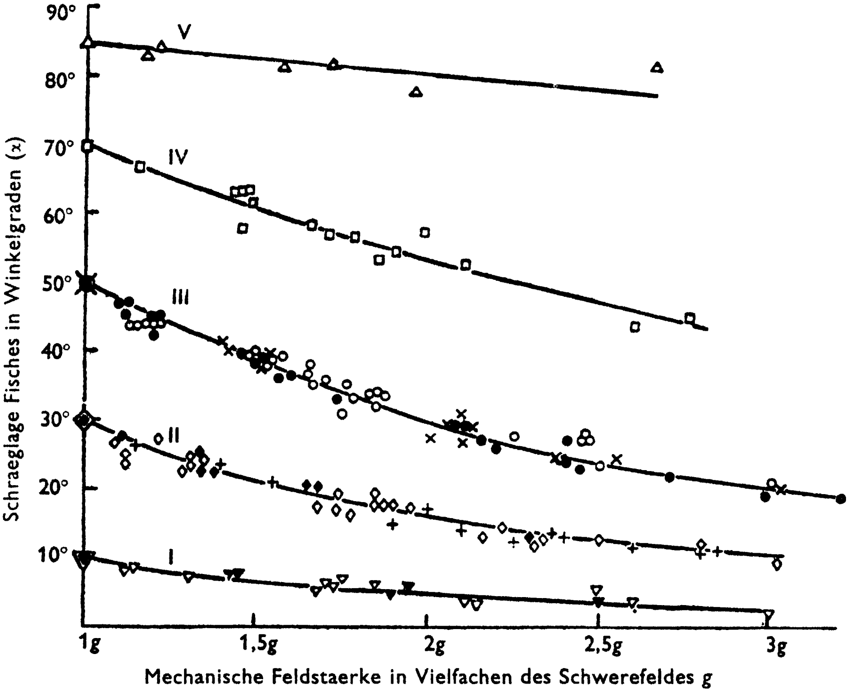

Abb. 5. Neigungswinkel α (Schräglage) der Fische in Abhängigkeit von der mechanischen Feldstärke für fünf verschieden starke Beleuchtungen, bzw. Lichtempfindlichkeiten (I–V). Die einzelnen Kurvenpunkte sind unkorrigierte Mittelwerte jedes einzelnen Zentrifugierversuchs. Helle Zeichen = *Gymnocorymbus ternetzi*; schwarze Zeichen = *Pterophyllum scalare*; die Werte von fünf weiteren Fischarten der Gattungen *Gasterosteus*, *Haplochromis*, *Lebistes*, *Platipoecilus*, *Hypessobrycon* sind gemeinsam durch Kreuze (× bzw. +) bezeichnet.

Ich brauche auf die komplizierten Einzelheiten der Anordnung nicht näher einzugehen. Wir können uns einfach denken, daß in diesem Versuch das 'Gewicht' der Statolithen in meßbarer Weise vermehrt wurde. Sie ersehen aus Abb. 5, daß mit der Zunahme des Statolithen 'gewichts' der Neigungswinkel α tatsächlich abnimmt. Die Meßwerte stammen von Tetra, Scalare und fünf weiteren verschiedenen Fischarten, das Ergebnis ist für alle Arten das gleiche: Der Neigungswinkel α ändert sich nur wenig, wenn der Ausgangswert von α nahe bei 0° oder bei 90° liegt. Dagegen nimmt α sehr stark ab, wenn der Ausgangswert von α um 45° liegt. Die fünf ausgezogenen Mittelkurven sind nun identisch mit mathematischen Kurven, die der einfachen Formel $ctg\,\alpha \sim F$ folgen. Der Fisch verhält sich so, als wäre er eine mechanische Waage, deren Arme durch ein senkrecht ziehendes veränderliches und ein wagerecht ziehendes konstantes Gewicht belastet sind (Abb. 6).

Es liegt nahe zu fragen, ob diese *Cotangensregel* auch noch gilt, wenn der Statolith *leichter* gemacht wird. Das ist durch einen Kunstgriff möglich: Wir haben zunächst in abgeänderten Zentrifugierversuchen festgestellt, daß eine Kraft, die an dem Statolithen in Richtung der Körperlängsachse wirkt, auf die Einstellung des Fisches um seine Längsachse, also auf den Winkel α ohne jeden Einfluß ist. Nun haben unsere Versuchsfische die schöne Eigenschaft, ihre Längsachse genau in die Richtung des Wasserstroms einzustellen, auch wenn die Strömung schräg oder senkrecht von oben oder unten her kommt. Bei einem Fisch, der auf diese Weise senkrecht schwimmt (Abb. 7A), wirkt die Schwerkraft g genau in Richtung der Längsachse, und der Fisch stellt sich folglich genau mit dem Rücken zum Licht ein. Wenn man nun durch Änderung der Strömungsrichtung den Fisch allmählich wieder in die Normallage bringt, so entsteht am Statolithen eine in Sinusform zunehmende wirksame Schwerekomponente K senkrecht zur Längsachse des Tieres. Gleichzeitig weicht der Fisch um seine Längsachse von der Richtung dieser wirksamen mechanischen Komponente um so viel ab, als wenn—bei

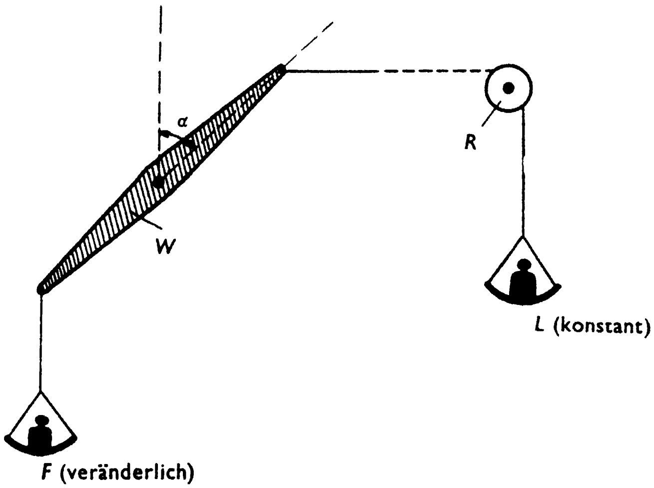

Abb. 6. Waage, die das Verhalten des Fisches bei konstanter Belichtung in verschieden starken mechanischen Feldern veranschaulicht (W = Waagebalken, R = Umlenkrolle, L = Lichtkomponente, F = mechanische Komponente; nur die Änderung der letzteren bestimmt in diesem Versuch das Verhalten des Fisches).

Einhaltung der Cotangensregel—der Statolith gerade dieses 'Gewicht' hätte. Damit ist gezeigt, daß die Cotangensregel für ein 'Statolithengewicht' von Null bis zum Dreifachen der Erdschwere gilt.

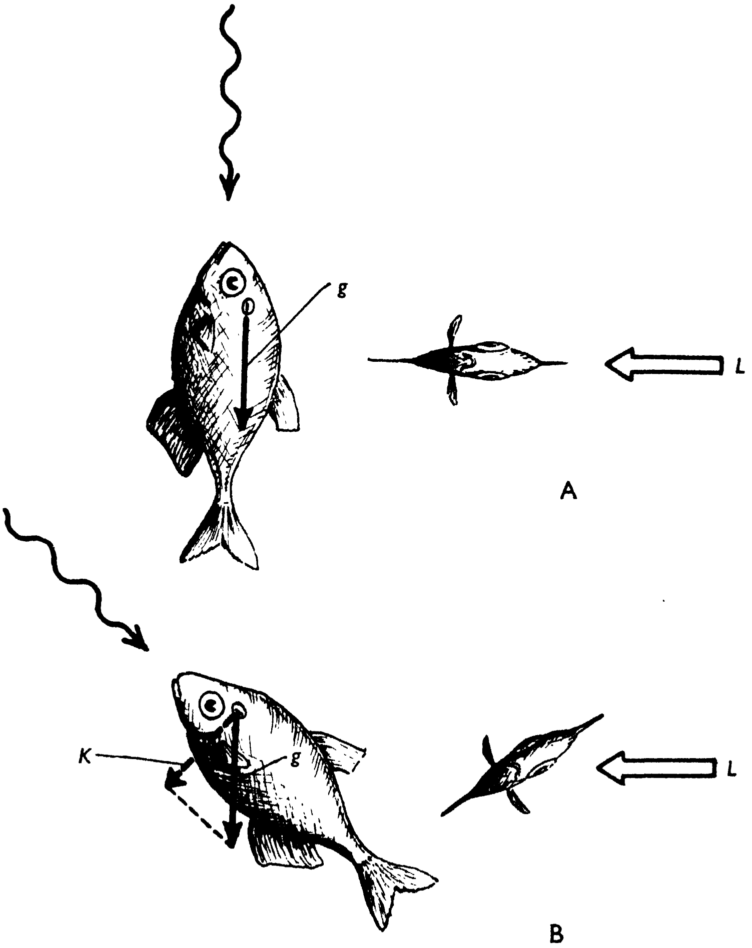

Abb. 7. Einstellung des Fisches bei horizontalem Lichteinfall (*L*) und senkrecht (A) oder geneigt (B) stehender Körperlängsachse. g = Statolithengewicht, K = Kraftkomponente senkrecht zur Längsachse des Fisches, ↯ = Richtung der Wasserströmung.

Diese überraschend einfache Beziehung legt die Vermutung nähe, daß zwischen Reiz und Reaktion ebenfals ein sehr einfaches Verhältnis besteht. Doch können wir es erst klären, wenn die Frage nach dem adäquaten Reiz beantwortet ist.

Im geschilderten Zentrifugierversuch ändern sich drei Größen: (1) die mechanische Kraft des Statolithen, (2) die Richtung, in der sie auf den Fisch wirkt, und (3) die Richtung des Lichteinfalls ins Fischauge, während nur die Helligkeit konstant gehalten wird. Wir haben noch eine Variable zu viel in unserer Rechnung. Doch ist es möglich, den Winkel, in dem das Licht in das Fischauge tritt, ebenfalls konstant zu halten und auf diese Weise die unbekannte Größe eines verschiedenen Lichteinfalls ins Auge zu eliminieren. Ich darf mir ersparen, Ihnen genauer zu berichten, wie wir den Versuch angestellt haben. Es genügt, wenn ich Ihnen den Kurvenverlauf zeige, der die Änderung von α, aufgetragen über Änderung der mechanischen Feldstärke F für fünf verschiedene Ausgangswerte von α wiedergibt, und zwar für den einfachen Fall, daß im Verlauf jeder dieser fünf Kurven die optische Gleichgewichtskomponente *genau konstant* gehalten wird (Abb. 8).

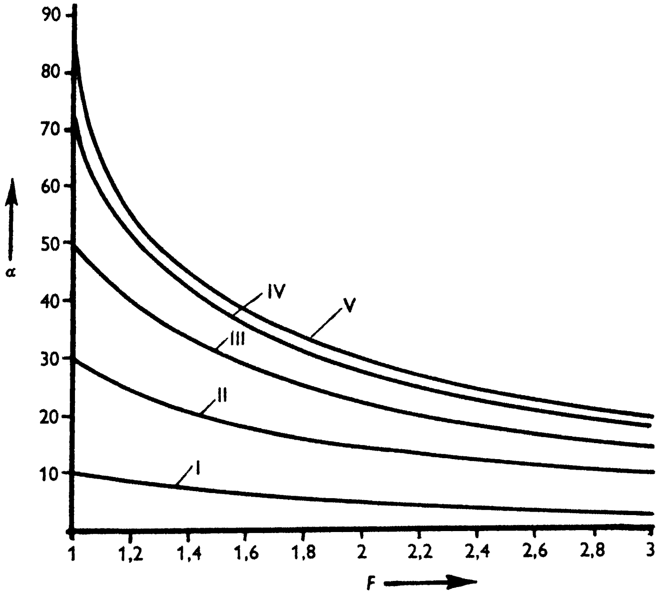

Abb. 8. Neigungswinkel α der Fische in Abhängigkeit von der mechanischen Feldstärke F (vergl. Abb. 5 und 6), jedoch bei Konstanthaltung des Lichteinfallswinkels β ins Fischauge für jede Kurve. Die Kurven I–V gelten für 5 verschieden starke Beleuchtungen (bzw. Lichtempfindlichkeiten).

Sie sehen, daß nun ein ganz anderes Bild entsteht. Je größer der Ausgangswert von α ist, desto wirksamer wird die Feldstärke F, wenn wir diese ansteigen lassen. Nun bedenken Sie bitte, daß wir ja stets reflexlose Normallagen vor uns haben, und daß ferner in diesem Fall die optische Reizsituation unverändert bleibt. Es ist daher nur eine Frage der Logik, daß der adäquate physikalische Reiz, auf den das Utriculusepithel anspricht, ebenfalls in jeder Kurve eine *konstante* Größe besitzen muß; denn sonst müßten ja Gleichgewichtsreflexe auftreten, die den Fisch in eine *andere* Lage bringen.

Diejenige physikalische Kraftkomponente, die in jeder dieser Kurven von Abb. 8 gleich bleibt, ist leicht zu finden: Es ist die Kraft in der Ebene senkrecht zur Dorso-ventral-Achse des Fisches (Abb. 9). In dieser Ebene aber liegen gerade die Utriculusstatolithen! Der *adäquate Reiz ist* folglich, wie schon Breuer (1891) im vorigen Jahrhundert angenommen hatte, die *seitliche Verschiebung* (*Scherung*) der Statolithen. Wenn wir die optische Situation konstant halten und das Statolithen'gewicht' z.B. erhöhen, dann stellt sich der Fisch ganz einfach immer so ein, daß der Scherungsanteil gleich bleibt, und das ganze Plus auf die Druckkomponente abgeschoben wird, auf die die Rezeptoren nicht ansprechen. Abb. 10 zeigt das an einem Beispiel. Ich füge noch ergänzend hinzu, daß die Rezeptoren auf Änderung des hydrostatischen Druckes ebenfalls nicht ansprechen, wie das von einer heute viel beliebten Theorie behauptet wird.

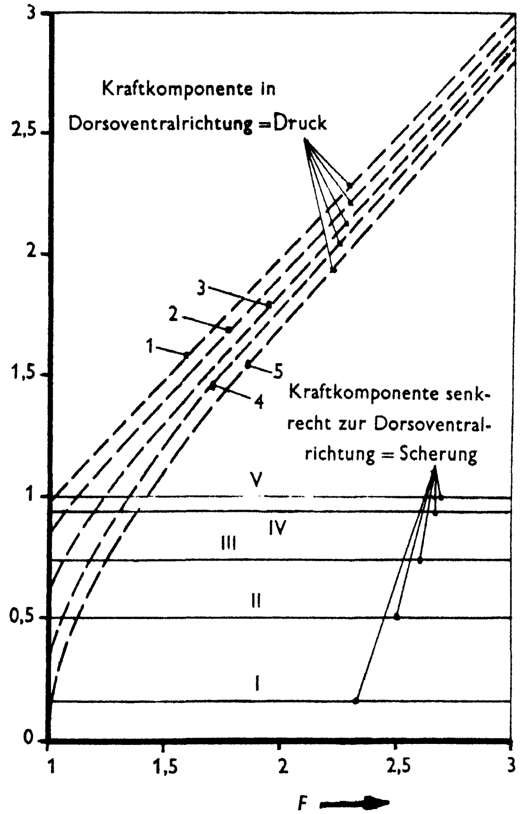

Abb. 9. Änderung der Scherungskraft (I–V) und der Druckkraft (1–5), welche am Statolithen angreift, wenn der Fisch sich im geänderten Schwerefeld F so einstellt, wie Abb. 9 es angibt. (K = Scherungs-, bzw. Druckkomponente.)

(2) *Die Zusammenarbeit der beiden statischen Apparate*

Damit ist Punkt 1 geklärt; wir kommen zu der Frage der *Zusammenarbeit beider statischen Apparate.* Dieses Problem ist bisher durch ein Phänomen besonderer Art verdunkelt. Schon Ewald hat im vorigen Jahrhundert (1892) aus seinen berühmten Versuchen an Tauben geschlossen, daß das Sinnesepithel der Bogengänge auch ungereizt ständig eine 'tonisierende' Erregung erzeugt. Den gleichen Schluß zog Magnus (1924) für das Statolithenepithel, und viele spätere Untersucher haben diese Annahme bestätigt, in letzter Zeit z.B. Ross (1936) sowie Löwenstein und Sand (s.O. Löwenstein 1948) durch Ableitung elektrischer Dauerentladungen des afferenten Nerven in normaler Ruhelage des Tieres.

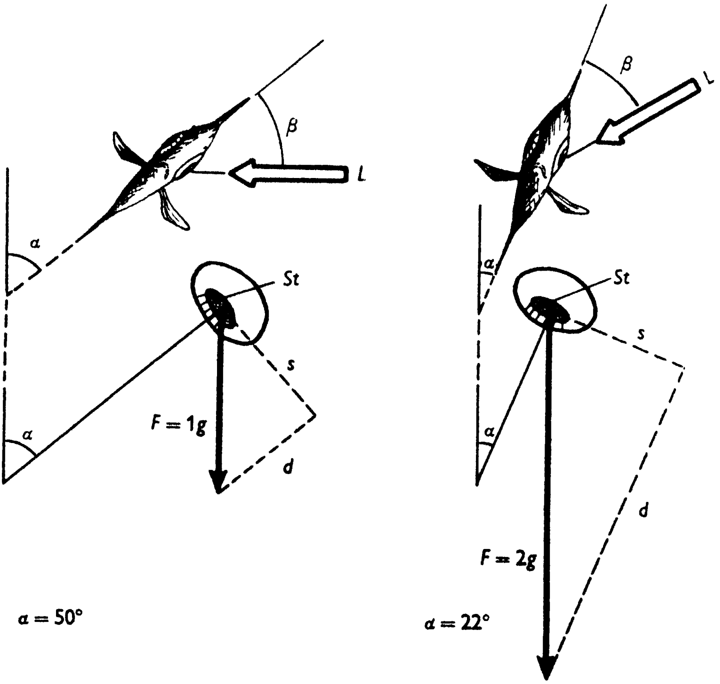

Abb. 10. Erläuterung der Fischeinstellung bei konstanter Helligkeit und konstantem Lichtwinkel β relativ zum Fischauge bei Verdoppelung der mechanischen Feldstärke F. Unter dem Fisch ist ein Statolith St skizziert; die an ihm angreifende mechanische Kraft F ist in eine Scherungskomponente s und eine Druckkomponente d zerglet. s bleibt konstant (vergl. auch Abb. 9).

Diese periphere Daueraautomatie ist schuld an einem Fehlschluß geworden, zu dessen Verbreitung auch ich früher beigetragen habe (1935): Wenn man wissen will, wie beide Utriculi zusammenarbeiten, so ist ein naheliegender Versuch die einseitige Utriculusausschaltung. Der Erfolg ist bei allen Wirbeltieren prinzipiell gleich. Es treten mit großer Intensität solche Augen- und Gliedreaktionen auf, *als ob* das Tier ständig nach der nicht operierten Seite hin um seine Längsachse geneigt würde. Es zeigt also lauter Reaktionen, die wir einer 'Drehtendenz' nach der Operationsseite hin zuschreiben können. Drehtendenz sei im Folgenden der zentrale Ungleichgewichtszustand genannt, der all diese tonischen und motorischen —artlich sehr verschiedenen—Asymmetrien verursacht.

Es liegt nun der Schluß nahe, daß dieses Phänomen durch den Fortfall des Reizes des einen Statolithen verursacht sei. Das würde aber bedeuten: Jeder Statolith bewirkt im Zentrum 'tropotaktisch' eine einseitige Drehtendenz, die durch die Gegenwirkung seines Partners in der normalen Gleichgewichtslage des Tieres kompensiert wird, während bei Neigungen die Reizwirkung eines Statolithen überwiegt. Dieser Schluß ist jedoch falsch! Wir haben nämlich jetzt gefunden, daß diese Drehtendenz tatsächlich überhaupt nichts mit dem Statolithenreiz zu tun hat, sondern allein eine Folge des einseitigen Ausfalls der eben erwähnten ständigen Automatie des *ungereizten* Utriculussinnesepithels ist. Durch diese Dauerautomatie hält das Utriculusepithel—ganz einfach formuliert—das Gleichgewichtszentrum auf der zugehörigen Seite in einem erhöhten Aktivitätszustand, der seinerseits die tonische Erregungsverteilung im motorischen Apparat im Sinne der genannten Asymmetrie verändert.

Es würde zu weit führen, die Versuche ausführlich mitzuteilen, die diesen Schluß sicherstellen. Ich will nur erwähnen, daß im Zentrifugierversuch die nach einseitiger Utriculusausschaltung entstehende Drehtendenz durch ein 'Schwerer'werden des übriggebliebenen Statolithen nicht etwa gesteigert, sondern gesetzmäßig vermindert wird, und daß ferner beim mit senkrecht stehender Längsachse schwimmenden Fisch, wo der Statolith keinen Einfluß auf die Einstellung um die Längsachse mehr besitzt (Abb. 7 A), die postoperative Drehtendenz doch quantitativ erhalten bleibt. Es genügt vielleicht, wenn ich zusammenfassend sage, daß der einseitig entstatete Fisch sich genau so verhält, wie die schon erwähnte Waage (Abb. 6), wenn man ihr durch Anfügen einer Rolle mit einem einseitigen Gewicht zusätzlich ein konstantes Drehmoment erteilt (Abb. 11). Bei Seitenlicht von der intakten Seite her (Abb. 11 A) steht der Fisch um einen bestimmten Winkelbetrag weniger, bei Seitenlicht von der operierten Seite (Abb. 12 B) um den gleichen Betrag stärker geneigt, als es bei Fehlen jener automatischen Dauererregung des intakten Utriculusepithels der Fall wäre.

Kurz nach der Operation ist diese Drehtendenz so stark, daß gewöhnlich weder die Gegenwirkung des einen Statolithen noch gerichteter Lichteinfall ein ständiges Rotieren des frei schwimmenden Fisches um seine Längsachse verhindern kann. Doch klingt dieser Effekt allmählich ab und verschwindet schließlich. Über diesen Kompensationsvorgang werde ich später noch sprechen.

Für den Augenblick interessiert uns nur die Tatsache, daß es möglich ist, die automatiebedingte postoperative Drehtendenz und die physiologische Wirkung des Statolithenreizes experimentell klar voneinander zu trennen. Es ergibt sich dabei, daß der eine Statolith (nach Abzug dieser Drehtendenz ebenso wie nach erfolgter Kompensation) bei Neigung des Fisches nach der einen wie nach der anderen Seite eine ganz *gleiche* wiederaufrichtende Wirkung entfaltet. Damit ist auch die zweite Frage beantwortet: Beide Statolithen arbeiten nicht tropotaktisch gegeneinander, sondern telotaktisch zusammen. In welcher quantitativen Weise, das werden wir gleich erfahren.

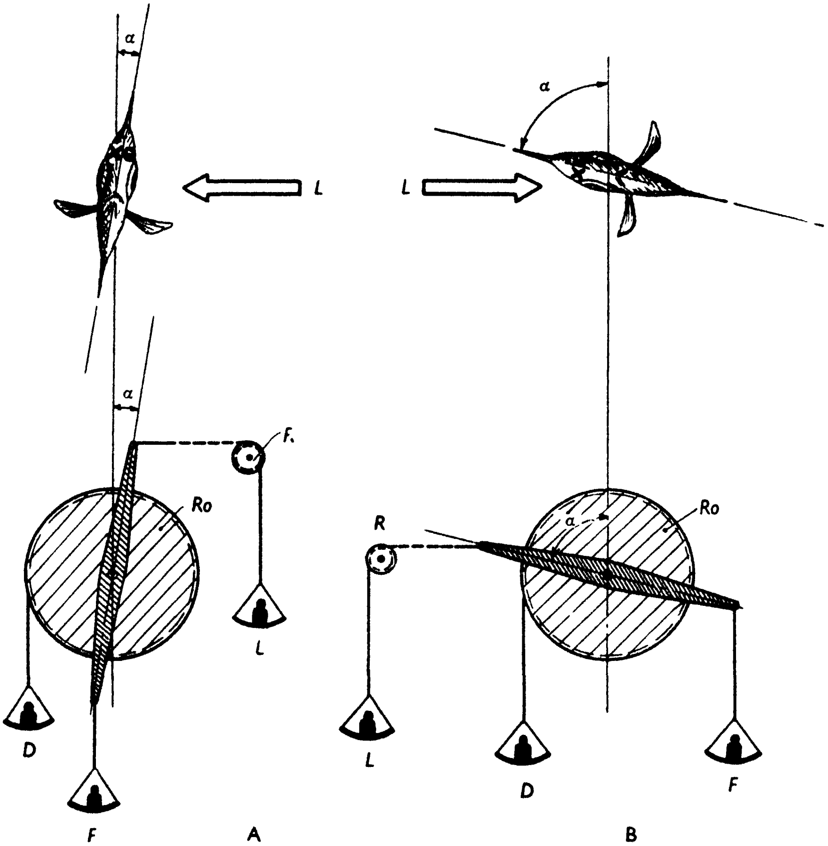

Abb. 11. Der einseitig entstatete Fisch stellt sich bei Licht von der intakten Seite (A), bzw. operierten Seite (B) so ein, wie die darunter gezeichnete Waage. Diese gleicht der Waage von Abb. 7, ist jedoch ergänzt durch eine am Waagebalken befestigte Rolle *Ro*, die durch ein Gewicht *D* ein konstantes Drehmoment erzeugt, das sich den übrigen Kräften überlagert.

(3) *Die quantitative Beziehung zwischen dem physikalischen Reiz und seiner physiologischen Wirkung*

Die dritte Frage nach der *quantitativen Beziehung zwischen dem adäquaten physikalischen Reiz*, der Scherung, und seiner *physiologischen Wirkung* im Gleichgewichtszentrum, ist nun schnell erledigt. Ich sagte schon, daß das Ergebnis der Zentrifugierversuche bei Seitenlicht auf eine sehr einfache Beziehung hindeutet: nämlich auf lineare Proportionalität. Nur eine sehr komplizierte Theorie könnte diesen Schluß jetzt noch umgehen. Die Entscheidung liefert das Verhalten nach einseitiger Utriculusausschaltung, wenn wir die automatiebedingte Drehtendenz eliminieren oder auch ihre zentrale Kompensation abwarten. Der Fisch mit nur einem Utriculus stellt sich nämlich bei horizontaler Beleuchtung wesentlich stärker zum Licht geneigt ein, als vor der Operation bei derselben Helligkeit. Der Neigungswinkel α nimmt *genau* den Wert an, den α vorher besaß, wenn das 'Gewicht' der beiden Statolithen gerade auf die Hälfte reduziert wurde. Anders gesagt: Das einseitig entstatete Tier nimmt, wenn man im Zentrifugierversuch das 'Gewicht' des einen übrig gebliebenen Statolithen verdoppelt, wieder denselben Neigungswinkel α ein, den es bei der betreffenden Helligkeit vor der Operation besaß (Abb. 12).

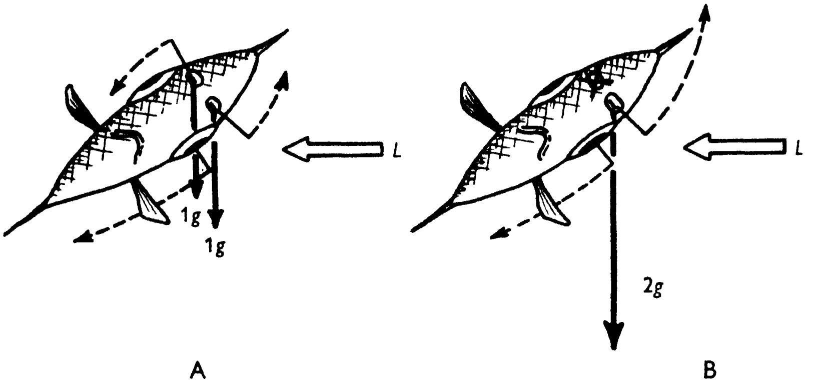

Abb. 12. Skizze zur Erläuterung der Einstellung des Fisches bei konstantem Seitenlicht vor (A) und nach (B) einseitiger Entstatung, wobei auf den einen Statolithen in B die doppelte mechanische Kraft wirkt. Die Gleichgewichtslage ist in beiden Fällen dieselbe; die jedem Sinnesorgan zugeordnete zentrale Drehtendenz ist als unterbrochener Pfeil eingezeichnet (vergl. als Gegenstück Abb. 11).

Wir erhalten also die gleiche Änderung der statisch bedingten Drehtendenz im Zentrum, wenn wir entweder den adäquaten physikalischen Reiz halbieren oder wenn wir durch chirurgischen Eingriff die Zahl der insgesamt das Zentrum mit Impulsen versorgenden Sinneszellen und Nervenfasern halbieren. Daraus ergeben sich unmittelbar zwei Folgerungen: (1) zwischen dem Scherungsreiz und seiner physiologischen

Wirkung im Zentrum besteht direkte *lineare Proportionalität*; und (2) die Wirkung eines Utriculusstatolithen *addiert* sich einfach zur Wirkung des anderen Statolithen.

(4) *Diskussion und Zusammenfassung der Resultate*

Diese Ergebnisse, die ich Ihnen hier nur kurz darlegen konnte, sind nach einer mathematischen Behandlung des Gegenstandes durch meinen Mitarbeiter, den Physiker H. Kaiser, nicht bloße Möglichkeiten, sondern sichere Schlüsse. Wenn ich nun noch hinzufüge, daß weder der periphere statische Apparat noch das Gleichgewichtszentrum irgend eine Form der Reizadaptation in unseren Versuchen erkennen ließen, so werden Sie mir beipflichten, daß wir hier den einfachsten Sinnesapparat vor uns haben, der sich wohl überhaupt denken läßt. Diese Einfachheit hängt gewiß damit zusammen, daß dieses Organ auf die Registrierung der Richtung einer ständig vorhandenen konstanten Kraft, nämlich der Erdschwere, angepaßt ist—oder ich sollte lieber sagen, daß die übrigen Sinnesorgane darum so komplizierte Reizübertragungsapparate sind, weil sie sich an so wechselnde Reizquantitäten anpassen müssen.

Wir haben nun erst alle Daten zur Hand, mit deren Hilfe wir zentrale Umstimmungen, die einen Einfluß auf die Gleichgewichtslage haben, quantifizieren können. Wir wissen Folgendes:

(1) Der adäquate physikalische Reiz, die Scherung, steigt in Sinusform an, wenn der Neigungswinkel α des Fisches zunimmt und erreicht bei Seitenlage, wenn $\alpha = 90^\circ$ beträgt das Maximum von 1 g (Erdschwere).

(2) Die physiologische Wirkung dieses Reizes, die wir *zentrale Drehtendenz* genannt haben, welche den Fisch in die aufrechte Lage zurückzubringen sucht, ändert sich proportional dem Sinus des Winkels α.

(3) Bei horizontalem Seitenlicht entsteht eine gegensinnige Drehtendenz optischer Herkunft, die den Fisch in Seitenlage ($\alpha = 90^\circ$) zu bringen sucht. Diese optisch induzierte Drehtendenz hat ihr Maximum bei $\alpha = 0$ und $\beta = 90^\circ$, wenn das Licht seitlich in Richtung der Augachse eintrifft, und sie wird $= 0$ wenn das Licht genau dorsal auftrifft, also $\beta = 0^\circ$ beträgt (vgl. Abb. 4). Es ergibt sich nun aus unseren Versuchen, wie am Waagemodell leicht einzusehen ist, daß auch die optisch induzierte zentrale Drehtendenz sich proportional dem Sinus des Winkels β ändert. Diese drei Tatsachen brauchen wir für das, was ich nun berichten möchte.

IV. DER BEGRIFF DER ZENTRALEN UMSTIMMUNG

Wenn der Fisch, als 'Gleichgewichtsmaschine' betrachtet, lediglich eine einfache Waage nachahmte, dann dürfte seine Einstellung nur von äußeren Faktoren, also von der Größe der Scherung im Statolithen und von Helligkeit und Richtung des Lichteinfalls abhängen. Doch so einfach ist, Gottseidank, sein Verhalten doch nicht. Tatsächlich unterliegt er Stimmungen, d.h. hier: er gleicht einer Waage, bei der unter bestimmten angebbaren Bedingungen das Längenverhältnis der beiden Waagebalken sich in bestimmter Weise ändert; und das ist ein Vorgang, der sich beim Fisch mehr oder weniger langsam im zentralen Nervensystem selbst abspielt.

Ein Beispiel: Ein Scalare steht bei horizontalem Seitenlicht im strömenden Wasser mit einer Neigung von $\alpha = 50°$; bei der gegebenen peripheren und zentralen Situation besteht ein Gleichgewicht zwischen optischer und statischer Drehtendenz, es treten keine Lagekorrekturen auf. Das Verhältnis von $\sin \beta : \sin \alpha$ beträgt in diesem Falle 0,85. Nun wird dem Fisch im strömenden Wasser etwas Preßsaft von Würmern (*Enchytraea*) zugeleitet. Sobald dieser Saft seine Nase erreicht, neigt der Fisch sich von 50° auf 65°, und zugleich bemerkt man, besonders am Spiel der Augen, eine gewisse motorische Unruhe. Das Verhältnis von $\sin \beta$: $\sin \alpha$ ist jetzt von 0,85 auf 0,47 abgesunken, obschon weder die optische noch die statische *äußere* Reizsituation sich geändert hat. Es muß also *im Zentrum* etwas anders geworden sein; nämlich die *Bewertung*, welche der optischen und der statischen Erregung zuteil wird. Und zwar ist die relative Wirkung der optischen Erregungszufuhr ganz erheblich angestiegen. Der Fisch ist, bildlich gesprochen, innerlich plötzlich fast 'ganz Auge'. Wäre dies nicht der Fall, so müßten ja Lagereflexe auftreten, die den Fisch von seiner 65°-Einstellung wieder zur 50°-Ausgangslage zurückbewegen. Diese Änderung der zentralen Bewertung peripherer Reize ist das, was ich eine *zentrale Umstimmung* nennen will.

Wir können das Ausmaß dieser Umstimmung leicht quantifizieren, indem wir angeben, mit welchem Faktor man den veränderten Quotienten $\sin \beta : \sin \alpha$ multiplizieren muß, damit er wieder seinen alten Ausgangswert erhält. In unserem Beispiel beträgt dieser *Umstimmungsfaktor* U etwa 1,8. Es ist also nicht der jeweilige Quotient $\sin \beta : \sin \alpha$ selbst für uns von irgendeinem Interesse, denn dieser hängt von peripheren Bedingungen ab, wie z.B. von der jeweiligen Helligkeit und von der Empfindlichkeit und dem Adaptationszustand des Auges. Sondern uns interessiert allein die *Änderung* des Quotienten, also der Umstimmungsfaktor U. Steigt U über 1 an, so bedeutet das, verglichen mit dem Ausgangszustand, eine relative Höherbewertung der optischen Erregungszufuhr im Zentrum, sinkt U unter 1 ab, so bedeutet es eine relative Geringerbewertung der optischen Erregungszufuhr. Da wir wissen, daß die einander kompensierenden Drehtendenzen dem $\sin \alpha$, bzw. dem $\sin \beta$ direkt proportional sind, so gibt uns der eingeführte Umstimmungsfaktor U ein sehr unmittelbares Maß für die zentrale Umstimmung.

Die Einführung dieses Umstimmungsfaktors an Stelle der bloßen Angabe des veränderten Neigungswinkels α macht die Situation vielleicht unanschaulicher, sie bringt aber dafür den großen Vorteil, daß in der quantitativen Erfassung des Phänomens die jeweilig verschiedene Ausgangslage des Fisches nicht mehr vorkommt, die ja durch periphere und konstitutionelle Faktoren mitbestimmt wird. Abb. 13 zeigt Ihnen beispielsweise die Winkeländerungen, die bei einem Umstimmungsfaktor von $U=0{,}8$; $U=1{,}2$ und $U=2$ auftreten, in Abhängigkeit von der jeweiligen Ausgangsschräglage. Sie bemerken, daß diese Winkelausschläge keineswegs unabhängig von der Ausgangslage sind, sondern nahe bei $\alpha=0^\circ$ und bei $\alpha=90^\circ$ ein Minimum, in der Gegend von $\alpha=45^\circ$ ein Maximum haben. Wenn der Fisch auf 45° geneigt steht, bewirkt also eine bestimmte zentrale Umstimmung einen großen äußerlich sichtbaren Effekt.

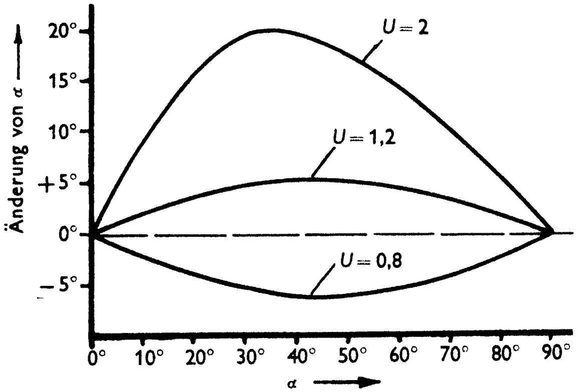

Abb. 13. Änderung des Neigungswinkels, aufgetragen über der jeweiligen Ausgangsschräglage α, für drei verschiedene Umstimmungsfaktoren U. Erläuterung im Text.

V. BEISPIELE VON ZENTRALER UMSTIMMUNG

(1) *Verändertes Bewertungsverhältnis optischer und statischer Gleichgewichtserregungen*

Lassen Sie uns nun endlich eine Anzahl verschiedener zentraler Umstimmungsvorgänge an Beispielen kennenlernen. Ich halte mich deshalb an einzelne Beispiele, weil unsere Versuche noch im Gange sind und weil hier, wo es sich um höhere zentrale Vorgänge handelt, nicht nur artliche, sondern oft erhebliche individuelle Unterschiede vorkommen—im Gegensatz zum bisher besprochenen Gleichgewichtsapparat, der bei allen untersuchten Fischarten übereinstimmend arbeitet.

Wenn ein Fisch näch längerem Dunkelaufenthalt wieder belichtet wird, dann bemerkt man an verschiedenen Anzeichen, daß er allmählich erwacht:

Er bekommt langsam eine andere Färbung, eine andere Atemfrequenz, die allgemeine motorische Aktivität und Irritierbarkeit nimmt zu, auch die Freßlust erwacht langsam, wie Sie noch genauer sehen werden. Diese Erscheinungen deuten auf eine allgemeine zentrale Umstimmung. Beleuchten wir den Fisch von der Seite, so manifestiert diese Umstimmung sich auch in einer allmählichen Zunahme der optischen Gleichgewichtskomponente, die bei genügend langem Dunkelaufenthalt (während des Schlafs) bis auf Null abgesunken war.

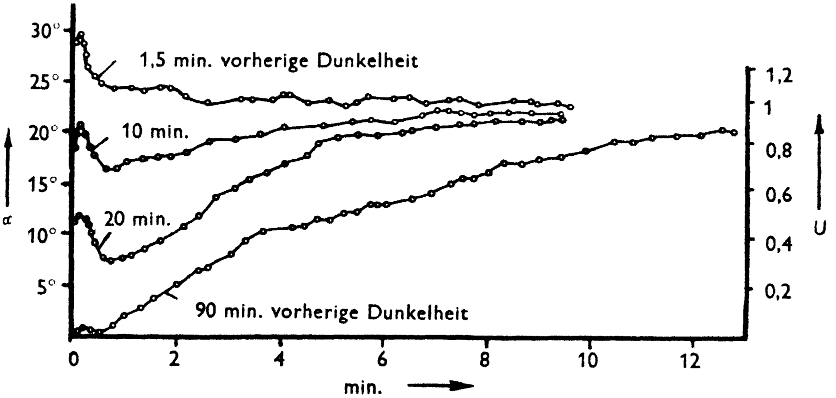

Abb. 14. Gleichgewichtseinstellung eines Tetra bei Seiteinlicht, aufgetragen über der Zeit in Minuten für vier vorhergegangene Dunkelzeiten von verschiedener Dauer. (Links der Neigungswinkel α, rechts der Umstimmungsfaktor U, wobei $U = 1$ der Ausgangslage vor Beginn der Verdunklung entspricht.)

Das Kurvenbild 14 zeigt dieses Verhalten an einem Tetra. Der Anstieg des Neigungswinkels α bei Seitenlicht geht nach einer Dunkelheit von mehr als einer Stunde ganz allmählich vor sich. Je kürzer nun die voraufgegangene Dunkelzeit ist, desto höher ist der Ausgangswert von α nach erfolgter Belichtung. Gleichzeitig macht sich ein sehr charakteristischer Anfangsgipfel in der Kurve bemerkbar. Dieser Gipfel geht auf das Konto der Dunkeladaptation des Auges, sein Wiederabstieg zeigt den Prozeß zunehmender Helladaptation an, also einen schnelleren peripheren Vorgang von *entgegengesetzter* Verlaufsrichtung, der sich dem zentralen Umstimmungsprozeß überlagert. Ich kann die Gründe für diese Deutung nicht näher ausführen, uns interessiert hier nur der zentrale Vorgang.

Wenn man die Winkelgeschwindigkeit, mit welcher der Fisch sich bei Seitenlicht um seine Längsachse mit dem Rücken zum Licht dreht, in Abhängigkeit von der vorherigen Dunkelzeit genau bestimmt, dann wird einem der Unterschied zwischen einer einfachen reflektorischen Gleichgewichtseinstellung und einem zentralen Umstimmungsprozeß eklatant deutlich. Bei Pterophyllum beträgt diese Drehgeschwindigkeit um die

Längsachse nach acht Sekunden Dunkelheit 0,05 sec. pro Winkelgrad, nach fünf Stunden Dunkelheit im Mittel 70 sec. pro Winkelgrad! Um das 1400-fache langsamer geht also die zentrale Umstimmung vonstatten, verglichen mit der einfachen Gleichgewichtseinstellung des bereits optisch gestimmten Tieres.

Wenn wir kurz nach der biologischen Bedeutung dieser Erscheinung fragen wollen, dann muß zuvor von der Aufgabe die Rede sein, die überhaupt dem optischen Gleichgewichtsanteil zukommt. Dieser ist für den Fisch von zweifachem Nutzen: (1) in turbulentem oder wellenbewegtem Wasser korrigiert das von oben einfallende Licht die ständigen Fehlanzeigen, die durch passive Beschleunigung des Fisches im statischen Apparat notwendig entstehen müssen. (2) Über unebenem, dunklem Untergrunde stellt der optische Gleichgewichtsfaktor den Fisch mit der Bauchseite zum festen Substrat; er wird der Kontur des Grundes gleichsam angeschmiegt und hat dadurch (im Gegensatz zum nur statisch orientierten Tier) freie Bewegung nach beiden Seiten. Unter natürlichen Bedingungen wird also die Wirkung des statischen Organs durch den Lichteinfall nur modifiziert. Erst wenn wir die anfangs geschilderte unnatürliche Situation schaffen, daß das Licht von unten her einfällt (Abb. 1), dann konkurrieren optische und statische Komponente miteinander, und es gibt bei gleicher zentraler Bewertung beider Komponenten einen Indifferenzzustand, wo jegliche Gleichgewichtsreaktionen ausgelöscht sind.

Da die optische Komponente nur nützlich sein kann, solange Licht vorhanden ist, so können wir ihr Schwinden in der Dunkelheit—also das Absinken des Umstimmungsfaktors *U* bis auf Null und sein allmähliches Wiederansteigen im Licht—als eine sinnvolle Anpassung an den Wechsel von Tag und Nacht betrachten.

Für die Richtigkeit dieser Auffassung sprechen nun zwei weitere Umstimmungsmöglichkeiten, die ich nur kurz erwähnen will: (1) Schaukelnde Bewegung des Wassers verstärkt manchmal (Scalare) sehr erheblich den optischen Gleichgewichtsanteil, der Umstimmungsfaktor kann bis auf das Doppelte ansteigen und geht, wenn das Schaukeln aufhört, langsam wieder zum Ausgangswert zurück. Das heißt also: Bei Wellenbewegung 'verläßt' der Fisch sich sozusagen mehr auf den zuverlässigeren optischen Gleichgewichtsanteil. (2) Erhöhung des hydrostatischen Druckes verringert bei vielen Fischarten mehr oder weniger die Wirkung der optischen Komponente; der Umstimmungsfaktor kann bei Druckanstieg von 10 cm. auf 100 cm. Wassersäule weniger als 0,7 betragen. Auch dieser Effekt schwindet allmählich bei Rückkehr zum Ausgangsdruck. Das bedeutet aber für den Fisch: Beim Herunterschwimmen in die sowohl dunklere als auch weniger bewegte Wassertiefe erhält der hier zuverlässigere statische Gleichgewichtsanteil eine höhere Bewertung im Zentrum. (Die Rezeptoren für diese Umstimmung liegen nicht im Labyrinth, sondern vermutlich in der Schwimmblasenwand).

Eine vierte von uns genauer untersuchte Umstimmung darf größeres allgemeines Interesse beanspruchen. Der *hungrige* Scalare, der *Beute fixiert* oder riecht, *neigt sich stärker* zum Licht, z.B. von 50° auf 65° bis 70°. Nach Erschnappen der Beute, oder sobald sie aus seinem Blickfeld verschwindet, geht er in etwa dreißig Sekunden wieder in die vorherige Ausgangslage zurück. Der Anstieg des Neigungswinkels α geht sehr schnell in 1–3 Sekunden vonstatten; der Abstieg ist langsam genug, um genaue Messungen zu gestatten. Abb. 15 zeigt den typischen S-förmigen Verlauf dieser Abklingkurve. Sie ist besonders dadurch charakterisiert, daß der Umstimmungsfaktor bei seiner Rückkehr den Ausgangszustand vorübergehend etwas *unter*schreitet, als wenn er gedämpft auspendelte. Auf den Anstieg folgt ein kompensatorisches Absinken, ein 'rebound'-Phänomen, das man vielleicht als 'zentrales negatives Erregungsnachbild' auffassen könnte.

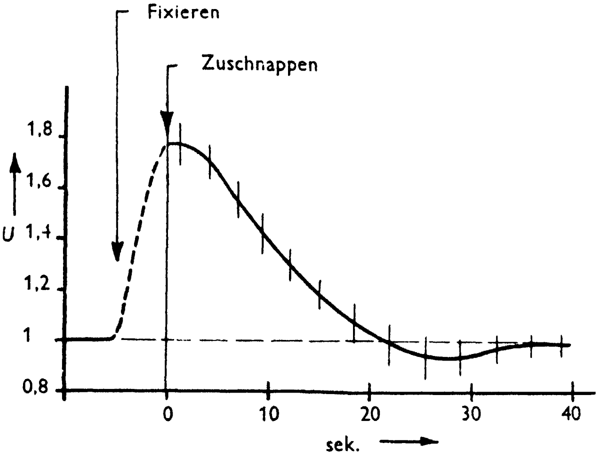

Abb. 15. Scalare; zentrale Umstimmung beim Fixieren und Schnappen von Beute, aufgetragen über der Zeit in Sekunden. Mittelkurve von zehn aufeinanderfolgenden Messungen (die senkrechten Striche bezeichnen die mittlere Streuung).

Die Höhe, bis zu welcher der Umstimmungsfaktor beim Erblicken von Beute ansteigt, hängt von folgenden Faktoren ab:

(1) Vom *Hunger*. Beim mehrere Tage nicht gefütterten Fisch beträgt der Faktor *U* oft mehr als 2, um mit fortlaufender Fütterung bald wieder auf 1 abzusinken. Die letzten noch geschnappten Würmer werden ohne jede Lageänderung fixiert und genommen.

(2) Die Größe von *U* hängt ferner von der *Beuteart* ab. Die kleinen

Cyclops bewirkten bei unseren Scalaren viel höhere, die größeren Daphnien geringere Ausschläge als die Würmer (*Enchytraea*). (Cyclops wird auch dann noch gefressen, wenn der Fisch Enchytraean und Daphnien nicht mehr beachtet.)

(3) Bei gleicher Futterart ist auch die *Größe* des Objekts von Einfluß: Größerer Wurm bewirkt stärkere Reaktion.

(4) Die *Temperatur* macht sich in dem Sinne bemerkbar, daß beim allmählichen Anstieg von 18° auf 30° sowohl die Freßlust als auch die Höhe der jeweiligen Gleichgewichtsausschläge immer mehr zunimmt.

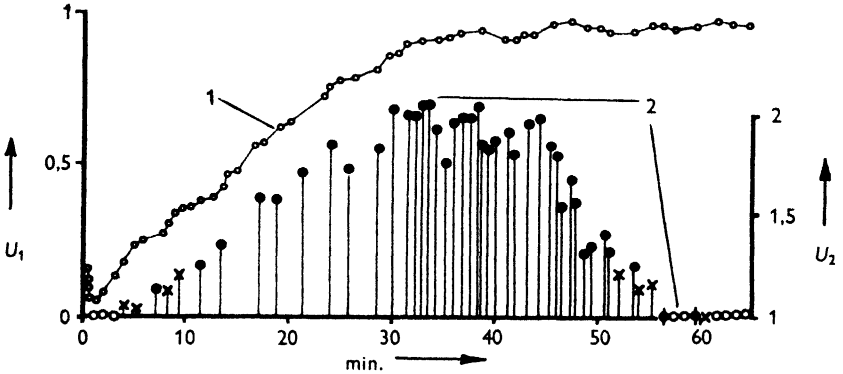

Abb. 16. Scalare; Kurve 1: Optisches 'Erwachen' nach acht Stunden Dunkelheit, aufgetragen über der Zeit in Minuten; der Umstimmungsfaktor U_1 ist links aufgetragen, als Einheit die Einstellung vor der Verdunklung gewählt. Dem Fisch wurden in Abständen Würmer geboten, die je nach der ausgelösten Reaktion durch 4 verschiedene Zeichen markiert sind. Für die durch jeden Wurm verursachte vorübergehende Umstimmung U_2 gilt als Einheit die Lageeinstellung im Moment des Fixierens. Es bedeuten in der unteren Kurve (2) ○ : vorbeischwimmenden Wurm nicht beachtet; × : Wurm fixiert, aber nicht geschnappt; ● : Wurm fixiert und geschnappt; ⧫ : Wurm geschnappt und wieder ausgespuckt.

(5) Schließlich ist auch der Grad des *optischen Erwachtseins* von Einfluß. Abb. 16 zeigt in der fortlaufenden Kurve 1 das schon bekannte langsame Ansteigen des optischen Gleichgewichtsanteils bei Seitenlicht nach acht Stunden Dunkelheit. Der Scalare hatte zwei Tage gehungert. Die senkrechten Stäbe geben die Größe des Umstimmungsfaktors für die nacheinander gebotenen Würmer wieder, die mit der Wasserströmung auf den Fisch zugeschwommen kommen. Die ersten Würmer, einige Minuten nach Einschalten des Seitenlichts, bleiben völlig unbeachtet. Die folgenden werden teils nur fixiert, teils auch geschnappt, aber mit nur geringer zentraler Umstimmung; erst nach dreißig Minuten gibt es maximale Reaktionen, die bei fortlaufender Fütterung aber bald wieder auf Null absinken. Auch die letzten Würmer werden wieder teils nur fixiert, teils lösen sie, obschon genommen, geringe oder überhaupt keine Gleichgewichtsreaktionen aus, und manche werden wieder ausgespuckt. Schließlich

wird kein Wurm mehr beachtet, als wäre der Fisch 'blind' für ein Objekt, das ihn kurz zuvor noch stark erregte.

Wir haben durch eine Reihe von Experimenten die Frage geprüft, ob an dieser Reaktion irgendwelche peripheren Faktoren, etwa Bewegungen des Auges oder retino-motorische Erscheinungen, die den Adaptationszustand im Auge ändern, beteiligt sind. Doch sind wir zu dem Schluß gekommen, daß es sich um ein rein zentrales Phänomen handelt. Es ist wohl nicht zweifelhaft, daß wir hier eine Auswirkung desjenigen Vorgangs messen, dessen psychisches Korrelat man bei uns Menschen den 'Appetit' nennt. Ich möchte daher diesen zentralen Umstimmungsprozeß als die *Appetiterregung* bezeichnen.

Sie ersehen aus dem Mitgeteilten, daß die Appetiterregung beim Fisch wie bei uns (außer von der vorausgegangenen Fastenzeit) von der Qualität und Größe des angebotenen Bissens abhängt; daß sie, ebenso wie bei vielen Menschen, nach dem Schlafen erst langsam wiederkehrt (auch wenn sie abends zuvor beliebig groß war). Ähnlich wie wir nimmt auch der gesättigte Fisch noch ohne Appetit gleichsam 'mechanisch' einige Bissen, die sich ihm bequem anbieten. Ob auch bei uns das erwähnte 'negative Erregungsnachbild' vorkommt, scheint mir einigermaßen zweifelhaft.

Es ist nun bemerkenswert, daß beim Fisch nach längerer Fastenzeit auch beuteähnliche Dinge, wie z.B. der eigene Kot, fixiert, gelegentlich auch geschnappt und wieder ausgespuckt werden, und dabei jedesmal eine gewisse, wenn auch deutlich kleinere 'Appetiterregung' auslösen, als z.B. die Würmer. Das ist ein gutes Beispiel für eine durch aufgestautes Entbehren verursachte 'Erweiterung des Schemas' im Sinne von Konrad Lorenz—wobei die Frage offen bleibt, ob dieses Schema hier angeboren oder erworben ist. Durch Atrappenversuche ließe sich hier wohl gut ein 'Beliebtheitsgefälle' quantitativ fassen.

Schließlich scheint mir noch die Tatsache erwähnenswert, daß der hungrige Fisch schon Beute in großer Ferne prompt bemerkt und fixiert, der halbsatte nur noch solche fixiert, die nahe vorbeikommt, und der gesättigte auch durch einen dicht vorbeischwimmenden Wurm zu keinerlei Augenbewegungen mehr veranlaßt wird. Wir müssen daraus wohl schließen, daß der Hunger einen bestimmten zentralen Dauerzustand erzeugt, den man, subjektiv formuliert, 'latente Aufmerksamkeit auf Eßbares' nennen könnte. Diese besondere zentrale Einstellung ist erst die Basis, auf der Fixieren und eventuelles Zuschnappen erfolgt. Man könnte auch so sagen: Je satter ein Fisch ist, desto weniger 'bemerkt' er eßbare Dinge seiner Umgebung. Eine solche *spezifische* latente Aufmerksamkeit auf bestimmte Dinge kennen wir auch von uns Menschen. Wie verschieden sind doch die Eindrücke, die wir empfangen, wenn wir ohne vorgenommenes Ziel in verschiedener 'Stimmung' die gleiche Landschaft durchwandern!

Ich habe Ihnen wohl genug Beispiele von solchen Umstimmungen gegeben, die sich in einem veränderten Bewertungsverhältnis der optischen und der statischen Gleichgewichtserregung äußern. Das ist nur *ein* Typus von derartigen Vorgängen. Ich möchte Ihnen nun zeigen, daß man auch solche Umstimmungen sichtbar machen kann, die—ohne daß optische Faktoren beteiligt sind—das zentrale Rechts-links-Gleichgewicht beeinflussen, und schließlich solche, wo das Zentrum als Ganzes in einen veränderten Aktivitätszustand versetzt wird.

(2) *Umstimmungen, die das zentrale Rechts-links-Gleichgewicht beeinflussen*

Zum Verständnis des Folgenden erinnere ich noch einmal an die Funktionsweise des Statolithenapparates. Das Sinnesepithel des Utriculus verursacht durch seine Daueraktivität jederseits eine einseitige Drehtendenz, der sich der Scherungsreiz des Statolithen additiv überlagert. Einseitige Utriculusausschaltung oder Zerstörung des ganzen Labyrinths erzeugt daher die bekannten Asymmetrien, die nicht nur bei Fischen, sondern sogar beim laufenden Kaninchen (Magnus) zu Rotationen um die Längsachse führen. Wir wollen nun das langsame Verschwinden dieser stürmischen Erscheinung, das bei Fischen einige Wochen, bei Vögeln, Säugern und beim Menschen Monate dauert, etwas genauer in Augenschein nehmen. Meine Mitarbeiterin Fräulein Schoen hat die Frage näher untersucht.

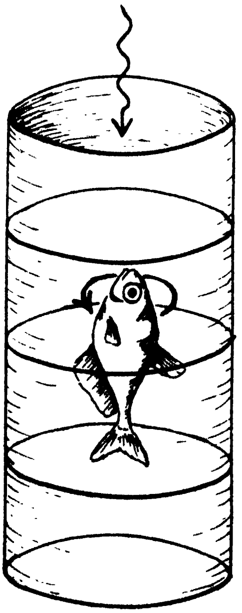

Abb. 17. Allseitig beleuchteter, von oben her durchströmter (↓) Zylinder, in dem ein einseitig entstateter Fisch in senkrechter Achsenstellung gleichmäßig rotierend schwimmt. Erläuterung im Text.

Ein einfaches Verfahren, die Größe der postoperativen dauernden Rotationstendenz in Reindarstellung sichtbar zu machen, besteht darin, daß der Fisch in einem senkrecht stehenden allseitig gleichhellen Zylinder nach oben oder nach unten schwimmt, wobei einige schwarze Kreise auf dem Zylinder ihm ein optisches 'Festhalten' gegenüber der Wasserströmung ermöglichen. (Abb. 17). Unter diesen Bedingungen rotiert z.B. der Tetra kurz nach der einseitigen Utriculusausschaltung mit einer Frequenz zwischen ein und zwei Umdrehungen in der Sekunde. Diese Rotationsfrequenz nimmt im Laufe der Wochen immer mehr ab. Aber selbst nach über einem

Monat dreht sich der Fisch immer noch ganz langsam, mit etwa ein Umdrehung pro Minute, um seine Längsachse. Dieses Verfahren ist demonstrativ und empfindlich, denn es läßt noch geringste Spuren eines zentralen Ungleichgewichts erkennen. Für eine Umrechnung in physiologische Erregungs- oder Umstimmungsgrößen ist es nicht geeignet.

Zu quantitativen Angaben kommen wir leicht bei Zuhilfenahme der statischen und optischen Gleichgewichtskomponente. Ich erwähnte bereits, daß der einseitig entstatete Fisch, der in horizontaler Strömung schwimmt, und seitlich beleuchtet wird, sich wie die schon demonstrierte Waage mit einem zusätzlichen konstanten Drehmoment verhält (Abb. 17). Dieses 'Drehmoment' und seine allmähliche Abnahme wollen wir messen und physiologisch verstehen, denn auch hier liegt ja ein Umstimmungsprozeß besonderer Art vor. Sie können sich am Waagemodell leicht davon überzeugen, daß es möglich ist, die Größe dieses 'Drehmoments' dadurch anzugeben, daß wir es durch eine bestimmte Scherungswirkung des erhalten gebliebenen Statolithen kompensieren. Wir können die Größe der postoperativen Drehtendenz quantifizieren, wenn wir als Einheit die durch eine Scherungsgröße von 1 *g* gerade kompensierte Drehtendenz wählen.

Die Kurve 18 gibt nun die Abnahme der postoperativen Drehtendenz wieder. Sie sehen, daß etwa nach einem halben Tage die zentrale Drehtendenz bis auf den Wert von 1 absinkt. Bis zu diesem Zeitpunkt rotiert der freischwimmende Fisch (bei allseitigem Licht), da die Gegenwirkung des einen Statolithen in keiner Stellung gegen die Rotationstendenz aufkommt. In diesem ersten Zeitabschnitt sind die Bewegungen meist recht turbulent, so daß der Kurvenverlauf nicht genauer festgelegt werden kann. Nach Passieren des Wertes 1 bemerken Sie einen zunächst rapiden Abfall der Kurve, die erst allmählich flacher wird und nach vierzig Tagen die Null-Linie noch nicht ganz erreicht hat.

Es entsteht die Frage, welcher Faktor diesen Kurvenverlauf bestimmt, ob es sich um eine rein zentrale Kompensation handelt, oder ob periphere Reize beteiligt sind? Wenn die Tiere gleich nach der Operation in eine Dauer-Zentrifuge gebracht werden, so daß das 'Gewicht' des Statolithen ständig auf das Doppelte erhöht bleibt, dann erfolgt diese Kompensation rund dreimal so schnell als bei den normal gehaltenen Kontrolltieren. Das spricht für eine starke Mitbeteiligung des statischen Apparates an diesem Kompensationsvorgang. Daß diese Korrektur in erster Linie vom erhalten gebliebenen Utriculus-Statolithen ausgeht, ist sehr wahrscheinlich. (Eine gewisse Mitbeteiligung der Lagena-Statolithen kommt ebenfalls in Frage. Aus Untersuchungen von Fräulein Schoen können wir nämlich schließen, daß auch die Lagena-Statolithen neben ihrer Hörfunktion auf

Scherung ansprechen. Sie bewirken zwar keine Lageorientierung, haben aber wohl einen gewissen 'tonisierenden' Effekt auf das Gleichgewichtszentrum. Doch diese Versuche sind noch im Gange.)

Es ist nun wichtig, daß nach erfolgter Kompensation, wenn auch noch der andere Utriculus entfernt wird, eine neue Drehtendenz auftritt, so als wäre der Utriculus auf der Gegenseite de facto noch vorhanden. Diese Drehtendenz, die wir mit Hilfe des gerichteten Lichteinfalls ebenfalls quantifizieren können, ist jetzt natürlich von der Raumlage des Fisches vollkommen unabhängig. Sie ist überraschender Weise von etwa derselben Größe, wie die Drehtendenz nach der ersten Operation und geht auch in einer ähnlichen Kurvenform zurück, wenn man die Fische in diffusem Oberlicht hält. Daraus folgt, daß die Kompensation auch ohne die Orientierungshilfe eines Utriculus-Statolithen vonstatten gehen kann.

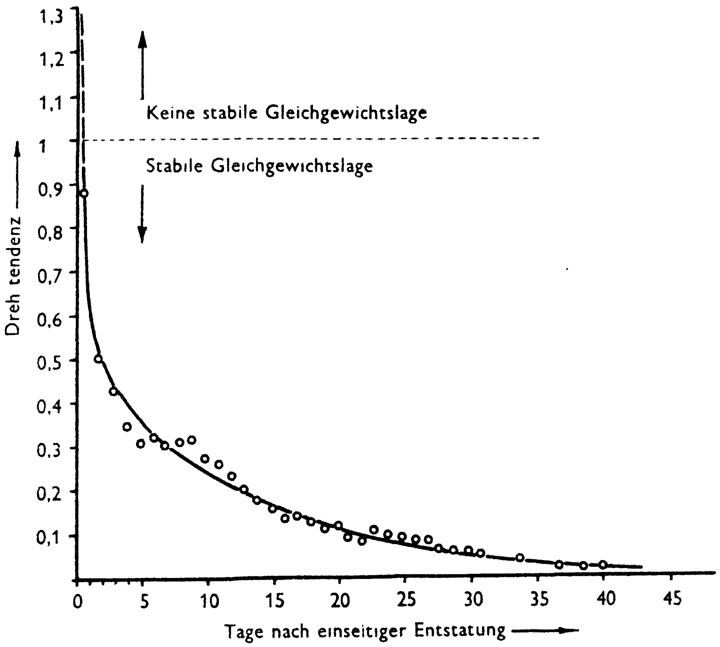

Abb. 18. Abnahme der Drehtendenz nach einseitiger Entstatung. Mittelkurve von zehn Fischen (vier Arten). Als Einheit ist die Drehtendenz gewählt, die durch einen Statolithen gerade kompensiert wird, auf den eine Scherkraft von 1 *g* wirkt.

Die Erscheinung, daß beidseitige Labyrinthausschaltung in zeitlichem Abstand eine Asymmetrie hinterläßt, ist bereits von vielen Wirbeltieren bekannt. Sie zeigt, daß die erste Kompensation im Neuaufbau einer zentralen Drehtendenz bestehen muß, die keiner Erregungszufuhr aus einem der Labyrinthe bedarf, und die vielleicht selbsttätigen-automatischen Charakter hat.

Wir können die Sache zusammenfassend so deuten: Chirurgische Abschaltung der ständigen Erregungszufuhr des einen Utriculus (bzw. Labyrinths) verursacht im zugehörigen Zentrum (dem gleichseitigen Vestibulariskern) ein katastrophales Absinken der Aktivität oder Erregbarkeit. Damit entsteht ein zentrales Erregungsungleichgewicht, das die enormen Asymmetrien von Bewegung und Haltung zur Folge hat, wie sie z.B. einer Taube den Kopf um mehr als 360° herumdrehen können. Die lahmgelegten Ganglienzellen erholen sich aber langsam wieder und gewinnen schließlich ihre volle Erregbarkeit zurück. Diese Erholung wird sehr gefördert durch solche peripheren Erregungen, die dem vorhandenen Ungleichgewicht im Zentrum entgegenwirken. Wenn späterhin auch der Utriculus der Gegenseite ausgeschaltet wird und hier der gleiche Zusammenbruch stattfindet, muß ein etwa gleichgroßes entgegengesetztes Ungleichgewicht im Zentrum mit entsprechenden motorischen Auswirkungen die Folge sein.

VI. ZENTRALE “AUFLADUNG” (ÄNDERUNG DER AKTIVITÄT)

Sie werden vielleicht fragen, warum ich mich bei der Erklärung dieses Phänomens so lange aufhalte? Es geschieht wegen einer *Konsequenz*, die sich aus dieser Deutung ergibt: Man kennt in der Physiologie zahlreiche Fälle, wo Sinnesreize die Aufgabe haben, ein Organ auf eine bevorstehende Beanspruchung vorzubereiten. So etwa wird das Verdauungssystem schon durch Anblick oder Geruch von Speise in zweckmäßiger Weise aktiviert. Ich stelle nun die These auf, daß das gleiche Prinzip auch im Zentralnervensystem gilt, und daß solche Sinneseindrücke, die eine bevorstehende Beanspruchung des Bewegungsapparates ankündigen, wo es auf Geschicklichkeit und schnelles Reagieren ankommt, das Gleichgewichtszentrum in einen Zustand erhöhter Aktivität versetzen. Selbstverständlich wird, wenn meine Behauptung zutrifft, dem intakten Tier davon doch nichts anzumerken sein. Sobald aber das Gleichgewichtszentrum einseitig weniger erregbar — nicht ‘gebahnt’ — ist, wird sich die von höheren Zentren eintreffende aktivierende Erregung nicht gleichmäßig ausbreiten können, sondern zu einem starken Übergewicht der erregbareren Seite, mithin zu einer plötzlichen zentralen Drehtendenz führen.

Sie erraten wohl schon, daß ich damit zu dem anfangs geschilderten absonderlichen Verhalten des Stichlings zurückkehre, der angesichts des drohenden Kampfes plötzlich zu rotieren beginnt (Abb. 2). Daß es sich hier um ein einseitig entstatetes, halbkompensiertes Tier handelt, hatte ich bisher unterschlagen. Wenn Sie meine Deutung akzeptieren, so können wir sagen, daß der Anblick der spezifischen Angriffsstellung des Rivalen eine ungeheure 'Aufregung' im Fisch erzeugt, die vor allem das Gleichgewichtszentrum aktiviert, das aber beiderseits sehr ungleich 'aufgeladen' wird.

Eine solche 'Aufladung' des Zentrums geschieht auch durch andere Sinnesreize, die einer erhöhten Bewegungsaktivität und -präzision vorauszugehen pflegen. So z.B. führt das Fangen eines Beuteobjekts, besonders wenn dieses verfolgt werden muß, ferner das Gejagtwerden (z.B. mit dem Fangnetz) und jedes Erschrecken, z.B. plötzliches Aufwecken aus dem Schlaf, zu einem Rotationsanfall. Daß die Erscheinung wirklich ein *zentrales* Phänomen ist, das mit Erregungszufuhr aus dem statischen Apparat nichts zu tun hat, ist daran zu erkennen, daß sie nach ***beidseitiger*** Entstatung in gleicher Weise auftritt, wenn beide Ausschaltungen in zeitlichem Abstand erfolgten. Es bietet einen ebenso illustrierenden wie erheiternden Anblick, wenn eine Anzahl in einem Becken bei Unterlicht gehaltene beidseitig entstatete Tetras, die schon in der Ruhe in umgekehrter Lage umherschwimmen, bei der Fütterung gar noch in Schraubenbewegungen ihre Daphnien verfolgen! Es handelt sich also bei der 'Rotation aus Aufregung' um einen echten, rein zentralen Umstimmungsprozeß.

Die Beobachtung, daß die Asymmetrien nach einseitigem Labyrinthausfall zunehmen, wenn das Tier erregt wird, ist schon alt und wohl keinem sorgfältigen Experimentator entgangen, obschon sich m.W. keine plausible Erklärung dafür fand. Schon Ewald beschreibt, daß seine Tauben, wenn er ihnen das Futter schwer erreichbar hinstellte, in der Anstrengung, hinzukommen, sich durch übermäßige Kopfverdrehung am Erreichen des Zieles selbst hinderten. Andererseits konnte er durch das bekannte sogenannte 'Hypnotisieren', d.h. auf den Rückenlegen, die Drehtendenz völlig koupieren: Die wieder aufstehende Taube ging in zunächst vollkommen symmetrischer Haltung davon. Wir können diese interessante Beobachtung jetzt als Herabsetzung der Aktivität des Gleichgewichtszentrums durch taktile Reize gut verstehen. Eine ganz entsprechende Wirkung haben taktile Reize auch bei Fischen: Läßt man einen frisch operierten ständig rotierenden Stichling sich in einem freischwimmenden kurzen Wollfaden selbst einrollen, dann kann er für lange Zeit zur Ruhe kommen; beim Auswickeln geht das Drehen wieder weiter.

Unser anfangs zitierter Stichlingsversuch ist nun deshalb von besonderem tierpsychologischem Interesse, weil wir diese 'Kampfaufregung' bei einem jung aufgezogenen Männchen entdeckten, das noch niemals zuvor gekämpft hatte. Das Angeborensein der 'Angst' vor dem Bild des drohenden Rivalen läßt sich wohl nicht drastischer demonstrieren! Es war dabei gleichgültig, aus welcher Blickrichtung dieses gegnerische Bild dem

Auge erschien, ob von vorne, seitlich oder schräg von hinten. In jedem Fall trat, ohne daß der Bedrohte Fixierbewegungen ausführte, der Rotationsanfall auf. Es ist folglich belanglos, auf welche Retinapartie die betreffende Reizkonstellation fällt; die entstehende 'Erregungsgestalt' findet immer ihren richtigen Weg.

Nicht gleichgültig ist dagegen die Häufigkeit der Auslösungen. Bei mehrfacher Kampfaufregung in Abstand weniger Minuten nahm die Rotationsfrequenz und -dauer schnell ab, obschon es nicht zu einem eigentlichen Kampfe kam. Das spezifische Erregungsreservoir leert sich schnell—wie wir ja von vielen ähnlichen Reaktionen wissen—es ist aber nach einigen Stunden wieder angefüllt (ein genaues Korrelat also zu der Appetiterregung).

Ich bin damit am Ende meines Berichtes, der Ihnen zeigen sollte, wie vielfältig und wirksam zentrale Stimmungen als Basis für motorische Reaktionen sind. Es ist wohl selbstverständlich, daß mit diesen Methoden nur ein Teil solcher Vorgänge überhaupt erfaßt werden kann. Ohne Zweifel spielen mannigfache ähnliche unsichtbar bleibende *Änderungen der Reaktionsnorm* eine große Rolle und sind Hauptursache für die scheinbare Unberechenbarkeit des tierischen—wie auch des menschlichen—Verhaltens.

Es ist vielleicht nicht ganz gleichgültig, wenn an einem Modellfall gezeigt werden kann, daß auch diese Vorgänge quantitativ erfaßbar sind. Es scheint ja heute Mode zu sein, daß Physiker (und andere biologische Laien) die angebliche Unberechenbarkeit des tierischen Handelns, zusammen mit dem sogenannten 'freien Willen' des Menschen, durch indeterminierte Quantensprünge im Gehirn und in den Sinnesorganen physikalisch 'erklären' wollen.

Diese merkwürdige Lehre, die manchen Beifall findet, ist bei Lichte besehen nichts als der Versuch, aus einer methodischen Not eine pseudo-'erkenntnistheoretische' Tugend zu machen. Wenn sie stimmte, dann wäre der Physiologe auf dem Gebiete der höheren nervösen Leistungen zu ewiger Resignation verdammt.

Dieser sterilen Idee gegenüber ist es Aufgabe des Physiologen, sich als der bessere Erforscher der Lebensvorgänge zu erweisen und auch das scheinbar Unberechenbare des höheren Verhaltens als kausalen Zusammenhang durchschaubar zu machen.

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ERKLÄRUNG DES TAFELS

Tafel 1. Zahnkärpfling (*Lebistes reticulatus*). Der Kopf ist entpigmentiert und erhellt, die Statolithen, die eine vom Knochen abweichende Lichtbrechung besitzen, sind in ihrer natürlichen Lage als weiße Körper genau zu erkennen. Von vorne nach hinten: Utriculus-, Sacculus-, Lagenastatolith. (Praeparat und Photo von D. Ahrens.)

* Die im Text citierte Literatur ist hier ausführlicher besprochen.

For explanation see p. 172

INSTINCTS, TAXES, ETC.

BEHAVIOUR PATTERNS IN LOWER INVERTEBRATES

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Behaviour patterns are sequences of an organism's activities directed to a goal. Some of these patterns seem stereotyped so that they can always be described in essentially the same terms. As Jennings (1915) pointed out and as anyone who has conducted laboratory demonstrations on behaviour is aware, this does not mean there is absolute fixity of response. But, particularly amongst the lower invertebrates, characteristic sequences of activities directed to a goal are repeatedly recognizable, and a great variety of responses and activities fall within this class. They vary, from direct reflex responses to instinctive behaviour patterns of great complexity. Such stereotyped patterns, particularly in the simplest animals, offer the most promising, even if limited, opportunity of studying the relation of behaviour to the underlying physiological machinery by which it is effected.

Some of the elementary behaviour patterns appear to be susceptible of complete analysis. This is true of the protective closure of the oral disk in sea anemones, such as *Calliactis parasitica*. Excessive stimulation leads to an obviously purposive response in which the marginal sphincter contracts, thereby protecting the delicate disk and tentacles. Analysis shows that mechanical or other stimulation of sufficient intensity generates impulses which travel over well-defined tracts in the body of the animal to the sphincter muscle. The threshold for stimulation is high, and adaptation is rapid in relation to the normal low frequency of impulses operating responses in the muscles. Consequently an adverse stimulus initiates a short group of impulses.

The impulses possess the properties of threshold and refractory period in the same way as the nervous impulses of higher animals (Pantin, 1935*a*, *b*, *c*). The tracts conveying the impulses constitute a through conduction system, and in some places, as in the mesenteries, it is possible to demonstrate the presence of organized tracts of single nerve fibres apparently consisting of a trellis of cells some 3–4μ in diameter running among the mesenteric muscles. The system conducts the impulse in an all or nothing way, normally without hindrance, though the effect of excess magnesium in the external medium shows that the system can be broken up into separate units (Ross & Pantin, 1940). Bullock (1943) has shown similar effects in Scyphomedusae. Bozler (1927) found the nerve-net tracts of Scyphomedusae to consist of cells making synaptic contacts. Woollard & Harpman (1939) found similar synaptic discontinuity in the net of *Tealia felina* and *Actinia equina*. Anatomical and physiological evidence thus indicates that the impulses are conducted by tracts in the nerve net consisting of chains of nerve cells in which normally the synaptic contacts offer no resistance to the passage of the impulse. The response of the sphincter muscle in *Calliactis* is governed appropriately by facilitation at some point between the through conduction system and the muscle (Pantin, 1935*d*). The rate of decay of facilitation is such that only the comparatively rapid sequence of impulses following strong stimulation of the animal will activate the muscle.

The properties of the neuromuscular junction are in part analogous to those of the simpler synaptic junctions in vertebrates and other animals. Each motor response in the muscle is directly related to the receipt of an individual nervous impulse; just as, in the mammalian sympathetic ganglion, post-ganglionic impulses synchronize with pre-ganglionic ones if the frequency is low (Bronk & Pumphrey, 1935). But in this particular neuromuscular junction of the Actinian there is nothing comparable to the excitatory state of the synapses of the vertebrate spinal cord which may lead to the prolonged discharge of motor impulses having no direct temporal relationship to those arriving at the cord. It differs also in the important feature that the facilitation at the Actinian junction endures far longer than do comparable states at junctions in the higher animals; up to several seconds, as opposed to a few hundredths of a second.

Notwithstanding these differences, analysis of the protective closure of *Calliactis* may be said to be substantially complete; that is, we can conceive of a mechanical model which would do the same thing in the same way, and be built of parts with physiological properties such as accommodation, impulses, through conduction and facilitation, with which we are familiar in the tissues of other animals.

When we turn to other animals we find that repeatedly and independently very similar physiological properties have been utilized in building up a purposive response similar to that of *Calliactis*, particularly for sudden protective movements. The special feature of the response mechanism of the latter is the through conduction system which conducts much faster than the rest of the nerve net, about 1 m. per second against a few centimetres per second. A comparable system is found in the retraction mechanism of Lumbricid earthworms which involves the through conduction system of giant fibres. These giant fibres consist of chains of segmental syncytia with large synaptic areas of contact (Stough, 1926). The work of Bullock (1945) and Rushton (1945, 1946) shows that each giant fibre conducts in both directions unhindered by its synapses. The middle fibre, and the two lateral ones acting together, each form independent units connected with different sensory fields.

Such a system reaches its greatest development in the enormous giant fibre of *Myxicola*, up to 1 mm. across. This forms a single syncytium including the motor nerves to the longitudinal muscles (Nicol, 1948*a*, *b*). Like the through conduction system of *Calliactis*, the giant fibre systems of both *Lumbricus* and *Myxicola* are activated readily by mechanical stimuli, to which there appears to be rapid adaptation. There are important differences of detail from the through conduction system of *Calliactis*. As in the giant fibre system of *Loligo* (Young, 1938*a*) a single impulse in the giant fibre system of *Myxicola* results in a contraction, so that the response is not controlled by neuromuscular facilitation. There are indications that the response is controlled in both *Myxicola* and *Lumbricus* on the afferent side of the system rather than at the neuromuscular junction. It is noteworthy that Pumphrey & Rawdon-Smith (1937) show that in *Periplaneta* there is a synaptic junction operating between the cercal nerves and a giant fibre system in the nerve cord. In this case a single impulse will pass to the giant fibre, but a rapid succession causes an adaptive failure of the synapse, in which condition, however, the synapse shows facilitation. Thus the position of the synapse governing the through conduction system is not always the same in different animals. It may be on the motor or on the sensory side of the arc, and the properties of the synapse may vary.

A second difference between the through conduction system of *Calliactis* and the Annelid worms is the size and speed of conduction of the nerve fibres involved. Conduction, presumably in the 3–4μ fibres, in *Calliactis* takes place at about 1 m. per second; in the vast *Myxicola* giant fibre it reaches 20 m. per second. But as Young (1938) points out for the system in *Loligo*, not only speed, but also synchronization of muscular action are essential features of the giant fibre system. Bullock (1944) in the same way shows the importance of synchronization in discussing the function of the giant fibres of Balanoglossids. The necessary speed of conduction required of these systems must be related to the speed of the contraction of the muscular systems involved. The small, 3–6μ 'giant fibres' of Balanoglossids are much larger than their other nerve fibres and may serve well enough, as do the through conduction tracts of the same thickness in Actinians, to permit synchronous contraction of their relatively slow muscles.

The property of through conduction is not utilized only when a protective response is required. The Scyphomedusae possess a well-developed through conduction system (Bozler, 1926*a*, *b*) concerned with normal locomotor contractions of the bell musculature in swimming. This has no relation to protection, but Bullock (1943) has shown that the through conduction system functions essentially in the same way as *Calliactis*, except for the time course of the facilitation process.

A comparison of through conduction systems shows that these have often developed independently in different animals where there is need for rapid conduction and synchronization. The cause of this need varies, though most commonly it concerns a protective response. The way in which the system is built up into the response machinery is not always the same. But the potentiality of relatively large and long cellular units to transmit impulses without hindrance is repeatedly 'utilized' by different animals for different purposes.

The incorporation of through conduction systems in the response mechanism is an example of the utilization by organisms of the properties of the material systems of which they are composed. By protective responses or other behaviour patterns the organism must meet its environmental needs. Whether through the agency of natural selection or otherwise, it must build up machinery to do this. It is open to the organism to devise machinery to meet these needs by utilizing any properties which are to hand in its component parts. If material systems were infinitely variable in their properties, we should not expect the behavioural mechanisms of any two animals to resemble each other in any degree. Fortunately for the prosecution of comparative physiology, many resemblances exist. The number of kinds of material systems and of their properties which organisms have at their disposal seem to be limited. This same limitation appears throughout comparative physiology, as in the very few kinds of respiratory pigment apparently available to organisms for increasing the oxygen carrying power of the blood (Pantin, 1932). For the transmission of excitation, action currents over the surface of cells provide a possible and convenient mechanism. The ability to carry such currents is one of the potential properties of cell membranes. It is not necessarily related to the transmission of excitation, as is evident in the case of the action currents which pass over algal cells such as *Halicystis* and *Valonia* (Osterhout, 1936). It can, however, be utilized for this purpose in both nerve and muscle. There do not appear to be many different methods by which excitation can be transmitted, so that this utilization of action current is resorted to again and again in different organisms. But in analysing response mechanisms we must constantly bear in mind that there are other ways of transmission of excitation, about some of which far too little is still known. This is particularly true of conduction in ciliary fields (Gray, 1928). Jennings's (1915) classical work on the Protozoa showed how close is the analogy of the behaviour of many Ciliates to the Metazoa, and the well-defined retraction response of *Stentor* and *Vorticella* resembles those of Actinians. Yet the machinery of this response must be different in these non-cellular organisms from the cellular and synaptic machinery of Metazoa, whatever view is taken of conduction systems of Ciliates.

From this point of view we can compare an organism to a functional structure made to meet environmental requirements which is not infinitely malleable, as if it were made of putty, but is subject to restrictions because it is made of standard parts; just as is the case with a mechanical model made by a child from a constructional set consisting of a set of standardized parts each with its special properties. Children building a crane from such a set will often use the same parts for this functional object, but they may not always do so, and it would be dangerous to say that all cranes made from such a set must necessarily be built of the same parts. This contains a principle which I believe is very important in comparative physiology. Let us compare, for instance, the organization and behaviour of two quite evidently closely related organisms such as *Hydra* and a sea anemone like *Anemonia*. The morphological plans of each are rather similar. The work of Jennings (1915) and others has shown how similar is their behaviour. There is the retraction of *Hydra* to adverse stimuli, and there is the succession of events accompanying feeding in which the food is seized by the tentacles. These co-operate to convey it to the mouth which opens and by peristaltic action conveys it to the interior. All this shows a detailed resemblance to what occurs in *Anemonia sulcata* (Pantin & Pantin, 1943). Nothing seems more natural than to assume that the neuro-muscular machinery underlying this behaviour is the same in both cases. It still may be so, but there are differences. In the first place the work of Kepner & Hopkins (1924) shows a curious deficiency of nerve cells and of nervous action in the endoderm of *Hydra*. In the endoderm there is no net and only isolated nerve cells. The peristaltic action of the peristome in particular appears not to depend on nervous action. Thus chloretone, which paralyses nervous response, actually frees the peristalsis of the body and the active movement of the peristome from a normal state of inhibition. But apart from this relatively low degree of development of the nervous system and its consequences, there is a more serious difference from the Actinians. McConnell (1932), in a careful study of the nervous system of *Hydra*, came to the conclusion that the nerve net in this animal was a true continuum without synaptic junctions. He arrived at this conclusion after fully bearing in mind the work of Bozler (1927) showing the presence of synaptic junctions in the nerve net of Medusae. In his paper he expressed the intention of giving the evidence for his conclusion that the net is non-synaptic in a subsequent paper, but, to the best of my knowledge, he never did so.

If the net of *Hydra* is truly non-synaptic, then the mechanism of much of its behaviour requires a different explanation from that which we apply in the case of sea anemones.

It still remains possible that with new and improved histological technique McConnell's conclusion might prove to be wrong, but even at the present time it is worth noting that it would be possible to conceive of a neuro-muscular machine which would give varied response even though there were no synaptic junctions, provided that the machine is on a sufficiently small scale. The size of *Hydra* is only a matter of millimetres, while the length of its longer nerve cells is only of the order of 100μ. Now we know that in the nerves of the higher animals stimuli below the threshold of a nervous impulse may yet produce electrotonic spread of a decremental kind. Such electrotonic spread may extend several millimetres down a nerve fibre (Barron & Matthews, 1936; Hodgkin & Rushton, 1946). Parry (1947) has produced evidence which suggests that electrotonic spread from the ocellus in *Locusta* may influence the response of this insect through a decremental electrotonic spread over a nerve of about 1 mm. in length. It is evident therefore that all parts of the body of *Hydra* may potentially be within range of electrotonic spread in a continuous nerve net. Such electrotonic potentials might in turn produce graded muscular response, for this is the interpretation which we might put on the graded local contractions which accompany the graded end-plate potential demonstrated by Katz & Kuffler (1946) in the neuro-muscular system of Crustacea. Together it seems possible that in this way graded activity of considerable complexity might be built up without the utilization of action currents by organisms if these are of sufficiently small size. I wish to make it quite clear that I am not saying that the behaviour of *Hydra* is certainly mediated in this way. What I do say is that the existing evidence places certain difficulties in the way of supposing that we have here a synaptic nervous system, and that because of the small size of the animal and what we now know of decremental electrotonic potentials, we cannot exclude the possibility that these alone would provide a machinery for the animal's activity, even though the total behaviour was essentially similar to that which we find in larger animals to be mediated by impulses and a synaptic nervous system. We cannot say that behaviour of a particular kind, even when it is complex, must necessarily be produced by the utilization of one, and only one, class of system.

The utilization of any convenient properties for the construction of the machinery for a response is very clearly shown in the feeding reactions of both anemones and *Hydra*. The tentacles of *Anemonia* respond to food in immediate contact with them, and provided the elementary sensory pattern is of the right kind, that is, a combination of mechanical stimulation from a solid object with chemical stimulation of a specific kind (protein as opposed to carbohydrate), a succession of local muscular responses conveys the food to the mouth (Pantin & Pantin, 1943). These responses are operated through impulses in the disk nerve net, with interneural facilitation. But before the feeding response gets to this stage, a vital part is played in food capture by the nematocysts. There is evidence that these do not discharge as a result of a nervous stimulus (Parker & Van Alstyne, 1932; Pantin, 1942), but that the nematoblasts are true independent effectors in Parker's (1919) sense. They respond selectively to food material because the threshold for the direct mechanical stimulus for their discharge is lowered by the simultaneous presence of surface-active substances in the food. These substances pass to the nematoblasts by direct contact between these and the food.

The feeding response thus begins with a selective non-nervous link in the chain of effector responses: the discharge of the nematocysts. Here we have the utilization of something quite distinct from the nervous system in the building up of the response mechanism. This same system can be utilized in other ways as the most interesting observations of R. F. Ewer show on the action of the nematocysts of *Hydra*. Both Ewer (1947*b*) and Jones (1947) show that the mechanism of discharge of nematocysts in food capture in *Hydra* is essentially similar to that which takes place in *Anemonia*. But *Hydra* is distinguished by the fact that it contains four distinct kinds of nematocyst, each with a separate function. Like the nematocysts of *Anemonia*, the *stenoteles* and *desmonemes* of *Hydra* have their threshold to mechanical stimuli lowered by the presence of food substances, and they are employed in food capture. They discharge to different levels of the intensity of mechanical stimulation. The *atrichous isorhizas* are not employed in food capture, but are concerned with the very remarkable 'somersaulting' progression of *Hydra* first described long ago by Trembley. The *Hydra* alternately attaches its tentacles to the substratum and then moves the point of attachment of its foot and by repeating this operation a number of times moves to a new position. This activity may be built into complex patterns of tactic behaviour related to light and gravity (Ewer, 1947*a*). In comparison with the *stenoteles*, the *atrichous isorhizas* have a low mechanical threshold, but the stimulus must endure for about 10 sec. The presence of food substances actually raises the threshold for this class of nematocyst, so that they are not employed in feeding, but are automatically employed during the long slow contacts associated with locomotion. Food actually inhibits locomotion. The fourth kind of nematocysts, the *holotrichous isorhizas*, have a high mechanical threshold. Ewer (1947*b*) produces evidence that, as in the *stenoteles*, the threshold is lowered by chemical means; not in this case by food substances but by the secretions of noxious animals. Thus the special mechanism of excitation of these independent effectors is utilized in different ways for different functions. Appropriate modification of thresholds of the system allow it to become a constituent part of more than one behaviour pattern. Moreover, we see that the machinery of such patterns is not arbitrarily restricted to neuromuscular mechanisms alone. The utilization of a non-nervous element in behaviour patterns shows clearly how an organism will meet environmental requirements by any means at its disposal.

Our study of these simple purposive responses thus leads us to the conclusion that a particular behaviour pattern does not necessarily correspond to a particular class of physiological mechanism at all. The common feature of such patterns is that they meet some particular environmental requirement. In different organisms, this may be met by machinery utilizing different properties of the material structures which compose them. It is often this element of 'environmental requirement' which characterizes the classes into which we place behaviour patterns, rather than the nature of physiological—or psychological—characteristics of the animals which exhibit them. Fraenkel & Gunn (1940) have given us a classification of the behaviour by which organisms orientate themselves. Orientation is an environmental requirement, and it can be met by the utilization of a variety of properties of the material systems which compose organisms. One of the methods by which an organism may achieve orientation is by photoklinotaxis. In this a particular kind of behaviour follows the variation in stimulation in a single intensity receptor as the organism moves in a beam of light. Many different organisms exhibit this class of taxis, but the physiological machinery which operates it in the Protistan *Euglena* obviously involves the utilization of different elements from those utilized in the photoklinotaxis of the maggot larva of *Lucilia*. Nevertheless, the number of kinds of system available for building up this taxis seems to be limited. In many different animals the physiological machinery of photoklinokinesis seems to be essentially the same. This results in a specious correspondence between photoklinotaxis and a particular physiological mechanism.

It is dangerous to draw general conclusions about the nature of behaviour patterns from the examples we have considered. Compared with those of the higher animals, the activities with which we have so far been concerned are extremely simple. It is true that they are directed towards a simple goal, but they lack certain of the most striking qualities of complex behaviour. In particular, the behaviour pattern consists of a succession of responses to stimuli, which may vary with the state of the animal but to which the animal contributes nothing by its own activity. There is no evidence of that active drive to achieve a goal, often by varied means, that characterizes complex behaviour.

Russell (1934) and many others have pointed out the inadequacy of describing behaviour in terms of reflex responses. Indeed, the simplicity of the behaviour we have been examining is in a great measure due to the fact that we chose to examine the simplest activities of simple animals and, trying to follow the principle of economy of hypothesis, have looked for the simplest explanation of their mechanism; that simplicity emerges in the answer is not surprising. There is no reason at all why new qualities should not be expected in more complex behaviour, and these may be related to the utilization of properties of living matter other than those with which we are familiar. Nor is there any reason why such behaviour should not be susceptible of analysis.

Even in Actinians we find behaviour patterns which consist of more than a simple succession of responses to stimuli. Let us consider certain reactions to food of *Metridium senile.* These are being investigated by Dr E. J. Batham and myself, and a fuller account of them will appear elsewhere. It has been recorded in some Actinians that, in addition to the direct response to food placed upon the tentacles, the presence of dissolved food substances in the surrounding medium brings about characteristic preparatory activity (Parker, 1919). This preparatory activity is more evident in *M. senile* than it is in many other species. The anemone may be resting in a relatively contracted state; but if a dilute food solution, such as about one part in a million by dry weight of molluscan mucus, be added to the sea water a series of reactions commonly, though not invariably, takes place. The disk, if not already open, expands, often very greatly. During the course of the next hour the column of the anemone may elongate so that the whole anemone appears much taller, with the tentacles extended freely in the surrounding medium. Presently, occasional slow swaying movements of the column may sometimes appear, so that the disk is bowed this way and that at random round the animal. The activities are not connected with the actual ingestion of solid food, but they are clearly purposive in character, in that if food is in the neighbourhood of the animal they increase the anemone's chance of coming in contact with it. It is activities of this kind, particularly the bending movements, which have been noted by earlier workers on the feeding responses of these animals (Pollock, 1883; Allabach, 1905).

It is one of the characteristics of this behaviour that it is extremely variable. While on the whole most anemones may show some effect of the presence of food solution, some remain unaffected. Some will not show the opening of the disk; not all will show the swaying movements of the column. The same anemone will vary in its responsiveness to food solutions on different days. The activity is not only variable but it is much more complex than the protective closure response. Each element involves a co-ordinated sequence of activities of several muscular systems, and this co-ordinated activity may continue for a long time after the application of the food-juice stimulus, even if this be removed.

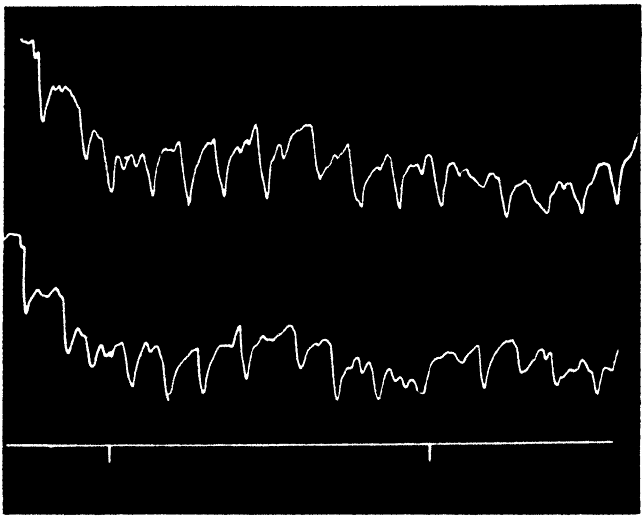

Fig. 1. Inherent activity in *Metridium*. Partially rhythmic contractions (downwards) and extensions of two opposite points on the body wall. Isotonic recording levers. Time interval 1 hr. Record runs from the left.

The response is not the simple consequence of a stimulus acting on a passive animal. It is essentially a change in the pattern of activity of an organism which is not at rest. Observation of an anemone such as *Calliactis* creates the impression that the 'resting' anemone is inactive. Anemones of other kinds, particularly *Metridium*, are in a constant state of activity. This is too slow to be easily appreciated except by the change of shape evident on examination at long intervals. Continuous active movement is, however, in progress and can be made apparent by 'quick-motion' cinematography, which also shows that the character of the movement continually changes.

Such activity of the normal animal can also be recorded by attaching light levers to it. Fig. 1 shows the slow changes which are registered when isotonic levers are attached to the body wall at two points on the circumference of *Metridium*. Contractions and extensions are apparently due to irregular alternate activity of the parietal and circular muscles of the column. Activity is continuous though extremely slow. It seems to originate within the organism itself. It is not caused by random changes of temperature, light, vibration or the bubbling of compressed air with which aquaria are aerated. All these sources of stimulation can be excluded experimentally. Animals were kept in a cellar at a temperature which varied by not more than 1° during the 24 hr., and they were insulated from vibration. In total darkness or constant light, with or without aeration, the activity continued. Indeed, it was as evident as in animals exposed to the fluctuations of light, temperature and vibration in an ordinary working laboratory.

The character of the activity itself is not consistent with excitation by random external stimulation. It frequently shows a slow rhythm, often with a period of the order of about 10 min. Fig. 1 shows a sample of activity of the column with a fairly marked rhythm. If each contraction of the column results from a random external stimulus, the contractions should be random and not rhythmic. The rhythmic element in the activity and the independence between activity and controllable external stimulation show that it is inherent in the organism.

Whether the activity originates as true automatic excitation in the nerve net, like that which is found in the swimming bell of Scyphomedusae (Bozler, 1926*a*, *b*), is uncertain. It might be maintained through something analogous to a chain reflex; each contraction engendering internal stimuli which initiate excitation of the next. The sequences of activity involve very small changes in pressure of the order of 1 or 2 mm. of water within the anemone, which might conceivably result in the stretching of parts of the animal and thereby initiate excitation. However, if the internal pressure is suddenly raised, even to several centimetres, by allowing water to pass into the animal from a cannula, it does not produce any marked reflex contraction; though large quantities of water at still higher pressures may do so. This suggests that activity is not the simple result of a chain reflex. But whatever the origin of this activity, it appears to be inherent in the animal and not initiated by casual external stimuli.

The nature of the rhythm and its extent varies with the state of the animal. The addition of food solution produces its effect by a change in the character of the inherent activity. This becomes clear if we examine the manner of elongation of the column. Fig. 2 shows the effect of adding an extract of *Mytilus* mantle up to a concentration of about one part in a million, dry weight, to the sea water containing a *Metridium*. The activity is recorded isotonically. It will be seen that before the solution is added the animal is in a continuous state of activity. About 10 min. after the addition of the food solution a steady lengthening takes place accompanied by expansion of the disk. Previous to the addition of food solution the activity of the animal could be seen to be due alternately to contractions of the longitudinal musculature of the body wall (the parietals) which cause shortening, and to waves of circular contractions of greater or less extent which cause elongation. Under the influence of the food solution this same irregular alternation of activity proceeds at about the same frequency, but the elongation phases due to circular contraction are relatively much greater in their effect than the parietal contractions which normally balance them. In the experiment the water was changed after about 2 hr. It will be seen that the activity of the animal continued at its new and greater length for a long period. After another 2 hr. the anemone gradually shortened. This shortening was due to a further change in the activity so that there was a preponderance of parietal contraction over the circular ones, the reverse of the initial elongation. The whole response involves a sequence of changes in inherent activity.

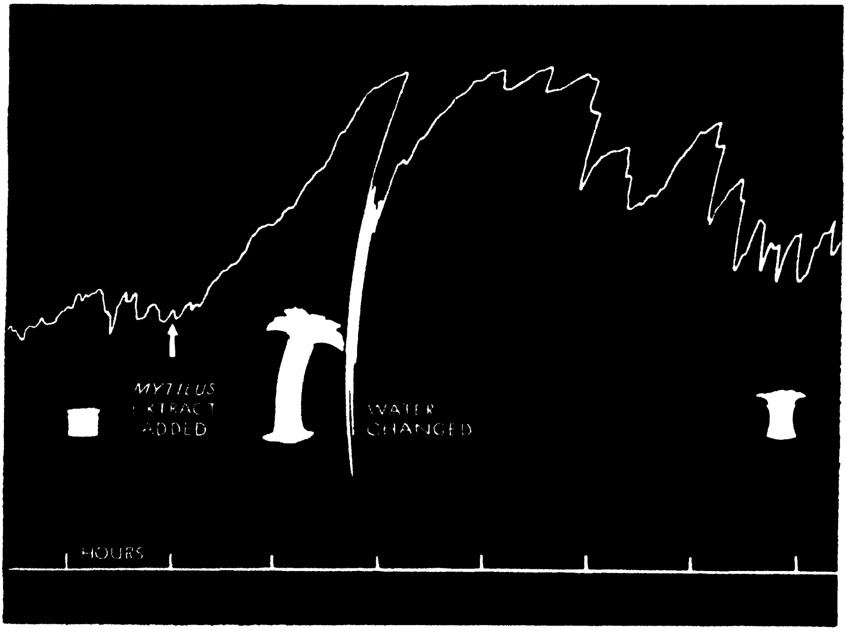

Fig. 2. Effect of addition of extract of *Mytilus* (about 1 part dry weight in 10^6 sea water), on activity of *Metridium*. Extension of column registered isotonically. Outline figures illustrate appearance of animal during each phase. Record runs from the left.

There is one other feature of this activity which should be noticed. Expansion, elongation and swaying are activities which may occasionally occur in the normal animal without apparent external stimulation. The whole pattern is already there in the normal animal, though it is usually only released by the presence of food. The threshold depends on the state of the animal, for like all elements of the feeding reaction these activities take place more easily in starved animals (Allabach, 1905).

Elongation results from modification of inherent activity of the parietal and circular muscles. Dr Batham and I have made a preliminary investigation of the properties of this parietal-circular system. In the first place, whereas the closure response and the reaction of the disk to the presence of solid food can be initiated by electrical stimuli, we have never succeeded in initiating elongation by this means. Nor, indeed, does electrical stimulation of the intact animal ever *directly* cause contraction of the circular musculature responsible for elongation. In the intact animal the only method of obtaining a direct contractile response of the circular muscles to stimuli is by the stimulus of touch upon the column. This may initiate a local or general ring of contraction.

The parietal muscles, on the other hand, which are chiefly responsible for the slow contraction of the column are susceptible to electrical stimulation and respond to batteries of some ten shocks sent in at the very low frequency of 1 per 5 or 10 sec. The existence of very slow responses of these muscles at very low frequencies of stimulation was already noted in *Calliactis* (Pantin, 1935*b*), and in *Metridium* (Hall & Pantin, 1937). In a general way the size of the response increases with the number and frequency of the stimuli, and at first it was supposed that we were dealing with a simple facilitation system essentially similar to that of the sphincter in *Calliactis* but acting at a much lower frequency. Further investigation in *Metridium* shows that in this case at least the system is much more complex. A succession of suitably timed electric stimuli (say 1 per sec.) will cause the sphincter of *Calliactis* to respond to every shock after the first with a latent period of only a fraction of a second. The extremely slow response of the parietals of *Metridium* frequently possesses an enormous latent period; on occasion it may not appear till about 30 sec. after the end of the application of a battery of low-frequency stimuli. This latent period is much greater than the through conduction time across the nerve net (about 80 msec. in *Metridium*).

When parietal contractions take place they do not increase in height with each individual shock of the battery of stimuli which initiates them. The contraction when it comes may be quite large, but it is smooth and does not have the step-like character of the *Calliactis* sphincter contraction. Under appropriate conditions, the circular muscle shows similar features of slow response to the parietals. Though it does not respond directly to electrical stimuli in the intact animal, it readily does so when isolated as a strip of tissue by cuts in the column of the anemone. The same effects of long latency and smooth contraction may then be recorded without complication due to activity of the rest of the animal (Fig. 3).

It is a remarkable fact that the extent of the responses of the parietal and circular muscles following a given stimulus vary enormously in different individuals and in the same individual at different times. The contractions appear to vary with, and on occasion to sum with, the inherent activity of the animal. There is evidence of a reciprocal relationship between the contractions of the parietals and the circular contractions. The spontaneous appearance of a circular contraction may in some cases inhibit the response of the parietals to an electrical stimulus which is fully adequate to produce

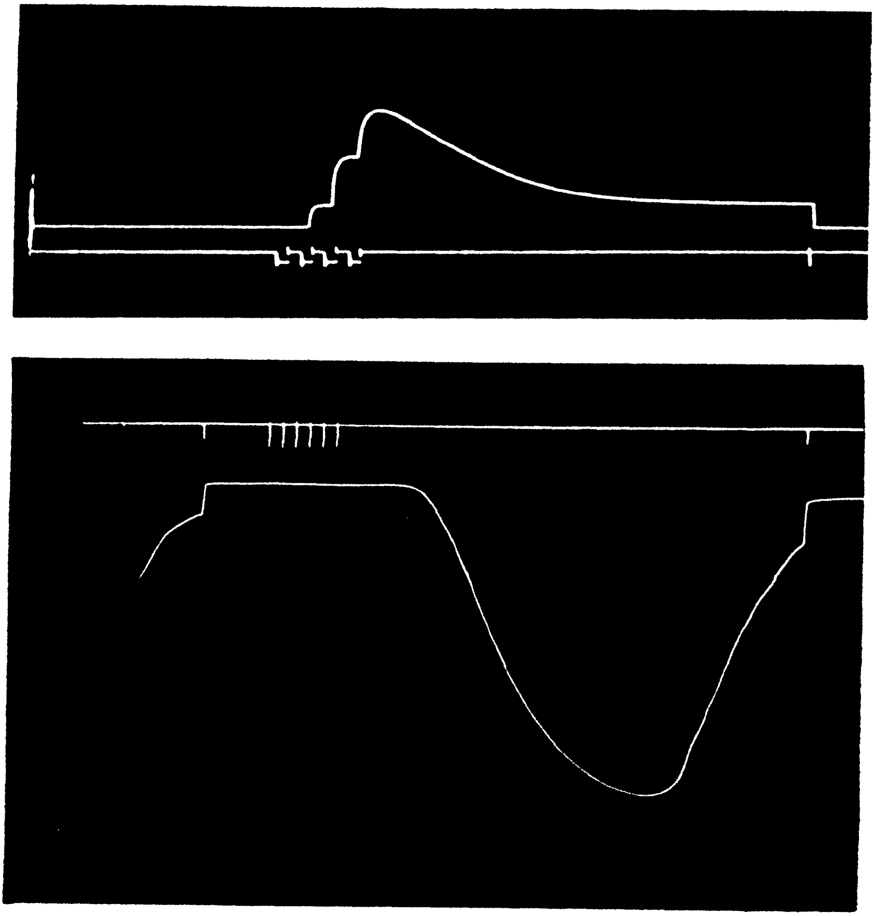

Fig. 3. Above: response of sphincter of *Calliactis* to four shocks at 1 per sec. frequency. Below: response of partly isolated strip of circular muscle of *Metridium* of six shocks at 1 every 5 sec. frequency. The shocks were applied to an attached vertical strip of body wall (with through conduction tracts intact). Note smooth contraction and very long latent period.

a contraction in them when the circular contraction has passed away. The same inhibitory effect may be exerted by the circular contractions induced by stroking the side of the column of the anemone. The system behaves as though there were reciprocal inhibition between the antagonistic circular and longitudinal muscles, and as though the effect of electrical excitation depended upon the state of excitation already present in this reciprocal system.

One further feature may be noted. In the case of the sphincter contraction of *Calliactis* the response of this muscle comprises almost the whole of the reaction. But stimulation which leads to contractions of the parietals in *Metridium* is commonly followed by a prolonged sequence of differential muscular activity. After the parietal contraction is over a slow 'circular' contraction begins in the region of the sphincter of *Metridium*, and from this point a wave of circular tone passes slowly and peristaltically down the column of the animal. This in turn may be followed by other activities which finally merge into a general base-line of inherent activity. The part played by the circular muscles is of interest because while electrical stimulation applied to isolated rings of tissue from the column will excite contractions, in the intact animal the response of all the circular muscle is in some way integrated into a pattern beginning with the response of the parietal muscle.

We may conclude that the very slow responses of *Metridium* involve a complex neuro-muscular pattern of inherent activity involving reciprocal inhibition and the successive activation of two antagonistic muscular systems. The system is normally active in varying degrees in different animals. The elongation of the column in response to food solutions takes place through modification of the pattern of inherent activity so as to increase the relative effectiveness of the circular as opposed to the parietal contractions.

The inherent activity clearly bears some parallel to patterns of activity which are to be found in the central nervous system of much more highly developed organisms, particularly in the alternating movements associated with locomotion. It does not necessarily follow that the machinery of such patterns of activity is always the same; though it is sometimes assumed to be so when the similar patterns of activity of two of the higher animals are compared. In the Coelenterates we must be particularly careful because all they do is so slow. Facilitation, conduction and above all latent period endure far longer than in corresponding phenomena in the higher kinds of central nervous system. But whilst it may be that the physiological system utilized for the production of these activities in Coelenterates differs from those concerned with processes like locomotion in the higher animals, it must not be forgotten that in the higher animals there are also many extremely slow processes going on in the nervous system. These may utilize slow systems like those of *Metridium*—though perhaps to a different end.

The preliminary activity initiated in *Metridium* by the presence of food solutions is built up by the utilization of much more complex physiological properties than is the protective closure of *Calliactis*, and this complexity shows parallels with complex co-ordinated activity in the higher animals. It occupies the first stage in the behaviour pattern of food capture. The subsequent links vary in character so remarkably that the manner of achievement of the goal, food ingestion, has an air of improvisation. Any kind of activity is utilized provided it furthers attainment of the goal. The complex initial phases of the pattern give way to the non-nervous but nevertheless selective and purposive action of the nematocysts. This is followed by the simple 'reflex' movements which convey the food to the mouth. Nor does the pattern end here. The food, once ingested, subsequently initiates changes in the state of activity of the animal, ending in defaecation over a period of many days.

Finally, let us note that the whole chain of events in the feeding behaviour bears a limited though significant parallel to behaviour of a much higher order, of the kind we see in instinctive behaviour. There is the same picture of a sequence of activities. The threshold for the appearance of each phase depends upon the state of the animal; and the activity may sometimes occur spontaneously. As in much instinctive behaviour, the chain begins with a variety of movements, some of which are random in character, but all of which appear to be directed towards a goal, that of obtaining a food object. The preliminary food responses resemble the preliminary taxes of an instinctive behaviour pattern. At the end, the pattern is brought to a close by the achievement of the goal, the ingestion of solid food, and the pattern of activity then changes.

There are, of course, some important differences between this and an instinctive behaviour pattern. At no point is the pattern of stimulation complex, though in the final stages it does involve a simple combination of chemical and mechanical stimuli from the food object (Pantin & Pantin, 1943). Further, we have no reason to suppose that the more complex behaviour patterns of instinct utilize only the simple physiological elements we have found here. But these observations and experiments do indicate how some behaviour patterns which possess the striking characteristics of purposiveness, drive and selection of varied activities to achieve a goal may be analysed sufficiently for one to conceive of a mechanical model which would do all that we know at present that the animal does.

As we pass from simpler to more complex behaviour we must expect the utilization of new and unforeseen properties in its machinery. There are no unequivocal examples of 'learning' except of the simplest kind in the Coelenterates. Learning may be considered as ability to respond suitably to sensory patterns which extend not only in space but also backwards in time. Provided the pattern is simple and the past temporal extension is not great, very simple properties may be utilized to build up a learning mechanism. Jennings (1915) showed that *Aiptasia* could become habituated to past stimuli. Doubtless the utilization of the property of sensory adaptation will suffice to account for this elementary 'learning'. In learning that relates to more complex patterns, and particularly with greater past temporal extension, new and more complex systems may be utilized such as the self-exciting nerve circuits of Lorente de Nó which Young (1938*b*) discusses in relation to learned responses in Cephalopods. It may be that several distinct classes of system can independently be utilized to allow response to complex temporal pattern. So far as we know there is no more need to suppose that there is only one 'physiological mechanism of learning' than that there is only one 'mechanism of photoklinokinesis'. It is fortunate for us that so far investigation indicates that in this Universe the number of kinds of system available to living organisms for the construction of their response mechanisms is limited. Similar phenomena of action currents, through conduction, synaptic facilitation and so on, are repeatedly and independently utilized in quite unrelated animals. But we must always be prepared for the organism to 'cheat' by using some new system to meet an environmental requirement in an unexpected way.

Let us say in conclusion that at no stage may we suppose that complex as yet uninvestigated behaviour mechanisms must necessarily utilize only the physiological properties that build up the simpler ones already known. We have no reason to suppose that all behaviour could be built up from the elementary properties of the reflex response. But once the behaviour patterns of an animal have been objectively described and their special qualities discerned, in the way Russell (1934) has so strongly urged, there is also no reason to suppose that they will not be susceptible of analysis. For the complete investigation of behaviour we need not only discernment of the qualities of the phenomena observed but also analysis of the mechanisms utilized in them. Not the least interesting result of such an investigation is that it brings to light the fact that these mechanisms are of few kinds and of unique properties, a limitation which appears to be a feature of the Universe we live in.

SUMMARY

1. Nowithstanding the purposive character of even the simplest responses of Coelenterates, such as the protective closure, their physiological mechanism can be analysed with substantial completeness. The response is operated by the utilization of certain physiological systems with standard properties. Similar systems are independently 'utilized' by quite unrelated organisms, as in the giant fibre systems operating the retraction response of Annelids.

2. Behaviour patterns of different organisms aiming at the same goal, such as protective responses, are not always operated by utilization of the same physiological systems, as we see by comparing the retraction mechanism of an Actinian and of *Stentor*. Conversely, the same physiological system may be utilized in different animals to different ends, as in the through conduction systems of Actinians and Scyphomedusae.

3. Consideration of the feeding responses of *Anemonia* and *Hydra* show the possibility that notwithstanding their essential similarity in both organization and behaviour, different physiological properties may be utilized in their response machinery.

4. The part played by nematocysts in Coelenterate feeding shows how any convenient property of living matter, even a non-nervous one, may be built into a behaviour pattern. The parts played by the different kinds of nematocyst of *Hydra* in its various behaviour patterns show the manner in which the same system comes to be utilized in different activities directed to different goals.

5. In the examples of behaviour first considered, the organism is a passive instrument, only responding to stimuli and contributing nothing to the behaviour by its own activity. Observations and experiments on the preliminary feeding activity of *Metridium* are described which show that the 'resting' animal is continually and inherently active, and that the response to certain food solutions takes place, not as a simple reflex, but through modification of this inherent activity. The modified inherent activity characteristic of the preliminary feeding reactions varies greatly in its extent according to the state of the animal. The threshold for its release may at times be so low that in starved animals it may occur without any food stimulus.

6. The physiological mechanism of this inherent activity bears an analogy to some complex activities in animals with a higher nervous system, particularly to locomotor activity. New and complex physiological properties are utilized in the anemone in building up this inherent activity, properties which are not utilized in the simple reflex closure of the disk.

The properties include co-ordination of reciprocally acting muscle systems.

7. As we go from simpler to more complex behaviour patterns we must always be prepared to find new physiological properties utilized to build up the machinery of behaviour. At no stage may we jump to the conclusion that the machinery of uninvestigated complex behaviour utilizes only the properties of systems utilized in simpler activities already investigated.

8. The whole behaviour pattern of *Metridium* relating to food bears a significant analogy to an instinctive behaviour pattern. There is modification of inherent activity of the animal, drive to achieve the goal by various means, and change of pattern on achievement of the goal (food ingestion). Nevertheless, there is every reason to expect that the physiological machinery of such activity can be analysed.

9. In complex as well as in simple behaviour, the need for a particular kind of behaviour pattern may be met by the utilization of different systems in different organisms; there is not necessarily only one physiological mechanism for 'learning'. Fortunately, present knowledge suggests that the number of kinds of system out of which an animal can construct its behaviour machinery is limited. Were it not so, the comparative analysis of behaviour would become impossible.

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SOME OBSERVATIONS ON THE NERVOUS MECHANISMS UNDERLYING THE BEHAVIOUR OF STARFISHES

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I. INTRODUCTION

Not least among the many advantages which the more simply organized animals offer for the analysis of behaviour mechanisms must be counted their ability to base the more striking and evident of their activities on the movements of relatively few systems of organs and parts. This is notably true of starfishes, brittle-stars, and other members of the phylum Echinodermata. All of the more generalized activities of starfishes, for example, are founded upon the movements of but two kinds of organ system, the muscular arm and the finger-like appendages of the arm, the tube feet, while a very wide range of behaviour in the starfish is based solely upon the activities of the feet.

A foot is capable of exhibiting a number of different kinds of movement and of posture, some simple and some complex, and the movements and postures of the individual feet can be variously combined into more extensive patterns of group activity, many of which patterns can be identified with particular courses of behaviour. It is thus possible, by studying the conditions of stimulation and innervation that are appropriate to the development of the variously integrated individual and group movements of the feet, not only to analyse the mechanisms which underlie the nervous integration of activity, but to assess, in general terms, the conditions of nervous control that are associated with the different behavioural states.

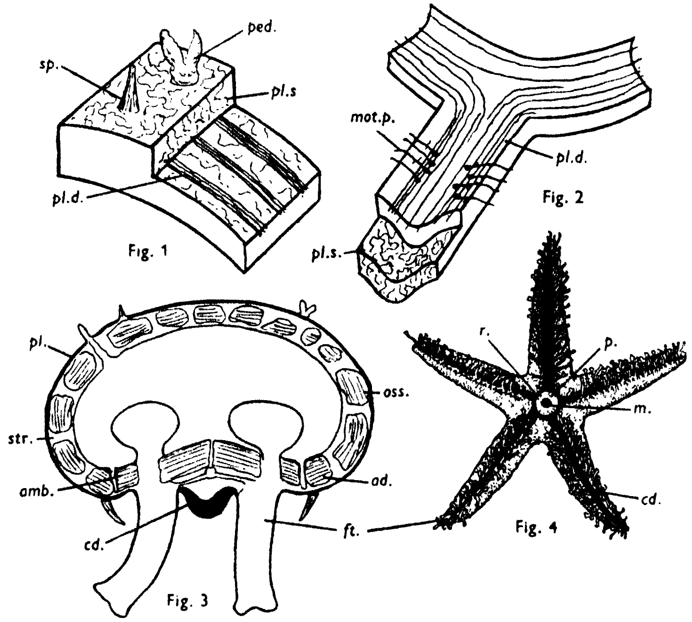
This kind of analysis has been gravely handicapped in the past, however, by the neglect of two lines of anatomical study. In the first place, until recently, practically nothing was known of the anatomy of the starfish nervous system beyond the gross features visible on external inspection; in no single instance, for example, had the nervous connexion between the sensory cells of the integument and the muscles of an effector organ been demonstrated. Secondly, the muscles responsible for the movements and postures of the tube feet and other organs had not in every instance been identified or their mode of action determined.

Some of these deficiencies have now been remedied. The distribution and fine anatomy of the principal systems of association and motor nerve tracts have recently been worked out in three of the commoner British starfishes (Smith, 1937, 1946; and work in the course of publication) by the examination of vitally stained and fixed material, and the routes through which excitation is conducted in its passage from the integumentary receptors to the various muscle systems of the feet and other movable parts defined. The muscular anatomy and the mechanics of movement of the podia have also been reinvestigated (Smith, 1947). The information gained from these anatomical studies has prompted a re-examination of some aspects of the nervous control of movement, the results of which are summarized in this contribution. A brief description of the nervous anatomy of the starfish and of the mechanics of movement of the feet is therefore given by way of introduction to the main, analytical, part of the account. Limitation of space has not allowed of the inclusion in the text of a complete series of references to work relevant to the analysis, but the contributions of Diebschlag (1938), Fraenkel (1928), Hopkins (1926), Jennings (1907), Kalmus (1929), Mangold (1908*a*, *b*), and Moore (1918, 1939, 1945), among other authors, have been freely drawn upon.

II. THE ORGANIZATION AND NERVOUS ANATOMY OF A STARFISH

Starfishes (Fig. 4) are radially symmetrical animals with a central disk and (usually) five radiating arms. The upper and lateral surfaces of the disk and arms are beset with a great number of more or less randomly arranged spines and pedicellaria (Fig. 1, *sp.*, *ped.*). Pedicellariae are pincer-like structures whose function is to seize, hold and paralyse small animals which come into contact with the integument. The under-surface of the disk is perforated centrally by the mouth (Fig. 4, *m.*) bordered by a membranous peristome (*p.*) with a much thickened margin. This thickening is the circumoral nerve ring (*r.*) which is continued along the under-side of each of the arms as a V-shaped radial nerve cord (Figs. 3, 4, *cd.*). On either side of the nerve cord is a row of feet (*ft.*), there being upwards of 200 feet in each arm.

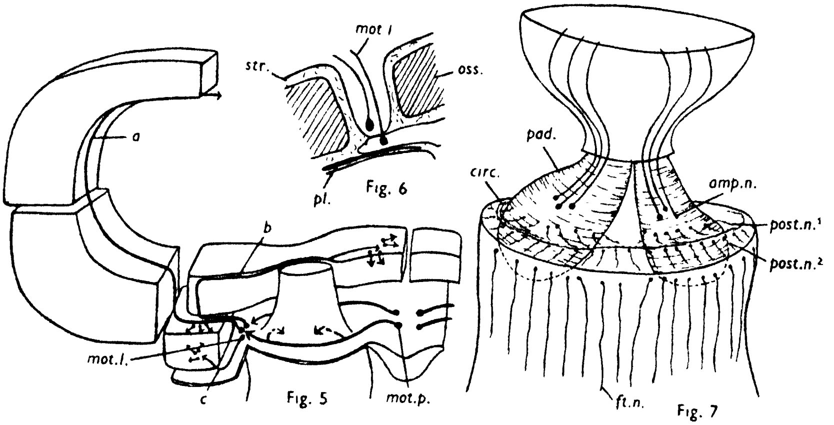
The internal anatomy of the starfish is somewhat complex and need not concern us here, but the body wall which bounds the internal cavities and viscera requires description because its structure bears directly on the architecture of the nervous system. The body wall (Fig. 6) has four main layers. An outer ectoderm comprises epithelial cells, mucus glands and sensory cells, the latter to the number of about 4000 per sq.mm. of surface. A nervous plexus (*pl.*) made up of the fibres of deep-seated ganglion cells lies below the epithelium, and with these the centripetal fibres of the sensory cells make synaptic contact. Over the dorsal and lateral surfaces of the integument the plexus is relatively thin and ill-developed, but in the radial nerve cord and nerve ring it is much thickened. The plexus appears always to be differentiated (Fig. 1) into a superficial zone (*pl. s.*) of randomly arranged fibres and a deep zone (*pl. d.*) organized into linear tracts. A stroma of mesodermal collagen fibres (Fig. 6, *str.*) lies to the inside of the plexus. Over most of the body wall it is much thickened, and its interstices are filled with calcite laid down in the form of separate but closely fitting ossicles (*oss.*). The inner face of the fibrous stroma, next the body cavity, is lined with an epithelium with which are associated muscles and motor nerve fibres. The nervous system of the starfish thus appears to be divided into two sections, one, the sensory and association pathways of the ectoderm, lying to the outside and the other, the motor tracts, to the inside of the stroma. Where the latter is thick and calcified the division is complete, there being no nerve fibres within the substance of the wall. Above the nerve cord and lateral to the feet (Fig. 6), however, the stroma is a thin, loosely woven, uncalcified lamella not more than 2–3 μ thick. The association pathways of the ectoderm (*pl.*) and the motor elements (*mot. l.*) of the mesothelia are here brought into close conjunction, and in some few instances synapses have been observed. The consequence of this arrangement is that excitation originating in the receptors of the integument is trans-



Figs. 1–4.

mitted to the motor neurons either by way of the nerve cord or via the lateral motor arcs.

The form of the body wall imposes on the nervous system a further character of great functional significance. Although the ossicles of the dorsal integument are developed rather at random, those which bound the margins and roof of the shallow ambulacral groove on the under-face of the arm are arranged in bilaterally symmetrical pairs along the length of the arm, the roofing (ambulacral) ossicles (Fig. 3, *amb.*) alternating regularly with the marginal (adambulacral) pieces (*ad.*). The tube feet correspond in number and position to the ossicles, and the arm thus comes to bear the imprint of segmentation. The nerve arcs, both in respect to their association and motor components, conform to this segmental pattern. Fig. 5 illustrates the arrangement of the principal motor pathways on one side of a segment, it being understood that the pattern is repeated along the arm in each of its 100–150 segments.



Figs. 5–7.

Excitation conducted through the association plexus is transmitted via the nerve cord to groups of motor neurons (*mot. p.*) lying in the floor of the so-called perihaemal sinus. These neurons have axons which encircle the foot to make junction with the neurons (*mot. l.*) of the lateral motor centre. The axons of the latter neurons extend in three main tracts (*a*, *b* and *c*) to various parts of the arm. They do not, however, directly innervate muscles but conduct excitation to groups of neurons (represented in the figure by small arrows) one of which accompanies each of the several muscle systems within the arm segment. This terminal motor complex may contain several neurons linked in series, but the last element only of the chain has its axon terminating on the muscle fibres.

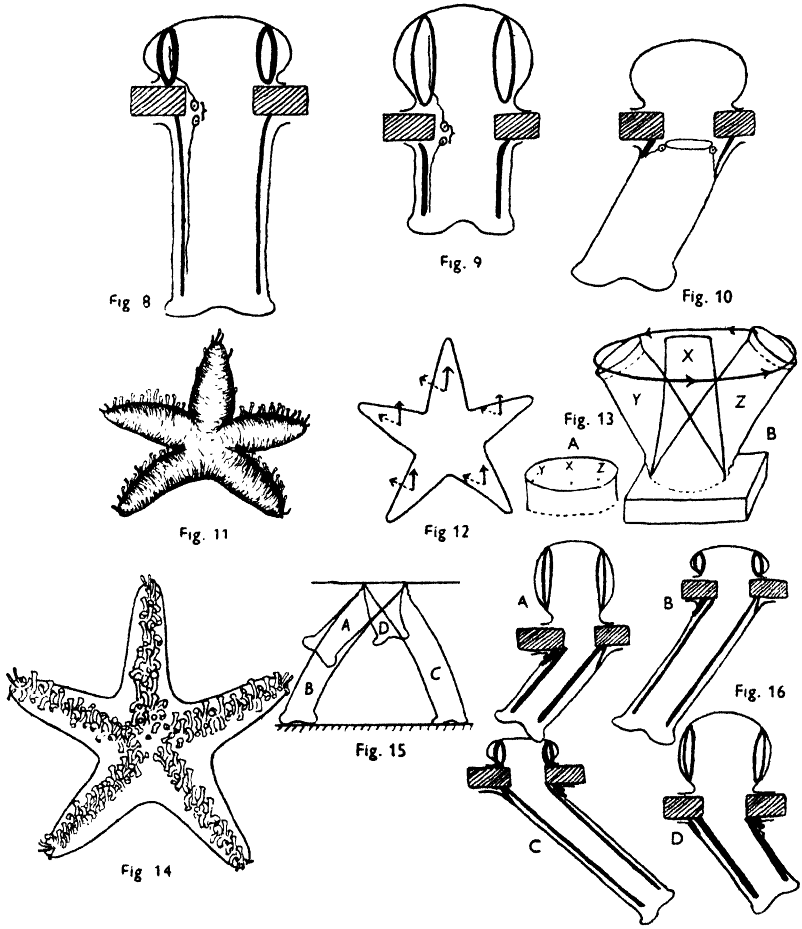
The axons of the motor neurons in the roof of the nerve cord, in encompassing the base of the foot, come to lie in close apposition to two pads of connective tissue situated medially and laterally within the cavity of the podium (Fig. 7, *pad.*). Within these pads are a number of multipolar neurons (not shown in the figure) whose function would appear, on anatomical grounds, to receive excitation from the extrinsic motor axons and to distribute it to three series of neurons also contained within the connective tissue pads. One group (*amp. n.*), situated in the core of the pads, has long axons which enter the neck of the ampulla to synapse with further neurons, the axon of which terminates on the ampulla muscles. The second series of neurons in the pad (*ft. n.*) innervate the retractor muscles of the foot. They are connected with the multipolar distributors through short internuncial fibres which, too, are omitted from the figure. The third group (*post. n.*[1]) has its cell bodies in the cortex of the pad. Their axons radiate to the periphery of the foot to connect with other neurons (*post. n.*[2]) whose short axons supply a ring of postural muscle fibres, later to be described. The several neurons of this third series are connected one with another through a ring of circumferentially disposed fibres (*circ.*).

Thus far the nervous system has been described as a number of arcs organized into discrete and strictly segmental series. The deeper plexus of the radial cord (Fig. 2, *pl. d.*) is, however, differentiated into tracts which run longitudinally along the arm, some of them continuing into the nerve ring and so down the other radial cords; the nerve plexus of the dorsal integument, on the other hand, lacks these longitudinal tracts. It would appear, therefore, that the segments of the arm are in nervous connexion chiefly, if not entirely, through the radial cord, and that the tracts of the cord are responsible for co-ordinating the activities of organ systems situated in widely separated parts of the body.

III. MECHANICS OF THE LOCOMOTORY STEP AND THE PATTERNS OF LOCOMOTORY ACTIVITY

Figs. 8–16 illustrate, schematically, the principal movements and postures of the feet. The locomotory step is shown in Figs. 15 and 16. A foot, when in the retracted position, is thrust out in the line of advance of the animal (A). It then protracts, applies the terminal sucker to the substratum (B), and with the sucker as the fulcrum, levers the arm forward through an angle of about 90°. Having reached the position (C), the foot is withdrawn, and during its withdrawal (D) is re-oriented in the forward direction. The cycle is then repeated.

The system of movements which make up the locomotory step derives from the contraction of four series of muscles, arranged in two opposing pairs. One pair, the ampulla muscles and the retractors of the foot, provide for the reciprocal movements of protraction and retraction (Figs. 8, 9). The vertically set, circumferential fibres of the ampulla, on contraction (Fig. 8), reduce the volume of the ampulla and drive fluid into the foot which protracts; retraction of the foot (Fig. 9) is brought about by the contraction of the cylindrical sheath of longitudinal fibres contained within the wall of the foot. Fluid passes, during the withdrawal of the foot, into the ampulla, the muscles of which relax to allow of its dilation.



Figs. 8–16.

Pointing of the foot (Fig. 10) is effected by the reciprocal contraction and relaxation of the diametrically opposed fibres of a ring of muscles which, originating on the under-surface of the ambulacral ossicles, are inserted into the wall of the podium near its attached base. The foot can be inclined to any point of the compass by the operation of different sets of diametrically opposed muscles; the postures *X*, *Y* and *Z* of Fig. 13 B, for example, derive from the contraction of the muscles *X*, *Y* and *Z* of Fig. 13 A, with the reciprocal relaxation of the muscles whose position is indicated by the corresponding broken letters.

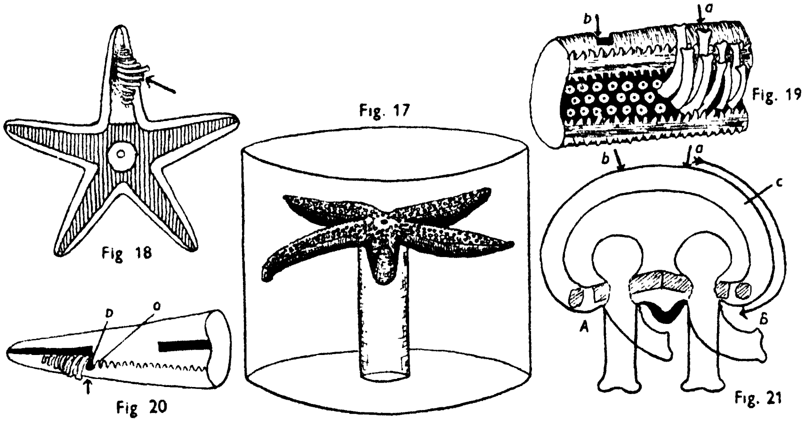
Stepping (Fig. 16 A, B, C and D) combines protraction, retraction and pointing in determinate combinations and sequences. The step can be analysed into four phases of static posture (A, B, C and D) linked together by four movements. Each posture is characterized by the contraction of one member of each of the two pairs of opposing muscles, and the linking movement is ushered in by a reversal of the contraction-relaxation relationships of one of the two pairs of mutually antagonistic muscles.

When a starfish walks, almost all of its thousand or so feet are engaged in stepping. The overall pattern of locomotory activity (Fig. 14) embodies two principal characteristics, namely, a complete absence of any determinate phase relationship in the movements of the several members of a stepping series, and (Fig. 11) a common direction of movement of all the stepping feet. The major variations in this arhythmic undirectional pattern of stepping are brought about in three ways: (*a*) by individual and general variations in the pace of stepping—the starfish *Asterias rubens* can vary the rate from about 3 to 10 steps a minute; (*b*) by disruptions of the generalized pattern of movement in consequence of some of the feet coming to rest or undertaking activities of a non-locomotory nature; and (*c*) by changes in the common direction of stepping (Fig. 12). Each attribute of stepping activity and each kind of variation provides the means of analysing, under appropriate conditions of experimentation, some particular aspect of the nervous mechanisms which lead to the development of integrated patterns of movement of the feet and to the pursuit of purposive activities by the starfish.

IV. THE SELECTION OF MATERIAL AND OF THE CONDITIONS OF EXPERIMENT

Before, however, any estimate can be made of the conditions of stimulation and of innervation appropriate to the development of the different kinds of individual and group activity of the feet, it is necessary first to ensure, so far as is practicable, that the animals are not exposed during the course of experiments and observations to uncontrolled extraneous stimuli, and that the starfishes used on different occasions are comparable in their inherent capacity for response.

The main difficulty attending the first requirement is to relieve the animal (and particularly its feet) from external contacts. It is useless merely to suspend a starfish in water, for the arms then twist and bend almost incessantly and set up surges of excitation against the fluctuating background of which it is impossible to estimate the significance of experimentally imposed stimuli. A more satisfactory way of setting up the animal is to invert it over the open end of a glass tube broad enough to support the margin of the disk while leaving the arms free (Fig. 17). An animal thus supported may for a time attempt to 'right' itself by twisting and dropping its arms, but if the feet are unable to acquire contact with the tube or dish the arms after a time cease to move and remain horizontally poised. Animals were rejected if after 5 min. in the inverted position they continued to twist and turn. So, too, were animals whose feet remained motionless after a similar interval, for such animals were usually found to be intractable to stimulation. Starfishes were regarded as 'normal' and suitable for experiment if after this time the arms were motionless but the feet were actively stepping.



Figs. 17–21.

V. EXTEROCEPTIVE STIMULATION AND THE SPREAD OF EXCITATION

The manner in which excitation is irradiated through the nervous system of a starfish, and the effects it evokes by virtue of its transmission through differently organized parts of the system, is very clearly illustrated by the movements which the feet and other action systems make in response to the gentle pressure of a probe laid against the dorsal integument of one of the arms (Fig. 18). Four distinct patterns of response are exhibited. They are of progressively increasing extension and are symptomatic of the spread of excitation into nerve tracts of increasingly wider distribution.

(1) *Responses elicited through the nerve net of the dorsal integument*

The pedicellariae and spines of the dorsal integument bend towards the stimulated area and the pedicellariae open and close their valves. The most remarkable feature of this pattern of response is its extreme localization. Spines and pedicellariae at a distance of 1–2 mm. show marked bending; at 3–5 mm. the movements are but feeble and transient, while at greater distances they are altogether absent. Exact analysis of the grading of the response in relation to the frequency and intensity of the stimulus is lacking, but there can be little doubt that the nerve plexus of the dorsal sheath, with its properties of decremental and diffuse conduction, exhibits qualities similar to those which Pantin (1935*a*, *b*) has demonstrated for the Coelenterate nerve net. The anatomy of the nerve supply to the spines and pedicellariae is fully consistent with this hypothesis. Both systems of organs are set on the surface of the integument, and the muscles by which they are moved originate from the outer layer of the ectoderm (Fig. 1). They are consequently innervated through the short, randomly arranged fibres of the superficial plexus which, by virtue of its numerous interneural junctions and presumed necessity for facilitation, is incapable of transmitting the centrifugally dispersed excitation for more than a short distance from its point of origin.

(2) *Responses elicited through the segmental nerve arcs*

A further consequence of the stimulation of the dorsal integument is to evoke the extension and ipsilateral bending of the foot (Fig. 18) lying immediately below the point of stimulation. Evidently, excitation originating in the receptors of the dorsal integument is capable of being irradiated beyond the limits defined by the responses of the spines and pedicellariae. The orientation of the tracts responsible for this more extensive transmission can be ascertained by a simple experiment (Fig. 19). When the integument of an arm, the feet of which are retracted, is stimulated at (*a*) the feet below the stimulated point, and on either side of it, protract and bend. If, however, a longitudinal cut of not less than about 2 mm. length be made in the skin, and the stimulus be applied on the dorsal side of the cut and in the same transverse plane (*b*), no response can be obtained from the underlying feet. The transmitted excitation is clearly confined to tracts running transversely round the arm with little or no longitudinal spread of excitation. Fig. 20 records the result of an experiment to show that the transverse tracts are strictly segmental in the sense previously defined (p. 199). The nerve cord is stripped from a part of the length of an arm. On touching the adambulacral spines (which are segmental in arrangement) of the denervated section no response can be elicited from the feet. Stimulation of the spine (*a*), for example, which is only 1 mm. distant, in the longitudinal direction, from the cut end of the nerve cord, is without effect. On touching the next spine (*b*, shown in black), however, the response is fully developed throughout the innervated section.

One further property of the transverse segmental tracts remains to be mentioned. When, as in Fig. 21, the dorsal integument is stimulated at (*a*), the feet *A* and *B* on either side of the nerve cord exhibit an ipsilateral response. Stimulation at (*b*) induces a contrary ipsilateral movement. If, however, the integument is cut at (*c*) and the stimulus reapplied at (*a*) there is no response. This shows that the segmental tracts conduct only in a ventral direction and that, as a conducting system, the arm is divided into two halves, with the mid-dorsal line as the excitation watershed. These various attributes of segmental conduction find their anatomical basis in the deep-lying segmental tracts of the ectodermal plexus (Fig. 1 *pl. d.*) which, from the nature of the reflex responses evoked through them, are polarized and through-conducting. Each transmits excitation to the nerve cord, and thence via the segmental motor neurons to the foot, thus completing the circuit of the segmental nerve arc.

(3) *Responses elicited through extra-segmental nerve arcs*

These responses are well exemplified by the lateral protraction of feet on either side of the stimulated segment (Fig. 18). They are dependent for their appearance on the integrity of the intervening length of nerve cord. As the figures show, the feet exhibit a progressively diminishing response the further they are from the stimulated segment, the pattern rarely extending beyond the limits of the stimulated arm. This visible manifestation of decremental conduction suggests that the tracts of the nerve cord may include chains of short-fibred intersegmental neurons. Neurons of this kind have not, however, as yet been seen in stained preparations.

(4) *Generalized, co-ordinated responses indicative of central nervous control*

One further effect of exteroceptive stimulation remains to be considered. The extra-segmental reflex responses of the feet have been shown to have a limited extension, the podia outside the range of induced reflex activity (represented in Fig. 18 by the shaded area) appearing to continue in their stepping as if unaffected by the stimulus. This is not, however, the case, for within 2 or 3 sec. of the application of the stimulus the pace of stepping rises and, more often than not, the direction of stepping is changed. The two kinds of change are contemporary and are general to all the stepping feet. On severing the nerve cord in one or more of the arms the feet distal to the cut or cuts fail to show a change of pattern, but transection of other parts of the nervous system is without effect. The alteration in the pace and direction of the step must therefore be symptomatic of a change of excitatory state of neurons within the cord and nerve ring that are capable of transmitting that state to all of the feet. The only neurons which appear, on anatomical grounds, to have this property, are the deep-lying neurons within the cord and ring (Fig. 2 *pl. d.*) whose fibres, organized into longitudinal tracts, run without interruption from one arm to another by way of the nerve ring.

In summarizing the conclusions to be drawn from these observations it may be noted:

(1) That the patterns of response which follow localized stimulation of the integument of a starfish reflect the irradiation of excitation into nervous pathways of progressively increasing extension, first to the superficial plexus of the integument, then, in order, to the segmental arcs and the extra-segmental arcs, and finally, to the central pathways of the radial cord and nerve ring.

(2) That the responses which are elicited through the four systems of nerve tracts, even when they concern the activities of one kind of organ such as the tube foot, differ not only quantitatively but also in quality, and are probably indicative of the modification of the excitatory state in consequence of its transference from one set of neurons to another.

(3) That the responses elicited through the more localized arcs tend to be developed to the exclusion of the generalized, co-ordinated activities which are an expression of central control.

This dual aspect of nervous control, the one peripheral and reflex, the other central and generalized, is of the utmost significance in the integration of the locomotory step from its component movements and postures and in the development of generalized patterns of movement of the feet.

VI. CONDITIONS OF DEVELOPMENT OF THE COMPONENT MOVEMENTS AND POSTURES OF THE STEP

(1) *Protraction and retraction*

These movements, when regarded as unoriented activities, developed independently of the postural attitudes with which they are associated in the locomotory step, are wholly reflex in character. They can be initiated in response to exteroceptive stimulation in single segments isolated from their neighbours by double transection of the nerve cord, or they can be elicited as extra-segmental responses, but neither retraction nor protraction can be induced as simultaneously and generally occurring responses after localized stimulation of the integument. It is true that if a wave breaks over a starfish all the feet retract simultaneously, and that if the intensity of photic stimulation is suddenly reduced all the feet protract, but in both instances the stimulation is general and the animal is behaving not as a unit but as a series of reflexly-acting segments.

Some indication of the nature of the excitatory states appropriate to retraction and to the reciprocal movement of protraction can be gained from observations on the responses elicited by stimuli of varying intensities applied to different parts of the surface of an arm segment. Contacts with the nerve cord (Fig. 22*a*) evoke a long-continuing retraction of the adjacent feet. Direct stimulation of the foot (*b*) also leads to retraction, but the response is usually limited to the stimulated podium. The consequences of stimulating the dorsal integument are more varied. If a probe is rubbed energetically against the ventral face of the integument (*c*), the foot retracts, but after a short interval it then protracts. Weaker stimulation at the same place, or stronger stimuli applied to a more dorsal area of the skin, have the effect of reducing the initial retraction response to a momentary flicker, the foot quickly protracting and bending over towards the stimulated region. Weak, dorsal stimuli (*d*) evoke protraction alone.

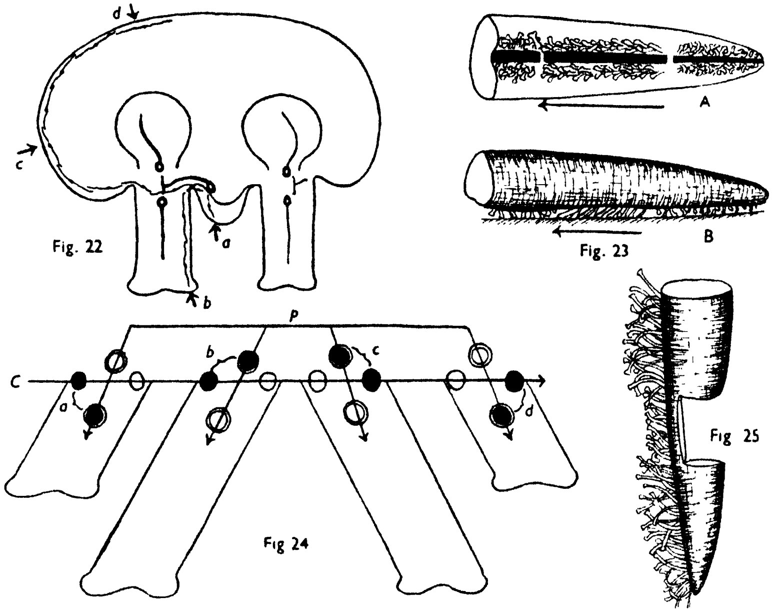


Fig. 22–25.

Protraction and retraction, as reciprocal movements, reflect reversible states of excitation and inhibition in the motor neurons of the foot cavity whose axons supply respectively the ampulla and foot retractor muscles.

The observations quoted imply that reciprocal excitation and inhibition of these terminal motor neurons are not a consequence of their independent innervation but is rather a measure of different states of excitation set up within a common afferent arc by stimuli of different intensities and (or) loci. This is in keeping with the anatomical picture of the two sets of neurons supplied through a common (segmental) association and motor path. One is tempted to suggest that retraction, as the primary response, is conditioned by the receipt by the terminal motor neurons of an initial high-frequency volley of impulses, and that protraction follows the receipt of low-frequency after-discharge effects, the two sets of neurons as it were resonating to different frequency ranges. The invariable retraction of the foot after stimulation of the nerve cord, where the receptors are only about 1 mm. distant from the final common motor path, would, on this basis, reflect the passage of excitation through relatively few neurons and a minimum of alternative pathways with the consequent transmission, through the final common pathway, of a rapid volley of impulses with little or no after-discharge. The tracts of the dorsal sheath, on the other hand, with their greater number of linked neurons and subsidiary side-arcs would, in consequence of the necessity for facilitation of the many interneural junctions, cause abbreviation of the primary volley and prolongation of the secondary reverberation. This would lead to the observed extinction of the retraction response and the promotion of the protraction movement.

It is consistent with this hypothesis that reflex protraction can be induced by narcotization of a starfish with magnesium salts, and by a reduction in the intensity of photic stimulation. These suppositions concerning the promotion of the retraction and protraction movements apart there remain, however, the established facts that the two movements reflect reversible states of excitation and inhibition of the intrinsic motor neurons of the foot, that these states are of local origin and significance, and that they are not directly conditioned by pre-existing states of central excitation.

(2) *Pointing and pivoting*

The assumption and maintenance by a foot of a position of postural pointing can be ascribed, in some instances, to reflex control, as when, for example, a podium stretches out and bends towards an area of the dorsal integument that has been stimulated (Figs. 18–19). This lateral orientation of the foot is not, however, a part of the step, it is rather a deflexion from stepping activity. In isolated arms the direction of stepping is along the line of the arm, and before stepping can occur the feet must first acquire this common line of posture. They cannot, however, do this unless they are connected with a certain minimum length of nerve cord. In inverted arms, where the feet are unable to make external contacts (Fig. 23A), the minimum length of nerve cord is 2–3 cm., though when the feet are allowed to touch the ground (Fig. 23B) patterns of unidirectional pointing can be established in pieces of shorter length. It would seem that the neurons of the foot which innervate diametrically opposed muscle fibres within the sheath of postural muscles require to be excited through tracts which have a distribution along the length of the nerve cord, and that it is not so much the absolute number of the neurons within these tracts as the product of their number and the level of their activity (conditioned, in the experiment cited, by the contact or lack of contact of the feet) which determines whether or not pointing shall occur. Mention has been made (p. 202) of the fact that patterns of unidirectional pointing and changes in the direction of common pointing are always manifested simultaneously and generally throughout the system of feet, from which it follows that the neurons most directly concerned in initiating and transmitting excitation to the postural neurons of the foot are the deep-lying and through-conducting systems of the radial nerve cords and circumoral nerve ring. These considerations might lead one to anticipate that the pivoting movement of the foot, which is an expression of the reversal of the excitatory and inhibitory states of the neurons supplying the operative muscles of the postural ring, is likewise governed by pre-existing conditions of central nervous discharge. This question of the origin of the pivoting movement is, however, more conveniently discussed in connexion with the integration of the locomotory step.

VII. THE NERVOUS INTEGRATION OF THE LOCOMOTORY STEP FROM ITS COMPONENT MOVEMENTS AND POSTURES

The conditions of excitation and inhibition affecting the intrinsic neurons of the foot during the performance of an 'idealized' step are set out in Fig. 24. Representative neurons of the systems supplying the ampulla and foot retractor muscles are shown by a double ring, those innervating the operative postural muscles by single circles. Excited neurons are figured in black, those in the inhibitory state are unshaded. Each postural phase of the step is characterized by the co-existence of a state of excitation within one member of each of the two pairs of mutually antagonistic neurons. The change from one posture to another is indicative of a reversal of the excitation-inhibition relationships of one of the two pairs of neurons, and the 'idealized' step can thus be expressed in terms of a cycle of successive excitations of different muscles by linked pairs of neurons (*a*, *b*, *c* and *d* in the figure).

Previous considerations have led us to suppose that the pair of neurons serving the ampulla and foot retractor muscles reverse their states of excitation and inhibition in response to localized conditions of excitation; they are essentially under peripheral control, a feature indicated in the figure by the guide-line *P*. The neurons responsible for postural changes, on the other hand, are supplied through central tracts and are presumably affected by central discharge *C*. The question now arises as to whether, when two neurons, one of each pair, exhibit contemporary excitation, the one member continues to be affected by peripheral and the other by central excitation, or whether an entirely new set of conditions is initiated by virtue of their linkage.

There is some evidence that they continue, even when so paired, to be subject to different and independently originating nervous influences. When, for example, a piece of integument is removed from a starfish arm (Fig. 25) the feet of the de-afferentated section continue to step as before, but the cycle of the step is conducted at about half the normal length of protraction. Evidently, although the linkages necessary for stepping have not been impaired, the one set of neurons responsible for protraction and retraction have been directly and independently affected by the changed circumstances of peripheral stimulation. The reverse condition, where the neurons responsible for orienting the feet and for evoking the pivoting movement are affected independently of the protractor-retractor neurons, is well exemplified by the events which led to variations in the pace of stepping. When a starfish is set up in the 1 saltted position, stepping is quickly established at a steady rate of about sunteps a minute, whereafter, over a period of several hours, the rate gradually declines to 2–3 steps a minute before muscle tone is lost and stepping ceases. The graph (Fig. 26) reveals the cause of the retardation. It shows the duration of the constituent phases of posture and movement in steps of different total duration. The slowing down of the step and its ultimate disruption is almost entirely due to the progressive prolongation of the phase of anteriorly oriented protraction, and is a measure of the increasing inability of the postural neurons to reverse their excitation-inhibition relationships. If now a starfish which has its feet 'frozen' in this position is gently stimulated, the pivoting movement is effected simultaneously, and generally throughout the system of feet and stepping is resumed. This observation, combined with the fact that retardations and accelerations of the step are common and equal to all the stepping feet and occur without any concomitant shortening of the step, clearly show that (*a*) the postural neurons of the foot are affected by changing states of central excitation, (*b*) the protractor-retractor neurons are unaffected by these changes, and (*c*) the state of excitation or of inhibition of the postural neurons can be affected independently of the contemporary states of excitation and inhibition of the retractor-protractor series.

There remains for consideration the question as to why the movements and postures of the feet are displayed in a particular and invariable sequence, or to put the question in another way: by what mechanisms is it ensured that the transfer of excitation shall affect the four representative neurons in an order which represents a sequence of alternating reversals of the excitation-inhibition relationships of first the protractor-retractor neurons and then the anterior and posterior postural neurons? It is evident that the rhythm of the movements, and therefore the order of the transfer, is not absolutely determined by pre-existing central rhythms of excitation for, if this were so, some determinate phase relationship would be expected in the movements of the several members of the rows of tube feet. There is, in fact, no such relationship; the movements are entirely arhythmic. It must be inferred therefore that while patterns of central nervous discharge serve to provide the conditions pre-requisite to the integration of the step, they do not directly dictate the sequence of its movements. Their rôle in this connexion is twofold. The first is passive in the sense that the centrally instituted patterns of excitation extinguish the local, reflexly developed states which tend to disrupt the step by deflecting the foot to other activities. The second is an active promotion in that central activity is prerequisite to the development within the neurons that innervate the postural muscles of the foot of the states of excitation and inhibition necessary for its pointing and pivoting.

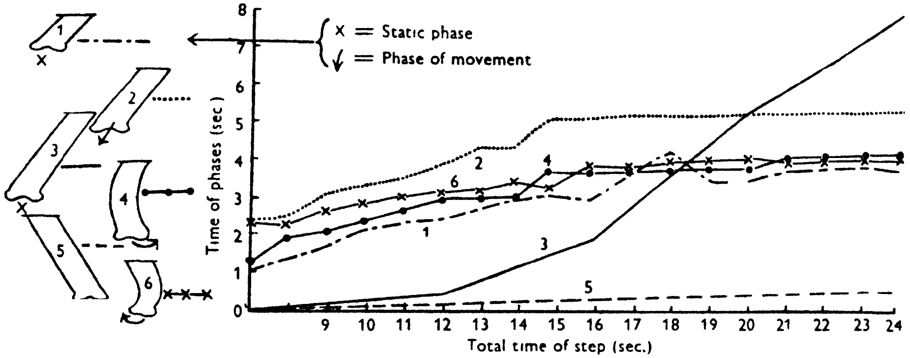


Fig 26

How then is the sequence of the step determined? If exteroceptive stimuli, acting through peripheral arcs or central tracts, fail to provide the timing mechanism, the integration of the step must be ascribed to cycles of excitation developed within the foot itself, either through proprioceptor activity or through the mutual interaction of the intrinsic motor neurons. There is, unfortunately, no anatomical evidence of the presence of proprioceptors within the muscles of echinoderms, though that is not to say that they may not be present, and though it is known that the intrinsic motor neurons of the foot are connected one with another (Fig. 7), the pattern of the connexions is too confused to permit of any final conclusions concerning the precise nature of the linkages. It is, however, possible that some light may be thrown on the linking mechanisms by a study of the effects of localized and graded stimuli applied to the foot at different phases of the stepping cycle and by a survey of the conditions of stimulation that are associated with different aberrations of the step. The possibilities inherent in this method of analysis may be illustrated by reference to a naturally occurring deviation of the actual locomotory step from the 'idealized' cycle. It is to be observed (Fig. 15) that the foot, having completed its backward pivoting movement (*C*), does not retract into the posteriorly oriented position as represented by phase *D* (Fig. 16D) of the 'idealized' step. The foot passes directly from phase *C* to phase *A* by a combined movement of withdrawal and forward re-orientation. The omission of phase *D* would imply an incompatibility of contemporary excitation of the neurons responsible respectively for posterior orientation and retraction. The evocation, under experimental conditions of stimulation, of other kinds of aberration might similarly serve to indicate the relative stability or instability of other linkages.

VIII. THE NERVOUS BASIS OF UNIDIRECTIONAL STEPPING

When a starfish walks, all the stepping feet within the five arms point and step in the line of progression. It is customary to refer to the anterior arm, in which the feet have a strictly longitudinal alinement, as the leading arm. As a first stage in the analysis of the orienting mechanisms it is necessary to determine whether the pattern of common orientation derives from the dominating influence of the leading arm or is to be regarded as the result of influences exerted by all five arms.

Hopkins (1926) and Diebschlag (1938) have noted that single arms, lacking connexion with the circumoral nerve ring (Fig. 27B), always (Hopkins) or almost always (Diebschlag) move with the base of the arm foremost, and that single arms which have connexion with a small piece of the nerve ring (Fig. 27A) always (Hopkins) or almost always (Diebschlag) advance with the tip foremost. My own observations show an approximate 97% tendency to proximal or distal progression in the two instances, the remaining 3 % representing a reversal of the direction of movement. The marked disposition of isolated arms, having connexion with the nerve ring, to step in a distal direction and thus to become incipient leading arms, and the significance of the occasional reversal of the direction of movement, is clearly brought out in the performance of an inverted starfish whose nerve ring had been transected in each of the five interradii (Fig. 29A, B and C). For the first 50 min. or so of stepping the feet of all five arms had a distal polarity (Fig. 29A). Within the next 20 min. the feet of one arm (Fig. 29, II) changed to proximal stepping, and at the end of 90 min. all the feet of all five arms had acquired a proximal polarity (Fig. 29C). After this the feet began to lose tone, became unoriented, and ceased to step. These observations would indicate that an arm behaves as a leading arm by virtue of a distal polarity conferred on the feet by an actively discharging 'centre' located in the nerve ring at its point of junction with the radial cord. When this centre becomes inactive, or is removed, proximal pointing ensues. The 3 % distal pointing of isolated arms, lacking a nerve centre, always occurs immediately after the severing of the arm and may therefore be ascribed to abnormal states of excitation following neurectomy.

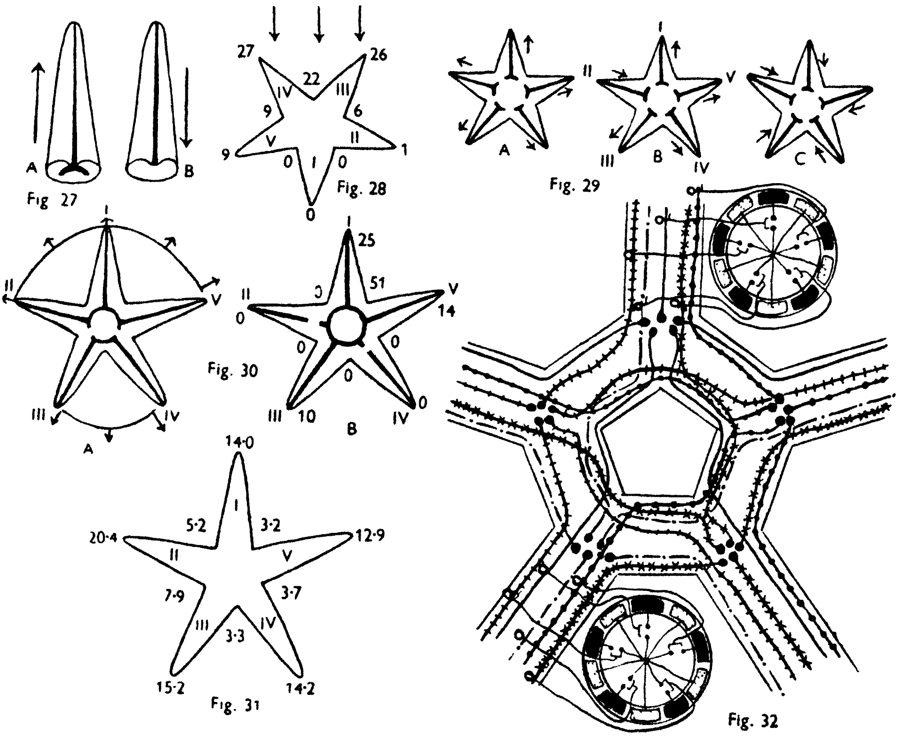


Fig. 27–32.

It may be inferred from these observations that, in the normal uninjured starfish, the distally pointing arm is truly dominant, and that it imposes its direction of movement on the feet of the remaining arms because of the dominant activity of its nerve centre. This conclusion is confirmed by other experiments, of which the two shown in Fig. 30A, B, may serve as examples. In the first (Fig. 30A), the nerve ring has been cut in the interradii II–III and IV–V. It was found that the feet of the arms V, I and II always conformed to a common direction of pointing as did the feet of III and IV, but that the range of common pointing was different in the two nervously isolated parts. If directional co-ordination were the result of the activity of all five centres, these patterns could not possibly be developed, but they are fully explicable in terms of the dominance of one centre. That the dominant arm is the arm with distally pointing feet is also evident from the limitation of the range of pointing of the podia of arms III and IV to the sector enclosed by these arms, and of the feet of V, I and II to the sector enclosed by V and II. In the second experiment (Fig. 30B) the radial nerve cords of II and IV were cut near their junction with the nerve ring. The directions of pointing of the feet were then recorded over a period of 3 hr., the time spent with each radius or interradius in the leading position being expressed as a percentage of the whole. Since the feet never once pointed in the directions II and IV it may be assumed that the nerve centres II and IV were effectively put out of action. This did not, however, prevent the display of unidirectional pointing in the other directions, and the establishment of dominance in each of the remaining centres.

It is of interest here to refer to the habit of many starfishes of reproducing asexually by the autotomy and subsequent regeneration of individual arms. Autotomy is effected in *Phataria*, for example, by the simultaneous distal stepping of the feet of two or more arms which, as it were, walk away from the disk and detach (Monks, 1904). It would seem that this capacity for autotomy reflects some underlying neurophysiological tendency towards the contemporary dominance of more than one centre in these starfishes, a condition that, except for a circumstance now to be examined, can only be induced in *Asterias rubens* by neurectomy.

We may now consider the question as to whether interradial pointing is due to the presence of interradial centres, or is the result of a contemporary dominance of two adjacent radial centres. Observations on many starfishes over a total period of some 65 hr. give the percentage pointing in the several radial and interradial directions shown in Fig. 31. There is a significant difference in the time occupied by radial and interradial pointing, the interradial positions being the less frequently used. It is also to be observed that feet in the interradial positions tend to oscillate from side to side, whereas in the radial positions they are more rigidly oriented. These observations, suggesting that interradial pointing is a resultant activity, receive a more satisfactory demonstration by the experiment shown in Fig. 30B. If specific interradial centres were present, one would expect to find, over a long period of observation, some pointing in every interradial direction; it occurs, in fact, only in the interradius V and I, which alone is flanked on either side by radial centres with an incipient capacity for dominance.

The conclusions to be drawn from these experiments are (1) that unidirectional pointing and stepping reflect the dominant activity of one of five neuron systems, each of which is situated at the base of a radial nerve cord, at its junction with the circumoral nerve ring, (2) that the states of excitation originating in these neurons are transmitted in a through-conduction manner via the circumoral nerve ring and radial cords to all the locomotory feet, (3) that the final motor elements of these tracts are the intrinsic neurons of the foot whose axons supply the postural muscles, and (4) that there are neurons within any one of the five nerve centres are ultimately connected with the postural muscles within the various feet having a like compass orientation. A scheme of innervation which would satisfy these four conditions and which, while going somewhat beyond the observed anatomical pattern (Figs. 2, 5 and 7), is consistent with the details so far ascertained, is presented in Fig. 32.

IX. CHANGES IN THE DIRECTION OF POINTING AND STEPPING

In an inverted starfish, not exposed to directional stimuli, changes in the direction of pointing and stepping tend to occur autonomously. The rate of change varies considerably from one animal to another and is by no means constant in any one animal on different occasions. There is however a certain persistence of disposition in most animals. Some starfishes, for example, are extremely lively and disposed to effect frequent changes, while others tend to fix upon one particular direction of stepping. The differences of disposition (as measured by the rate of change of the direction of movement) of male and female, young and old, starved and satiated, and other antithetic states of starfish life make an interesting study which must however remain outside the scope of this review, but there are two circumstances connected with directional pointing that are of sufficiently general occurrence to be worthy of mention.

The first is the almost invariable tendency for autonomous transfers of dominance from one centre to another to be made in rotation in oscillating clockwise and anticlockwise sequences. It would seem that the neurons of each centre are subject to a periodic rise and fall of activity, and that, by some mutual interaction between the neurons of adjacent centres, a decline in the activity of the one centre is accompanied by, and is related to, a building up of excitatory state in an adjacent centre. The relative slowness of the build-up and the spatial limitation of the transfer suggests that excitation spreads from one centre to another by way of a diffuse and somewhat indirectly coupled system of nervous pathways rather than through organized and definitive tracts. It is thus possible that the relatively unorganized net-like superficial plexus of the nerve ring mediates these transfers.

The second general characteristic of pointing is the notable tendency (in *A. rubens*) for arm II to be the most frequently used leading arm. Although the overriding dominance of nerve centre II is not always apparent over short periods of observation, it is clearly expressed as characteristic of the species in long-term performances such as that shown in Fig. 31, where some 7000 changes of direction were recorded over a period of 65 hr. The tendency for arm II to dominate the locomotory pattern is not to be ascribed to any obvious organizational feature such as greater arm length or a greater number of podia. It appears rather to reflect some intrinsic feature of nervous organization such as, perhaps, the retention of traces of the bilateral symmetry of larva.

In normal environmental conditions the direction which a starfish pursues and the arm it most frequently uses is conditioned more by imposed conditions of external stimulation than by any intrinsic tendency to bilateral behaviour. This can be readily put to test in inverted animals, where, for instance, the intensive stimulation of a leading arm invariably causes that arm to assume a trailing position. Energetic stimulation evidently induces a state of excitation in the nerve centre of the stimulated arm that is incompatible with dominance, and causes the centres farthest removed from the stimulus to take control. The effects of directional light on the pointing of an inverted animal may be cited as a further example (Fig. 28). The arms nearest the light source dominate the locomotory pattern. Those which are farthest away from the light only infrequently come into the lead. They are not directly inhibited from leading, but fail to do so because the transfer of dominance from one centre to another is, as it were, weighted in favour of changes in the direction of III and IV, each transfer in a contrary direction becoming an increasingly improbable event.

X. THE ADAPTIVE NATURE OF THE PERIPHERALLY AND CENTRALLY INITIATED PATTERNS OF ACTIVITY OF THE FEET

The emphasis laid in this account on the nervous mechanisms which underlie the development of the variously integrated patterns of activity of the feet may have diverted attention from their behavioural purport. Behaviour is purposive in the sense that its component activities are of a kind which tend to maintain the animal in an environment favourable first and foremost to its preservation and secondly to growth and reproduction. The function of the nervous system is to take apprisal of environmental changes, and to promote responses which lead to favourable adjustments. It will be appropriate, therefore, by way of conclusion, to underline the regulatory character of the nervous mechanisms we have been considering by showing, in a few selected instances, how environmental stimuli of different qualities and pattern lead to responses which are clearly in the nature of adaptive adjustments to the predisposing environmental situations.

A starfish moving about in a pool or walking over the sea floor is subject to external contacts, variations in light and shade, and to different concentrations of carbon dioxide, oxygen and other substances dissolved in the sea water, all of which, together with other stimuli, are presented in changing patterns affecting different parts and areas of the sensitive integument. The behaviour of an animal, in its normal environment, will be largely determined by the patterns of conjoined reflex and centrally controlled activity induced by a particular pattern or succession of patterns of exteroceptive stimulation to which it is exposed. In this matter of pattern of stimulus it will be recalled (p. 206) that given identical intensity of contact stimulation, the tube feet, dorsal sheath and nerve cord do not possess equivalent capacities for evoking reflex and centrally controlled activities. In particular, sustained and gentle contacts of the feet, while of little effect in evoking reflex activity, are remarkably potent in inducing and maintaining a state of activity in the central neurons. One might therefore suppose that the normal orientation of a starfish with its oral surface towards the substrate and its many podia continually renewing their contact with the ground, is favourable to the maintenance of a state of movement which, under the influence of other superimposed stimuli, can be canalized into more specifically directed activities.

Let us then consider the possible significance, in nature, of responses resulting from superimposed stimuli impinging on the dorsal integument and nerve cord of the starfish. The primary reaction of the feet to stimulation of either area is a reflex retraction, though with stimuli of moderate intensity the movement is momentary and limited to the affected part of the arm. The adaptive value of such a movement, however transitory, is, no doubt, that it screens the foot from any incipiently harmful stimulus until the qualities of the latter have been further tested. If the stimulus is of low intensity, the foot (after the primary movement) will protract, but an intense stimulus, with nociceptive potentialities, evokes a long-continuing retraction which keeps the foot away from the harmful stimulus. These localized responses would, however, have little significance in the life of the organism as a whole were they not attended by the movement of the animal away from the source of injury. But, as has already been observed (p. 208), intensive stimulation of local application, in addition to producing local reflex retraction of the feet, affects the central neurons in such a way as to induce the stepping podia to accelerate their movements and to reorientate the step in a direction which takes the animal away from the stimulus.

One may also visualize situations in which a starfish is subjected to sudden and perhaps intensive stimulation over the whole of its surface; a wave washing over it is a case in point. The animal immediately retracts all its feet which, if previously in contact with the substrate, attach by suction. The starfish is, as it were, instantly transformed, by the generalized condition of stimulation, from a centrally motivated animal into a series of reflexly-acting segments, each with its feet under reflex control. Not until the abnormal conditions of stimulation have passed, and the animal is subjected to a less violent background of contact stimulation, is central control reintroduced and the animal re-established in its co-ordinated locomotory activity.

The circumstances attending reflex protraction of the feet likewise illustrate the adaptive nature of the response. The podia retract under two conditions: (1) as a secondary response to stimuli of normal intensity affecting the dorsal sheath receptors, and (2) on reducing the sensitivity of the receptors or otherwise depressing the general level of excitation within the nervous system. The receipt of non-harmful stimuli is followed by conditions of discharge within the segmental and extra-segmental reflex arcs which favour the protraction of the feet and the exploration of any substance or body coming into contact with the skin that is not inherently noxious. The movement is of adaptive significance in that it may lead to the consummation of some act of potential value to the animal such as attachment to a solid object or the capture of food.

The second of the two situations mentioned above is only likely to arise, in nature, under somewhat abnormal circumstances. When a starfish is kept for a time in a dish of sea water and is allowed partially to exhaust the oxygen dissolved in the water, its podia protract to the full, though later they become flaccid and bent. One may suppose, in view of the sequence ot these events, that protraction is attended by the depression of activity of some or all parts ot the nervous system in consequence of an oxygen lack or possibly because of an excess of carbon dioxide. Protraction of the feet has the effect of exposing a greater area of the thin integument of the starfish to the water and if, as Meyer (1935) has shown, more than half of the total oxygen uptake of *A. rubens* is through the tube feet, and if it is indeed oxygen lack that initiates the movement, the adaptive significance of protraction under conditions of low oxygen tension is obvious.

These observations, though necessarily selective, will, I think, serve to show that the reflexly and centrally controlled patterns of activity of the feet of starfishes are related to the general pattern of exteroceptive stimulation in ways that ensure that the movements contribute to the preservation of the organism and to its maintenance in an environment most suited to its needs.

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THE COMPARATIVE METHOD IN STUDYING INNATE BEHAVIOUR PATTERNS

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I. INTRODUCTION

Like many other branches of biological research, comparative ethology owes its existence to a discovery. The discovery of a new *particulate* process, the function of which is comparatively independent from the function of the organism as a 'whole', always opens a new line of analytical approach. The nature of the process then determines the method most favourable for its experimental investigation, and this method, in its turn, determines the direction in which analytical research continues to proceed. There are many cases in which the development of a new and independent branch of biological science has thus been determined by the character of one particularly favourable object, modern genetics being the most obvious example.

The distinct and particulate physiological process whose discovery may be identified with the origin of comparative ethology as an independent branch of science is represented by a certain type of innate, genetically determined behaviour patterns. Charles Otis Whitman, who was the first to discover them, called them simply 'Instincts'; Oskar Heinroth, who, ten years later, independently rediscovered them, spoke of 'arteigene Triebhandlungen'; I myself have called them 'Instinkthandlungen', 'Erbkoordinationen' and 'Instinktbewegungen' successively, thus further mixing up terminology. I shall, in the conference on terminology, included in the programme of this Symposium, propose the term *endogenous movements* for this type of innate behaviour pattern. Endogenous movements were not only discovered and recognized as a very distinct phenomenon by C. O. Whitman as early as 1898, but also systematically studied and evaluated as taxonomic characters. Nevertheless, their extreme importance as independent elements of behaviour was not generally realized until much later. It was only about 1930 that the discovery of endogenous activities began to act as a centre of crystallization, about which concerted efforts to analyse innate behaviour patterns began to become organized. From then on, however, a quickly growing number of investigators began to apply the methods dictated by the nature of the favourable object which had been discovered so much earlier by Whitman and Heinroth. Thus comparative ethology developed, and therefore it is distinguished by a particular set of methods from all other schools also occupying themselves with the innate behaviour of animals and men. To convey some idea of this particular set of methods is the task I have set myself in this paper.

I shall set about this task from two sides. Before trying to explain what comparative ethology is trying to do, I propose to state, at least as clearly, what it is trying *not* to do. I deem it most necessary to show what particular errors of method, committed by the vitalistic and by the mechanistic schools of behaviour study, we are meticulously trying to avoid, also to make it quite clear why these errors have prevented some fundamental facts about innate behaviour from being discovered half a century sooner than they actually were. After thus defining our own methods *per exclusionem*, I shall proceed to describe them in some detail.

This plan involves some serious criticism of both vitalistic and mechanistic schools, on 'purposive psychology' and some branches of 'Gestalt' psychology, as well as on behaviourism and Pavlov's school of reflexology. I confidently assert that this criticism is irrefutable from the methodological point of view. But I want to make it absolutely clear at once that comparative ethology has no right whatsoever to claim credit for not having repeated the methodical errors of which we accuse vitalists and mechanists. A preconceived idea is a very terrible danger indeed to all inductive research, the very essence of which is unprejudiced observation. The narrow path of inductive natural science is hemmed in on both sides by methodological pitfalls, and is, therefore, by far easiest to walk along blindfolded. And this is exactly what Whitman and Heinroth did. Happily ignorant of the great battle waged by vitalists and mechanists on the field of animal behaviour, happily free from even a working hypothesis, two 'simple zoologists' were just observing the pigeons and ducks they loved, and thus kept to the only way which leads to the accumulation of a sound, unbiased basis of induction, without which no natural science can arise. Small tribute is due to them for not tumbling into the methodological traps, into which vitalists and mechanists succeeded in shouldering each other, as I shall at once proceed to explain. No very great tribute either is due to them for applying the phyletic method to the study of innate behaviour. Being comparative morphologists, it was only natural for them to do so. But by doing it, they discovered a fact which could not be discovered from any but the phyletic point of view; they discovered an independent, particulate function of the central nervous system which, as an element of animal and human behaviour, is, at the very least, equally important as the reflex or the conditioned reaction.

II. CONSEQUENCES OF THE DISPUTE BETWEEN VITALISTIC AND MECHANISTIC SCHOOLS OF BEHAVIOUR STUDY

(1) *Antagonistic exaggerations*

Without any doubt the dispute between vitalism and mechanism has created and exaggerated a number of erroneous preconceptions which subsequently developed into a serious obstacle to analytical research. It would be a difficult task for the historian to decide which side originally sent the pendulum swinging and was responsible for the whole dispute. One must not forget, however, that vitalism is much older than mechanism, that the concept of entelechy comes from Aristotle, and that Johannes Müller and Claude Bernard were quite decidedly vitalists, though they also undoubtedly were the pioneers of analytical physiology. Furthermore, the quarrel has had particularly disastrous results for the analytical investigation of such life processes as embryonic development, regeneration and instinctive behaviour, which, because of their 'wholeness', their 'directedness' and their apparent spontaneity, have, since the very beginning of the dispute, constituted the stronghold of vitalism. Last, but not least, the theoretical and philosophical position of vitalism is much more fundamentally wrong than the few much less portentous methodical errors, of which we accuse the mechanistic schools. For all these reasons I think that we are justified in regarding the vitalistic errors as primary and the reciprocal errors of the mechanists' reactions justified in themselves and only erring through exaggeration.

Vitalists base all their arguments on the purely dogmatic assertion that all life processes are governed by an essentially non-explainable, preternatural 'factor', termed vital force, entelechy, whole-producing factor, and so on. The legitimate answer to this is obviously that no man can know to what extent causal analysis is going to succeed in explaining the processes of life, and that, if a man prefers to meditate upon the supernatural instead of trying to explain things in a natural way, a lamasery is a much more suitable place to do so than a research institute. Instead of which, mechanists replied that all life processes could be explained on the foundation of the laws of classical mechanics. If they relinquished this position later, they only did so because modern physics did.

If vitalists asserted that the existence of organic systems was due to a whole-producing factor (Müller's *ganzmachende Kraft*), and therefore not explainable by way of synthesis, mechanists answered that organic systems could be explained very simply as a sum of very few sorts of elements. They even grew quite dogmatic, in some cases, as to what these elements were.

If vitalists asserted that life was the result of a directing force, mechanists altogether neglected the fact that life processes do, in some cases, continue to run in a certain direction. If vitalists regarded the spontaneity of some life processes as a wonder and as the direct effect of their preternatural factor, mechanists replied by denying the very existence of spontaneous processes. If all the vitalistic factors, vital forces, directing forces, entelechy, instinct and however they were called, were, if we come down to fundamentals, nothing else than the old, preternatural, immortal *soul* in a new guise, mechanists tried to build up a psychology without a soul, and went so far as to neglect the existence of subjective phenomena altogether, even where introspection can tell us some most important facts about our own ways of acting and reacting.

The very nature of these antagonistic exaggerations, into which vitalism and mechanism were forcing each other, makes it intelligible that of all fields of analytical research the investigation of *behaviour* suffered most. Its well-defined character as a 'whole' or system, its directedness and purpose and, in some cases, its evident spontaneity, brought animal behaviour into the very focus of the great dispute. Especially innate behaviour suffered from this, mainly because 'instinct' was one of the cardinal points of dissension. To make clear the methodical point of view held by comparative ethology, I think it necessary to explain in some detail the reciprocal errors which both the vitalistic and the mechanistic schools of behaviour study committed regarding the items mentioned above.

(2) *Reciprocal errors in the treatment of systems*

The conception of the 'whole' was to vitalists the very essence of what never could be explained, being the direct consequence of a preternatural factor. Particular stress was laid on the thesis that a whole could never be explained by synthesis of particulate elements. To this fatal resignation of analysis on the vitalistic side mechanists replied by trying to synthetize all the systems of behaviour on the basis of too few elements. This 'atomism' is an error very characteristic of mechanistic schools. This optimistic attempt was, of course, doomed to failure, but not before it had brought valuable results. Even very crude simplisms have done less damage to the progress of science than resignation.

One of the most deplorable consequences which resulted from the 'atomistic' attempts at explaining behaviour was the counter-recoil of 'Gestalt' psychology. It is an everlasting merit of Gestalt psychologists to have been the first consciously to introduce the method of a truly correlative analysis of organic systems. They were the first to prove the inherent fallacy of the atomistic method of artificially isolating a single chain of causation where in reality there was an immeasurably complex system of interaction. Gestalt psychology should have undertaken to correct the atomistic errors of behaviourism and of reflexology and to introduce the method of a correlative analysis into the study of behaviour. But it did not. Instead of correcting the errors mentioned, it merely committed the reciprocal errors. That is to say, the conception of 'Gestalt' has assumed, with a good number of Gestalt psychologists, a character dangerously akin to that of a vitalistic factor. To very many authors 'Gestalt' is something that neither stands in need of, nor is susceptible to, a natural, physiological explanation. Also, 'Gestalt' has been very badly overrated as an explanatory principle. The characters of 'Gestalt' were uncritically attributed to all 'wholes' and therewith to all organic systems in general. I want to show that this is just as much of an error as it is to regard organism as 'sums' or 'mosaics' consisting of only a few elements.

There is not a single organic system which is really a 'Gestalt', nor one that is a mosaic. Every real organic system is built up on *both* principles, mutual interaction of correlated parts playing a role as well as particulate elements influencing the whole in one-way causation. It is extremely important to know, in every single instance, with what kind of relation analysis has to deal as its method has to conform to the actuality of its object. It is as much a methodological error to treat a one-way causality as if it were an 'amboceptoric' interaction, as to mistake mutual interaction for linear one-way causation.

It is a pre-eminent characteristic of that phenomenon of perception, to which alone the term 'Gestalt' should be applied, that it is largely independent of the elementary parts out of which it is built up. A melody, for instance, retains its particular 'Gestalt' quality, whether it is played on a violin or on a piano, whether it is reproduced in one key or the other. Of course, no real objective system is in the same way independent from its component elements; even the examples chosen by Wolfgang Köhler in his paper on 'Physikalische Gestalten', such as the electrical charge on the spherical conductor, the soap-bubble, etc., decidedly are not. It seems absurdly commonplace to state that a spherical conductor cannot be charged with soap solution and that one cannot blow bubbles from electricity. But this very error has been just as crudely committed again and again by sociologists and group psychologists who were misled by a total contempt of the particulate element. This contempt of the particulate element is legitimate exclusively in the study of 'Gestalt' as a phenomenon of *perception*. In the study of all other kinds of 'wholes' it is disastrous! Every Gestalt is a whole, but not every whole is a 'Gestalt'.

Otto Koehler has defined the organismic whole as a self-regulating system of universal causal interaction of all its parts.* This conception of the whole has nothing metaphysical about it, and the most convinced mechanist must concede that very many organic systems are, at least partially, just this kind of a whole. The system of endocrine glands is a very good example. So far from being a 'Gestalt', a living organism is not even completely a whole in this much wider sense. No organism is a system of really universal interaction of its parts, because every organism contains a number of discriminate parts which, while certainly influencing the form and the function of the whole by a linear one-way causation, are not in turn influenced to an appreciable extent by the whole. Skeleton elements, at least in their definite state of development, are good examples of this kind of independent constituents. Even in the embryo, where interaction generally is much more universal than in the grown organism, there are instances of constituent parts behaving with an amazing independence of the whole, the cells of the two-cell stage of the ascidian embryo being the classical example. Spemann's useful distinction between 'mosaic' embryos and 'regulative' embryos can be, *mutatis mutandis*, applied to any other organic structure or function. The application of an analogous distinction to behaviour seems to me particularly advantageous. The behaviour of the sea-urchin, for instance, is quite literally a mosaic of the independent functions of its organs and can be as literally 'synthetized' by tying a broken-up sea-urchin shell together again with a piece of string. Uexküll, in his drastic manner, has said: 'When a dog runs, the dog is moving his legs, when a sea-urchin runs, the legs are moving the sea-urchin'—which beautifully expresses the difference between the mosaic system and the system of universal interaction.

I do not think that there are any other organic systems, in which independent, mosaic-like constituents and regulative systems of mutual interaction alternate and interlock in so utterly incalculable a manner as they do in the behaviour systems of higher animals. It is, therefore, of superlative importance to ascertain, as early as possible, to which type of system a given object of investigation belongs. It is an extremely pertinent question, whether the dog moves his legs, or the legs the dog, quite especially in group and social psychology. We may summarize the reciprocal methodological errors of vitalists and mechanists by saying that the former dogmatically assume that it is exclusively the whole which is influencing its parts, while mechanists as dogmatically confine their attention to one-way causalities, leading from the part to the whole. Vitalists overrate the 'whole' and totally neglect the particulate element, mechanists neglect

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* Maybe it is necessary to state that Gestalt psychologists strictly reject this definition as a definition of the Gestalt, asserting definitely that a Gestalt is *more* than the sum of all interrelations possible between its elements

regulative interaction and overrate those particulate independent elements which they happened to succeed in isolating. Of these errors the mechanistic one is obviously far less detrimental to research than the 'Gestalt' psychological one. Linear causal influence, acting exclusively from an independent part towards the system as a whole, *does* exist, at least in some cases, and the atomistic investigator is not guilty of any methodological error, as long as he really is examining a comparatively independent constituent part. It is just because they may legitimately be isolated theoretically and experimentally that the discovery of independent constituents always is such a tremendous step forward in analytical research. On the other hand, linear causal influence leading from the whole to the part, as assumed by those overrating the 'Gestalt' principle, simply does not exist, any part influenced from the side of the whole always reacts upon it.

The causal interaction which constitutes wholeness in an organic system is, of course, a very real thing. It is therefore evidently absurd to expect 'wholeness', comparable to that of Gestalt perception, in the behaviour of animals lacking the complicated nervous system which serves as an apparatus of integration and renders possible so universal a form of interaction as occurs in the perceptual functions of higher animals and man. When Alverdes repudiates von Uexküll's conception of the 'reflex republic' of the sea-urchin, on the grounds that it is 'incompatible with the fiction of wholeness' ('der Fiktion der Ganzheitlichkeit widerspreche'), then the misunderstanding is centred in the belief that 'wholeness' is a 'fiction'. Where wholeness in our sense of universal interaction of constituent parts *does* exist, there it is anything but a fiction, and there we have to conform to its reality by applying the slow and cautious method of correlative analysis on a broad front. Where it does *not*, there we may bore in with linear analysis and with experiments isolating constituent parts. But *whether* it exists, and to what extent, is not a question that can be settled out of hand by metaphysical speculation or by the dogmatic misapplication of a slogan, but one that must be decided for every single particular case by patient inductive research.

(3) *Reciprocal errors in the treatment of directedness of behaviour*

The undeniable facts that animal behaviour in most cases develops a definite survival value and that, in some cases, it is directed towards a certain purpose, have, in consequence of the vitalistic-mechanistic dispute, received a treatment very similar to that accorded to the whole.

Survival value and purposivity of innate behaviour did not, to vitalistic thinkers, appear to offer any problems. 'Instinct' and 'purpose' were, by them, spelled with very big capitals and were regarded as direct effects of the non-explainable directive factor of life. Thus *two* problems were hushed up by one pseudo-explanation and therefore appeared as one. Whether an animal is strenuously striving to attain some end or goal, changing its behaviour time and again adaptively to reach it, or whether a stereotyped behaviour pattern automatically develops some survival value, the 'directive factor' is, in the opinion of purposive psychologists, one and the same: the 'infallible' instinct is telling the organism what it has to do. Therefore it is only consistent to identify the survival value of any kind of innate behaviour patterns with the end or goal, at which the organism as a subject is aiming.

It was Wallace Craig who cleared up this confusion and who, once for all, exploded the myth of the 'infallibility' of instinct. He did so by showing, with a wealth of observational evidence, that the animal as a subject is certainly not aiming at the survival value of its activities, but merely at the *discharge* of certain actions, termed *consummatory action* by Craig. The recognition of this indubitable fact is one of the utter commonplaces which are so amazingly hard to discover. Introspective self-observation makes it superlatively obvious that the purpose of what Craig termed *appetitive* behaviour is the discharge of instinctive action and not its survival value. I cannot stop myself eating, though it is my purpose to lose weight. However obvious and even commonplace Craig's discovery may *seem* on close inspection, it nevertheless undoubtedly was one of the most decisive steps forward towards a real understanding of behaviour. As Goethe says: 'Das ist das Schwerste von Allem, was dich am leichtesten dünket, mit den Augen zu sehn, was vor den Augen dir liegt.'

The greatest damage done to the analytical investigation of behaviour by the teachings of vitalists was, however, not caused by the confusion of purpose and survival value of behaviour, but by confounding finality with causality. It is a fateful mistake to believe that the teleological 'understanding' of behaviour (or, for that matter, of any process of life) makes it superfluous to gain insight into its causation. If Bierens de Haan says 'Wir betrachten den Instinkt, aber wir erklären ihn nicht' ('We contemplate instinct, but we do not try to explain it'), our answer to this thesis is very clear. It is, of course, perfectly legitimate to meditate upon the obvious finality of any organic structure or function. It is even possible to reach, by this contemplation, a very valuable 'understanding' of it—in the teleological sense of the word. But this sort of understanding does not invest us with the power to *change* the natural sequence of events. Mankind owes its power over nature to its insight into causality. As regards wholes or systems, they have a disconcerting way of getting out of order and thereby supply us with a strong motive for wanting insight into their causal texture.

My teleological understanding of my car is not worth a brass farthing if a drop of water has got into the jet of the carburettor, and Medicine, the queen of all applied natural sciences, is forever in exactly the same position. No whole-producing factor helps the man in whose appendix a cherry stone has got stuck. What I strongly resent is the ever-recurring vitalistic aspersion that our emphatic quest for causal understanding implies materialistic blindness to the existence of the great goals of humanity. Without full recognition—teleological recognition!—of these goals, our quest for causality would lack its purpose. Without insight into causality the active pursuance of these goals would be impossible. We have particularly urgent reasons to want insight into the causal context of 'instinct'. With atomic bombs in its hands and with the endogenous aggressive drives of an irascible ape in its central nervous system, modern humanity is a whole or system which has got very thoroughly out of balance. No teleological meditation will help us, we shall have to *do* something about it, and this implies the necessity of causal insight.

If vitalists persistently ignored the question *why* behaviour develops survival value, or why it is purposive, one should expect mechanists to stress the urgent necessity of putting just these questions. Instead of doing this, the mechanistic schools treated the very *fact* of survival value and purpose exactly as if it were just another vitalistic superstition like entelechy, instinct and the like, that is to say, they flatly ignored it. It is perhaps too much to say that the question 'What for?' was strictly barred from the contemplations of behaviourists and reflexologists, but certainly no sufficient consideration was given to it. This effectively obstructed the mechanists' way of approaching the problems of innate behaviour from a selectionistic point of view, which, though certainly not 'vitalistic', is only possible if the survival value of a behaviour pattern is drawn into consideration.

In saying above that no mechanist has ever raised the question after a causal explanation of directedness and purposivity of behaviour, I have neglected one memorable instance. No less a man than I. P. Pavlov has not only raised this question, but actually tried to give an answer to it. In a paper published in 1916 he writes: 'Analysis of the activities of animals and men has led me to the conclusion that, amongst other reflexes one particular reflex, the reflex of the goal (рефлекс целм) must be conceived, a striving for the attainment of one definite object sending out stimuli' (translated from the Russian). Later on, he adds that this reflex is standing in a close relation to the unconditioned reflexes of taking food and of copulation. It is quite obvious that here purposive behaviour, in the special form of appetitive behaviour, has obtruded itself to Pavlov's notice, also that, observing it chiefly in dogs and humans, he believed that food appetite and sexual appetite were the only ones in existence. It is a subject for deep meditation that the great mechanist did not see how closely akin this new 'reflex', created with the sole intent of explaining something hitherto unexplainable, is to any vitalistic factor introduced for the very same purpose.

(4) *Reciprocal errors in the treatment of spontaneity*

In a strictly analogous way, as the vitalistic-mechanistic dispute prevented a sensible analytical treatment of the whole, and of survival value and purpose of behaviour, it also obstructed the way to a causal explanation of spontaneity. Exactly as in the cases already discussed, the vitalists saw the phenomenon in itself, but regarded it as a 'wonder' and refused to ask for its natural explanation. William McDougall has certainly gained very great merit by stressing the importance of spontaneity of behaviour as an argument against the chain-reflex theory of the mechanistic schools. His sentence that 'it is evidently inadmissible to speak of a *re*-action to a stimulus not yet received' is something we ought to keep well in mind when formulating our modern terminology of behaviour. Also, his slogan, 'The healthy animal is up and doing', which he threw into the teeth of the chain-reflex theory, is worth remembering. But he and other purposive psychologists did not confine themselves to using the fact of spontaneity as an argument against the chain-reflex theory, but regarded it also as an argument against the general assumption that behaviour is causally explicable. At least none of them ever made the least attempt to offer a physiological explanation of spontaneity.

Instead of unrelentingly demanding this explanation, behaviourists as well as reflexologists evaded the problem by the simple means of ignoring the fact. In my opinion it is the most serious accusation against the working hypotheses of mechanists that they conducted only such experiments as were beforehand destined to confirm the theory. This is about the worst fault a working hypothesis can have. With exceedingly few exceptions, the experiments of mechanists confined themselves to letting some sort of stimulation impinge upon the organism and then to record its answering reaction to this stimulation. This kind of experiment could not but create and confirm the opinion that the function of the central nervous system was restricted to receiving and reflecting external stimuli. No mechanist ever thought it worth while to observe what healthy animals do when left to themselves. So the central nervous system, poor thing, never got the opportunity to show that it could do more than answer to stimulation.

Again there is one exceptional case, in which a reflexologist did take notice of spontaneity, and again it is I. P. Pavlov himself who did so. In describing his experiences with a certain small and very lively dog who would on no account keep still when tied to the framework, to which reflexologists attach their dogs, Pavlov actually has introduced a new reflex to meet the case, the 'reflex of freedom'. The most confirmed vitalist could not have done better by introducing an instinct of freedom, and, curiously enough, he would have been far nearer the truth than the great mechanist. It is very far from my mind to make fun of Pavlov. On the contrary, I regard this jarring *contradictio in adjecto*, the 'reflex of freedom', as a reminder of the limitations of the human mind!

(5) *Reciprocal errors in the treatment of innate behaviour*

The conception of 'instinct' is one of the doubtful legacies left to us by the scholastic philosophy of the middle ages. From the first, this conception was introduced to offer what appeared to be an explanation for such types of animal behaviour as were not explicable on the familiar terms of insight and intellect and yet had a definite survival value to the animal. Medieval science was very prodigal with just this kind of 'explanation'. The *horror vacui*, the 'phlogiston' and many other conceptions are further examples. John Dewey, in his book *Human Nature and Conduct*, has given so irrefutable a critique of this type of explanation that it is really superfluous to add even one word. If we accept a 'homing instinct' as an explanation for the fact that a pigeon flies back to its loft, then, next time a child asks me what makes the train go, I shall answer that this is caused by a special factor, called the locomotive force. The justification in both cases is absolutely the same. If we concede it as a scientifically legitimate sort of proceeding, to bridge any arbitrarily chosen gap in our present understanding of nature by assuming an obliging little wonder, then all scientific research becomes a pure farce.

The obvious answer to the vitalistic assumption of the 'wonders of instinct' would have been to explode these wonders one by one, by giving a sensible physiological explanation for each of them, just as hosts of similar vitalistic 'wonders' have, since the days of Johannes Müller and Claude Bernard, been shattered by the progress of analytical research. It is a *real* wonder that no mechanist ever seriously tried to do this! Maybe innate behaviour, with its evident character of a system, its obvious survival value and its undeniable spontaneity, did not seem attractive to the mechanistic methods of research; maybe it was only the great stress vitalists laid on 'instinct' that made it distasteful to behaviourists and reflexologists. Anyhow, none of the mechanists ever systematically investigated innate behaviour. The few reflexologists who deign to mention innate behaviour patterns at all, confine themselves to the rather obvious statement that they consist of chains of unconditioned reflexes, while some behaviourists, chief among them J. B. Watson, go so far as to deny the existence of any more highly differentiated forms of innate behaviour, conceding only that of simple 'motor mechanisms'.

It is hardly an exaggeration to say that the large and immeasurably fertile field which innate behaviour offers to analytical research was left unploughed because it lay, as no man's land, between the two fronts of the antagonistic opinions of vitalists and mechanists. Small wonder, indeed, if it became 'the sporting ground of fruitless philosophical speculation', as Max Hartmann said on a memorable occasion.

(6) *Lack of observational basis*

A short account of a philosophical quarrel, such as the one just given, of necessity, does an injustice to both sides. In fact, every abridged rendering of a philosophical system is an impudent caricature, tending to make the philosopher look a fool. It is, on principle, impossible to summarize philosophical opinion in the same way as we are wont to do with the results of our research. This must be borne in mind, lest my representation of the reciprocal errors of vitalism and mechanism seem an insolent libel of men whose immense merit I would be the last to depreciate. I am quite aware of the immense over-simplification of all that has been said above and of the many exceptions that have been left unmentioned. I only wanted to make quite clear the *general* influence which the great vitalistic-mechanistic dispute has had upon the investigation of *innate* behaviour. I may have over-estimated and exaggerated this influence, and on this point I am open to discussion and very ready to make amends where I have erred.

There is one point, however, in our methodological criticism on the vitalistic and mechanistic schools of behaviour study on which I do not think that serious discussion is possible. It means striking at the very roots of the teachings of a scientific school if one accuses it of insufficient knowledge of facts, of insufficiency of basis of induction. Yet I do not see how this reproach can be spared to either of the great schools of behaviour study. It is an inviolable law of inductive natural science that it has to *begin* with pure observation, totally devoid of any preconceived theory and even working hypothesis. This law has been broken by one and all of the great schools of behaviour study, and this one fundamental, methodical fault, is at the bottom of all the errors of which we accuse vitalists and mechanists. To put it crudely in two examples. If William McDougall had known all H. Elliot Howard knew about 'reactions incomplete through lack of intensity', he would never have confounded survival value and purpose.

If J. B. Watson had only once reared a young bird in isolation, he would never have asserted that all complicated behaviour patterns were conditioned. It was a really crushing blow to cherished ideals when, as a young student, I first realized that the great authorities on 'instinct', such as Lloyd Morgan and W. McDougall, *did not know* the relevant facts about innate behaviour with which I, ignorant boy though I was, was mentally struggling even then; reactions not attaining their goal because of lack of intensity, vacuum activities and the innumerable ways in which innate behaviour patterns were miscarrying, were evidently unknown to the great theorists.

I know of only two students of animal behaviour who really *knew* the animals about which they wrote and who were, at the time of their writings, considered 'scientists' and not just 'bird lovers'. One of them is H. S. Jennings, who may, in a loose sense, be considered as a behaviourist; the other is Jakob von Uexküll, who certainly was a vitalist. In spite of the world-wide discrepancy of their philosophical positions they have one fundamental point of departure in common: both of them hold that the observation *of all there is to be observed* in the behaviour of a species must go *before* the quest for explanation of the single items of behaviour. This means that both of them treat the behaviour of a species as it must unconditionally be treated: as an organic system. To Jennings we owe the conception of the *system of actions* of a species, and though J. v. Uexküll gave a vitalistic name (*Bauplan*) to the same reality, he also approached it with the same method as Jennings, with the method of a truly correlative analysis, proceeding on a broad observational front.

If there is one behaviorist or reflexologist of Pavlov's school, or one purposive psychologist, who also approached the problems of behaviour by the obligatory method of correlative analysis, that is, who began by observing all there is to be observed in a species, making an inventory of its system of actions before forming a working hypothesis, then I am very sincere in asking his forgiveness; I am not a very well-read man and have failed to hear of his existence. But all other professional students of animal behaviour have been guilty of the one unpardonable offence against the most fundamental law of inductive natural science: they have one and all formed a hypothesis *first* and proceeded to look for examples to confirm it *afterwards*. The protean multiformity of organic nature and quite particularly of the behaviour of higher animals is such that a circumspect search for examples can never fail to detect a wealth of evidence for literally *any* theory, however arbitrarily you chose to invent one. The *facts* in themselves may be quite correct, but *choice* of facts in itself is ever a falsification of the inductional basis. And this statistical falsification of the very foundation of natural science can only be prevented in one way: unprejudiced observation of all there is to be observed must go temporarily *before* the building up of hypothesis.

III. METHODS PECULIAR TO COMPARATIVE ETHOLOGY

(1) *Observational basis of induction*

It is a fact worthy of very serious contemplation that very nearly all the relevant details of innate behaviour, the ignorance of which so seriously impaired the theories of the two great schools of behaviour study, mechanism and vitalism, have long been known to and fully appreciated by *bird lovers.* H. Eliot Howard, Edmund Selous and many other men who would have been considered mere 'amateurs' by the 'scientific' schools, have been conversant with these facts, without, however, knowing how badly these facts were needed by psychology. Also the professional zoologists whom we consider as the pioneers of comparative ethology, such as C. O. Whitman, O. Heinroth, Julian Huxley and Jan Verwey, at first regarded their observational work more as a hobby or at best as a very secondary occupation. Indeed, sitting in a blind observing birds, or just staring into an aviary with pigeons, or on a pond with a collection of ducks, or into an aquarium, does not, at first sight, appear to be as 'scientific' as the tremendous experiments of mechanists or the deep philosophical speculations of vitalists. Yet it is very far from being accidental that just this kind of observation yielded facts which remained unknown to the great schools.

The development of any inductive natural science proceeds through three indispensable stages: the purely observational recording and describing of fact, the orderly arrangement of these facts in a system, and finally the quest for the natural laws prevailing in the system. These three steps have been termed the idiographic, the systematic and the nomothetic stage by Windelband. For rather obvious reasons, which I need not expound here, the relative importance of the strictly observational basis of any natural science is in direct proportion to the degree in which its object bears the character of a whole or system: the greater the number of constituent parts of a system, the more complicated their interaction, the more necessary it evidently becomes to get an *inventory* of these parts, before beginning the analysis of their correlations. Now the system of actions of any animal is at least as much of a 'whole' and possesses at least as many particulate constituent parts as its body. Therefore the only legitimate manner of proceeding in the study of the behaviour of any species of living organisms is to begin, quite exactly as H. S. Jennings has done, with what I would call a morphology of behaviour, by a thorough observation and description of *all* the behaviour patterns at the disposal of the species.

Now this, in higher animals, is a tall order. If the morphologist must spend months in getting an approximate survey of the anatomy of a species, the ethologist must spend years to do the same regarding its system of actions. And that is exactly where the 'fancy' of the 'amateur' comes in. I confidently assert that no man, even if he were endowed with a superhuman patience, could physically bring himself to stare at fishes, birds or mammals as persistently as is necessary in order to take stock of the behaviour patterns of a species, unless his eyes were bound to the object of his observation in that spellbound gaze which is not motivated by any conscious effort to gain knowledge, but by that mysterious charm that the beauty of living creatures works on some of us!

(2) *The keeping of animals as a scientific method*

In many natural sciences, such as botany, zoology, mineralogy and others, scientific activity has begun with collecting, and I do not doubt that this collecting was, in most cases, at first motivated much more by 'fancy' for attractive objects than by cognitive purpose. No comparative ethologist of my acquaintance has ever denied that his scientific career began in the same manner. Heinroth was ten when he started collecting and keeping ducks and geese; I myself was still younger when I did the same. Whitman is said to have been addicted to pigeon keeping at about the same age. Though having done this undoubtedly is not a merit, it nevertheless was the methodologically correct thing to do, and I think I am justified in ranging the keeping of animals in captivity first among the methods peculiar to comparative ethology.

By 'keeping' an animal I do not mean the mere attempt to keep it alive in captivity for as long as possible, but the endeavour to make a given species unfold its whole system of actions under constant, controllable conditions. Keeping, therefore, always implies the attempt to *breed* the species in question.

It is far from me to disparage the advantages of field observation and the merits of field observers. But for the purposes of correlative analysis it is, as I have already stressed, of the first importance to get an inventory of the particulate behaviour patterns of a species and to get some notion to what extent these constituents of behaviour patterns are woven into a regulative 'whole'. I have already emphasized (p. 226) the necessity of ascertaining, at an early stage of analysis, how far a system of actions is a regulative whole and how far it is a mosaic of relatively independent elements. This question is extremely difficult to decide in field work, because in the natural surroundings of a species its system of action is apt to *seem* much more adaptive and its several activities much more purposive than they really are. Thus adaptedness is easily confounded with adaptability. *It is only by miscarrying that any behaviour pattern can show its nature of a particulate element.* Now, of course, it is possible to notice miscarrying behaviour patterns in field observation, as H. Eliot Howard has sufficiently proved. But it is quite impossible *not* to see it in observing animals kept in captivity.

It is hardly possible to exaggerate the importance of miscarrying behaviour patterns as a source of our knowledge. W. Craig's great discovery that it is the discharge of consummatory actions and not the survival value which is the goal of appetitive behaviour was exclusively due to the observation of behaviour patterns being executed without attaining their 'normal' survival value. The existence of innate releasing mechanisms would never have been discovered and their function would not have been possible to analyse if it had not been for the observation of cases, in which they were activated 'erroneously' by stimulus situations, in which the released activity was thoroughly miscarrying. The whole set of phenomena connected with the process of accumulation of action-specific energy (such as lowering of threshold, explosion activity, etc.) also could only be discovered by observing innate behaviour patterns miscarrying when discharged at an inadequate object.

It is not only the miscarrying of reactions caused by the absence of normal environmental stimulation which makes the observation of animals kept in captivity so valuable. The physiology of the central nervous system has gained much of its knowledge about particulate functions by studying cases in which some functions had dropped out, because of pathological processes, or had been experimentally destroyed. Very much the same manner of proceeding has led comparative ethology to analogous results. Very slight disturbances of the general 'condition' of captive animals are apt to cause surprisingly far-reaching disintegrations of their systems of actions. Endogenous activities lose much of their normal intensity or drop out altogether; innate releasing mechanisms lose much of their selectiveness. The general disintegration of the species' system of actions caused by these two main processes is essentially *reversible.* If one starts keeping a *new* species, with whose needs one is not yet familiar, one automatically gets an opportunity to observe this particular form of disintegrated behaviour, very often a jumble of unconnected behaviour patterns whose normal survival value is often very difficult even to guess. Yet this jumble of disconnected behaviour patterns is extremely valuable for the purpose of taking stock of the particulate, genetically fixed 'mosaic stones' of behaviour. When, later on, one learns how to keep the species in question and when, with the improvement of technique, the animals are got back into the pink of condition, then the jumble of disintegrated parts is slowly reassembled into a functioning system which fully delivers its normal survival value. I hardly know a more *instructive* object of observation than just this type of disintegration and reassembling of the system of actions in animals kept in captivity. It is, in fact, an actualized example of analysis and resynthesis of behaviour!

If disintegration is a valuable source of our knowledge about behaviour and, indeed, the most valuable fulcrum for its analysis, it must also forever be remembered as a possible source of error. I want to give one warning example of this. The red-backed shrike, *Lanius collurio L.*, has got a very beautifully differentiated endogenous movement for impaling insects on thorns. This activity has a taxis component generally directing it to branches or twigs, but apparently none that directs it to a thorn. The reaction to the thorn was indubitably acquired by the trial-and-error method by the shrikes I observed as early as 1932, and in a paper then published I enlarged upon this particular case of innate behaviour patterns interlocking with trial and error and conditioning. Now G. Kramer has recently reared red-backed shrikes with a view to studying their migration activities and incidentally observed the development of their reaction to the thorn. What he saw at first was in perfect accord with what I had written in 1932; the shrikes showed the movement first and got conditioned to the thorn by trial and error. Kramer is a past master in rearing birds, and you may rest assured that these shrikes were in the best of condition. And yet, when he tried still further to improve his feeding technique and started breeding silkworms for the young shrikes, the birds thus reared needed no conditioning to the thorn, but most amazingly proved to have an innate directive mechanism reacting to the specific optical sign stimuli emanating from a sharp end or thorn. This particular source of error must be kept in mind.

As a method of analysis of animal behaviour, *keeping* truly deserves the adjective 'correlative', because it very strictly compels the investigator to consider the behaviour patterns of a species in correlation to the environmental conditions to which they are adapted. Again, it is the observation of miscarrying behaviour patterns, from which the keeper must be able to deduce what particular conditions of the artificial environment of the animal he must *change*, to make those behaviour patterns attain their normal survival value. Just as he would deduce from the morphological characters of a mole's forepaws that this species needs earth to dig in, so he must, from slight 'hints' of miscarrying behaviour patterns, be able to deduce the corresponding environmental exigencies of the species. Perhaps the most important cognitive value of this proceeding lies therein, that it forcefully compels the observer to treat the several behaviour patterns of a species exactly as he would treat organs. The observer is very convincingly taught that behaviour patterns are not something which animals may do or not do, or do in different ways, according to the requirements of the occasion, but something which animals of a given species 'have got', exactly in the same manner as they 'have got' claws or teeth of a definite morphological structure.

From the recognition of this fact it is only a very short step to the systematic *comparison* of the innate behaviour patterns characteristic of allied species. It is, indeed, only in keeping animals that this comparison obtrudes itself to the observer's notice. The discovery of *phyletic homology* between innate behaviour patterns was unavoidable, once a scientist conversant with the methods of comparative morphology got the opportunity to observe closely a number of species belonging to the same systematic group. It is there that C. O. Whitman's 'fancy' for pigeons and O. Heinroth's partiality to Anatides have played a very decisive part. A man knowing the single system of actions of every species as they knew it could not fail to notice that certain innate behaviour patterns were just as characteristic of a species, a genus or a family, as any morphological character. As early as 1898, C. O. Whitman wrote the sentence that marks the birth of comparative ethology. 'Instincts and organs are to be studied from the common viewpoint of phyletic descent.'

(3) '*Comparative anatomy*' *of behaviour*

With the discovery of phyletic homology of behaviour patterns the study of behaviour may be said to have grown out of the purely idiographic stage of its development and to have reached the second systematic stage. This discovery was of the greatest importance in several respects. Not only could innate behaviour patterns be used as very valuable and certainly very welcome new taxonomic characters in ascertaining the phyletic relations between allied forms, but the special form of certain innate behaviour patterns became accessible to a causal explanation based on the understanding of their phyletic origin. Both of these facts, though certainly important enough in themselves, attain an even greater secondary importance by proving the great independence of the behaviour patterns in question, as *particulate elements* of behaviour. Thus not only the well-tried method of comparative morphology became applicable to the study of behaviour, but it also became possible to *isolate* a very distinct physiological process as an independent constituent of behaviour and to study it separately, in a legitimate departure from the otherwise obligatory method of correlative analysis on a broad front. Therefore, physiological analysis followed closely on the heels of the comparative and systematic study of the elementary process in question.

Zoological systematics and comparative morphology are, by many, considered tedious and rather mummified branches of research. It is too easy to forget that we owe them the most revolutionary discovery of the last hundred years, the discovery of evolution. Though I emphatically deny the charge that comparative morphology is a spent science which has already borne all its fruits, I should concede that it certainly has borne the most important of them. Now there is some danger that the same might be thought, very prematurely, of comparative ethology. In the study of behaviour the phyletic viewpoint has yielded, as a very valuable result, the possibility of isolating and studying in linear, experimental analysis an important, particulate central nervous function, the endogenous activity. In consequence of this, a second, nearly as independent *perceptual* function, the so-called innate releasing mechanism, has become experimentally accessible. Each of these two functions, as a constituent of behaviour, doubtless plays as important a part as the reflex and the conditioned response, and there is a very great temptation to repeat the error of which we have reproached behaviourists and reflexologists, by believing that we have got hold of 'all' the necessary 'elements' to explain 'everything', and to plunge into linear, experimental analysis without giving any further thought to the necessity of further collecting purely observational facts. Of course, the fulfilling of this duty will not keep us from eagerly following up the leads to linear, experimental analysis which we have discovered. But it is well that we should keep in mind the extreme youth of our branch of science and that we should cherish no illusions about the breadth of the observational basis of induction that has hitherto been attained. A precipitate transition from systematics to nomothesis would be particularly disastrous to our branch of research, and the longer and the more we lay stress on the *descriptive* side of comparative ethology, the better it will be in the long run.

Since the days of Charles Darwin the term 'comparative' has assumed a very definite meaning. It indicates a certain rather complicated method of procedure which, by studying the similarities and dissimilarities of homologous characters of allied forms, simultaneously obtains indications as to the phyletic relationships of these forms of life and as to the historical origin of the homologous characters in question. I need not enlarge on the details of this method which is a commonplace to biologists and physiologists. We all know perfectly well what we mean by 'comparative' anatomy, morphology, physiology and so on. But it is all the more misleading if psychologists, who evidently are not familiar with what we mean when we speak of the comparative method, apply the same term in a very loose sense to all behaviour studies concerned with different forms of life. I must confess that I strongly resent it, not only from the terminological viewpoint, but also in the interests of the very hard-working and honest craft of really comparative investigators, when an American journal masquerades under the title of 'comparative' psychology, although, to the best of my knowledge, no really comparative paper ever has been published in it.

Phyletic comparison is slow and painful work, even in morphology, where the comparable, homologous characters are immediately and permanently accessible to the anatomist's knife. It is obvious how the difficulties are increased in the study of innate behaviour patterns which are not there continuously, just to be looked at and described, but for which one must wait in patient observation. It is therefore easy to understand that only very few systematic groups of animals have hitherto been thus studied with any appreciable degree of thoroughness. Historically the first and perhaps still the most thoroughly studied group is the order of pigeons which was investigated by Whitman. Second are the order of Anatidae, as studied by Heinroth, and one family of this order, the Anatinae, more especially studied by Heinroth and by myself. If, as a third group, I add the cichlid fishes, investigated by A. Seitz, G. P. Baerends & Baerends van Roon and A. Steiner, whose paper on dwarf cichlids is, however, not yet published, our list is complete. There are some very good papers on lizards which can, to a certain extent, be evaluated comparatively, though wide gaps still remain between the known species, and there is a comparative investigation on herons by O. Koenig nearly finished. The only paper aiming at giving even a superficial survey of the comparative ethology of a group of mammals, is the paper by O. Antonius on Equidae. Concerning invertebrates, O. Plath has used the behaviour patterns of nest building and provisioning of humble-bees as taxonomic characters, and analogous work was done by A. Petrunkewitch with spiders. There are, of course, hosts of unconnected facts known that may eventually, when gaps are bridged, become accessible to comparative evaluation.

The immense field of observation which is still waiting to be systematically exploited needs whole armies of investigators. These armies are, however, already in existence, at least two of them: the bird-lovers and the fish-fanciers. It is a superlative merit of a book like that of the Rev. E. A. Armstrong that it calls the amateurs' attention to the important details which we need to know. There can never be too many such really scientific and yet generally intelligible books on behaviour. I have already explained why the bird or fish 'lover' is in some respects the ideal observer. The task is, to enlist him to help us in concerted effort

The methodologically first task is, without any doubt, the *intensive* study of all of the innate behaviour patterns of a restricted group of forms. Besides this, it is a legitimate way of proceeding, *extensively* to study throughout the animal kingdom one given homology of behaviour pattern. O. Heinroth (1930), in a paper as interesting as it is short, has given us a survey of the extension and distribution of some exceedingly widely spread and evidently exceedingly old behaviour patterns of vertebrates, such as yawning and scratching the head with the hind leg. Curiously enough, I do not know of another paper proceeding in this way, though this way of pursuing a behaviour pattern as a homologous character throughout a large group is interesting work and gives quick results in comparison with other comparative investigations. At present I am collecting notes on the scratching movements of mammals, particularly of rodents. In this group, and also in primates, the areas scratched with the hind leg and with the forepaw respectively are a taxonomic character whose distribution is most interesting.

Only in two groups (in ducks and cichlid fishes) have our intensive studies of the single species and our extensive studies of the several behaviour patterns progressed far enough to make possible what in comparative morphology is quite a commonplace thing, that is, to represent both lines of investigation in a tabular index. In one of my papers (1947) I have given such an index concerning a number of behaviour patterns of sixteen species of ducks belonging to different families (Anatinae, Cairininae and Casarcinae). This method of letting, metaphorically speaking, two lines of investigation cross each other at right angles, is fundamental to every kind of phyletic investigation of homologous characters. Only this kind of broad survey can give us the possibility of forming a firm opinion about the relative age and phyletic conservativity of any taxonomic character.

In some cases which are particularly favourable to this kind of investigation, it has been possible to form a quite well-founded opinion concerning the lines along which the evolution of certain behaviour patterns has taken place. Always keeping in mind that there are *no* 'primitive' forms of life, and that therefore any linear taxonomic arrangement of living animals or plants is necessarily sheer nonsense, it is nevertheless possible and legitimate to attribute the quality of relative primitivity to *single characters*. It is a dangerously loose and misleading expression to call any recent form of life, however many primitive characters it may possess, a 'primitive' animal. In regard to all the characters of his mouth and teeth, man is much more primitive than the *Platypus*. What alone may be arranged in a linear sequence are the different forms of actualization which one and the same homologous character shows in related forms of life. The ramifying 'line of differentiation' thus obtained does, very probably, correspond to the actual stages of evolutional development of the character in question. A number of indubitable sequences of differentiation could be established among innate behaviour patterns.

In all cases where it has been found possible to do this, the innate behaviour pattern in question was a 'releasing ceremony'. This is far from being accidental. There are two papers being read here on the subject of social releasers, so I must be very short. A social releaser is a device—either a property of colour and/or shape, or a special sequence of movements, or, for that matter, of sounds, or a scent—specially differentiated to the function of eliciting a response in a fellow-member of the species. To every releaser, as an organ for sending out sign stimuli, there corresponds a perceptual correlate, an 'organ' to receive sign stimuli and to activate the answering reaction. This we call an innate releasing mechanism (*auslösendes Schema*). The function of social releasers and of answering innate releasing mechanisms is very much like that of a human signal code, or of that of human word language. Exactly as the several forms of the single word symbols of our language do not have any direct connexion with their meaning, but are only fixed by the *convention* of one particular sign code, so also is the particular form of any social releaser determined by an intraspecific 'convention' between the sender and the receiver of sign stimuli. The important consequence of this is that we may exclude from our consideration the possibility of convergent adaptation when comparing similarity and dissimilarity of releasers. It is immeasurably improbable that the similarity of the words *mother*, *mutter*, *mater*, *μήτηρ* and мать, in English, German, Latin, Greek and Russian, should be due to anything else than to their common derivation from a mutual Indo-European 'ancestral form'. If, therefore, the comparative philologist is fully justified in neglecting any other possibility, then the very same holds true for any resemblance between releasing 'ceremonies' of phyletically allied species. This is why we know more about the origin and the evolution of releasing ceremonies than we do about any other innate behaviour patterns. This is also why, on the basis of releasing activities used as taxonomic characters, it is, in quite a number of cases, possible to ascertain phyletic interrelations of species with a certitude and a wealth of detail, hardly ever attainable on the basis of purely morphological characters.

We know of two phyletically distinct ways, by which non-social, mechanically effective endogenous activities may develop into social releasers: in one case the so-called 'intention movement' (*Intentionsbewegung*, Heinroth), in the other the so-called 'displacement activities'. Both types of movement are, in their primary form, mere by-products of action-specific excitation and certainly devoid of any survival value. The intention movement is nothing but a slight hint of a certain innate behaviour pattern, as will occur whenever action-specific excitation only reaches a very low level of intensity. Displacement activities are the result of a very different physiological process. If action-specific excitation is at a comparatively high level of intensity and finds its path to its normal outlet suddenly blocked—for instance, by activation of an antagonistic drive or by sudden disappearance of the adequate object—it 'sparks over', as Makkink very expressively describes it, into a nervous path not normally its own and finds its expression in behaviour patterns belonging to a quite different action-specific excitation. Makkink, Tinbergen, Koortlant and E. A. Armstrong have studied displacement activities very extensively.

Intention movements as well as displacement activities are, to an observer well conversant with the system of actions of a species, very reliable indicators for the present 'mood' of an animal, that is, in objectivistic terminology, for its present internal state of specific readiness for certain activities. Now in very many animals an analogous 'understanding' of the intention movements and the displacement activities of a fellow-member of the species has evidently been developed on the basis of innate releasing mechanisms. (It seems well worth mentioning that as yet we do not know of a single instance in which a similar 'understanding' is brought about by conditioning!) In other words, the characteristic movements in question developed a totally new function as social releasers. From that point onwards both types of releasing movements underwent an exceedingly characteristic process of differentiation. The primarily important, mechanically effective constituent parts of the movement are lessened in strength and amplitude, while all *optically* effective features of the movement are exaggerated and emphasized in a very peculiar and striking way. We know to-day of a very great number of examples of this particular process of evolution; there are all possible gradations between movements, as yet hardly different from their original form and behaviour patterns, whose differentiation along the lines described above has gone so far as to transform them into grotesque 'ceremonies' or 'dances' whose actual homology to the primary intention or displacement activity can only be ascertained through a thorough study of intermediate forms—if such happen to exist. Releasing ceremonies derived by this over-accentuation or 'mimical exaggeration' from intention movements were called 'symbolic movements' (*Symbolbewegungen*) by Heinroth. In the case of displacement activities a terminological difference has not yet been made between primary displacement and fixed, ritualized, mimically over-accentuated ceremonies.

In a very great number of known cases, the differentiation of a homologous releasing behaviour pattern has, in allied species, taken place along divergent lines. Very often different morphological devices have been evolved to accentuate the optical effect of a ceremony, thus emphasizing different parts of one homologous behaviour pattern in different species.

In surface-feeding ducks there are a good many instances of this. The evolutive process described makes it easily intelligible why in many instances the behaviour pattern should be—as it evidently is—phyletically very much older and much more conservative than the morphological devices, colour and/or structure, that help to accentuate it. Another notable fact is that the sequence of movements, constituting a releasing ceremony, is, in very many cases, much more conservative than its 'meaning', than the innate releasing mechanism activated by this particular set of sign stimuli in a fellow-member of the species. The extensive comparative study of one distinct releasing behaviour pattern often leads to amazingly similar results, as the comparative study of a root word in the historical development of language. Just as the meaning of one word symbol may split up into different and even opposite meanings of its derivatives (for instance, in the English and German words *knight* and *Knecht*, which have both been derived from a common root describing an armed follower of a war lord but have assumed the opposite meanings of a lord in English and of a serf in German), so does, to cite only one instance, the behaviour pattern originally expressing inferiority in cichlid fishes assume the exactly opposite meaning of a threatening gesture in the 'dwarf cichlids' of the genera *Nannacara* and *Apistogramma*. What is more, we know the phyletic development by which it has done so.

A good example of a line of differentiation of mimetically over-accentuated intentive movements is offered by the releasing behaviour patterns which, in cichlid fishes, elicit and direct the young fishes' reaction of following after their parents. There are two elements in the normal movements of a fish starting to swim which are particularly effective in an optical way and suitable for mimetic over-accentuation. One is the sideway swing of head and body, the second is the movement of the median fins which, in cichlids as in most other acanthopterygians, are furled when the fish starts to swim and re-erected whenever it stops. Both these elements have undergone an independent and divergent differentiation and also a 'splitting up' of their 'meaning' in the course of the evolution of cichlids. In the most widely spread and doubtlessly most primitive form of the releasing behaviour pattern in question, the swinging of the head and the furling and erecting of median fins are still coupled in the same obligatory way as in the original movement which has not yet got a releasing function. In this primitive form of the releasing and directing behaviour pattern, it differs from a normal swimming start only in that, after all the grand preparation, the fish does not get farther than 4 or 5 cm. and then stops again. Also in this primitive form, as we find it in *Aequidens*, *Hemichromis*, *Geophagus* and most species of the genus *Cichlasoma*, the *directive* function of the sideways swing of the head is very clear. The swarm of young 'obediently' turns to the left or to the right accordingly, which is especially striking, when the young are swimming 10 or more cm. in front of the guiding parent. Even in some of these species the movement of the median fins is becoming independent of the body movements, and a quick lowering and raising of fins can be observed, especially when the parent fishes are a bit alarmed. There is an indubitable correlation between these independent movements of the median fins and their colouring: the dorsal fin is richly beset with 'jewels' in species, in which the movement is developed. In *Hemichromis bimaculatus*, in which the dorsal fin is particularly richly adorned, the up-and-down movement has taken the form of an exceedingly quick twitching that makes the jewels on the fin flicker like a heliograph. Also this movement, in its higher intensities, has assumed a specialized meaning; it is used quite particularly when the young are called together and tucked up for the night in the nest-hole.

In the genus *Apistogramma* and *Nannacara*, on the other hand, the sideways swinging of the head has taken an independent path of differentiation. Without any concomitant movement of the median fins, the females of these species (which alone lead the brood) twitch their head sideways in a lightning jerk. The body and tail are not moved, and the homology with the original form of the movement is only apparent when the fish really starts to swim. The brooding females of these species wander about very little, but 'browse' their flock of youngsters for long intervals in one spot, all the time executing their sideways flicking of the head with the regularity and about the same frequency as a mother hen utters her clucking call note. In old *Nannacara* females the flicking movements can be elicited by putting the fish into a dense swarm of *Daphnia*. Though the fish will eat single *Daphnias*, it will refuse to eat them if they are too close together, in which case it proceeds to 'brood' them. In all species of *Apistogramma* the broody female has a bright black and yellow patterning of the head and throat which goes to accentuate the optical effect of the flicking movement. Steiner's experiments to investigate the releasing and directing function of these colour patterns on the young were interrupted by the war.

In *Herichthys cyanoguttatus* (formerly *Neetroplus carpintis*) a movement doubtlessly homologous to the 'call' of the dwarf cichlid females has assumed the function of a *warning* signal to the young. *Herichthys* resembles the dwarf cichlids in a number of ethological traits. The female has a particular brooding colour, being jet black on the throat and along the underside of its body, and undertakes most of the brooding of eggs and young, while the male takes only short spells of these functions and is chiefly concerned with defending the territory. When the fishes are alarmed by strong stimuli, as very big fish in their tank or the experimenter's hand approaching them, the female begins a furious sideways twitching movement of head and body. The fish remains absolutely stationary all the time, and the young, as if drawn by a strong magnet, converge from all sides and lie down on the bottom just under their mother, at the same time 'becoming heavy' through contraction of their swimming bladder, just as they do whenever one of the parents catches them in his mouth. The releasing and directing value of the female's movement is easy to prove; any black object, e.g. a fountain pen, twitched sideways between the fingers, will attract the young *Herichthys* in exactly the same way, and if the object is blacker and twitched more furiously than the mother's body, it will even draw the swarm away from the mother, notwithstanding the male's furious attacks upon the substituted object! The warning movement of the *Herichthys* female is, in a way, farther differentiated from the original swimming-away-movement than is the head flicking of the female *Nannacara* and *Apistogramma*, because no intermediates between it and the original behaviour pattern could be observed, while frequently enough occurring in the latter species.

This kind of 'comparative philology' of releasing behaviour patterns is not only a fascinating study in itself, but it may, once we know more about its object, develop a very practical value. I would stress the fact that the human expression of emotion is largely built up on exactly the same kind of intention movements as Charles Darwin knew long ago. In man, in whom innate behaviour patterns are, to a great degree, rudimentary, the study of these innate expressions of emotion may become a most valuable clue to the human 'instincts'!

(4) *Approach to physiology*

(*a*) *The accumulation of action-specific energy*

C. O. Whitman and O. Heinroth were phylogenists and not physiologists. Their chief interest in innate behaviour patterns was of a systematic and taxonomic nature. If they had, as we have reasons to believe, some shrewd suspicions of the physiological singularity of the innate behaviour patterns which they so accurately described, they never said so in so many words and they certainly did not separate them conceptually from other innate behaviour patterns which are of a reflex nature, as taxes, innate releasing mechanisms and others. But while systematically describing and arranging what they called 'instincts' and 'arteigene Triebhandlungen' respectively, they did, maybe quite unconsciously, discriminate a very distinct type of innate behaviour pattern from all others. On the grounds of what we know to-day, it is quite obvious why the endogenous behaviour patterns are much more useful as taxonomic characters than reflex ones. Maybe it was only this that made the pioneers select endogenous activities for their object. But *by* selecting them and grouping them together as something distinct, they brought to light certain striking characteristics which seemed to be clamouring for a causal, physiological explanation. And this is exactly how, in a healthy inductive science, nomothesis will automatically grow out of systematics.

What particularly seemed to demand an explanation was a very unexpected correlation which evidently existed between the *spontaneity* and the *invariability* of the innate behaviour patterns in question. According to the vitalists' opinion, spontaneous activity must automatically be considered as purposive, and must, therefore, show adaptive variability in the pursuit of its end or goal. According to the mechanists' opinion, any innate and individually invariable behaviour pattern must be considered to be a chain of unconditioned reflexes and must, therefore, be totally devoid of spontaneity. In defiance of both these dogmas, just those highly differentiated innate sequences of movements that not only were absolutely invariable individually, but even in phylogeny were rather conservative and slowly changeable characters, proved to possess a very distinct and striking kind of spontaneity.

At the level of superficial observation the innate behaviour patterns in question appeared reflex-like in that they were set off by a sort of 'trigger-action' in a very specific stimulus situation. But on closer inspection it became apparent that these activities are, at bottom, to a very high degree independent from external stimulation. Captive animals, deprived of the normal object or releasing situation of an innate behaviour pattern, will persist in discharging the same sequences of movements at a very inadequate substitute object or situation. The longer the normal stimulation is withheld, the less necessary it becomes, in order to set off the reaction, to supply *all* of the stimuli pertaining to it. The longer the reaction does not go off, the finer the trigger that releases it seems to become set. In other words, the threshold of the stimulation necessary to release this type of innate reaction, is not a constant, but is undergoing a continuous process of lowering, going on throughout the time during which the reaction is not released. This gradual lowering of threshold does, in a good many cases, actually reach the theoretically possible limit of zero, that is, the activity in question will finally go off *in vacuo*, with an effect somewhat suggestive of the explosion of a boiler whose safety valve fails to function. This occurrence has been termed 'Leerlaufreaktion' in German, vacuum reaction and explosion reaction. I would move the general acceptance of Armstrong's term 'energy accumulation activity' for reasons discussed later.

The consequences of the 'damming up' of a certain innate activity are, however, not confined to the threshold of the mechanism (whatever that mechanism may be) which releases the activity. It is not only a facilitation of the releasing process, not only an increase of passive excitability that takes place, but, quite on the contrary, an active and peculiar excitation. Any one of these particular innate behaviour patterns, however small and unimportant it may seem in itself, develops into an active source of excitation which influences the whole of the organism whenever it finds its outlet blocked. In this case, the undischarged activity becomes a *motive* in the literal and original sense of the word, derivated from *movere*, 'to move'. In the simplest and most primitive case the organism shows undirected, 'random' locomotion, *kineses* as we term it. In more highly differentiated types these kineses are interlaced with taxes orienting the organism's locomotion in space, or even with conditioned responses and all the most complicated and least analysed forms of animal and human behaviour, which, for lack of a better term, we are wont to describe as 'intelligent'. Though the activities thus elicited comprise the whole range of behaviour, from its simplest to its most complex form, they have one decisive character in common: they are all *purposive* in the sense which E. C. Tolman has given to this term, that is to say, they all tend to bring about, by *variable* movements, an *invariable* end or goal, and they go on until this goal is reached or the animal as a whole is exhausted. The invariable end or goal is represented by the releasing stimulus situation and, therewith, the discharge of the specific behaviour pattern that had been dammed up. The purposive behaviour striving for this discharge was called *appetitive* behaviour by Wallace Craig, the behaviour pattern finally discharged was termed *consummatory action.*

I want to emphasize what a great wealth of observational evidence is underlying the facts condensed into the two preceding paragraphs. It took the life's work of at least three excellent observers to gather that evidence: Whitman, Heinroth and Craig. All these facts are strongly suggestive of a very definite assumption, and it is eminently characteristic of these three men that every one of them has conscientiously recorded those facts while none of them put this assumption into words. This is all the more significant of the value they set on observation free of any hypothesis, as they must have found it quite hard to avoid descriptive terms like damming up, discharging, etc., which already imply the assumption *that some sort of energy, specific to one definite activity, is stored up while this activity remains quiescent, and is consumed in its discharge.*

This hypothesis is, roughly speaking, identical with the assumption that the behaviour patterns in question are caused by processes of endogenous generation of motor stimuli, such as have been studied by von Holst, P. Weiss and others. The parallels between both types of processes go so far that, in my opinion, there cannot be any serious doubt as to their fundamental identity. The difference between what von Holst calls an automatic rhythm and what we call endogenous activity lies exclusively in the level of integration, as Prof. Tinbergen will explain to you presently.

(*b*) *The innate releasing mechanism*

The conception of a wound-up spring implies the existence of a trigger mechanism, holding it back until the right moment and setting it off when this moment arrives. W. Thorpe says of endogenous activities that 'they are set off by a kind of trigger action'. J. A. Portielje has, at a very early date, fully recognized this double nature of endogenous activity which always is an 'Aktion-und-Reaktion-in-Einem', an action and a reaction in one, as he expresses it. While it is obviously inadmissible to speak of a *re*-action to a stimulus not yet received, for instance, when the organism is striving by trial and error to attain a certain releasing stimulus situation (appetitive behaviour in W. Craig's terminology), the organism's answer to this situation, once it is attained, just as obviously *is a re*-action in the truest sense of the word. Indeed, this reaction has all the earmarks of what I. P. Pavlov would call an unconditioned reflex. With the recognition of the peculiarity and independence of endogenous activity as a distinct physiological process, there evidently arises, as a physiological problem by itself, the question about the 'trigger' mechanism releasing the accumulated action-specific energy. The statement that this mechanism is an unconditioned reflex, though indubitably correct, does not help us any further, because the essential part of the problem does not lie in the reflex process as such, but exclusively in its perceptual side. The intriguing problem lies in the *selectivity* of the reaction. The observational facts are suggestive of a mechanism akin to a filter, letting through only certain particular stimuli while strictly excluding others, or of a complicated lock which can only be unlocked by a very specific key. The adaptation of the perceptual organization to certain characteristic key stimuli is very evident.

Through the work of a considerable number of recent investigations some very peculiar facts have become known about the perceptual organization of these innate releasing mechanisms. What acts as a 'stimulus' is, in the great majority of cases, not a simple physical influence of *absolute* quality and quantity, but a *relational* property. These *innate* reactions to relational properties differ from reactions to acquired Gestalt perceptions only by their extreme simplicity. In acquired reactions, the Gestalt that elicitates the response consists of an indivisible unit of literally hundreds of interdependent relational properties. In innate releasing mechanism we do not yet know a single case in which the innate and immediate reaction is elicited by a relational property comprising the relation between more than *two* elements. The innate releasing and directing mechanisms of the gaping activity of young thrushes (*Turdus*) are a good example. The nestlings will gape at (*a*) the nearer of two objects, (*b*) the higher of two objects and (*c*) the smaller of two objects, the optimum relation of the smaller to the bigger being 30%. All three of these relational properties are characteristic of the normal object of the reaction, the parent's head. Each of them, considered by itself, is a true, if extremely simple, 'Gestalt', showing all of Ehrenfels' 'Gestalt' criteria, most important of all, transposability. Each of these relational properties represents a key-stimulus setting of the *same* innate releasing mechanism, but each of them does so quite independently from the other. Unlike the immeasurable number of relational properties inextricably woven into the whole of a 'Gestalt' perception, *these single relational key stimuli act merely as a sum of non-interdependent elements.* This process of summation of key stimuli, belonging to one and the same innate releasing mechanism, has been termed 'Reiz-Summen-Phänomen' by A. Seitz, who was the first to study it intensively. N. Tinbergen translated this into English by 'law of heterogeneous summation'. What I have said about the innate releasing mechanism suffices for the understanding of the subsequent section on dual quantification, especially as the subject will probably be expounded in detail in the papers that are to be read on social releasers.

A few words must be added about the term. The mechanisms in question were first discovered in their function of setting off endogenous activities; they can, indeed, most advantageously be studied in this particular function, for reasons explained in the next section. But evidently the very same type of perceptual organization as the one that receives the key stimuli setting off endogenous activities also plays a part just as important in a great many quite different functions. The perceptual side of taxes may be organized in exactly the same manner, appetitive behaviour may be activated by evidently identical processes and so may specific inhibitions. Especially important is the function of innate releasing mechanisms in the hierarchical system of moods, as explained in N. Tinbergen's paper. In his investigation of the gaping reactions of young thrushes, Tinbergen distinguished between releasing and directing mechanisms, according to whether they activate discharge of endogenous activity or a taxis. I think that this terminological differentiation is not advisable. Of course, it is not very elegant to talk of an innate mechanism 'releasing' a taxis, or, still worse, a social inhibition. But somehow we ought to express in our terminology the fundamentally important fact that it indubitably is *the same* innate organization of perception that is filtering and selecting the key stimuli activating these very different responses.

(5) *The method of dual quantification*

A very considerable percentage of all animal activities consists of the typical successive links of appetitive behaviour, attainment of a desired stimulus situation, to which an innate releasing mechanism responds and sets off the discharge of accumulated endogenous action. In the vast majority of cases where we find an organism responding specifically and without previous experience to certain stimulus situations, closer investigation will reveal one or other of the innumerable variations to this theme, always leading up in one way or the other to the final discharge of consummatory actions. What we can objectively observe is exclusively this discharge. But this discharge is dependent upon two absolutely heterogeneous causal factors: (1) the level attained by the accumulated action-specific energy at the moment and (2) the effectiveness of external stimulation. None of these two factors is directly accessible to our observation. Absolutely identical reactions can result, in one case, from an extremely low level of endogenous accumulation and strong stimulation, and, in the other, from a high level of accumulated action-specific energy and a very weak external stimulation, or even, in the case of explosion activity, from internal factors alone, external stimulation not taking any part in the activity at all. This has to be taken into very serious consideration in the experimental study of perceptual organization. If, after the elimination of one or more single stimuli, the activity can still be elicited in its normal form, this does not in any way justify the conclusion that these stimuli are ineffective in activating the releasing mechanism pertaining to the activity in question. If Stone's (1923) rats discharged certain innate behaviour patterns apparently normally, although they were deprived of important sensory organs, this is in no way astonishing. A mother rat who, in spite of the removal of her olfactory bulbs, continues to foster her young, is in no other position than an old virgin Scotch terrier bitch who, with a sufficient lowering of threshold, proceeds to discharge homologous reactions with a cushion for a substitute object.

What is constant is not the effect actually produced by a certain key stimulus at a given moment, but the relation between this effect and the organism's momentary internal state of accumulation of action-specific energy. The constancy of this correlation only becomes apparent when both the internal and the external factors are quantitatively investigated *simultaneously*. The method of doing this truly deserves the name of a *correlative* analysis. In a dabbling and uncertain way I sensed the possibility of this method as early as 1926, when I was experimenting with my first free-flying tame jackdaw. The observations I then made are still very vivid in my memory, and though it has taken me years to see their real purport, they are a good and simple illustration of what I am trying to explain. The following reaction of a hand-raised and fully fledged young jackdaw (*Coloeus monedula*) is elicited by a small number of single stimuli which, though apparently simple, nevertheless imply the necessity of assuming an innate perceptual organization responding to *relational* properties. The experimenter who wants to elicit the reaction which the young birds give to the stimuli emanating from its parents guiding it, must do at at least *one* of three definite things. He must either more or less quickly move *away from* the bird, or *upwards* from its position, or he must utter a good imitation of the call-note of the species. (A fourth very effective stimulus, pertaining to the same releasing mechanism, is the sudden unfolding of a pair of black wings, but this is not so easy for the human experimenter to imitate. Its existence is, however, immaterial for our present concern.) When I walked abroad with that young jackdaw, the bird would, at first, follow me very willingly. It would fly up in pursuit even when I walked away from it quite slowly. (Though it was always possible to get away from the bird, without having it following after me, by the method of letting the stimulus 'creep in', walking away with extreme slowness.) After a time it became necessary for me to walk away *abruptly*, over-accentuating my movements very much in the same way as a parent cichlid does with his swimming-away movements. After a few more performances I had to *add* another stimulus, that is, I had either to call, or to crouch low to the ground beside the sitting bird and jump up in starting. At last, I had to do *all* of these things simultaneously and with the utmost intensity, crouching close to the jackdaw, jumping up suddenly, running away as quickly as I could and yelling jackdaw-calls all the time, in order to make the bird take to wing at all. In this simple experience two important facts are obtrusively apparent: (*a*) the activity is *exhaustible* independently from the general state of exhaustion of the organism as a whole, (*b*) the stimuli which release it are *interchangeable* and the general releasing effect of a situation is dependent on the *sum* of the single releasing stimuli contained in it. Furthermore, another fact mentioned earlier is again illustrated: internal and external motivation may add up to exactly identical results if the weakness of one is compensated by strength of the other.

Whenever we put stimulation in front of an organism and register its answer to this stimulation, we have to deal with an equation containing *two* unknown factors. The quantification of each of these factors is, on principle, impossible without simultaneously ascertaining the quantitative effect of the other. What is visible to us is (*a*) the stimulus situation we are putting before the animal, and (*b*) the discharge of a specific activity thereby released. The varying internal state of specific excitability is only accessible to us through the means of these two indicators. If we are looking for an object favourable to an exact solution of this equation containing two unknowns, we must obviously search for an activity, the discharge of which has a number of clearly distinguishable grades of intensity, and the releasing mechanism of which consists of an appreciable number of distinct stimuli, so that by the addition of these stimuli we may obtain a gradation of different releasing values.

A very extensive observational basis is needed to obtain a certain knowledge of all the different forms of movement activated by *one* quality of action-specific excitation. The internal state of heightened action-specific excitability may betray itself by small intention movements, and from the merest hint of these up to the activity of full intensity there are all possible gradations. For endogenous activity as a whole, the very contrary of an 'all-or-nothing law' holds true. (Not, however, for the single neural elements of endogenous activities which certainly do obey the all-or-nothing law, as von Holst has clearly shown. The differences of form and of amplitude which endogenous activities show at different levels of action-specific excitation are due to the fact that the single neural elements, pertaining to the same quality of specific excitation, have slightly different thresholds, so that different numbers and, in some cases, different kinds of elements are activated at different levels of reactional intensity.) To an observer who is familiar with the systems of actions of the species in question, these finely graded intention movements can tell very exactly what to expect from the animal at the next moment. But, because the slight intensive movements grade imperceptibly into the full activity, it is difficult to gain an objective criterion for absolute quantification.

Luckily for our analytical purposes, this is not true for such intention movements as have, by the evolutionary process described (p. 242), developed a new function as social releasers. The intensity scales of these consist, in the majority of cases, in a series of behaviour patterns which do not grade into each other, but each of which has not only a very definite and distinctive form of movement, but also a quite distinct threshold that must be reached by action-specific excitation in order to activate it. To describe only one of the many examples obtruding themselves: the welling-up of the excitation specific of fighting activity in the cichlid fish *Astatotilapia strigigena*, activates a sequence of not less than five behaviour patterns in the succession of their respective thresholds: (1) taking on display colouring; (2) standing parallel to the adversary with median fins maximally spread; (3) distending of gill membrane; (4) sideways beating of the spread caudal fin; (5) ramming the adversary. In *Betta splendens*, an osphromenid fish, there are two more steps distinguishable in the same ladder. Of course, each one of these single activities may be executed with greater or lesser intensity, thus giving opportunity for further differentiation; but even without this, a graduation of five steps, not to be confounded with each other, is a tremendous help for quantitative study.

For the purposes of dual quantification it is necessary that not only the intensities of the activity released, but also the releasing effect of external stimulation should be accessible to an exact graduation. This is obviously best in cases in which the innate releasing mechanism is activated by a comparatively great number of independent stimuli, in other words, in the most complex and most highly differentiated releasing mechanisms. These, indubitably, are the ones that correspond to social releasers. In this respect, the fighting reactions of certain fishes again prove to be an admirable object, being released by a number of visual stimuli which not only are easy to reproduce in a dummy, but also very different from each other as to their respective releasing values.

Before describing in detail how we proceed in our simultaneous quantitative study of endogenous generation of action-specific energy and of the respective effectiveness of single releasing stimuli, I want to emphasize what a tremendous amount of purely observational work has to be done, to furnish us with the *measure* with which we quantify these factors. The observer has to get thoroughly familiar with *all* the innate behaviour patterns of the species with which he is going to experiment, in order to know what movements are correlated to what independent quality of action-specific excitation. He must possess an exact knowledge of the sequence, in which the single behaviour patterns correspond to different levels of intensity of this specific excitation. The task of correlating single behaviour patterns to specific qualities of excitation is not made easier by the frequent occurrence of displacement activities which also must be drawn into consideration and which, in higher animals, tend to complicate matters immensely. Also, the experimenter must already have attained a rough working knowledge of the stimuli pertaining to certain releasing mechanisms. If these conditions are thoroughly fulfilled, the ethologist is, in a good many cases, in a position to prove the correctness of his hypotheses in the most exact manner known to natural science, that is, by correctly *predicting* what will happen in the situation he creates experimentally. My friend Seitz, who is, what every comparative ethologist ought to be, a past master of the motion-picture camera, had a really uncanny way of predicting what his cichlids were just going to do. When demonstrating some experiment on fighting or courtship activities of his fishes, he always quite unconsciously dropped into the same manner of speaking as when demonstrating a film that he knew by heart, forever anticipating by a few seconds in his explanations what the fishes were doing, calling the attention of the onlookers to the minutest detail of behaviour which he *knew* would occur in the next moment.

The practical way of proceeding in experiments of dual quantification is obvious, after what has already been said. Presenting the animal with a given stimulus situation and recording the intensity of its reaction presents us, as I have explained, with an equation containing two unknowns: we do not know how much of the intensity recorded is due to internal accumulation of action-specific energy and how much is due to external stimulation. The obvious thing to do, is to let *maximal* stimulation impinge upon the organism immediately after the first experiment, in order to see how much specific energy is 'left'. This already gives us a definite notion about the *relative* effectiveness of the stimulation supplied in the first experiment. What we are doing is best illustrated in a hydro-mechanic model which, in spite of its extreme crudeness and simplicity is able to symbolize a surprising wealth of facts really encountered in the reactions of animals. In Fig. 1 the tap *T* supplying a constant flow of liquid represents the endogenous production of action-specific energy; the liquid accumulated in the reservoir *R* represents the amount of this energy which is at the disposal of the organism at a given moment, the elevation attained by its upper level corresponds, at an inverse ratio, to the momentary threshold of the reaction. The cone-valve *V* represents the releasing mechanism, the inhibitory function of the higher centres being symbolized by the spring *S*. The scale-pan *SP* which is connected with the valve-shaft by a string acting over a pulley represents the perceptual sector of the releasing mechanism, the weight applied corresponds to the impinging stimulation. This arrangement is a good symbol of how the internal accumulation of action-specific energy, and the external stimulation are both acting in the same direction, both tending to open the valve. It can also easily and obviously represent the occurrence of explosion activity. The activity itself is represented by the spout discharged from the jet *J*. The intensity of the reaction is symbolized by the distance to which the jet springs, in other words, by the speed of the outflow. This automatically corresponds to the proven fact that the consumption of action-specific energy in the time unit is in direct proportion to the intensity of the reaction. The intensity of the reaction can be read on the scale *G*. To this apparatus we can easily attach a gadget exactly symbolizing the way in which a sequence of different movement patterns belonging to one scale of action-specific excitation is activated. A row of little funnels attached below the gradation will meet the case where, with the attaining of a higher level of excitation, the activities corresponding to lower levels are discontinued (as, for instance, in the taking-to-wing ceremony of the greylag goose). It is, however, much more usual that the movements activated at the lowest levels of action-specific excitation are continued unceasingly all the while those corresponding to higher levels are discharged. We can symbolize this by fixing below the scale *G* an oblong trough *Tr* which has an oblique bottom perforated by a number of holes. The outflow from these holes then represents the intensity scale of a sequence of different activities, such as fin-spreading, gill-membrane expanding, etc. For reasons subsequently to be expounded, we have arranged the scale tray representing the receiving section of the innate

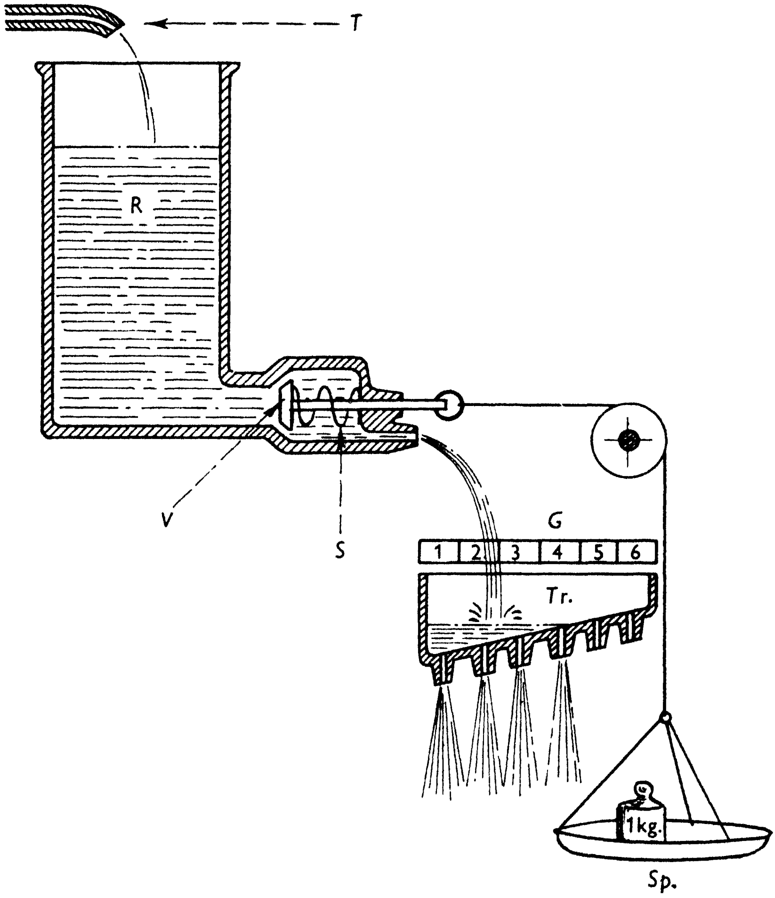

Fig. 1

releasing mechanism in such a manner as to let some of the ultimate flowing out of liquid impinge on it in a diffuse way.

This contraption is, of course, still a very crude simplification of the real processes it is symbolizing, but experience has taught us that even the crudest simplisms often prove a valuable stimulus to investigation. As an instrument for the quantification of external and internal stimulation this model has already proved to be of some value. Let me explain its use. Suppose we present an organism with a stimulus of unknown effectiveness. All we can immediately record is, as already explained, the intensity of the reaction. In the terms of our model, we do not know what weight we have applied to the pan. In order to ascertain it, we must try to get some notion of the pressure pushing on the valve from the inside. The simplest way to do this is to open the valve altogether and record the distance which the spout delivered by the jet will now attain. In other words, we shall present our animal with the *normal* object of the reaction which may be roughly (though not theoretically) identified with its optimal object, and record the intensity of which the reaction is capable at the moment. Out of both data the relative effect of the first stimulus can be roughly calculated, as well as the pressure acting from within. In other words, we have now got two equations with two unknowns.

There can be a very great number of variations to the intrinsically identical method of calculation described above. Which of them is the most favourable largely depends on the object and on the particular questions which are in the experimenter's mind at the moment. If, as it is most advisable at the very start of any investigation, we are interested in taking stock of all the stimuli that activate the innate releasing mechanism, it is a very good way of proceeding, to 'pump out' the reservoir of action-specific energy gradually. We begin by presenting a comparatively simple dummy which is reacted to only with little intensity and only for a short time. When the reaction to this dummy noticeably begins to flag, we 'improve' upon the dummy by introducing additional stimuli. In the terms of our hydromechanical model, we are lowering the internal pressure to such an extent, that the releasing weight x ceases to open the valve, while the weight x plus 1 still will do so. We get the threshold of the reaction exactly *between* the releasing values of the two successive dummies. We may continue with this procedure until we arrive at dummies whose releasing value cannot be increased any more. In many cases, the objects thus attained by far surpass the releasing effect of the natural object of the reaction in question, a fact which in itself is a serious blow to the vitalistic belief in the infallibility of 'instinct'. And not only has the experimentation of human scientists succeeded in discovering such 'supernormal' objects, but the evolutionary adaptation of certain social parasites to the releasing mechanisms of their hosts has evidently done the very same thing. The cuckoo, for instance, is obviously presenting a superlatively strong stimulation to the innate mechanisms releasing the feeding activities of many small passerines, far excelling the one emanating from young of the respective species. Heinroth, in his drastic way, once said that cuckoo feeding may become a real *vice* indulged in by most of the occupants of an aviary. Though meant as a joke, this utterance contains a very serious truth, because some human vices are evidently nothing more than a continued search for supernormal stimulation. What is true for the cuckoo very probably is also true of many social parasites of termites and ants. All these organisms are a challenge to the ambitious ethological experimenter.

If a releasing mechanism contains the perceptual correlates to a comparatively large number of key stimuli, it is possible to construe an immense number of combinations and permutations of these stimuli. By this we obtain the further possibility of comparing the stimulating effect of objects whose releasing value is approximately the same, but is brought about by a summation of entirely different constituent key stimuli. By patiently constructing a great number of dummies of approximately equal releasing value, but different elementary stimuli, A. Seitz (1942) was able to show rather conclusively that the releasing value of the single constituent stimulus is absolutely constant in all possible combinations. This is what he termed 'Reiz-Summen-Phänomen' in German, and what Tinbergen translated into English by 'Law of heterogeneous summation'. Wolfgang Schmidt (to be published) investigated the human reaction to the visual stimuli of laughing with exactly the same method and obtained strictly analogous results. The effect of heterogenous summation could be demonstrated even more clearly in this case, because in experimenting with humans it is possible to compare directly the releasing values of two dummies, by applying the choice method. In experimenting with animals, especially with the lower forms, this method has a very serious drawback: it frequently occurs that the stimuli, activating an innate releasing mechanism, are *not identical with those that direct it in space*, and therefore very misleading results can be obtained by letting an organism 'choose' between two dummies. As Tinbergen has shown conclusively in the greyling butterfly, *Satyrus semele*, it is quite possible that one object elicits the discharge of endogenous activity, while the second is sending out directing stimulation guiding the organism's reaction to itself.

There are endogenous activities which have a rather quick generation of action-specific energy, but, speaking in the terms of our hydromechanical metaphor, a narrow reservoir in which to hold it. The gaping activity of young passerines, for instance, 'fills up' from total exhaustion to explosion activity within half an hour or an hour and, in smaller species, is exhausted after a discharge lasting only a fraction of a minute. In rearing such birds by hand, it is, in very many species, quite impossible to feed all of the nestlings during one gaping 'burst'. If there are six nestlings, nos. 4, 5 and 6 will cease to gape, before one has finished feeding nos. 1, 2 and 3. This also very clearly shows how the activity is not motivated by a directive 'food instinct' or 'hunger'. In such quickly exhaustible activities the enormous inconstancy of the level of action-specific energy is a very serious obstacle to the comparison of releasing values of different stimuli. Even the obvious method of presenting the stimulus suspected to be 'stronger' immediately after the reaction to the weaker stimulus has ceased, does not give reliable results. It is very possible that a stimulus which is really quite appreciably stronger than the preceding one, fails to elicitate any reaction when thus presented. Here we have to take into consideration an effect which has been very aptly termed *inertia* of reaction by A. Seitz. When we suddenly deprive an animal of the object of its reaction, the activity never breaks off abruptly but nearly always continues a considerable time *in vacuo*. Doubtless it is a consequence of the same phenomenon that the 'momentum' gained by any activity will carry it on for an appreciable time after the moment when its releasing threshold, rising continually throughout the duration of the discharge, has reached the value corresponding to the external stimulation impinging at the moment. This is also the reason why an organism that is left continually in the presence of a releasing object does not continually react to it with a constant intensity, as otherwise would be expected. The inertia of a reaction carries the threshold high above the value corresponding to the ever-present stimulating object. After the reaction has ceased, the gradual lowering of the threshold during its period of quiescence acts exactly as a correspondingly slow increase of stimulation would act upon a constant threshold, that is, it results in the well-known phenomenon of 'creeping in' of stimulation. Because of this, the new burst of activity does not occur until the threshold is very appreciably *below* the value corresponding to that of the constant stimulation. The result of this is the usual form of discharge, in rhythmically recurring 'bursts' of activity. The heightening of threshold, caused by inertia of reaction, may be so considerable that it can supersede a quite substantial difference between the stimulating effects of two dummies. If we let the animal react to one combination of stimuli until activity ceases and then *fail* to elicit any response by the presentation of another set of stimuli, we are not yet in possession of conclusive proof that the second combination is not quite considerably stronger than the first. For obvious reasons this fact is all the more important, the more quickly the activity in question is exhaustible.

It is probable that the *initial* inertia of endogenous activities and their propensity to *continue* longer than corresponds to present stimulation, are two entirely different phenomena, requiring different physiological explanations. The way in which quiescent activities respond to stimulation is more suggestive of initial *friction*. They 'behave' exactly as if the valve releasing their discharge was a bit sticky. Furthermore, there arises the question whether there is not a distinct relationship between creeping in of stimulation and what we call habituation. Contrary to these phenomena of an initial resistance to stimulation, the continuance of activity after cessation of adequate stimulation is easily explainable on the assumption that the activity is *self-stimulating*. A strong argument for this assumption lies in the fact that this type of inertia of an activity is evidently in exact direct proportion to the intensity the discharge has attained. If in our hydrostatical model we arrange the scale-pan receiving the weights representing stimulation in such a way as to let part of the outflow of the activity impinge upon it in a somewhat diffuse way (Fig. 1), we are able to reproduce a very exact replica of the avalanche-like way in which the endogenous activities tend to grow after being released. Also we can account for the fact that the valve stays open much longer than corresponds to the added values of internal pressure and weights on the scale-pan. A very considerable part of all endogenous activities is in this way self-exhausting and self-stimulating at the same time, a fact which has been stressed by Julian Huxley long ago.

(6) *Analysis of taxis and kinesis constituents of 'instinct'*

As long as the whole of innate behaviour was considered a chain reflex, there was no reason to make any particular distinction between the single constituent reflexes which are building it up. The discovery of endogenous generation of action-specific energy has considerably changed this position. I have already shown in what way the recognition of the very peculiar physiological character of these functions forces us to conceive of endogenous activity and of the perceptual organization releasing it as of two very distinct physiological processes which, though they are strictly interdependent constituents of one mutual function, each demand a different method of analytical approach. In very much the same manner as the discovery of endogenous activity has influenced our conception of the releasing mechanism, it also necessitates some corrections of our notions about the mechanisms *directing* activity in space. Correlative analysis is like the solving of a crossword puzzle, in that the correction of one word which had been put in erroneously makes it necessary to revise our notions about all the parts interlocking with it. I need not say anything here about the interdependence of endogenously automatic activities and taxes as constituents of innate behaviour; a much better authority on the subject will do so.

I would, however, say a few words in answer to an evidently widely spread misconception about our conceptional distinction of physiologically independent constituent functions. It is in the very nature of analysis that it leads to a progressive narrowing in of formerly wider and more general conceptions. What formerly was very simply conceived of as 'an instinct' is shown by the advance of analysis to be a very complex mechanism of very distinct and very different constituents, such as endogenous automatisms, releasing mechanisms, taxes, kineses and, maybe, quite a number of further as yet unrecognized particulate functions. For this we have been reproached by many psychologists, all of them more or less under the influence of vitalistic and finalistic preconceptions. We were accused of pulling to pieces what really was a whole, and it has been said of us what Goethe said of a certain type of analytical science: 'Sie haben die Teile in der Hand, fehlt, leider, nur das geistige Band.' I would emphatically deny this charge. When we distinguish independent and particulate constituent functions of innate behaviour, we are just as much justified in doing this as the physiological anatomist is justified in distinguishing between the bones, joints, muscles and nerves of, let us say, a human arm or leg. The conceptional distinction of constituent parts and of their particular qualities does not in any way preclude the fullest cognizance of the general mutual interdependence and interaction of these parts. It does not, in any way, prevent us from seeing the organism as a whole or system. This will seem a very commonplace thing to say to physiologists, as, indeed, it really *is*. But it is a deeply regrettable fact that it seems to be exceedingly necessary to say it again and again to some psychologists.

(7) *The hierarchy of moods*

Doubtless a quite considerable percentage of all the activities of animals and men are compounded of the three successive links described in the classical diagram given by Wallace Craig and further differentiated by Tinbergen and myself: (1) accumulation of action-specific energy giving rise to appetitive behaviour; (2) appetitive behaviour striving for and attaining the stimulus situation activating the innate releasing mechanism; (3) setting off of the releasing mechanism and discharge of endogenous activity in a consummatory action. Doubtless this tripartite organization of behaviour does occur. Pessimists assert that yesterday's truth is to-day's error. In biological research work it is certainly more correct to say that the truth of yesterday is, not the error, but the *special case* of to-day. In biological research, an all-too-cautious abstaining from forming a hypothesis would get us nowhere, and we must have the courage to formulate preliminary hypotheses, though we are well aware that these preliminary formulations are much too simplistic and correspond, at the best, to a particularly simple special case. In fact, the discovery of a natural law has been, in many instances, identical with the discovery of a special case, in which it was actualized in a particularly simple manner. We are therefore neither surprised, nor pained, that the original, tripartite diagram of the organization of innate behaviour has proved a typical example of this kind of simplification. That is to say, it meets a good many cases, but is much too simple for most cases.

It was a most decisive step forward in our understanding of innate behaviour when Baerends (1941) pointed out that appetitive behaviour by no means always leads immediately to the discharge of consummatory action. In the vast majority of cases, the appetitive behaviour with which an activity begins is of a much more *generalized* nature. The releasing situation attained by this first step of appetite and the innate releasing mechanism activated in this situation, do not lead to the discharge of the final consummatory act, but, as the next step, to another form of appetitive behaviour of a distinct and *more specialized* form, striving for another, also more specialized, releasing situation. A very general 'mood', in the sense of a readiness to certain activities, as, for instance, the 'reproductive mood' of a male stickleback, which comprises the several readinesses to a very considerable but finite number of consummatory acts, is, step by step, narrowed down to the discharge of one of these. There is, in other words, a hierarchical order of wider and narrower readinesses or moods. The action-specific appetite and the discharge of the consummatory action are the *lowest* rung in this ladder of superimposed commanding instances or 'centres'. Baerends has extensively studied the 'Hierarchy of moods' in the digger wasp, *Ammophila campestris*, and Tinbergen in the stickleback. As the latter is going to read a paper on the subject himself, I need not say more here.

From the methodological viewpoint, which is the subject of this paper, it must be emphasized that the conception of a hierarchy of 'instincts', at which we have arrived, is something entirely different from what W. McDougall and other purposive psychologists conceive of as chain appetites, first and second order drives and the like. These conceptions have been arrived at from the opposite direction of approach. We have not gone out from finalistically considering what the animal *ought* to do, in order to sustain itself and its species, but from what it actually *does*. We have not started from the hypostatization of a 'reproductive instinct', deduced from the fact that sticklebacks reproduce their kind, but from the observation and inventory of the lowest rung of the hierarchical ladder of integration, with the consummatory actions, and worked our way inductively *up* that ladder instead of deductively down. The conceptions of the successive levels of integration are therefore determined *causally* and not teleologically. Therefore Tinbergen's and Baerend's conception of hierarchically superimposed 'centres', though determined exclusively from a functional point of view, may prove a most valuable hint to the experimenting physiologist as to the number of localizations for which he has to look.

(8) *The psychological aspect of comparative ethology*

There is an amazingly widely spread prejudice that a given process of behaviour can only have *either* a physiological *or* a psychological explanation. In F. Hempelmann's otherwise admirable text-book this fundamental error keeps recurring every few pages. Of course there simply is no psychological process which does not have its physiological correlate and which does not demand a physiological explanation as well as a psychological one. The serious consequence of the erroneous 'either-or' lies therein *that it implies the superfluity of physiological explanations in all cases where a psychological explanation can be found.* On the other hand, there are a lot of processes comprised in animal behaviour which do not have a psychological explanation. In other words: every psychological process has its physiological side, but not every physiological process is correlated to psychological phenomena.

Though comparative ethology is resolutely and exclusively concerned with an *objectivistic* study of behaviour, as long as it is concerned with animals, we do not, by any means, shut our eyes to one important fact: just those particular physiological processes that are the main object of our investigations, undoubtedly belong to the kind which *does have a correlated psychological side to it.* This is true of all the three most important elementary processes of innate behaviour, of endogenous-automatic activities as well as of innate releasing mechanisms and of taxes.

There cannot be the least doubt that the discharge of accumulated action-specific energy is accompanied by very intense and very specific subjective phenomena. I fully agree with W. McDougall in his fundamental assertion that man has just as many 'instincts' as he has qualitatively distinguishable emotions. Jan Verwey, an indubitably objectivistic student of animal behaviour, is evidently of the same opinion when, in his famous paper on the grey heron (1930), he writes: 'Where reflexes and instincts can be distinguished from each other at all, there the reflex is functioning mechanically, while instinctive activities are accompanied by subjective phenomena' (translated from the German). Heinroth used to answer to anybody's assertion that animals were reflex machines by saying jocularly: 'Quite on the contrary, animals are exceedingly emotional people, possessing very little intellect'. The same opinion is evidently underlying Heinroth's conception and treatment of 'moods' (*Stimmungen*). Our firm conviction that there exists a subjective, emotional side to 'moods', as well as to the discharge of action-specific energy, does not in any way imply our making illegitimate assertions about the nature and quality of an animal's subjective experiences. These are, and ever will be, inaccessible to our knowledge. I would lay great stress upon the fact that Heinroth's conceptions of 'moods' can one and all be strictly defined from a purely objectivistic point of view, as specific internal states of readiness to discharge a certain complex of behaviour patterns. Even Heinroth's terms are not derived from human subjective phenomena, but from the objective activity itself, as, for instance, 'Flugstimmung', 'Fortpflanzungs-Stimmung' (flying mood, reproductive mood) and others. We still hold that a real 'psychology' of animals is on principle impossible. But in its application to *man*, the fact that the discharge of certain endogenous activities is correlated to certain distinct emotional phenomena may become of tremendous importance.

The psychological aspect of innate releasing mechanisms presents some parallels to that of endogenous activities. We know for a certainty that the attainment of the releasing stimulus situation represents the end or goal to which appetitive behaviour is directed. We can give an exact and purely objective definition of this kind of directedness or purpose (p. 248). In all human behaviour, which also objectively fits this definition, we furthermore know for certain that the organsim, as an experiencing subject, is striving for certain pleasurable subjective phenomena accompanying as well the perception of the releasing stimulus situation as the discharge of the accumulated endogenous activity. I do not think that any observer really familiar with appetitive behaviour in higher animals will ever doubt the fact that the animal as a subject also experiences intense sensual pleasure as the subjective correlate of attaining the releasing stimulus situation. W. Craig gives a convincing description of the behaviour of a young male dove on attaining the specific situation eliciting the nest-calling activity: When 'a ready-made nest is put into his cage, the inexperienced dove does not recognize it as a nest, but sooner or later he tries it, as he has tried all other places for nest-calling, and in such trial the nest evidently gives him a strong and satisfying stimulation (the appetitive stimulus) which no other situation has given him. In the nest his attitude becomes extreme; he abandons himself to an orgy of nest-calling (complete consummatory action), turning now this way and now that in the hollow, palpating the straw with his feet, wings, breast, neck and beak, and *rioting in a wealth of new, luxurious stimuli*' (italics mine). Again, we cannot say anything about the specific quality of the animal's subjective experiences. But again the laws we have found in animal behaviour find an enormously important application to the special phenomena of human psychology. We do not go far wrong if we suspect the existence of an innate releasing mechanism, wherever we can introspectively ascertain a specific quality of sensual pleasure. To give a good example of this, and quite a proper one at that: it is a distinct and indubitably sensuous pleasure to fondle a nice plump, appetizing human baby. The stimulation emanating from such a baby even elicits one of the very few motorically innate behaviour patterns of our species, a quite distinct movement of taking the infant on one arm, holding it with the other. In fondling the baby, we behave to its 'sweet' stimulation very much like Craig's pigeon does to the nest. By introspection I can ascertain that the pleasure I feel in fondling and petting the baby is certainly qualitatively different from any other kind of sensual pleasure, especially, whatever psycho-analysts may assert to the contrary, from that of a sexual nature. Indeed, I can assert that my pleasurable sensations in fondling a sweet human child are of the same quality as those I experience in fondling a chow-puppy, or a baby lion. There is not even an appreciable difference of intensity between these reactions; indeed, it is questionable whether a young lion is not, in some respects, what we call a supernormal object to my reaction. But I would seriously warn any psycho-analyst against telling me that I am reacting sexually to that lion! In this case, the existence of a true innate releasing mechanism in man has been clearly proven, the relational properties which the object must possess have been analysed, and the fact that their common effect is obeying the law of heterogeneous summation is quite evident. Also, the objective and subjective reactions activated by the mechanism are clearly distinguishable. A normal man—let alone a woman—will find it exceedingly difficult to leave to its fate even a puppy, after he or she has enjoyed fondling and petting it. A very distinct 'mood', a readiness to take care of the object in a specific manner, is brought about with the predictability of an unconditioned response. Quite especially a strong inhibition to hurt or kill the 'sweet' baby is activated by the innate releasing mechanism in question. When, much against my emotional inclination, I once forced myself for rational reasons to kill a number of young hooded rats who still were in a 'sweet' stage of development, I acquired a very slight, but indubitable neurosis; that is to say, I repeatedly *dreamt* of the occurrence in an emotionally super-accentuated way. This particular innate releasing mechanism of our species is, for obvious reasons, an exceptionally favourable object for the method of approach just described.

But there is no doubt that in many more cases introspection, circumspectly applied, can lead to similarly important discoveries.

Perhaps an even greater theoretical interest is due to the psychological aspect of *taxes*. It can be shown irrefutably that it is not possible to draw a sharp distinction between taxes and *insight* either from the objectivistic or from the psychological point of view. Considered from the objectivistic viewpoint, taxes, as constituents of appetitive behaviour, are represented in all possible gradations of complexity, ranging from simple and clearly analysable directing reflexes to those complex processes of spontaneous solution of spatial problems that we are wont to call 'insight'. The former merge gradually and imperceptibly into the latter, without giving us an opportunity to draw a distinction between both. Neither is it possible to arrive at a clear conceptual distinction between taxis and insight from the psychological, introspective side of the matter. The subjective experience of insight which Karl Bühler so very expressively has termed the 'Aha-Erlebnis', always characteristically takes place in the exact moment when disorientedness gives way to orientation. But in this also there is no essential difference between the simplest and the most complicated processes of 'orientation'. The specific experience of the 'Aha' crops up in the moment when we attain an 'illumination' concerning some very complicated problem, but it also does in the case of a simple and indubitable tropotaxis. When, for instance, our tropotactic orientation to gravity has been removed, let us say by narcosis, or, as I have experienced it twice, in a vasomotoric collapse, then the reorientation sets in again with what I should metaphorically call an audible click, and this click is accompanied by a superlatively strong and qualitatively distinct 'Aha-experience'!

In my opinion, every physiological process which can, in the manner just described, be approached simultaneously from the objective and from the subjective side is of a paramount theoretical and practical importance. The cardinal problem of psychology, the question of the interdependence of body and mind, cannot be inductively approached in any other way than by studying those not too common cases, in which the intrinsic unit of one of these highest life processes *can* be studied from the objective, physiological side as well, as from the subjective, psychological one. To refrain from introspection in such cases would mean renouncing a superlatively valuable source of knowledge for purely dogmatic reasons which would be about the worst thing a natural scientist could do. On the other hand, it is high time that social and group psychology began to occupy itself with the physiological side of behaviour and more especially with the innate processes of which I spoke above. It is high time that the collective human intellect got some control on the necessary outlets for certain endogenously generated drives, for instance 'aggression', and some knowledge of human innate releasing mechanisms, especially those activating aggression. Hitherto it is only demagogues who seem to have a certain working knowledge of these matters and who, by devising surprisingly simple 'dummies', are able to elicit fighting responses in human beings with about the same predictability as Tinbergen does in sticklebacks.

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DIE ANALYSE DER TAXISANTEILE INSTINKTARTIGEN VERHALTENS

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I. EINLEITUNG

In ihrem fast mütterlich anmutenden, grundsympathischen Buch *Vom Wesen des Tieres* (*The Nature of the Beast*) sagt Mrs Noble (1946) vom Orientierungsproblem nicht viel mehr als: 'frankly, no one knows.' Einem Philosophen, der immer gleich alles in einem wissen will, würde ich ähnlich antworten. Aber wir, unter uns, sind gewohnt, die Grenzen unseres Wissens ins Auge zu fassen und an ihnen unsere Weiterarbeit zu orientieren.

Wir gehen aus vom gesicherten Wissen. Im Grunde orientieren sich *alle* Lebewesen auf die gleiche Weise: sie reagieren im Rahmen ihrer *ererbten* Reaktionsbreite auf *Außen*reize. Außenfaktoren und innere ererbte Mechanismen wirken zusammen; die Methoden, jene physikalisch-chemisch, diese physiologisch zu erfassen, sind bekannt und bewährt.

Die *Tropismen* der im Boden *fest*gewachsenen Pflanzen beruhen auf Wachstumskrümmungen, gehören also der Entwicklungsphysiologie an. Die *Taxien frei*beweglicher Organismen sind letzten Endes Aufgabe der Reizphysiologie.

Vermöge ihrer Sinne nehmen die Tiere Außenreize wahr, die unter anderem auch Taxien steuern. *Sinn* ist das Vermögen eines Sinnesorgans, im einfachsten Fall *einer* Sinneszelle, äußere Reize in physiologische Erregung zu verwandeln und diese dem Nervenzentrum zuzuleiten. Hier setzt sie einen keineswegs starr, jedoch *zwangs*läufig arbeitenden, angeborenen Mechanismus in Gang, eben die *Taxis*, mit dem effektorischen Enderfolg der *orientierenden Wendung*.[1]

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[1] *Anm. bei der Korrektur:* Es war die Absicht dieses Vortrages, den Begriff der *Taxis* einzuengen *allein* auf *die orientierende Wendung*. Was *bisher* Taxis hieß, wäre demnach *Verschränkung* eines lokomotorischen (oder der 'Gleichgewichtserhaltung' dienenden usw.) zentralnervösen Automatismus im Sinne v. Holsts (oder mehrerer solcher) mit mindestens einer orientierenden Wendung (oder meist deren vielen). Ebenso wie K. Lorenz (1937*a*, *b*; 1939; 1943) den alten Begriff der Instinkthandlung auflöste und als Verschränkung einer Instinktbewegung (oder mehrerer) mit mindestens einer Taxis (oder mehreren Taxien) deutete, so wäre hier per analogiam der alte, weite Taxisbegriff vielleicht mit 'Orientierungshandlung', die einzelne orientierende Wendung mit 'orientierender Wendung' zu bezeichnen gewesen. Die von mir vorgeschlagene Sprechweise, die also das Wort Taxis dem Einzelteil dessen vorbehält, was früher als Ganzes Taxis hieß, schien mir den Vorteil zu haben das *Wesentliche*, das allen, noch so ver-

Mit den 'unbedingten' *Reflexen* haben die Taxien gemeinsam, daß sie der *Auslösung* von außen her unter allen Umständen *bedürfen*. v. Holstsche Bewegungsautomatismen können bekanntlich spontan anlaufen, Lorenz'sche Instinktbewegungen können leerlaufen. Solches beides kann die Taxis nicht, sie arbeitet immer nur auf Außenbefehl und immer nur 'ins Reine'. Der zwischen den sensiblen und den effektorischen Sektor eingeschaltete Mechanismus der Taxis ist ganz gewiß sehr viel verwickelter als der der einfachen Reflexe (Sherrington, P. Hoffmann u.a.); hier sind die Lokalisation, die Zahl der beteiligten Neurone, die Zeitverhältnisse bereits weitgehend in Arbeit. Vergleichsweise sei demgegenüber an W. R. Hess' (1941) wundervollen Aufsatz über die Motorik als Organisationsproblem erinnert, wo man, durch Modelle veranschaulicht, die Zusammenarbeit der sechs Augenmuskeln im Dienste optischer Zieleinstellung dargestellt findet ('gelenkter Reflex', der 'dreischenklige Reflexbogen', quantitative Summationsfähigkeit der innervatorischen Erregungsübertragung [quantitative Zentrenlehre]. Interferenzphaenomene, positive und negative Werte überlagern sich, nur das Resultat wird an die ausführenden Organe weitergegeben, die nur im Betrag der Resultante mobilisiert werden). Da die Neurophysiologie der Wirbellosen weit weniger durchgearbeitet

schiedenen Fällen *Gemeinsame* zu betonen, die *Vergleichbarkeit* so recht und schon im Wortlkang deutlich zu machen. Die dritte Möglichkeit wäre es natürlich, den alten Taxisbegriff im alten Sinne beizubehalten und für das Neue, die orientierende Wendung also, ein neues Wort zu prägen. Hiergegen schien mir die außerordentliche Divergenz der heute verwendeten Taxissysteme und Taxisterminologien des alten, weiten Sinnes zu sprechen, die ja soweit gediehen ist, daß bereits die ersten terminologischen Tabellen erschienen sind (Fraenkel & Gunn, Soulairac u.a.), mit je einer Säule für jeden Autor, aus denen man ablesen, kaum mehr aber im Kopfe behalten kann, wie verschieden dieser oder jener dieselben Termini verwendet und gegeneinander abgrenzt, so daß am Ende womöglich sich niemand mehr durchfindet und damit die ganze Problematik einfach liegen bleibt. Mein Vorschlag ging also dahin, wenn ich hier ganz subjektiv reden darf, das so gut eingebürgerte, zudem durch seine Adjektivierbarkeit und Zusammensetzbarkeit überaus bequeme und kurze Wort Taxis für den Bestandteil zu reservieren, der es alleine verdient und allein durchsetzbar schien, eben die orientierende Wendung.

In Cambridge versuchten wir, die drei Möglichkeiten gegeneinander abzuwägen, erörterten das Für und Wider, kamen jedoch aus Zeitmangel und weil wichtige zum Mitraten Berufene fehlten, zu keiner Entscheidung. Ich selbst aber entdecke beim Wiederlesen meines Manuskriptes—die Korrektur muß morge nerledigt sein!—daß ich in meiner Darstellung, die ja die Durchführbarkeit meines Vorschlages belegen sollte, keineswegs ganz selten offenbar mehr oder weniger unbemerkt in die alte Redeweise zurückgeglitten bin, so daß das Ganze geradezu unverständlich wird, wenn der Teil bald als solcher, bald aber das Ganze den gleichen Namen Taxis trägt! Ich habe mich kurzerhand entschlossen, einfach ein (*n*), was 'neu' heißen, soll hinter Taxis bezw. -taktisch zu setzen, wo die orientierende Einzelwendung gemeint war, und (*a*), d.h. 'alt', wo mir beim Schreiben des Manuskriptes der alte Wortsinn, die gesamte Orientierungshandlung also, vorschwebte. So belegt der Vortrag in der nunmehr zu Druck gehenden Form die unbedingte Notwendigkeit, alsbald die Entscheidung herbeizuführen, damit weiterhin allgemeinverständlich, ohne terminologische Lexika geredet werden kann. Nach wie vor hoffe ich, daß mit der Zeit der neue Gebrauch sich durchsetzen möchte. Der Begriff der Orientierungshandlung ist so weit—fast jede sinnvolle Handlung ist orientiert—daß er entbehrlich scheint.

ist als die der Wirbeltiere, und da unser Begriff der Taxis, der vergleichenden Verhaltenslehre entnommen, sich in der Neurophysiologie kaum eingebürgert hat, so ist damit die wundeste Stelle unseres Begriffsgebäudes bezeichnet und der durchaus provisorische Charakter,* den meine Ausführungen zu dem anspruchsvoll genug—ebenso wie die Zwischentitel nicht von mir selbst formulierten—Thema haben, ein wenig entschuldigt.

II. DER BEGRIFF DER TAXIS

Es ist kaum zu erwarten, daß der Begriff der Taxis in der hier vertretenen Universalität seiner Anwendung in naher Zeit ein durch das ganze Tierreich durchgehendes morpho-physiologisches Korrelat finden werde. Schon an der Grenze zwischen Ein- und Vielzelligen wird das erschreckend klar. Jenen gesteht man allgemein und unbedenklich Taxien zu, muß ihnen jedoch die Sinne verweigern, da diese an Sinnesorgane geknüpft sind und *eine* Zelle bestenfalles Organelle haben kann. Aber wir stehen mit solchen Kalamitäten nicht allein, sie liegen im Wesen der Sache. So kennen wir Farbempfindlichkeit bei Einzelligen und Farbensinn bei Vielzelligen mit morphologisch recht verschiedenen Lichtsinneszellen, die in noch weit verschiedener organisierte Augen eingebettet sind. Trotzdem ist eine gemeinsame Bearbeitung des Farbsehproblems möglich und notwendig. Echte Lernfähigkeit kennen wir bei Organismen mit Strickleiternervensystemen und höchst verschieden hoch organisierten Gehirnen. Die neurophysiologischen Korrelate des Lernvermögens müssen auch hier denkbar verschiedene sein; dennoch hat man denselben Begriff dafür. Wenn jemand bisher alles in der Wohnküche verrichtete, wofür er nach dem Umziehen in eine größere Wohnung viele Zimmer verwendet, so bleibt er deswegen doch derselbe und behält seinen alten Namen. Das darf auch für die Taxis gelten.

Der hier ins Auge gefaßte Begriff der Taxis (*n*) ist ganz unvergleichlich viel enger als alle früheren Definitionen. Der Vogelzug z.B. ist weder eine Taxis (*a*, geschweige *n*), noch gar ein Instinkt, noch ist eine Taxis (*a*, *n*) ein Instinkt (Bierens de Haan, 1937, 1940), noch auch ein Instinkt je eine Reflexkette usw. Nimmt eine *Galathea* den bewegten Sehreiz wahr und folgt seiner Bewegung lediglich mit der zweiten Antenne, ohne sich selbst vom Platze zu rühren (Doflein, 1910), so ist das eine schöne Taxis (*n*), ebenso, wenn ein Frosch, vor dessen linkem Auge ein Mehlwurm auftauchte, linksherum fährt, so daß sein Maul genau vor dem Mehlwurm steht. Fällt nun der Mehlwurm herunter und ist weg, so schnappt der Frosch trotzdem wiederholt dorthin, wo vordem der Mehlwurm war. Das ist eine *Instinktbewegung*

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* Vergl. Anm. S. 269.

im Leerlauf. Fällt aber der Mehlwurm nicht herunter und wird richtig erschnappt, so war es dieselbe Instinktbewegung 'ins Reine', d.h. sie erfüllte ihr biologisches Ziel, und zwar deshalb, weil sie *verschränkt* war mit soviel Taxien (*n*), wie das Zappeln des Mehlwurms sie notwendig machte, damit der Frosch zu seinem Mehlwurm kam. Der Flug des Zugvogels gegen das Leuchtturmfenster ist *Verschränkung* des zentralnervösen Automatismus (v. Holst 1938–9), der Erbkoordination des Freifliegens mit immer neuen Taxien (*n*), nach jedem Windstoß, der ihn abzutreiben droht, eine neue, wenn nicht ein halbes Dutzend. Ob ich da, wo ich stehe, den Leuchtturm anblicke, oder ob ich dann auch zu ihm hingehe, hinschwimme, rudere oder fliege, stets waren Taxien (*n*) im Spiele, im ersten Fall, am Ort ohne Ortsbewegung, dieselben wie jene, mit denen alle ferneren Fälle anhoben, nur kamen dann später auf der Reise immer neue hinzu, jedoch von derselben Art wie die ersten schon. Ob die Krabbe seitwärts, schräg vorwärts, ob mit allen zehn Beinen oder nur mit neun, mit sieben oder gar nur mit drei Beinen zum Köder eilt oder, am Platz verharrend, lediglich ihre Augen und Stromrichtorgane spielen läßt, immer sind es dieselben Taxien (*n*), gleich mit was für noch so verschiedenen Fortbewegungstypen sie sich verschränken. Besonders schöne Beispiele für Ziel*handlungen* als *Verschränkungen von Instinktbewegung und Taxis* (*n*) gaben uns Lorenz & Tinbergen (1938) für das Zunestrollen eines Eies durch die Graugans, Tinbergen & Küenen (1939) für das Ansperren optischer Reize durch nestjunge, unerfahrene Singdrosseln.

Selbstverständlich rechnen wir auch alle Einstellungsreaktionen, alle Kompensationsbewegungen zur Erhaltung der *Normallage* im Raum, gleich ob sie am Ort oder in der Ortsbewegung stattfinden, mit zu den Taxien (*a*, *n*). In diesen Zusammenhang gehört auch der sog. *Umdrehreflex* (*a*). Man lege nur hundertmal nacheinander einen Seestern oder einen Kartoffelkäfer auf den Rücken und vertiefe sich in die geradezu verwirrende Fülle der Möglichkeiten, die hier dem Tier endlich wieder zur Normalhaltung zurückhelfen, um zu erkennen, welchen Mißbrauch man mit dem Reflexbegriff getrieben hat. Schier unerschöpflich erscheint hier der Vorrat an Bewegungskoordinationen, die alle sich mit den gleichen Taxien (*n*) verschränken, solange, so unermüdlich wiederholt in immer neuen Varianten, bis endlich das Ziel erreicht ist.

III. DIE EINTEILUNG DER TAXIEN

(1) *Einteilung nach dem Sinn*

Es ist allgemein üblich, die Taxien (*a*) *nach dem* sie bedienenden *Sinn* (Chemo-, Geo-, Phototaxis usw.) bezw. nach der durch sie zu erzielenden bezw. erzielten *Einstellung zum Reizfelde* (positiv, negativ, transversal, schräg usw.) einzuteilen. Das ist so eingebürgert, daß es sich nicht mit einem Federstrich abchaffen läßt. Nur soll man sich darüber klar sein, daß solche Aussagen lediglich beschreibenden Wert haben. Sie ordnen den Vorgang mit in einem bestimmten Sinne vergleichbaren Vorgängen zusammen, ohne jedoch auch nur im mindesten etwas zu erklären, noch auch darüber Gewißheit zu bieten, ob der Vergleich nicht rein äußerlich bleibt und recht wesensverschiedene Vorgänge zusammenfaßt. Prechts (1942) Einteilung (durchweg *a*) nach der physikalischen Beschaffenheit der Kraftfelder ist unterrichtend zu lesen, aber zum praktischen Gebrauch insofern wenig tauglich, als sie Zusammengehöriges auseinanderreißt und zu lauter Wiederholungen zwingt. Mit Soulairacs (1949) Kritik an einem noch zu besprechenden Begriffssystem gehe ich in mehreren Punkten einig.

(2) *Einteilung nach dem Ziel. Zwangscharakter. Fraenkel und Gunns Einteilung*

Die *Ziele*, auf die eine Taxis (*a* und *n*) sich richtet, sind oft durch *angeborene Schematen* festgelegt, welche die Grenzen bestimmen, innerhalb welcher dann *Lernakte* und Erinnerung weiter spezifizieren können. Tinbergen & Küenen (1939) haben wohl als erste nachgewiesen, daß für die Taxis (*n*, *a*) ein anderes angeborenes Schema bestehen kann, als für die mit ihr verschränkte Instinktbewegung. Da die Ziele einem weit höheren psychologischen bezw. neurophysiologischen Niveau als dem der Taxis angehören, sollen sie ein für allemal und ganz unbedingt *aus dem Taxisbegriff* (*a* und *n*) *herausbleiben*. Ob ein Mensch sich dem blütenduftgeschwängerten Winde, dem Telefonhörer oder seiner Frau zuwendet, ob er sich anständig hinstellt oder im Manuskript eine Formel nachschlägt, ob ein Heuschreckenmännchen dem Gezirp des artgleichen Männchens nachläuft oder nur ersteinmal die Fühler in Richtung auf die Schallquelle ausstreckt, ob endlich ein Affe den anderen laust, der Taxisanteil (*n*) aller dieser Begebenheiten ist durchaus in voller Strenge vergleichbar. Ein und dasselbe Tier kann, je nach Stimmung, jetzt einen Lichtfleck vor dunklem Grunde, jetzt umgekehrt das schwarze Loch in der weißen Wand ansteuern, beidemal nach genau demselben *Mechanismus*, und *nur* eben *nach ihm* wünschen wir die Taxien (*n*, auch *a*) *erklärend* einzuteilen. Deshalb sind Termini wie Skototaxis untunlich. Wo kämen wir hin, wollten wir für jedes ansteuerbare Ziel—ihre Reihe ist ohne Ende—eine besondere Taxis aufstellen! Die Art des Zieles lehrt uns so gut wie nie etwas rechtes über die Natur des Mechanismus der Taxis, die im Einzelfalle zum Ziele führt.

Auch der so weit verbreitete Widerstand gegen den *Zwang*scharakter der Taxien (*n*, *a*) beruht zum guten Teil auf der Verwechselung von Ziel und

Taxis. Wären freilich die Ziele Zwangsziele, wie es noch Loeb (1913) sogar dem Menschen zumutete, so wäre solcher Widerstand nur zu berechtigt. Aber schon *Paramaecium* wechselt je nach Begleitreizen das *Vorzeichen der Taxis* (*a*); bald schwimmt es aufwärts, bald abwärts (Fox, 1925), das Studium der Umstimmbarkeit des Vorzeichens der Taxis (*a*, *n*) ist ein Kapitel für sich, das die ganze Breite der Reizphysiologie und Psychologie umfaßt. Ich wähle meine Ziele gerne frei, wenigstens in den Ferien; meine Taxien (*n*, *a*) aber, die mich zum jeweils gerade gewählten Ziele führen, sind glücklicherweise ebenso zwangsläufig wie die beste Maschine; es wünscht sich niemand ein Auto mit freiem Willen. Die Zuverlässigkeit der Maschine beruht auf völligem Mangel an Freiheiten. Der freie Wille des Fahrers lenkt sie aufs cm. genau, und sie gehorcht blind. Solche guten Maschinen sind unsere Taxien (*n*, *a*).

Soviel ich dankbar aus Fränkel & Gunns (1940) schönem Buche gelernt habe, so glaube ich doch nicht, daß ihre Terminologie sich durchsetzen werde. Schon Kühns (1919, 1929) erheblich einfacherem Begriffssystem, das sich bis heute immer wieder aufs beste bewährte, blieb die allgemeine Anerkennung z.B. in Amerika bisher weithin versagt. Auch Fränkel & Gunn trennen eng Zusammengehöriges nach in unserem Sinne untergeordneten Gesichtspunkten (vgl. die Sonderrubrik für Transversaleinstellungen), teilen auch nach den Fortbewegungen ein, die wir aus dem Taxisbegriff (*n*) herauslassen wollen (Kinesen), und vor allem klammern sie, uns ganz unbegreiflicherweise, den Menschen aus, wie schon so viele andere vor ihnen. Das ist höchst unpraktisch, denn es trennt uns von den Medizinern, von denen wir sehr viel lernen können und denen, wie wir hoffen, auch unser Wissen hie und da einmal nützlich werden kann und wurde. Jenen vollends, die den Vergleich mit Tieren verabscheuen, ist es Wasser auf ihre Mühle. Ich will keinem der Taxienforscher, die solches tun, wünschen, sie möchten einmal plötzlich alle ihre Taxien (*n*, *a*) verlieren. Wollten sie, in ihrer völligen Hilflosigkeit zur Verzweiflung getrieben, sich erschießen, so ginge die Kugel gewiß ganz weit daneben.

(3) *Die Kühnsche Einteilung*

Allein die Kühnschen Kategorien, die *rein nach dem Mechanismus* trennen, der die Erregung vom sensiblen Sektor auf den effektorischen überleitet, haben voll erklärenden Wert. Nur sie lassen uns die grandiose Konstanz der Taxien (*n*), allen Artunterschieden zum Trotz, völlig klar bewußt werden. Die Taxien (*n*) einen den Menschen mit allen Tieren in fast so engem Verband, wie der gemeinsame Besitz von Protoplasma, Kern, Chromosomen, Mitosis, Meiosis und Zygotenbildung uns zugleich auch mit den Pflanzen eint.

Ein jeder Sinnesreiz kann mehreres zugleich wirken. In jedem Falle lädt er das Zentralnervensystem mit *unspezifischer* Erregung auf und erhöht die Handelnsbereitschaft. Nach Strümpell soll ein Patient nach Verlust auch seines letzten Sinnes nur noch geschlafen, bei künstlicher Ernährung vegetiert haben. Sinnesorgane wie die Halteren, denen er noch keine spezifische Funktion zuzuschreiben wußte, nannte v. Buddenbrock (1928) Stimulationsorgane eben um dieser Leistung willen.

Zweitens können wir zu allermeist eine *spezifische Wahrnehmung* nachweisen, die der adaequaten Reizart im Rahmen einer zugehörigen Modalität entspricht. Im jeweils angeborenen Rahmen leistet sie innere Abbildung von Außenbezügen.

Und drittens kann der Sinnesreiz eine Taxis (*n*, auch *a*) auslösen.

IV. DIE BEZIEHUNG DER KINESIS ZUM TAXIENSYSTEM

Man hat die Auslösung einer Bewegung des vorher ruhenden Tieres oder auch die Beschleunigung einer vorher schon bestehenden Ortsbewegung durch Intensitätssteigerung von Sinnesreizen als *Kinesis* bezeichnet. Auf die Reizart bezw. Modalität kommt dabei wenig an, sie ist durch eine andere meist weithin ersetzbar. Da wir nun—und das ist der einzige Unterschied unseres Ansatzes zu demjenigen Kühns—nach Lorenz' Anregung die Ortsbewegung als solche aus dem Taxisbegriff (*n*) ausklammern, so muss, im neuen Sinne, auch die Kinesis fallen, da sie ja nur die mit der Taxis (*n*) verschränkte, selbst aber nicht Taxis (*n*) darstellende Ortsbewegung betrifft. Jedoch kann *Kinesis* zu *Ansammlungen* führen, und darin liegt, im alten Sinne, ihre Beziehung zum Taxiensystem (*a*).

(1) *Ortho- und Klinokinesis* (Fränkel, Gunn)

Wenn Asseln in feuchter Luft sich langsamer und seltener bewegen als in trockener, so nennen Fränkel & Gunn diesen zu passiver Ansammlung führenden Effekt *Orthokinesis.* Zumindest für das Aufscheuchen aus der Ruhe würde vielleicht das gebräuchliche Wort *Alarm* genügen; ob reine Orthokinese für sich allein häufig vorkommt, bleibt abzuwarten.

Hängt anstatt der Beschleunigung der Ortsbewegungen die Häufigkeit der Wendungen von der Reizstärke ab, dergestalt daß sie die Winkelgeschwindigkeit steigert, so sprechen Fränkel & Gunn von *Klinokinese. Ein lediglich unterschiedsempfindlicher* Rezeptor genügt; die Bewegungen sind relativ zum Reizfelde ungerichtet. Wie bei der Orthokinese—vermutlich kommt beides nicht selten zusammen—ergeben sich passive Ansammlungen, aber schärfer begrenzte, z.B. bei *Paramaecium* und konzentrischem Diffusionsgefälle in Ringform. Wie man sieht, ist Klinokinesis ein neues

Wort für Kühns auf Jennings zurückgehende *Phobotaxis* (*a*).* Fränkel & Gunn wünschten den psychologischen Beiklang zu vermeiden. Uns schreckt er nicht, zumal es abermals für die Taxis (*n*, *a*) durchaus gleichgiltig ist, ob sie in bewußte oder unbewußte Abläufe eingeschaltet ist. So habe ich manchmal beim Quartettspiel meine Bratschenstimme prima vista zur Zufriedenheit der Mitspieler abgeleistet und hinterher feststellen müssen, daß mir von der ganzen Musik schlechterdings nichts bewußt geworden war. Es waren nämlich während des Spielens ganz andere Dinge in meinem Kopfe umgegangen. Kein Zuschauer hätte aus den Spielbewegungen die Achtlosigkeit abgelesen; sie waren gewiß unverdächtig dieselben, wie wenn ich mit ganzer Seele dabei gewesen wäre. Ebenso kann man bei starker Ermüdung ganze Seiten lesen, sie rechtzeitig umschlagen usw., ehe man gewahr wird, dass allein die Augen und Hände am Werke waren, nicht aber der Verstand. Bei kleinen Jungen nennt man es 'schmökern'.

In Gunn & Walshes (1940) Studie über die Klinokinese von *Paramaecium* kommt die *Schreckreaktion* gar nicht vor. Und doch ist sie etwas ziemlich Festumschriebenes, dergestalt daß sie ausgesprochen schädlich wirken kann. Normalerweise begegnet das Tier schädlichen Reizen mit dem Vorderende, und dazu paßt das Zurückfahren. Nähert man aber die aufs Deckgläschen aufgesetzte Heiznadel dem *Hinter*ende eines dahinschwimmenden Paramaeciums, so fährt es *ebenso sicher rückwärts* wie bei Hitzereizung von vorn. So kann es schnurgerade in den Tod rennen, und nur die ungeheure Geschwindigkeit und der geringe Durchmesser der totbringenden Hitzezone retten es, wenn die Nadel noch nicht lange verweilte (Koehler, 1939, 1942). Wer solches sieht, dem wird der Ausdruck Schreckreaktion vertraut, ich möchte ihn nicht mehr missen; der Anthropomorphismus ist zu grob, um ernstgenommen zu werden.

Und in der aufsteigenden Tierreihe kommt er wohl wirklich seinem eigentlichen Wortsinn immer näher. 'Versuch und Irrtum' wird man heute vom Infusor nicht mehr gerne sagen, aber daß die Schlange nach der gebissenen und wieder freigelassenen Maus '*sucht*' (Baumann, 1929)—einer von vielen Teilen des heute so genannten *Appetenzverhaltens*—und zwar erbarmungslos solange bis sie sie hat, das ist wohl zu sagen erlaubt. Solches Suchen ist ein 'Zurückschrecken' vor all den Orten, wo das Gesuchte sich nicht findet.

Erhöhte Wendungsfreudigkeit im Reizfelde kennen wir in schier zahllosen Fällen, so auch im *diffusen*, völlig gefällefreien Duftfelde, wo jede Richtungskomponente fehlt (Murr-Danielczick 1930 bei *Habrobracon* in Raupenatmosphaere, Warnke 1931 bei *Geotrupes* vor Mist, Flügge 1934

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* Die alte Phobotaxis erweist sich, im neuen Sinne, als Verschränkung normaler Lokomotion mit einer meist großen Zahl von Schreckbewegungen, d.h. von Phobotaxien im neuen Sinne.

bei *Drosophila* über Larvenfutter). Die biologische Bedeutung des Verhaltens ist klar: je engere Bahnen jedes Flächenelement treffen, um so größer die Wahrscheinlichkeit des Findens.

Im Paramaecienversuch löst das *Reizgefälle* an beiden Ringgrenzen, d.h. ober- und unterhalb der indifferent ('optimal') wirkenden Konzentration um so sicherer Schreckreaktionen aus, je steiler es ist, d.h. je schneller das unterschiedsempfindliche Tier den kritischen Schwellenunterschied durchschwimmt. Hier dagegen, im gefällefreien Duftfelde, können wir keinen äußeren Grund angeben, warum die Schlupfwespe, der Käfer, die Taufliege gerade hier und nicht dort, warum hier um zwei, dort um drei Rechte wendet. Wir suchen nach einem Wort dafür und finden kein anderes als eben *Suchen*. Auf S. 279 Anm. kommen wir noch einmal darauf zurück.

V. DIE TERMINOLOGIE DER TAXIEN

(1) *Pseudotopotaxis oder Klinotaxis*

Auf der Grenze zwischen Kühns Phobotaxis (*a*) und Topotaxis (*a*), bezw. Fränkel-Gunns Ortho-Klinokinesis und Taxis (*a*) schlechthin steht die *Pseudotopotaxis* alter Nomenklatur, von Fränkel-Gunn als *Klinotaxis* umbenannt. Der Ausdruck der Mittelstellung, sozusagen des Bastardcharakters, ist beidemal durch Nebeneinanderstellen der Grenzwertbegriffe erreicht, wie wenn man Rotgelb statt Orange sagte. Es kommt eine, im ganzen gesehen, gerichtete Zielbahn zustande, aber vermöge vieler aufeinanderfolgender Schreckreaktionen. Die Spur erinnert an den sympodialen Verzweigungstyp des Botanikers, wie ihn auch das *Obelia*-Polypenstöckchen zeigt.

Hierher gehört bekanntermaßen Masts blow-fly-Larve und *Euglena*; und wir können uns in die Lage eines solchen Wesens mit nur einem lediglich unterschiedsempfindlichen, zudem exzentrisch liegenden Photorezeptor versetzen, indem wir ein Auge schließen und das andere durch Vorhalten eines schwarzen beiderseits durch je eine Milchglasscheibe verschlossenen Rohres auf bloßes Helligkeitssehen reduzieren. So bleibt uns lediglich Unterschiedsempfindlichkeit in der Zeit. Trotzdem können wir im Dunkelzimmer das einzige darin brennende Licht nahezu geradlinig ansteuern. Wir drehen uns auf der Stelle solange hin und her, bis die gesehene Helligkeit maximal ist. Dadurch lassen wir uns zum Abmarsch alarmieren und trachten, daß es dabei nie dunkler, sondern nur immer heller wird. Dann wird die Wegspur die der Pseudotopotaxis (*a*) = Klinotaxis sein.

Aber auch bei zweiäugigen Wesen kommt dieses Spurbild vor. *Planaria lugubris* kann, sogleich vom Alarm aus oder erst nach ungerichteten

Suchbahnen, entweder in echt tropotaktischem (*a*) Zielmarsch streng geradlinig oder mit dauernd beidseits symmetrisch zum streng geradeaus gleitenden Hinterkörper hin und wider pendelndem Vorderende den Köder erreichen (Koehler, 1932). Dieses Ausschlagen verbreitert die Basis für das tropotaktische (*a*, *n*) Zusammenwirken beider Auricularsinnesorgane, so wie es bei der stereoskopischen Tiefenmessung geschieht (optische und akustische Entfernungsmesser); das stabile Hinterende zeigt das Integrationsergebnis an. Reine Klinotaxis im Sinne der Definition von Fränkel & Gunn scheint mir das nicht ganz zu sein. Vielleicht dürfte man eher von echter *Tropotaxis auf verbreiterter Basis* (*a*, *n*) reden, wobei jedes der beiden Sinnesorgane sowohl simultan (*n*) mit seinem Gegenüber, wie successiv (*a*, *n*) mit sich selbst bei Links- und Rechsstand 'vergliche'; und damit brauchen die intrazentralen Kombinationen noch keineswegs erschöpft zu sein. Ähnlichen *Simultan-Successiv-Verschränkungen* begegnen wir vielerorten, z.B. beim Längenschätzen eines nahebei an uns vorübersausenden Eisenbahnzuges.

A. Öhmig (1940) sah Raupen des kleinen Fuchses (*Vanessa urticae*) mit nur einem freigelassenen Stemma eine Lichtquelle ansteuern. Hundertmark (1936, 1937) behauptete Formensehen für *Lymantria*raupen, die er dunkle Figuren auf hellem Grunde ansteuern ließ. Das wirkt überraschend, da ja das Stemma nur ein einziges Rhabdom besitzt. An der gleichen Gattung stellte unser gefallener Doktorand A. Kühn (muß unveröffentlicht bleiben) erneut fest, daß tatsächlich ein Stemma genügt, um einen schmalen Dunkelstreif im Hellen sicher anzusteuern, während er hinsichtlich des Formensehens erheblich zurückhaltender urteilte. Beim gut gerichteten Lauf pendelte der Kopf 'klinotaktisch' hin und her, wenn auch in etwas asymmetrischer Haltung, das sehende Stemma dem Ziele angewandt. Es muß wohl der Kopf beim Übergang von Schwarz nach Weiß ins Schwarze zurückgewendet haben, mehr oder weniger regelmäßig abwechselnd an der linken und rechten Streifengrenze. Es ist das von S. Exner (1891) an *Copilia* demonstrierte Prinzip, deren einziges Rhabdom in der Bildebene einer riesigen, ausgezeichnet abbildenden Linse deren ganzen Öffnungswinkel ständig äußerst geschwind durchpendelt. Exner traut ihr ein Bildsehen zu, ebenso wie auch wir unsere fovea successiv über die Teile des Gegenstandes schweifen lassen, ohne es zu wissen, und nehmen subjektiv *gleichzeitig* wahr, was die Stelle des deutlichsten Sehens *nacheinander* aufnahm.

Baumanns (1929) Viper verfolgt die *Spur* der von ihr gebissenen und wieder freigegebenen Maus in engen Windungen, dem Äskulapstabe vergleichbar. Physikalisch gesehen ist die Mäusespur ein langgestrecktes Duftmaximum, das zu beiden Seiten rasch abfällt, wie die Seiten eines steilen Walmdaches. Die Schlange muß sozusagen den Dachfirst entlang laufen, sich ständig auf gleicher Reizhöhe halten, jeden Abfall vermeiden, ganz wie wir mit dem Milchglassrohr. Sie würde vor jeder Reizminderung zurückschrecken, jedes *Spurverfolgen* wäre *Pseudotopotaxis* (*a*).

(2) *Kühns Topotaxien* (*a*)

Wir kommen endlich zu Kühns *Topotaxien*, von Fränkel-Gunn Taxien (*a*) schlechthin genannt—was ich nicht mitmachen möchte, da ich für Beibehalten von 'Alarm', Phobotaxis (*n*, *a*) und Pseudotopotaxis (*a*) eintrete. Definiert sind die Topotaxien (*n*) als *im Sinne des Reizfeldes gerichtete* orientierende Wendungen; der orientierte Zustand verlangt mindestens zwei Sinneszellen bezw. mindestens eine Sinnes*fläche*, wahrend Phobotaxis (*a*, *n*) schon mit einer einzigen Sinneszelle möglich war. Es gilt an *verschiedenen* Stellen der Körperoberfläche *gleichzeitig* Reizunterschiede wahrzunehmen. Wir behalten Kühns Einteilung der Topotaxien (*n*) in *Tropotaxis*, *Telotaxis und Menotaxis* (alles *n*) bei, womit wie gesagt stets lediglich die orientierenden Wendungen gemeint sind; von der etwa damit verschränkten Ortsbewegung soll abgesehen sein.

(*a*) *Tropotaxis* (*n* und *a*)

Der indifferente, orientierte Zustand der *Tropotaxis* (*n*) war definiert als Erregungsgleichgewicht spiegelbildlicher Rezeptoren; die beiden gegensinnigen Befehle heben sich bei gleicher Stärke auf. Ist der linke Rezeptor stärker erregt, so setzt sein Befehl sich durch; das Tier wendet bei positiver Stimmung nach rechts, zur Reizquelle hin, bei negativer nach links, von ihr weg. In jeder Stimmung kann also der Rezeptor *nur einerlei* Befehl geben, er ist ein *einsinniger Lenker*, schon je eine einzige Sinneszelle beiderseits kann für Tropotaxis (*n*) genügen. Ausschaltung eines der beiden spiegelbildlich symmetrischen Sinnesorgane macht tropotaktische Einstellung unmöglich, es sei denn daß andere Sinnesorgane helfend eingreifen. Auch bei radiärsymmetrischen Tieren gibt es echte Tropotaxis, so im Zusammenwirken der Randkörper von Medusen (Fränkel, 1925; Bozler, 1926).

Außer dem Schmerzsinn können wohl *alle* bisher bekannten Sinne den Erbmechanismus der Tropotaxis bedienen (Koehler, 1931). Beim chemischen Sinn ist es vor allem der *Geruch* auf die Ferne: die linksseitig entfühlerte *Drosophila* (Flügge, 1934) macht im diffusen, anlockenden Duftfelde Rechtskreise, im abstossenden Linkskreise* ($\Sigma n = a$). *Planaria*

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* Diese Tatsache beweist Tropotaxis ($\Sigma n = a$). Die normale Taufliege wendet, wie schon oben mitgeteilt, im gleichen diffusen, anlockenden Duftfelde gleich oft und gleich viel nach beiden Seiten. Daraus könnte man eine gewiße Berechtigung herleiten, dieses oben unter 'Klinokinese' = Phobotaxis (*a*) behandelte Verhalten auch als Tropotaxis (*a*) zu deuten,

lugubris läßt sich, zwischen zwei gleichstarken Lockdüften 'eingegabelt', im tropotaktischen Gleichgewicht weithin aufgezwungene Bahnen führen, so recht wie Buridans Esel, ohne je das Ziel zu erreichen (Koehler, 1932). Butenandt (1939) konnte Seidenspinnermännchen durch Hinhalten eines Glasstabes, dessen äußerste Spitze er in ein extrem verdünntes Extrakt (0,018 %) aus weiblichen Duftdrüsen getaucht und dann sorgfältig getrocknet hatte, anlocken und beliebig weit führen. Für den *Geschmack* sei an Romanes (1885) Versuch mit der Meduse *Tiaropsis indicans* erinnert, die sogleich den Magenstiel gegen denjenigen Randtentakel hinbewegt, der Nahrung erbeutete. Ließ man den gegenüberliegenden Tentakel etwas ebensolches erbeuten, so blieb der Magenstiel im tropotaktischen Gleichgewicht hängen. *Thermotropotaxis* wies Homp (1938) bei der Kleiderlaus nach. *Planaria alpina* wendet im Zusammenfluß zweier gleichstarker Ströme zum kühleren; die Unterschiedsschwelle gab ich nach Messungen in beiden Strömen vor dem Zusammentreffen mit 3° C. an; die im Mischgebiet vom Tier wahrgenommenen Differenzen dürften kleiner gewesen sein. *Rheotropotaxis* zeigen ebenfalls Planarien, wiederum *alpina* am schönsten; sie folgten feinen Pipettenströmen in ruhendem Wasser und ließen sich, inmitten zweier gegensinnig genau aufeinandertreffender gleichstarker Ströme eingegabelt, im tropotaktischen Gleichgewichte ebenfalls führen (Koehler, 1932). Als Beispiele für *Vibrotropotaxis* mögen dienen Spinnen (Rabaud 1921*a*, *b*, 1922; Grünbaum, 1927; Lassen und Tolzien, 1940), der Rückenschwimmer (Fisahn, nicht veröffentlicht), Fische und Amphibien (Matthes, 1924; Dijkgraaf, 1933, 1947*a*). *Stereotropotaxis* wies Crozier (1924) beim Mehlwurm nach, *Geotropotaxis* bei *Paramaecium* Koehler (1922, 1930), mittels des Muskelsinnes Crozier & Navez (1930) bei Gehäuseschnecken, mittels Statocysten am schönsten Kühn (1914) beim Flußkrebs, für den horizontalen Bogengang der Eidechse (Kühn und Trendelenburg, 1908), in welchem, ebenso wie beim Hecht (Steinhausen, 1934, 1939*a*, *b*) als typisch einsinnigem Lenker lediglich der ampullopetale Strom wirkt. *Schall*lokalisation belegten beim Hund und Huhn Engelmann (1928), bei Heuschrecken Regen (1914, 1923, 1926), Jacobs (1944), Autrum (1936, 1940–42), bei Fledermäusen Hartridge (1945–46) und Mitarbeiter, zuletzt Dijkgraaf (1946). Beim Lichtsinn ist reine *Phototropotaxis* (*a*, *n*) nur bei Tieren mit sehr primitiven Augen zu

nämlich unter Verzicht auf das Bestimmungsstück, daß sich spiegelbildlich gleich starke Erregungen in ihrer orientierenden Wirkung aufheben. Die beiden im diffusen Felde stets gleichstarken gegensinnigen Befehle würden es unterlassen, sich gegenseitig aufzuheben, sei es daß im Zentrum die beiden Antagonisten zu ähnlichen Successivumschlägen führen, wie unsere positiven und negativen optischen Nachbilder es tun, oder daß, vom Rezeptor aus gesehen, die Empfindlichkeiten links und rechts ein wenig schwankten, oder was sonst. Im Freien wird übrigens ein streng diffuses Duftfeld wohl kaum vorkommen, zumindest nicht bei biologisch wesentlichen Düften.

erwarten (vgl. A. Müller (1925) bei Asseln, Fraenkel (1927*a*) bei Copepoden). Der *galvanische* Strom endlich richtet Infusorien über Plasmapolarisation kathodenwärts, indem die kathodennahen Cilien vorwärts schlagen. Im orientierten Zustande besteht tropotaktisches Gleichgewicht. Bei Vielzellern sind die Verhältnisse unübersichtlich (Koehler, 1926).

(*b*) *Telotaxis* (*n* und *a*)

Telotaxis und Menotaxis erfordern beide schon differenziertere Sinnesflächen, die als *mehrsinnige Lenker* wirken. Für Telotaxis, wörtlich *Zielsteuern*, ist kennzeichnend, daß eines der beiden Sinnesorgane dasselbe leistet wie beide zusammen. Das Hinterende des Polychaeten *Branchiomma* (v. Buddenbrock, 1913) gräbt sich senkrecht in den Sand, gleich wie der Vorderkörper orientiert sein mag. In der orientierten Normallage drückt der *Statolith* auf den Caudalpol der nahe dem Vorderende liegenden Statocyste; er ist ein Indifferenzpunkt, das Eingraben geschieht wendungsfrei geradeaus abwärts. Statolithendruck auf jeden anderen Punkt gibt einen Ausschlag des Hinterendes. Die Längsmuskulatur kontrahiert sich in dem Meridian, auf welchen der Statolith drückt, und das um so mehr, je größer der Winkelabstand des gedrückten Meridianpunktes vom Caudalpol ist.

Ganz Entsprechendes gilt für *bildsehende Augen.* Ihre Stelle des deutlichsten Sehens, die Fixierstelle entspricht dem Caudalpol der *Branchiomma*statocyste; sie ist der Indifferenzpunkt, dessen Reizung allein keine Wendung auslöst. Im orientierten Zustand liegt also das Abbild des Zieles auf der Fixierstelle. Ein jeder passende Reiz aber, der andere Netzhautstellen trifft, löst eben die Augendrehung aus, die den Reiz der Fixierstelle zubringt. Ganz wie in der *Branchiomma*statocyste dreht sich das Auge im gereizten Meridian um soviele Winkelgrade, wie die gereizte Sehzelle von der fovea absteht (Kühn 1919). Wie es sich besonders schön am Leuchtkäferchen zeigte (Mast, 1912, vgl. auch 1923–4), kann einmalige noch so kurze Reizung genügen, um hinterher die jeweils richtige Zieleinstellung im Dunkeln zu erzwingen. Nach einmaligem Aufleuchten eines elektrischen Funkens (für 1/10000 sek. und weniger) saßen alle *Photinus pyralis* ♂♂ mit der Körpermediane in Richtung auf den Punkt, der vorher geleuchtet hatte, manche flogen ihn im Dunkeln an. Die Netzhaut*peripherie* des Wirbeltierauges ist ein *automatischer Sucher*, der alles, was sein Besitzer sehen 'will', zwangsläufig sogleich der Fixierstelle zubringt. Man muß einmal einen Patienten mit allein sehtüchtiger fovea in seiner Hilflosigkeit gesehen haben, um zu ermessen, was wir unseren Taxien danken.

(*c*) *Menotaxis* (*n* und *a*)

Menotaxis endlich bedeutet *Beibehalten* einer gerade gegebenen Reizverteilung auf der Gesamtsinnesfläche durch aktive Kompensationsdrehungen. Um das radiär strahlende Licht kreisen Nachtinsekten in jeweils konstantbleibendem Kurswinkel. Bei 90° Kurs zum Radius ergibt sich ein Kreis, bei spitzerem Winkel verengt sich die Spirale zum Lichte hin, das Tier verbrennt im Ziel; bei stumpfen entkommt es in einer sich erweiternden Spirale. Im parallelstrahligen Licht der Sonne zeigen Ameisen, die Honigbiene und andere Insekten Lichtkompaßsteuerung (Santschi, 1911; Brun, 1914; v. Buddenbrock, 1928; Wolf, 1926, 1927; Fraenkel 1927*b*; v. Frisch, 1946*a*, *b*, 1948*a*, *b*, 1949). Während Tropotaxis (nur beidäugig, *n*) und Telotaxis (*n*) (auch einäugig) nur Positiv-, Negativ- bezw. Transversalkurs steuern ($a = \Sigma n$) können, ist die Anzahl der Kurse bei der Menotaxis umbegrenzt. Die Biene erlernt jeden Kurs, in den sie einmal geraten ist, auf der Stelle beizubehalten und sich seiner noch eine Zeitlang so genau zu erinnern, daß sie ihn vorweisen kann Der sog. Lichtrückenreflex (v. Buddenbrock, 1928) hält Tiere in der Normallage, da im Wasser ja das Licht von oben kommt. Ein der Labyrinthe beraubter *Crenilabrus* (v. Holst, 1935) schwimmt im von unten her beleuchteten Aquarium rückenabwärts in um 180° verkehrter Gleichgewichtslage. Intakte Fische zeigen bei Seitenbeleuchtung Resultanteneinstellung zwischen Auge und Labyrinth, die durch zusätzliche Zentrifugierung bei konstanter Seitenbeleuchtung äußerst exakt quantitiert wurde (v. Holst, 1948*a*). Entsprechend der Unveränderlichkeit der Gravitationskonstante fehlen dem Statolithenorgan Reizgewöhnung und Adaptation. Bietet man hungrigen Pterophyllen (v. Holst, 1948*b*), die im Seitenlicht konstante Resultantenstellung eingenommen haben, Futterreize, so neigt sich ihre Medianebene kurz vor dem Zuschnappen, insbesondere während der beidäugigen Fixation, noch stärker dem Lichte zu; nach dem Zuschnappen (gleich ob erfolgreich oder nicht) nimmt sie langsam wieder ab, wobei die Ausgangslage vorübergehend unterschritten werden kann ('negatives Erregungsnachbild'). Damit ist ein vortrefflicher 'Stimmungsmesser' gegeben, der nach Dunkelaufenthalt erst ein allmähliches 'optisches Aufwachen', danach 'Nahrungsaufmerksamkeit', endlich die oben beschriebene 'Appetiterregung' bezw. Zuschnappbereitschaft sehr sauber anzeigt. Das Tier ist dann 'ganz Auge', die optische Erregung 'fließt ins "Gleichgewichtszentrum" ab'.

Die angebliche Rheotaxis (*a*) der Fische im Fluß hat schon Lyon (1904–7), die des Rückenschwimmers Schulz (1931) und Lüdtke (1935–40) als Photomenotaxis entlarvt: sie wehren sich gegen das Abgetriebenwerden, indem sie dem Strom mit dessen Geschwindigkeit entgegenschwimmen und so das Gesichtsfeld der Ufer bezw. auch des Grundes konstant erhalten. Die Libelle auf dem schwankenden Schilfrohr braucht nichts aktiv hinzuzutun, um ihr Blickfeld konstant zu erhalten, denn das besorgt der im stabilen Gleichgewicht am Hals aufgehängte Kopf von selbst (v. Holst, unveröffentlicht). Der Krebs dagegen erzielt die gleiche Blickfeldkonstanz unabhängig von seiner Körperlage durch menotaktische (*n*, *a*) Ausgleichbewegungen seiner Augen, ganz eben so wie eine Eidechse, die Taube oder wir selbst. Die nystagmischen Augen- bezw. Kopfbewegungen von Amphibien (Birukow, 1937) können gleicherweise vom Auge wie vom Labyrinth her ausgelöst werden. Jeder Verschiebung des Blickfeldes, sei es durch Eigenbewegung des Körpers gegen ruhende Umgebung oder durch bewegte Umgebungsreize gegen den ruhenden Körper (sog. Optokinese, optomotorische Reaktion), wirkt die langsame Phase des optischen Nystagmus in einer Kette menotaktischer (*n*) Gegendrehungen weitestmöglich entgegen. Sowie der in Gegendrehung fixierte Gegenstand aus dem Auge kommt, springt es—die rasche Phase bleibt uns unbewußt—voraus und faßt sich einen neuen Fixierpunkt. Derselbe Nystagmus kann, z.B. bei Passivdrehung im optisch indifferenten Felde, auch rein labyrinthär ausgelöst werden (Birukow, 1937; Dijkgraaf, 1933; Steinhausen, 1934, 1939*a*, *b* beim Hecht). Im Wechselrhythmus beider so oder so auslösbarer Phasen haben wir wohl einen zentralnervösen Automatismus von gegebener erblicher Variationsbreite zu erblicken, zwischen deren Grenzen die aufs Auge bezw. das Labyrinth wirkenden Außenreize das Zeitmaß der langsamen Phase bestimmen.*

VI. DAS ZUSAMMENSPIEL VERSCHIEDENER TAXIEN (*n*)

Es bedarf wohl keiner besonderen Betonung mehr, daß höhere Tiere und wir selbst zugleich über *alle* genannten Taxien verfügen und uns ihrer aller wechselweise, wie in oft schier unauflösbarem Zusammenspiele bedienen, ferner daß ein jeder Sinnesreiz, gleich welcher Modalität immer angehörig,

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* Bei Katzen konnte Hess (1949) durch elektrische Zwischenhirnreizung denselben Nachnystagmus auslösen, wie er nach Zwangsdrehung vom Labyrinth her ausgelöst wird. Auch die von Magnus (1924) so eingehend untersuchten Koordinationen zur Hals- und Körpermuskulatur werden dabei ebenso deutlich, wie auf der Drehscheibe selbst. Nach ihrem Anhalten läuft das Kaninchen bezw. die Katze (Bartorelli & Wyss, 1941–2) im früheren Drehsinne weiter im Kreise, ohne Nystagmus zu zeigen (Körpernystagmus); hält man den Kopf fest, so zeigen sie Kopfnystagmus; wird auch der Kopf fixiert, dann ist der Augennystagmus vollkommen. Entsprechend verfolgen manche Menschen beim Lesen die Zeilen statt nur mit den Augen, vielmehr unter nystagmischen Kopfdrehungen. Den optomotorisch wie labyrinthär gleicherweise und gleichgut auslösbaren menschlichen Nystagmus untersuchten Jung (1948), sowie Jung und Tönnies (1948). Das Nystagmuszentrum suchen sie mit Lorente de No (1931, 1938) in der substantia reticulosa von Mittelhirn und Brücke, in Edingers motorischem Haubenkern.

jede Taxisform bedienen kann, wofern der sensorische Sektor hinreichend differenziert ist, um alle Taxisformen zu gestatten. Schon *Paramaecium* beantwortet die verschiedensten Reizarten durchweg mit derselben Schreckreaktion; andrerseits vermag es denselben Schwerereiz je nach Begleitumständen ('Stimmung') bald phobisch, bald topisch zu beantworten (Koehler, 1922). Und um Benachbartes zu erwähnen, so hat v. Gavel (1940) genau gemäß der Voraussage von M. Hertz (1934*a*, *b*; vgl. aüch Gaffron, 1934) jenen Richtungsumschlag gesehener Bewegung für das Komplexauge von *Drosophila* physiologisch gesichert, der uns im Film zwingend sehen läßt, daß am vorwärtsfahrenden Wagen die Räder sich rückwärts drehen. Das Fliegenauge vermag ebensowenig wie das unsere wirkliche und gesehene Scheinbewegung zu unterscheiden. Fische und Hühner unterliegen denselben optischen Täuschungen wie wir selbst.

Wollten wir Kühns Telotaxis nach Fränkel & Gunns Vorschlag (*a*) etwas umdefinieren, so hülfe es uns auch das nicht über die vor allem von Lüdtke (1935–40) am Rückenschwimmerauge gesicherte Tatsache hinweg, daß einzelne Augenteile in höchst variabler Weise zusammenspielen, selbst im gleichen Orientierungsakte (*a*) mindestens zwei, wenn nicht drei ja vier Motive (*n*) zugleich anschlagen, die wir gewohnt sind, als Phobo- Tropo-, Meno- und Telotaxis (alles *n*) sonst streng zu scheiden, und vor allem daß hier wieder einmal sämtliche Vorstellungen von starren Bahnen zwischen bestimmten Sinneszellen und bestimmten Effektoren gründlich versagen. Je nach der Reizlage und ihrer Beantwortung läßt sich der Augenquerschnitt in drei bezw. vier sehphysiologisch verschieden tätige Sektoren zerlegen, deren jeder seinen spezifisch eigenen Anteil an der gesamten Orientierungsleistung nimmt. Dieselbe ist nun vom ersten Larvenstadium an bis zur Imago durchweg gleich vollkommen; andrerseits wachsen von Häutung zu Häutung immer neue Ommen nach und entfalten sich bei der Häutung als Halbmond, der die bereits vorhandenen Ommen umgreift. So wird der Augenquerschnitt schrittweise bis auf das gut sechsfache verbreitert. Demgemäß wechseln die allermeisten Ommen bei jeder Häutung ihre Sonderaufgabe. Nur relativ zur Gesamtfläche ist das Sektorenverhältnis festgelegt, keineswegs jedoch absolut. Nur vom Ganzen her bestimmt sich die besondere Orientierungsleistung des einzelnen Ommas für jedes Larvenstadium neu.

VII. DAS PROBLEM DES HEIMFINDENS

(1) *Einleitung*

Wie das *ABC* zum Faust, so verhält sich das Taxisproblem, das wir soeben besprachen, zu dem des *Heimfindens* (Koehler, 1943, 1948). Selbst der Tierverächter wird hier vor Leistungen den Hut abnehmen, die schier unglaublich klingen und doch sicher belegt sind. Dementsprechend sind der vorwegnehmenden Lösungen nicht wenige. Wir wissen genau, wie wenig wir wissen und wieviel wir wissen müßten, um vom Heimfinden verbindlich zu reden. Trotzdem tun wir—auf den Vorwurf der Engstirnigkeit hin, den wir ertragen müssen—das einzige, was uns in solcher Lage zu tun möglich scheint: wir gehen abermals aus vom Wissen über die Sinne, Taxien, Schemata, Lernvermögen usw. und versuchen, die Grenzen ihrer Anwendbarkeit auf unser Problem so zu zeichnen, wie sie uns heute erscheinen.

Ich fragte eine hilfsbereite junge Dame, die schon zwölf Jahre in Freiburg lebte, nach einem bestimmten Geschäft. Sie nannte ein anderes, um mir von dort aus den Weg zu beschreiben, und als ich auch das nicht kannte, gab sie auf. Nun bat ich um Angabe der Himmelsrichtung, in welcher ich das Geschäft zu suchen habe, und erregte heftigen Unwillen. Niemals in ihrem Leben, nirgends habe sie nach Nord und Süd, geschweige gar nach West und Ost gefragt und sei doch überall recht gut durchgekommen. Es gibt nicht wenige solche Menschen. Sie mögen den Stadtplan, die Karte der näheren Umgebung, die Karte ihres Landes und die von Europa einigermaßen im Kopfe haben; doch sind sie unfähig, sie in Gedanken zu koordinieren. Sie wissen nicht, durch welche Straße sie ihre Stadt verlassen müssen, um zur Nachbarstadt zu radeln, sie können zuhause in ihrem Zimmer auch nicht ungefähr die Richtung weisen, in der Paris, Rom oder London liegt.

Käme solch ein Mensch des Nachts in eine fremde Stadt, führe im geschloßenen Wagen ins Quartier und verließe es erstmals am nächsten Morgen, so würde er vor der Haustür sich erst einmal umdrehen, um es nebst seiner Umgebung sich gut genug einzuprägen, um es beim Heimweg wiederzuerkennen. Danach tritt er seinen ersten Gang an, indem er sich durchfragt, sich jeweils die Straßenecken und die Art merkt, ob und wie er dort wenden muß. Dann kann er den so dem Gedächtnis eingeprägten Weg wieder zurückfinden, indem er die Markenreihe von hinten aufsagt und alle Drehsinne ins Spiegelbild verkehrt. Diesem ersten nunmehr bekannten 'Wechsel' durchs Unbekannte folgen weitere Weg-Dressuren, die, abgesehen vom gemeinsamen Ausgangspunkt, vorerst noch keine Lagebeziehung zueinander zu haben brauchen.

Erst durch zufällige Entdeckung von Überkreuzungsstellen zweier solcher Wechsel, von Durchblicken, die Abkürzungen bedeuten, und ähnliches festigt sich das bisherige lose Radienwerk der Einzelwege zu einem soliden Wegenetz, endlich zu voller Kartenkenntnis des Ortes, die es ihm gestattet, von jeder Stelle wo er schon einmal war, auf kürzestem Wege nachhause oder sonstwohin zu gehen, und das alles immer noch ohne

Ahnung von Himmelsrichtungen. Wesentlich beschleunigen kann er die Erwerbung, wenn er auf den Kirchturm steigt, die Stadt überfliegt oder sich möglichst früh eine Karte kauft.

(2) *Mnemotaxis* (*a*)

Ganz ähnlich hat man sich offenbar bis noch vor kurzem die Orientierung der heimfindenden Insekten vorgestellt.

So beginnt ja die erstausfliegende Biene mit dem *Orientierungsflug*, d.h. sie pendelt wie der Glockenklöppel beim Anläuten mit zunehmendem Ausschlag um die durchs Flugbrettchen gehende Medianlinie, und manchmal sieht man sie an den Wendepunkten, die links wie rechts ziemlich genau auf zwei sich im Flugbrettchen schneidenden Geraden liegen, in kurzem Schwirrflug verweilen. Genau so halten es die ausfliegenden Wespen (Freisling, 1938), und keine Sammlerin fliegt nach gutem Erfolg von der Fundstätte ab, ohne zuvor einige Flugrunden darüber gelegt zu haben. Daß all das auf ein *Anpeilverfahren* herausläuft, wie es auch der Küstenschiffer anwendet, das beweist das Vorspielen der heimkehrenden Sammlerinnen, wenn man den Bienenstock auch nur um wenige Meter verschob, genau dort in der leeren Luft, wo vordem das Flugbrettchen stand (Wolf 1926–7). Auch der Sandregenpfeifer (*Charadrius hiaticula*), dem man das Nest samt den Eiern spurlos versandete, sucht es nach genau demselben Prinzip und findet den Ort trotz Fehlens aller Nahmarken allein durch Fernmarkenpeilung auf wenige cm. genau (Koehler, 1940, Laven, 1940). Es handelt sich immer wieder um die Kombination vieler telotaktischer (*n*) Anzielreaktionen (deren jede recht gut auch einäugig stattfinden könnte) mit dem Prinzip der symmetrisch zur Mittelsenkrechten sich verbreiternden Basis, und gewiß unter voller Ausnützung aller sonstiger Kriterien der Tiefenschätzung, die diesen Tieren eignen mögen.

Danach legt die erstausfliegende Biene ihre erste Wegspur. Sie fliegt auf eine Marke los, wendet kurz vor ihr zur nächsten, von ihr zur dritten und so fort. Denselben Marken in umgekehrter Reihung folgend kehrt sie heim.

Dieses Vermögen nannte Kühn (1919) *Mnemotaxis* (*a*). In unsere ersten Kapitel paßte sie nicht, um so besser in dieses. Sehen wir heute schon in Kühns 'elementaren' Taxien, also in seiner Phobo-, Tropo-, Meno- und Telotaxis (alles *a*) zu allermeist Verschränkungen mindestens eines lokomotorischen zentralnervösen Automatismus (einschließlich Aufrechterhaltung der Normallage im Raume) bezw. einer Instinktbewegung bezw. mehrerer solcher mit meist vielen Einzeltaxien (*n*) gleichen Namens oder auch aller möglichen—wir lernten ja bereits Orientierungshandlungen kennen, bei denen mindestens Phobo- und eine, wenn nicht gleich alle Arten von Topotaxien mitbeteiligt waren (Planarie, Rückenschwimmer und andere)—so gilt solches in noch unvergleichlich weit höherem Masse von der Mnemotaxis (*a*). Sie stellt eine Reihung von vielleicht hunderten der elementaren Taxien dar, verschränkt mit Fortbewegung, geordnet und geleitet am Bande der *Erinnerung*. Der orientierte Zustand des Weiterfindens besteht jeweils in erlebnismäßiger Erfüllung dessen, was die erinnerte Marken- und Winkelmelodie jeweils erwarten ließ. Und unter Marken sind die Einzelziele verstanden, wobei alles Erdenkliche zum Ziel werden kann, wenn es nur passend am Wege lag. Bei der Orientierung zur Einzelmarke mag Telotaxis (*a*) mit Basisauspendeln vorwiegen, wenigstens anfangs; später schleifen sich die Winkel ab, es kann abgekürzt werden, der Winkelflug nähert sich allmählich der Luftlinie. Bleibt eine Marke aus, solange sie noch gebraucht wird, so wird sie gesucht, in phobischen (*a*) Bahnen unter jeweiligem Zurückschrecken (*n*) vor dem hier Unerwarteten. *Mnemotaxis* ist *homophoner Ablauf der Folge realer Reizsituationen mit der Erwartungsmelodie* (Kühn, 1919), ist *Wegfinden nach der Erinnerung*. Wo man schon einmal gewesen ist, da findet man sich zurecht; im fremden Gelände ist man hilflos.

Ich sah den ersten längeren Ausmarsch eines erst vor wenigen Stunden geschlüpften *Sandregenpfeiferjungen* aus dem Nest mit an. Vorher kann er höchsten ein oder zweimal ein par Schrittchen herausgekommen sein, bis der Brüter ihn wieder zurückholte. Ich ging aufs Nest los, um des Junge zu beringen. Erst drückte es sich, dann machte es sich davon recht unbeholfen noch, oft knickte es zusammen, raffte sich aber immer gleich wieder auf. In etwa 40 m. Abstand verlor ich es aus den Augen, ging in meinen Unterstand zurück und wartete. Da kam es heran, genau aus der Richtung in der es fortgegangen war, haargenau gerichtet zur Nestmulde und legte sich mitten hinein. Rundherum waren zahllose windverwehte menschliche Fußstapfen, die für mich genau so aussahen wie die ebenso verwehte, kaum mehr kenntliche Nestmulde. Ich wäre völlig außerstande gewesen, den Nestort auch nur auf ein paar Meter genau anzugeben, hätte mir nicht eine Stöckchenmarkierung geholfen, die dem Tier bestimmt nichts sagte. Das volle Vermögen, sich im Nu auf Fernmarken einzupeilen und mnemotaktisch (*a*) den einmal begangenen Weg zurückzufinden, ist *angeboren*.

(3) *Die Rolle der Kinaesthetik*

Besonders augenfällig sind die Wechsel der *Kinaesthetiker*, z.B. der Wasserspitzmaus. Als Lorenz (1943, S. 336/7) ein Kistchen fortnahm, das auf dem Weg zur Futterschale gestanden hatte, sprangen alle Wasserspitzmäuse genau an der gewohnten Stelle in die leere Luft, stellten sich nach unsanfter Landung auf die Hinterbeine und tasteten mit Schnurrhaaren und Händen dort herum, wo der vordem stets angesprungene Kistenrand hätte sein sollen. Ganz ähnliches gilt für Wüstenspringmäuse; ja es wird wohl nur wenige Tiere geben, bei denen nicht Kinaesthetik früher oder später die höheren Sinne beim Wiederfinden ihres Wechsels (alter Wegspur) mehr oder weniger ablöste. So weitverbreitet die Vorstellung zu sein scheint, Mnemotaxis sei ein rein optisches Vermögen, so unhaltbar ist sie. Jeder andere wache Sinn kann mithelfen; die Propriozeptoren vor allem bei kinaesthetischer Orientierung. Ich stehe nicht an, menschliche verwickelt orientierte Bewegungsfolgen etwa wie Blindschreiben auf der Schreibmaschine oder die Beherrschung eines Musikinstrumentes, orientierungsphysiologisch gesehen, als ganz vorwiegend kinaesthetische Mnemotaxis zu bezeichnen. 'Erst hat mans im Kopf, dann in den Fingern.' Was sich anfangs in voll bewußten, rein intelligent geleiteten Willensakten unter vor allem optischer Führung mühsam, quälend langsam vollzog, das verlegen wir immer mehr und endlich völlig in den Bereich unbewußter Kinaesthetik hinab. Ebenso beginnt die Ratte im Labyrinth, indem sie sich sehr viel Zeit läßt, alles beschnuppert, zögernd wählt. Am Ende saust sie wie ein Pfeil zum Ziel. Wieweit Kinaesthetik selbst beim beseeltesten Künstler mitspricht, ja ihm das Oberbewußtsein für das Eigentliche, die Beseelung des Handwerks erst freigibt, das ermißt man nicht ohne Enttäuschung beim da capo, wo sich selbst Nichtdazugehöriges, etwa bei der Sängerin das Zusammendrücken des Taschentuchs in den verschränkten Händen, an genau derselben Stelle haargenau wiederholt.

(4) *Kreisflüge der Hummeln*

Der von Frank (1941) und Haas (1946, 1949) entdeckte Kreisflug der Hummelmännchen, auf dem sie den größeren Teil ihrer Wachzeit verbringen sollen, ist ein weiteres anschauliches Beispiel für Mnemotaxis (*a*). Die Männchen verlassen nach dem Schlüpfen das Nest auf Nimmerwiedersehen. Wohl gemäß angeborenen Schematen, deren Artunterschiede die Darstellung gut belegt, fliegt das Männchen z.B. eine Baumwurzel an, setzt sich und verwittert den Ort, wenn die Verhaltensdeutung sich bestätigen sollte, mit teils auch der Menschennase wahrnehmbaren artspezifischen Düften. So geht es von Marke zu Marke, bis der Kreis sich schließt und das Tier, 150 mal und mehr am Tage, immer im gleichen Drehsinne dieselbe Tour beschreibt, jetzt natürlich nur vorspielend; neu verwittert wird nur, wo es nottut. Der Verwitterungsduft könnte dem Spurleger selbst helfen, seine Erstbahn wiederzufinden; auch mag er benachbart kreisende Männchen einfangen, so daß Bahnteile mehrerer

Männchen sich decken, und endlich soll er Weibchen anlocken, die, gleichwohin sie sich wenden, in dem immer dichter werdenden Netz männlicher Rundbahnen überall gute Begattungschancen haben. Bis zu zwölf Tagen sahen die Autoren ein markiertes Männchen alle vier Minuten dieselbe Marke anfliegen, stets aus gleicher Richtung, was invarianten Drehsinn auf dem wochenlang gleichbleibenden Rundflug bedeuten soll, der nur durch kurze Pausen der Futteraufnahme und des Sichsonnens unterbrochen wird. Manche flogen konstant links, andere konstant rechts herum, kein einziges flog 'razemisch'. Großäugige Männchen (*B. mendax* z.B.) sah man häufiger in angespanntem Lauern auf der Stelle. Sie flogen pfeilgerade, vergleichbar auch den *Eumenis semele* Männchen in gleicher Stimmung (Tinbergen, 1943), auf ziemlich beliebige bewegte Sehdinge, z.B. vorüberfliegende Fliegen los, und wendeten erst kurz vor dem falschen Auslöser zum Ruheplatz zurück.

Die allmähliche Erweiterung des deskriptiv bekanntwerdenden Flugfeldes der Biene wird bewiesen durch Verfrachtungsversuche nach Aufstellung des Stocks in neuer Gegend. Läßt man Bienen vor dem ersten Orientierungsflug auch nur auf wenigem Abstand vom Stock auf, so findet keine heim, obwohl sie sein Bild ja genugsam kennen. Später kann man sie täglich weiter weg aussetzen, ohne sie zu gefährden. Nach etwa zwei Wochen kennen sie das gesamte Flugfeld des Volkes bis zu seinen äußersten Grenzen (1 bis 4 km. Durchmesser je nach Größe des Volkes) und finden von jedem beliebigen Punkt in Luftlinie heim (v. Frisch, 1923).

Bei *Ammophila campestris* (Baerends, 1941) sei an unmittelbar Vergleichbarem hervorgehoben das Aufsteigen der Wespe auf *Aussichtspunkte*, wenn sie im Jagdgebiet nach Beutefang nicht weiterweiß, der *spiralige* Abgang, das *Geradlinigwerden* des Heimwegs bei Anschluß an wieder bekanntes Gelände, die nachweisliche *Markenführung* längs versetzten künstlichen Baumreihen, die Überlegenheit des alten Nest*ortes* über das um nur wenige Dezimeter zur Seite verlegte Nest selbst (genau wie bei Honigbiene und Sandregenpfeifer). Wie Tinbergen (1932, 1935, 1938*a*, *b*) und Beusekom (1948) am Bienenwolf *Philanthus triang.* feststellten, werden auch Nahmarken am Nest stark beachtet, wobei ihre Gesamtkonfiguration mindestens ebensovel bedeutet wie ihre Einzelbeschaffenheit. Im Kreis von Kienäpfeln zielen die Weibchen die leere Mitte an; legte man sieben Kienäpfel wie die Sterne des Großen Bären (Wagen) aus, so flogen sie die leere Mitte des 'Wagenkorbes' und das Zentrum des Bogens der Deichselsterne an. Vielleicht darf man ein solches Zielen ins Leere als *Telotaxis im bewegten Blick* bezeichnen. Es ist vergleichbar dem Schießen auf eine Konturscheibe; das kann einäugig geschehen, indem man den Durchmesser verfolgt und nach der Halbzeit abdrückt, es sei daß die

Grenzen der Scheibe im indirekten Sehen gleichzeitig mitwahrnehmbar sind und wieder einmal simultane mit successiven Vermögen kombiniert werden.

Selbst der Ansatz des Ehepaares Heinroth (1941) zur Erklärung des Heimfindens der *Brieftaube* (*Columba livia*) rechnet offenbar nicht mit den Himmelsrichtungen, sondern lediglich mit den Methoden jener Freiburgerin. Auch diese in sicher fremdem Gelände einzeln aufgelassenen Tauben schroben sich in konzentrisch um den Auflaßort sich erweiternden Spiralen empor (vgl. *Ammophila*). Reichte ihr Fliegemut soweit, bis sie bei ihrem Kreisen irgendwo endlich auf bekanntes Gelände stießen, dann konnten sie direkt nachhause fliegen. Knieriem (1942, S. 137) sah seinen vielfach preisgekrönten Tauber Derby bei nicht weniger als 28 Heimflügen jedesmal den 3 km. hinter dem Schlag liegenden Kirchturm ansteuern, auf dem er beim ersten Heimflug, bei erschöpftem Fliegemut, übernachtet hatte. Er gewöhnte sich den 6 km. weiten, haarnadelförmigen Umweg ebensowenig ab wie Lorenz' Wildgans Martina (1943, S. 338) jenen ebenfalls beim Erstbesteigen der Haustreppe durch Erschrecken erworbenen Umweg auf dem Treppenabsatz während voller dreier Jahre.

Wenn jene himmelsrichtungsscheue Freiburgerin auch die Begriffe Rechts, Links, Vorn Hinten, Oben, Unten verweigert hätte, so wäre damit jede Verständigung über Orientierungsfragen unmöglich geworden. Wir beziehen diese Wortsinne auf unsere *subjektiven Raumkoordinaten*, deren Nullpunkt etwa in der Mitte des Kopfes bei Normalhaltung liegt. Wer also eine Weg-*Erinnerung* haben soll, dem sollte man solche subjektiven Raumkoordinaten zutrauen.

(5) *Subjective Raumkoordination*

Friedländer (1931) und Wiechert (1938) konnten Honigbienen auf Farb- und Formpaare dressieren, die an der Vertikalwand des Futterkästchens über und unter dem Flugloch angebracht waren (z.B. Gelb oben, Blau unten als Positivmerkmal; Blau oben, Gelb unten als Negativmerkmal). Bei Wegnahme des Flugloches als Bezugspunkt blieb die Dressur erhalten; einer Schrägdrehung des Farbpaares hielt das Unterscheidungsvermögen um 80° noch stand; d.h. wenn oberhalb der nun in keiner Weise mehr anschaulich gemachten Raumhorizontalen auch nur eine Spur mehr Gelb war als darunter Blau, so achteten sie es noch positiv, bei 90° Drehung (gleich viel Gelb wie Blau sowohl über wie unter der Raumhorizontalen) reagierten sie indifferent. Ferner glückte die fluglochfreie Dressur auf Links-Rechts-Farbpaare in der Vertikalebene und genau so gut auch auf der horizontalen Tischplatte, R und L verstanden im Sinne der aus konstanter Richtung anfliegenden Biene, wie überall bei ständigem automatischem Platzwechsel, und endlich hier auch, abermals im Sinne der Anflugrichtung der Bienen, die Dressur auf Vorn Blau, Hinten Gelb gegen Hinten Blau, Vorn Gelb, alles ohne festen Bezugspunkt, d.h. fluglochfrei, bei gleicher Drehtoleranz wie in allen bereits erwähnten Versuchen. Demnach besitzt die Biene nachweislich den unseren streng vergleichbare *subjektive Raumkoordinaten.* Da nun die Dressur in der Horizontalanordnung voll erhalten blieb, als weiterhin plötzlich die Anflugsrichtung regellos bis zu 180° wechselte, so reichen nunmehr die subjektiven Koordinaten zur Erklärung des nachgewiesenen Vermögens nicht mehr hin: *auch* der *äußere* Raum muß für die Biene seine *eigenen* Koordinaten haben, so daß sie es merkt, wann und wie sie gegen diese ihr subjektives Koordinatensystem verdreht. Natürlich kann hierfür in erster Linie die reiche Markentopographie des Versuchsgartens verantwortlich gemacht werden. Dann blieben wir immer noch im alten Begriffsystem unserer Freiburgerin. Doch ist zu fragen, ob Mnemotaxis (*a*) allein nach Marken das einzig verwendete Prinzip war. Das war es nicht.

(6) *Die Lichtkompaßreaktion*

Tatsächlich übertrifft die Biene die Freiburgerin, und zwar vermöge ihrer menotaktischen (*a*) *Lichtkompaßreaktion*, wie sie besonders Wolf (1926/7) auf dem markenarmen Riesenflugplatz nachgewiesen hat; von seinem seither wohl noch nicht wieder nachgeprüften 'Fühlersinn' sehen wir hier ab.

Darüber hinaus hat neuerlich K. v. Frisch (1946*b*, 1948*a*, *b*) eindeutig bewiesen, daß die Biene bei schlechterdings jedem Fluge auch in markenreichstem Gelände den Lichtkompaß des Ausfluges aufnimmt und ihn zudem bis nach der Heimkehr im Gedächtnis behält. Denn sie tanzt im dunklen Stock auf der *vertikalen Wabe* den Schwänzeltanz, dessen Geschwindigkeit den Abstand, dessen geradlinig durchschwänzelte Mittelstrecke den Lichtkompaß der Luftlinie vom Stock zur Tracht angibt, gleich ob sie selbst Luftlinie oder Umwege geflogen ist. Liegt die Trachtquelle vom Stock aus gesehen genau in Richtung zur Sonne, so legt die Finderin ihre richtungweisende Mittelgerade genau senkrecht *aufwärts*. Alle weiteren vorkommenden Kurse gegen den jeweiligen Sonnenstand symbolisiert die Tänzerin durch entsprechendes Schrägschwänzeln gegen die Raumvertikale, d.h. *geomenotaktisch* ($\Sigma n = a$). Die hinter der Tänzerin mitlaufenden Neulinge *lernen* geomenotaktisch den Kurs, den die Tänzerin im Freien *photomenotaktisch* ($\Sigma n = a$) erfuhr und dessen sie sich beim Tanze entsinnt. Nun fliegen die Neulinge aus und halten zur Sonne den Kurs, den die beim Mittanzen erlernten. Jede Sammelbiene, die am Gemeinschaftstanz teilnimmt, macht also dieselbe Transposition in beiderlei

Richtung und in dreifach wechselndem Sinne. Als Vortänzerin transponiert sie von horizontal auf vertikal, als Nachtänzerin umgekehrt; jene erinnert drinnen das photomenotaktische Erlebnis, diese draußen das geomenotaktische; jene reproduziert das draußen optisch Erlernte drinnen nach der Schwerkraft, diese das im Stock nach der Schwerkraft Erlernte draußen relativ zur Sonne.

Stellt man jedoch die *Wabe horizontal*, so entfällt diese Art der Richtungweisung. Und nun zeigt die Finderin die *direkte Richtung zur Tracht* an, unabhängig von der Tageszeit. Im dunklen Stock freilich ist sie dazu nicht imstande, wohl aber, wenn blaues Himmelslicht auf die Wabe fällt. Die Sonne selbst braucht sie nicht zu sehen, sie darf auch bewölkt sein. Es genügt ein beliebig kleiner blauer Ausschnitt des Himmelsgewölbes, so klein wie der Querschnitt eines Ofenrohres ihn ausspart. Frischs Spiegelversuch (1948*a*) nebst dem mit der Polarisationsfolie (1949) lehren, daß das *teilweise polarisierte Himmelslicht*, selbst in so kleinem Ausschnitt, in voller Deutlichkeit den Sonnenstand anzeigt. Daher kann die Tänzerin hier den erinnerten Sonnenkompaß, der zur Tracht führt, direkt vortanzen, ohne die Sonne zu sehen. Bewölkt sich der Ausschnitt im Ofenrohr, so versagt das Vermögen, die Tänze sind ungerichtet. Wie aber die Biene im Freien auch unter ganz bewölktem Himmel den Sonnenkompaß zu nützen versteht und wo in ihrem Auge der Analysator sitzt, das zu klären ist v. Frisch gegenwärtig bemüht. Das Vermögen dürfte auch anderen Insekten eignen. Schon Santschi sah seine Ameisen ihren Sonnenkurs unter einem eisernen Schirm beibehalten; freilich schloß er daraus, sie sähen bei Tage die Sterne und navigierten nach ihnen.

(7) *Gibt es einen 'Orientierungssinn'?*

Da die Biene auf jedem Fluge den jeweiligen Kurs neu aufnimmt und sich der einmaligen Wahrnehmung hinreichend entsinnt, um ihn im Dunkeln gegen die Raumvertikale transponiert den Genossinnen vorzuführen, was beides zusammen keine fünf Minuten dauern dürfte, so sind hier Mißweisungen infolge des Sonnenganges nicht zu befürchten. Der *Zugvogel* aber ist nicht Minuten, sondern Tage, Wochen, wenn nicht Monate auf Reisen. Wie sollte ein Vogel jene Methode ersetzen, nach der wir mit Hilfe des Zifferblattes einer Ortszeit weisenden Uhr aus dem Sonnenstande die Südrichtung zu bestimmen lernen. Und wie soll ein Brutvogel wissen, in welcher Richtung man ihn blind verfrachtete?

Andrerseits aber sind nun einmal Beobachtungen verfügbar, die es höchst unwahrscheinlich machen, daß alle Orientierungsleistungen verfrachteter bezw. ziehender Tiere sich allein als Mnemotaxis (*a*) deuten ließen. So erinnert Gätke (1900) an die Millionenschwärme von Gamma-Eulen (*Plusia gamma*), die, seiner Angabe nach ausschließlich Männchen, gleichzeitig, gleichgerichtet (von Ost nach West) und in vergleichbarer Mengenabstufung mit den herbstziehenden Vögeln fast alljährlich in Augustnächten über Helgoland fliegen und an Englands Küste landen. Für drei Nächte stärksten Fluges verzeichnet sein Protokoll schwachen Südwind, Wind Südost bei 'schönem stillen Wetter', Windstille. Eine Verdichtung der etwa breiten Front—auf dem Meere wird man kaum beobachtet haben—durch das Leuchtfeuer will er ablehnen, da auch tags, 'während des Lerchenzuges' (Oktober) *Hibernia defoliaria* (das Weibchen ist flügellos) und *aurantiaria* in großen Scharen auf der Insel eintreffen. Sie alle können ja nur einmal im Leben ziehen, Erfahrung scheidet hier ebenso sicher aus, wie Landmarken im weiten Ozean. Immerhin ist es schwer, diesen Männchenschwarmbewegungen ein Ziel und einen biologischen Sinn zugeben, ebenso bei den weit weniger regelmäßigen Libellenzügen, die gleichfalls sehr gut Richtung halten.

Bei wilden Altvögeln wird man nicht leicht die Möglichkeit abstreiten, daß sie recht weit herumgekommen seien, aber auch das hat seine Grenzen. So kommt denn gerade hier die Rede vom 'sechsten Sinn' auf, konkreter gesprochen vom 'Kompaßsinn', ja kurzerhand vom 'Orientierungssinn', der den Wildtieren wie dem menschlichen Waldläufer, dem Tundra- und Wüstenbewohner eigne, dem zivilisierten Menschen und Haustieren wie der Brieftaube dagegen abhanden gekommen sei. So unbefriedigend unser Wissen im Verhältnis zu den beobachteten tierischen Leistungen auch immer ist, so muß doch mit wiederholter Schärfe betont werden, daß es nichts hilft, wenn man seinem Unwissen Namen gibt, die ein Wissen vortäuschen. Ein Sinn fordert ein Sinnesorgan; die Behauptung neuer Sinne, ohne auch nur die geringste Vorstellung von ihrem Wesen und Wirken, hilft uns nicht. Jene bisher durchaus unerklärlichen Höchstleistungen reisender Tiere stellen dem Sinnes- und Reizphysiologen neue Aufgaben, ohne ihm bisher zu ihrer Lösung einen Weg gewiesen zu haben. Der Sinnes- und Orientierungsphysiologe fühlt den Aufruf in dem offenen Eingeständnis: 'frankly, no one knows', das mir lieber ist als insbesondere die unselige Vokabel vom 'Orientierungssinn', die schier unausrottbar scheint.

Zwei ausgesprochen negative Befunde werden dem Optimisten des 'Orientierungssinnes' wenig sagen, um so mehr aber dem, der versucht, mit dem was wir wissen, möglichst weit zu kommen.

Rüppell (1941) ließ fünfzehn aus dem Nest genommene Jungstare fast ein Jahr lang am Geburtsort in einem 2,50 m. hohen Flugkäfig halten, in dem sie endlich auch erfolgreich brüteten. Als man sie nun von Winsen an der Luhe nach Hannover, 114 km. weit, verfrachtete, fand keiner heim. Von dreißig Winsener Altstaren, die man ebenfalls ein Jahr lang im gleichen Flugkäfig hielt und, als sie darin brüteten, genau wie die Jungen verfrachtete, kamen siebzehn heim, nach drei Tagen der erste, fünf nach mehr als zwanzig Tagen. Ich kann hieraus nur den Schluß ziehen, daß die Alten heimfanden, weil sie das Luftbild ihrer Heimat ein volles Jahr im Kopfe behalten haben; die Jungstare fanden nicht heim, weil sie kein Heimatbild im Kopfe hatten, da der Flugkäfig zu niedrig war. Daß sie nicht aus mangelndem Fliegemut versagten, das beweist der Erfolg der genau ebensolang gefangen gehaltenen Alten; beide Gruppen brüteten. Kurz, die Ortskundigen fanden, die Ortsunkundigen nicht. Das Versuchsergebnis entspricht genau dem der Bienenverfrachtungsversuche.

Griffin & Hock (1948) verfrachteten siebzehn Basstölpel (*Sula bassana*) von der kleinen Meeresinsel, auf der sie brüteten, 100 Meilen aufs Festland, d.h. da sie selbst niemals landeinwärts fliegen, in bestimmt unbekanntes Gebiet. Neun wurden vom Auflaßort mit dem Flugzeug begleitet, 500 bis 800 m. über dem Vogel, acht flogen ohne Geleit. Von beiden Gruppen kamen gleich viele heim (63 %), der erste nach 24, der letzte nach 75 Stunden. Das begleitende Flugzeug hat also nicht gestört. Die vom Flugzeug aufgenommenen Startrichtungen gehen gleichmäßig nach allen Sektoren der Windrose rein zufallsmäßig streuend auseinander, die beobachteten Bahnen sind reich an mächtigen Kurven, ja Kreisflügen, keine einzige weist auch nur annähernd in Heimatrichtung. Dies Ergebnis entspricht genau der Erwartung, wenn man Heinroths (1941) Brieftaubenansatz auf den Wildvogel überträgt: Blindes Spiralsuchen um den unbekannten Auflaßort, bei zufälligem Anschluß an Bekanntes (hier also an die Küste) mnemotaktisch (*a*) gerichteter Heimflug. Der Umstand, daß Landung den Tölpel stark gefährdet—zum Auffliegen braucht er starken Gegenwind und 33 m. freien Anlauf—mag ihren Fliegemut (über Land flogen sie sozusagen ums Leben) hinreichend gestärkt haben, in gutem Prozentsatz die rettende Küste zu erreichen, deren Topograhie sie kannten. Die Zufallswahrscheinlichkeit, Küste zu sichten, ist am Auflaßort sehr groß, noch grösser, als in Watson und Lashleys Verfrachtungsversuch (1915). Verf. hält nicht viel vom 'Orientierungssinn' und glaubt, daß alle Wildvögel, so wie seine Tölpel, sich weithin auf mnemotaktische Wegmarken verließen ('by exploration').

So hat der erste Versuch, mit dem freigelassenen Vogel mitzufliegen, also den Weg zu beobachten, statt ihn zu behaupten, die unter Ornithologen weitverbreitete Annahme, er schlüge alsbald die Luftlinie zum

Heimatort ein, gleich als wäre er durch ein gedehntes Gummiband mit ihm verbunden, gründlich widerlegt. Aber der Stachel bleibt. Rüppels (1934–40, 1944) Sternverfrachtungen Berliner Brutvögel ergaben Heimkehrbestzeiten von London in 10 Tagen, von Madrid in 7 (Star), Wendehälse von London in 12, Venedig in 10, Saloniki in 12 Tagen, ein Neuntöter von Madrid in 11 Tagen. Auf den Luftlinien ergäbe die beste Bestzeit eine Flugleistung von nur 270 km. am Tage. Doch kamen verhältnismäßig viele heim, über 1000 bis 1700 km. hinweg; und es ist wenig wahrscheinlich, daß ausgerechnet der nach Saloniki verfrachtete Wendehals vorher schon einmal am Südbalkan war, der in Madrid aufgelassene Star in Spanien, oder gar jeder Berliner Brutvogel an allen diesen Auflaßorten.

Inzwischen ist uns Anregung von Physikern erwachsen, die rechnerisch theoretisierend Möglichkeiten äußerer richtungweisender Schlüssel erwogen haben, wie die Erddrehung (Ising, 1946) und dazu die Vertikalkomponente des Erdmagnetismus (Yeagley, 1947). Kramers (1948) erschöpfender Kritik an Yeagleys Versuchen ist nichts hinzuzufügen. Jede neue physikalische Denkmöglichkeit ist der Erwägung wert, auch wenn sie in ihrer ersten Formulierung der biologischen Prüfung nicht standhält. Der Biologe kann gar nicht eng genug mit allen Grundwissenschaften zusammenarbeiten; doch sollte auch der Physiker, wenn er Tiere als Meßinstrumente benützt, sich die Erfahrungen des Biologen als eines Mitarbeiters nicht entgehen lassen.

Neuhaus (1948) setzt seine Versuche fort, am radiärsymmetrischen Labyrinth, in das Mäuse von unten her eingesetzt werden, so daß die Eintrittsrichtung ihnen keinen Schlüssel gibt, den ‘Kompaßsinn’ nachzuweisen. Dijkgraafs (1947*b*) Versuche, Singvögel auf die Südrichtung zu dressieren, verliefen völlig ergebnislos.

Mit gutem Recht hat schon Wachs (1926) davor gewarnt, das Orientierungsverhalten nach Verfrachtung und auf dem Zuge in allem gleichzusetzen. Aber die Zugvögel warten mit vielleicht noch erstaunlicheren Leistungen auf. Die durch Schüz (1934) aus Ostpreußen nach Essen verfrachteten Jungstörche, lange nach Abzug der dortigen Störche in mehreren Trupps nacheinander aufgelassen, schlugen sämtlich dieselbe S.O.-bis S.S.O.-Richtung ein, die sie zuhause ‘herkunftsgemäß’ an den Bosporus geführt hätte, wohin die Oststörche ziehen. Die Weststörche dagegen ziehen nach S.W. auf Gibraltar zu. Die letzten Versuchsstörche sah man in der Po-Ebene. Das in sich überaus stimmige Ergebnis spricht für einen der geographischen Rasse eigenen *angeborenen* Herbstkurs. In seine letzten Arbeit, die die lange Reihe des früheren (1934–41) krönt, schließt Rüppell (1944), der am Kurischen Haff auf dem Frühjahrszug gefangene Nebelkrähen nach Flensburg, Essen und Frankfurt verfrachtete, aus den in vorbildlicher Weise gesammelten und verarbeiteten 176 Rückmeldungen auf *angeborenen Kurs* des Frühjahrszuges (nach N.O.), denkt an die Sonne als Richtungsweiser, zumal die Krähe nur tags zieht und stets früh aufbricht, und spricht von Parallelverschiebung des Zugbildes sowohl nach Richtung wie Länge der zurückgelegten Strecke. Somit wäre nunmehr auch der Genetiker mitaufgerufen. Demgegenüber steht jedoch wieder der allerdings noch umstrittene Befund an jenen *Lachsen* (Scheer, Huntsman, 1947), die als Eier in ein weit entferntes Quellgebiet verfrachtet, als geschlechtsreife Tiere aus dem Ozean in ihre Adoptivheimat, anstatt zur Geburtsstätte zurückkehrten, so daß man auf erlerntes Wegfinden schließen müßte. Denken wir vollends an die den Ozean überfliegenden Arten, den auf Laysan brütenden Albatros und wieviel anderes mehr, so bleibt es bei: 'frankly, no one knows.' Wir legen inzwischen ein Steinchen zum anderen und glauben, Überraschungen wie jene, die uns die Fledermäuse und Bienen brachten—Spallanzanis Versuch ist nach 160 Jahren geklärt; die Perspektiven des Polarisationsbefundes (v. Frisch, 1949) wage ich noch nicht auszumalen—sollten uns neuen Auftrieb geben, auf altbewährten Bahnen fortzuschreiten und die Geduld nicht zu verlieren. Gnadengeschenke lassen sich nicht erzwingen, und solche Neuigkeiten sind nicht alltäglich. Stets wird der Freilandzoologe der Pionier bleiben; je direktere Methoden (Mitfliegen!) er wählen kann, um so besser. Mithelfende Laien sind vor Rekordsucht zu warnen; die negativen Fälle sind genau so wichtig wie die positiven. Dem Sinnes- und Orientierungsphysiologen aber mögen sie sein Kritteln verzeihen. Hans Spemann nannte es in der Sprache des Archäolgen: die Bruchflächen in Ehren halten.

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COMMENT BY DR D. L. GUNN

It has been a great pleasure to hear and see Professor Köhler in person. I am not so happy about some of the detailed ideas he has assembled for us. They are rooted in Kühn's *Orientierung der Tiere im Raum* (1919), as indeed are those of Fraenkel and myself in *Orientation of Animals* (1940). Unfortunately, during the last ten years or so, the Continental workers and ourselves have been moving in different directions, so that we use the same words to mean different things. Unless we can come to some agreement, this divergence will lead to a great deal of confusion and will hold back progress, not only in the small field of behaviour with which Fraenkel and I dealt, but also in the wider one opened up by Lorenz and Tinbergen.

By the word taxis (Gunn, Kennedy & Pielou, 1937) in the simplest case we mean an orientated locomotory reaction leading directly towards (or away from) an undifferentiated source of stimulation. We made no important assumptions about neuro-physiological mechanisms, and the limiting relationships considered between stimulus, receptor, and behaviour were essentially geometrical. We excluded behaviour requiring training, or memory, or depending on a highly differentiated stimulus like a flower of a particular shape and colour. By this rather narrow use of the word, with other similar modifications of Kühn's system, we believed we had created a useful shorthand for investigations of the manœuvres in the simpler kinds of behaviour—especially of insects—in nature, and we have been encouraged in that view by the use made of the terminology since 1940.

As I understand Professor Köhler, he is restricting the word *taxis* to the turning components in such reactions and at the same time extending it to cover turning movements of any animal whether in locomotion or not.

Tinbergen (1950) and Lorenz (1950) seem to go even further, dividing instinctive actions into two components—innate automatisms responsible for locomotion or other basic movement pattern, and turning responses to external stimuli responsible for steering; it is only the steering component which they call the taxis component. According to them, once an instinctive action has been initiated or released by a stimulus, it requires no further stimulus but proceeds automatically to its end, as far as the innate automatism component is concerned, but it may be steered by the taxis-component (Lorenz & Tinbergen, 1938). This usage is bound up with the explicit idea that locomotion does not require stimuli for its maintenance; such a usage will probably be changed again if these workers become convinced that external stimuli are important in the co-ordination of locomotory movements (Gray, 1950). In any case, why not use an expression like *steering component* or *turning movement* or *topic component* without any unnecessary assumptions about neuro-physiological mechanisms? Why appropriate a word which is required elsewhere for something which cannot be adequately named in two common words? If we are not careful, *taxis* will go the same way as *tropism* and *instinct*, which have had to be virtually abandoned altogether because they had been given so many different and inconsistent meanings.

This is not the time for answering all of Professor Köhler's criticisms of our book. I hope he will re-examine carefully and with an open mind our attempt to provide a group of word symbols for use in limited fields of behaviour and ecology. I will, however, take him up on the so-called phobotaxis of *Paramecium*. It at first appears that *Paramecium* simply turns away from both higher and lower concentrations of the stimulating chemical and so remains in a region of middling concentration. That is, however, merely a special case which is seen in its more general form in a gradient which has no specially steep regions, as was shown by Ullyott (1936) for *Dendrocoelum* and later substantially confirmed for *Paramecium* itself (Gunn & Walshe, 1941; Gunn, 1942). Like ortho-kinesis, this type of behaviour has a statistical probability element which is absent from any taxis (in our sense) and it does not lead directly towards the source of stimulation, and we therefore ally it with ortho-kinesis as *klino-kinesis* and do not use the word phobo-taxis.

Finally, may I appeal once more to workers in behaviour not to take part in the pointless destruction of a limited but useful system in this merely incidental way, nor to begin again fruitless discussions of whether any behaviour is forced or free, but to study behaviour as a subject in its own right, without depending upon doubtful generalizations from more elemental subjects.

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THE HIERARCHICAL ORGANIZATION OF NERVOUS MECHANISMS UNDERLYING INSTINCTIVE BEHAVIOUR

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As long as workers on instinct focused their attention on to the fact that instinctive behaviour as a whole is often highly variable and plastic, while the only constant aspect was considered to be the end towards which it is directed, there was little hope of finding nervous mechanisms underlying the behaviour.

Although some writers called attention to the relatively rigid and simple innate activities that do exist, the majority of writers considered these rigid activities to be of minor importance; they were either considered to be no 'true' instinctive activities, or it was attempted to show that even they were not rigid but 'variable'. In pointing out this variability the need for sharply distinguishing between intrinsic variability and effects due to rigid responsiveness to variable external factors was rarely felt.

We begin to realize now that the fact that an animal may use various behaviour patterns in turn in order to attain one special end does not necessarily mean that this plastic behaviour is not dependent on nervous mechanisms, but that it might also, and certainly does, mean that the underlying nervous mechanisms are much more complicated than was expected before. The notion that a relatively limited number of mechanisms are responsible for plastic behaviour gains in probability when one obvious fact is better realized, viz. that in each case of plastic behaviour, however complicated it may be, there are many more ways in which an animal could, yet does not, try to attain the end than there are methods which it does use. One instance may make the point clear. When one of the three eggs of a gull is taken out of the nest and put at a foot's distance in front of the sitting gull, the bird will 'retrieve' it. This it does by bringing the bill behind the egg, and shovelling it back while carefully balancing it on the relatively narrow edge of the lower mandible. When watching the repeated clumsy attempts of the bird, which have often to be repeated quite a number of times before they meet with success, one is impressed by the bird's obvious 'stupidity'. Why does it not shovel the egg back by one sweep of the extended wing? Or with one of its webbed feet? The answer is, of course, the effectors are there all right, effectors much better suited to this task than the bill, but the animal simply does not have the central nervous mechanisms to employ these effectors in this situation. In psychological terms, it does not occur to the bird to retrieve the egg in a more intelligent way.

This recognition of the probability that an animal may have a limited (although admittedly sometimes great) number of nervous mechanisms in the service of the attainment of one biological end is an important step in the study of underlying nervous mechanisms.

Another, even more important, step has been the recognition that the nervous mechanisms are organized in hierarchical systems. The first suggestion of such a hierarchical organization is given by the fact that the relatively simple movements are often elements, building stones, of the more complicated movements.

Two sciences, originally working in isolation from each other, have contributed toward our knowledge of central nervous hierarchy: ethology and neurophysiology.

I will approach the problem by ethological study first. Here the principle was first discovered in the three-spined stickleback.

The male three-spined stickleback hibernates in the sea or in deep fresh water. With the awakening of the reproductive instinct, it migrates towards shallow fresh water. A rise in temperature and visual stimulation by a special type of vegetation make it settle on a 'territory'. To this territory all its reproductive activities are confined. It fights off other males, it builds a nest; when this is finished, it courts females which spawn in the nest, after which the male fertilizes the eggs. The eggs and young are guarded by the male.

All these activities are partly dependent on internal impulses and partly upon external stimuli. The responsiveness to the external stimuli, such as, for instance, those releasing fighting, or building, is, however, dependent on the activation of the reproductive instinct as a whole, which is primary. While a temperature and a visual stimulus (vegetation) determine whether the fish will settle and begin with fighting, building, etc., these subordinated activities are dependent on special additional stimuli. Fighting, for instance, is released by the visual stimulus situation 'male in nuptial markings intruding', nest building by visual stimuli from certain plants.

Now fighting may consist of very different movements; there are at least five different methods of fighting. Which type will be shown depends on additional, still more specific, stimuli from the intruding male. Biting will evoke biting in return, escape evokes pursuit, etc.

This type of evidence suggests a hierarchical system in the central nervous system, including partial systems at different levels of integration.

The idea of well-defined central nervous mechanisms is further rendered probable in view of the fact that, at each level, special causal factors evoke special responses. This is most obvious at the lowest level; the relatively simple and stereotyped motor response 'biting' is released by a simple tactile stimulus.

At the higher levels, equally simple stimuli ('sign stimuli') have an equally specific, though less clearly recognizable, effect. This effect, it is true, cannot be described as a special motor response, yet it is a narrowing down of the potential responses in the sense that it increases the animal's readiness to perform a special limited set of responses, at the same time decreasing its readiness to perform all other types of activity. Thus fighting as a whole (that is to say, the readiness to respond with one of the types of fighting) is released by the stimulus 'red male intruding'.

This can mean but one thing: this hierarchical system is a system of nervous 'centres', the higher centres controlling a number of centres of a next lower level, each of these in their turn controlling a number of lower centres, etc.

In order to understand what these 'centres' (which are, provisionally, to be thought of as functionally characterized systems) are actually doing, it is necessary to analyse the motor responses a little further.

As Lorenz (1937), partially referring to the studies of Craig (1918), has shown, instinctive behaviour often consists of two successive parts of very different kinds. An animal, in which an instinctive urge or drive is activated, starts 'random', 'exploratory' or 'seeking' behaviour. When this type of behaviour is closely observed, it is found that it is typically purposive in the sense of McDougall. Further, it is continued until the animal comes into a situation that provides the sign stimuli necessary to release the motor response of one of the centres of the lowest level. To mention an instance: a peregrine falcon in which the hunting drive becomes active, searches for prey until it is found. The sight of the prey releases the motor response of catching, killing, eating, which is a chain of simple, relatively rigid, responses. Or, a female rat runs through a maze, keeps searching, until it finds its young, which releases the maternal motor responses. Or again, an animal migrates toward the end of the day to a quiet place, where it can sleep (Holzapfel, 1940).

The final motor response, bringing the striving of the animal to an end, is called the consummatory act (Craig, 1918), the preparatory searching behaviour: appetitive behaviour. Whereas the analysis of the consummatory act has made a good start already, that of the much more complicated appetitive behaviour has not yet proceeded very far.

Baerends (1941), who has analysed the behaviour of the digger wasp, *Ammophila campestris*, along these lines, has succeeded in carrying the analysis one step further. I will take as an example the hunting behaviour of a peregrine falcon, because this happens to be familiar to me. What I said above on the hunting behaviour of this species was purposely simplified.

A peregrine falcon in which the hunting urge becomes active leaves its perch and begins to roam about its hunting territory, which may measure several, up to at least ten, miles in diameter. It flies more or less aimlessly around, on the look-out for potential prey, perhaps purposely visiting special locations where it has met with success before. However, it will depend upon the type of prey sighted what type of hunting it will show. It may take a starling, a lapwing or a teal out of a flock, it may pick up a weak gull or lapwing from the water, it may even take a small mammal from the ground. Now the important point is, that the sight of one of these prey will not immediately call forth the consummatory act, but it releases another, more special type of appetitive behaviour. For instance, upon the sight of a flock of teals, the falcon will not at once try to catch one of them, but it will make sham attacks and continue them until one of the teals fails to keep up with the quickly manœuvring flock and gets isolated. This stimulates the falcon to the final swoop, which is a still more specific type of purposive, appetitive behaviour, and only if the swoop brings it into a favourable position will the falcon catch the prey, which is a real consummatory act.

This shows that activation of the centre of the highest level results in appetitive behaviour of a generalized kind. This is carried on until a new stimulus with a more restricted effect releases a subordinated type of appetitive behaviour. This again is continued until the next stimulus releases a still more restricted type of appetitive behaviour, and this is carried on until the consummatory act is released.

Next we have to consider the part played by the external stimuli. Certain facts, not to be entered upon here, point to the conclusion that the releasing stimuli are not calling forth the response in the way of a reflex, however involved this reflex response might be. We must rather assume that they merely remove a block and thus provide free passage for the motor impulses coming from the activated centre. The instinctive centres seem to be in a state of readiness, they are constantly being loaded from within, but their discharge is prevented by a block. If there were no such block, continuous simultaneous discharge of all centres and, as a consequence, chaotic movement would be the result. The adequate sign stimuli act upon a reflex-like 'innate releasing mechanism' (I.R.M.), and this mechanism, upon stimulation, removes the block.

Each centre, on each level, has such a block with a corresponding I.R.M.

As long as this block is not removed by stimulation of the I.R.M., the centre cannot 'get rid' of its motor impulses.

This hypothesis fits in very well with what scanty knowledge we have of so-called displacement activities. In short, these seem to be the result of accumulated motivational 'tension' in a centre which cannot be discharged because the block is not removed. The impulses under certain circumstances find an outlet through neighbouring centres. Lack of space does not permit to elaborate this further; I may refer to Kortlandt (1940), Tinbergen, (1940), Tinbergen & van Iersel (1947) and my forthcoming book on instinct.

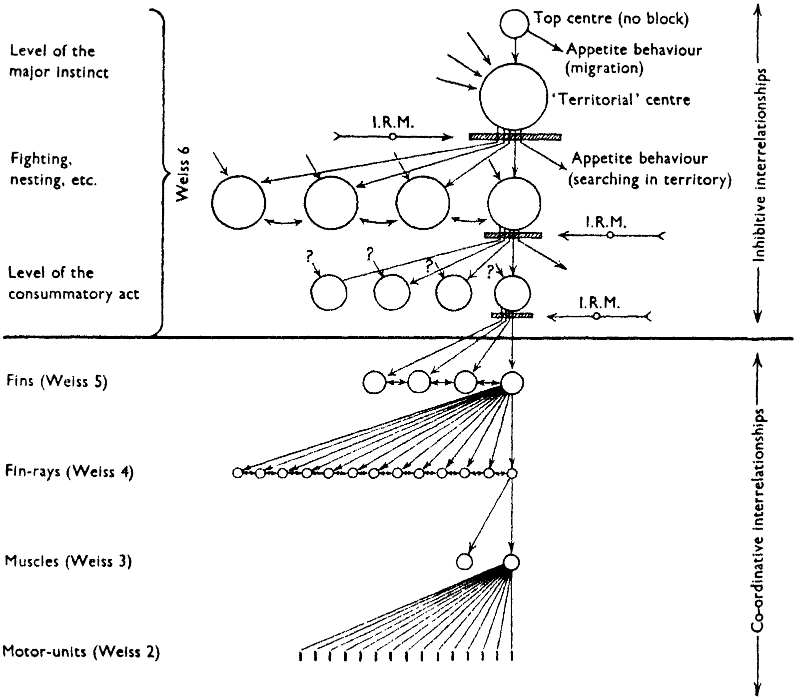

Fig. 1. Symbolic representation of the hierarchical organization of 'centres' playing a part in instinctive behaviour. Explanation in text.

I have attempted to develop a graphic model of the organization of such an instinctive centre. It is based upon the instinct with which I happen to be familiar, the reproductive instinct of the male three-spined stickleback (Fig. 1). 'Centres' are represented by circles, causal factors by arrows, blocks by shaded rectangles, innate releasing mechanisms by schematic pictures of a nerve cell, and motor paths by drawn lines.

The centre on the highest level has no corresponding block. This seems to be typical for the highest levels, as indicated by the fact that activation of a major drive always results in (the highest type of) appetitive behaviour.

If there were blocks, even at this highest level, the animal would have no possibility of getting rid of impulses, which, so far as we know, must lead to neurosis.

In the case of the stickleback, day-lengthening, through various endocrine glands increasing the level of gonadal hormones in the blood, activates the highest centre in early spring. The impulses generated by this centre can travel one of two ways. They can travel toward the centre of the next lower level, but as this centre is blocked at the distal end, these impulses cannot go further. The other possible way is through the appetitive behaviour. The appetitive behaviour belonging to this highest centre is migration from the sea, or deep fresh water, to shallow fresh water. This migration is carried on until the sign stimuli adequate to activate the I.R.M. of the next lower centre are met with. These stimuli are, as said before, a sudden rise in temperature, and visual stimuli provided by the vegetation. These stimuli remove the block, and thereby provide free passage to the impulses. The result is that the animal stops migrating. This state of affairs leads to the hypothesis that the threshold for the activation of the highest appetitive behaviour must be higher than that for the activation of the lower type of appetitive behaviour.

On the level of the lower centre, the 'territorial centre', the situation is similar to the one we have just seen. Here again the impulses can flow to the next lower level of centres, those of fighting, or building, etc., or they may flow to the appetitive behaviour. As long as the blocks of the fighting, building, etc., centres are not removed by the adequate sign stimuli, the animal will perform the appetitive behaviour. This is a type of restless swimming all over the territory, while the animal is on the look-out for rivals and for nesting materials. This is carried on until, for instance, an intruding male appears. This removes the block of the fighting centre; all impulses flow to this centre, and the animal stops its aimless wandering over the territory and attacks. The type of attack, that is to say, the activation of one of the five next lower centres, is decided by the behaviour of the intruder; his movements finally provide the stimuli which call forth (or rather enable the fish to perform) one special type of fighting which is a consummatory act.

So much for the interpretation of the ethological evidence. Though this is not the place to dwell on the neurophysiology of instinct, it should be mentioned that there are certain neurophysiological data which lend support to the views presented above.

First, the existence of internal, intrinsic central nervous mechanisms responsible for and controlling co-ordinated motor patterns of an order of complexity of the consummatory acts has been made highly probable by the work of von Holst, Gray & Lissmann, and Weiss. Moreover, their work shows that the relatively low centres, of the level of the consummatory act and locomotion, have their anatomical basis somewhere in the spinal cord.

Further, it is of the greatest interest that Hess & Brügger (1943) discovered that certain behaviour patterns, which according to his descriptions must be considered the result of activation of the highest centres, can be called forth by direct electrical stimulation of certain strictly localized centres in the hypothalamic region of the brain. In cats, Hess succeeded in calling forth sleep, fighting and eating with the appetitive behaviour patterns belonging to these activities. This work, when seen in connexion with the work on spinal mechanisms, suggests the possibility of parallelization and mutual fertilization of ethology and neurophysiology and opens wide perspectives.

Still, in another way it is possible to link up ethological work with neurophysiology. After the above views on the hierarchical organization of instinct were developed, I read Weiss's paper on self-differentiation of central nervous patterns (1940). In this paper, Weiss emphasizes the hierarchical organization of central nervous mechanisms, but his considerations apply to levels lower than the consummatory act. In fact, the highest level of his system of six levels, called by him the level of the behaviour of the animal as a whole, is equivalent to the whole complex of centres we have been considering here. In other words, his highest level is again a complex of several levels, and our system, being an analysis of what Weiss considered the highest level, can be fitted without any trouble into his system. Weiss's analysis of the levels below that of the consummatory act shows interesting parallels to von Holst's work on co-ordination in fish.

In my figure I have indicated a number of horizontal double-headed arrows between centres of the same level. These represent interrelations. In the levels above the heavy line these interrelations must be supposed to exist on the ground that the centres of the same level mutually suppress each other's activities. Further, the existence of displacement activities suggests something of the kind. Below the solid line, the interrelations are not of an inhibitive type, but they are responsible for the co-ordinative phenomena. Especially the phenomena of superposition and the magnet effect, discovered and analysed by von Holst, must be based on some kind of nervous interrelationships.

These considerations, however provisional they may be, enable us to see the problems of instinct much more clearly than twenty years ago. Most of the older writers considered the directiveness of instinctive activities as one of the main characteristics of an instinct. Instincts were distinguished on the ground of their being directed to special ends: escape, feeding, reproduction, etc.

At present we are in a position to formulate neurophysiological arguments in favour of the distinction of several instincts. Although it is too early to give a definition of 'an instinct', we are justified in concluding that in any definition of an instinct its neurophysiological foundation will have to be mentioned just as well as the end toward which it is directed. The hierarchical structure will have to be mentioned, the dependence of internal (motivational) and external factors, and the innate and self-differentiating character will have to be stressed.

The fact that neurophysiological, or, to put it in more general terms, objectivistic research no longer confines itself to the relatively lower levels but, for the first time, embarks upon a study of the levels above the consummatory act, creates a peculiar and new situation. Objectivistic research begins to discover the functioning of mechanisms in activities that, as introspection teaches us, are accompanied by subjective phenomena, viz. the instinctive emotions in McDougall's sense. No doubt, there will be psychologists who will see this situation as a conflict. In my opinion, however, results of the type discussed here must not necessarily be in conflict with psychological results obtained by means of introspection. It will be of the greatest importance for future ethological research to clarify the relations between these two types of research.

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AN EXPERIMENTAL ANALYSIS OF INTERSPECIFIC RECOGNITION

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I. INTRODUCTION

Every object within the visual perceptual field of an animal is seen—that is to say, its image is part of the pattern of colour patches received upon the retina. If in respect of certain objects, or characters of objects, the perceiving animal shows behaviour, these objects or characters possess, in the term of Russell (1934), 'valence' for the perceiver. Reaction to a valent object is evidence that it has undergone the process of 'recognition'; that its image has ceased to be a mere part of a total in which all the components are equivalent and has become a subject of special reference. The various combinations or selections of visual characters which give valence in the perceptual field to animals of species other than that of the perceiver are the subject of this paper.

Definitions. It is a commonplace of the study of visual perception that the image upon the retina is no more than a mosaic of colour patches, variously toned and showing fixed or changing relationships to one another in successive impressions. All other percepts are elaborations from this pattern of colours and tones. The perception of outline is emphasis upon the boundaries between tone and colour patches. The perception of solidity is a development from the differences in tone upon surfaces which from their colour and relative fixity of spatial relationship appear to be parts of one object; it is probable that experience plays a large part in this interpretation of differential illumination. 'All the sensations which enable us to appreciate depth and distance, modelling and texture of the objects around us come to have their special significance only as a result of individual experience' (Cott, 1940). The perception of the movement or the immobility of objects is the interpretation of the change or fixity of position of groups of colour patches in relation to one another. The perception of scale and distance is a process in which experience and innate powers of triangulation have both a part to play.

Every object is possessed of some or all of the visual characters here listed, characters which are either directly perceived or are developments from the primary percepts of colour and tone.

(1) Shape, composed of: (*a*) outline; (*b*) contour or solidity.

(2) Coloration, composed of: (*a*) colour, which may be due either to pigmentation or, more rarely, to structure; (*b*) pattern, or organization of coloured areas upon the surface.

(3) Tone, the relative darkness or pallor of surfaces. The tone of any surface is affected by: (*a*) the saturation of its pigment; (*b*) the texture, or structural capacity to contain shadow.

(4) Orientation, in relation to the rest of the perceptual field.

(5) Scale, a percept dependent upon: (*a*) powers of triangulation and comparison; (*b*) comparisons based upon a combination of triangulation and experience.

(6) (Animate objects.) Behaviour, composed of: (*a*) pose, or orientation of mobile parts in relation to one another; (*b*) movement.

The recognition of predators. The valency of an object in the perceptual field of an animal can be gauged only by the reactions to it. The more dramatic or clear-cut the reactions the more valuable they are as evidence of recognition in observational or experimental work. It is for this reason that the processes of recognition of sex partners and of enemies have been important subjects for investigation. In work upon interspecific recognition much attention has been given to the processes by which predators are known to their victims, for enemies are the members of other species which most often call forth strong reactions, reactions which are easily recognizable and readily described.

The reactions of small birds to the appearance or discovery of a predator are several. They may take refuge in flight or cover, sometimes accompanying or following the reaction with 'alarm' cries; by gesture, voice or bearing they may exhibit uneasiness or vigilance, without seeking refuge; they may (seemingly) ignore the predator; or they may mob it. In a mobbing the predator is approached by one or more birds, which follow or circle it with outcry and gesticulation each after its kind, until the object of the attack departs or until its persecutors presently move away to other activities. Mobbing behaviour is to be distinguished from aposematic or pseudaposematic displays undertaken defensively, and from 'diversionary displays' (Armstrong, 1949) in that a mobbing is not a reaction to an actual attack by the enemy. It is not proposed here to discuss the possible survival value of the mobbing habit. This survival value is obscure, for often the predator seems to be in no way disconcerted by the demonstrations. Occasionally, mobbing behaviour seems to be positively disgenic, for there are records of an attacking bird being killed in the assault (Mason, 1915; Ryves, 1942; Brown, 1947).

Both 'fear reactions' (the seeking of refuge or the demonstration of uneasiness) and mobbing behaviour have been used as the bases for the experimental analysis of the recognition of predators. The account which immediately follows describes a series of experiments in which mobbing behaviour was the criterion of recognition. Since the word is repeatedly used in the account, and since it is desirable that the implications of the term should be exactly understood, a definition is here offered:

'A mobbing is a demonstration made by a bird against a potential or supposed enemy belonging to another and more powerful species; it is initiated by the member of the weaker species, and is not a reaction to an attack upon the person, mate, nest, eggs or young of the bird which begins it.'

In this definition stress is laid upon the fact that a mobbing is not provoked by hostile actions. It is a reaction to a dangerous aspect.

II. FIELD EXPERIMENTS ON THE RECOGNITION OF OWLS

In 1939 the writer began a series of experiments on the willingness of wild birds to mob stuffed owls and a variety of other objects. The original purposes of this work were to study the deportment of the mobbing birds under advantageous conditions, and to test the theory of Nicholson (1927) that owls are mobbed by other birds because of their 'strangeness' of appearance, that '...owls are mobbed not so much because they are enemies as because they are outside the general freemasonry'. The main interest of the experiments was soon shifted to the problem of the visual characters by which an owl is recognized as an object for demonstrations of hostility. Experiments were made at several different places in England from November 1939 until the summer of 1941, and from the spring of 1945 onwards.

The experimental technique was simple. A stuffed or model bird or some other object was placed in a suitable position, and there left for a period of 60 min. The experimental object was observed from a concealed post, and a record kept of the birds seen near it, and of their reactions or lack thereof. The 'suitable' position had to fulfil four requirements.

(1) It must be such a place as an owl might reasonably perch upon. The choice of such sites was wide: twigs, branches and tree-stumps, the tops of walls and buildings, posts, rails and gate-posts were all used. The heights at which objects were exposed ranged from 2 to 20 ft. (0·6–6 m.) above the general ground-level. A live tawny owl, *Strix aluco sylvatica*, has been seen to be mobbed while perched upon a stump only 18 in. (0·5 m.) high, so that the lower level used in the experiments was not open to objection as unduly low.

(2) The perch on which the experimental object was placed had to be

near cover suitable for small birds. It would be misleading to place the objects far out in the open, as there might be a reluctance in defenceless species to venture near a predator at any distance from refuge.

(3) The area must be known to be possessed of an adequate population of small birds. Care was taken not to put any experimental object near a known or suspected nest, since the mere intrusion upon the nest site might unduly dispose a bird to demonstrations of hostility or alarm. In 1947 and 1948 no experiments were made in the breeding season.

(4) The area must be reasonably free from interruption.

Experiments were made in gardens, orchards, hedge-rows and the borders of woods and shrubberies.

When a positive reaction had been obtained to an object on any one perch no more experiments were made at that place until at least 14 days had elapsed. By the application of this rule it was hoped to avoid conditioned reactions to an experimental site, such as had been found by Nice & Ter Pelwyk (1941).

The 'standard' duration of an experiment was 1 hr. Occasionally an experiment was cut short by rain or (especially in the war years) by some intrusion, and not infrequently the object was left in position for a little more than 60 min.

Working in the open it was impossible to control or standardize the environmental conditions. No experiments were made in hard frost, in heavy rain, in mist or when the wind was of more than force 4 on the Beaufort scale.

Experiments with wild birds have certain disadvantages and certain advantages when compared with experiments upon captive birds under controlled conditions. The disadvantages are:

(1) The impossibility of guaranteeing that the experimental object will be seen at all. In an experiment without reaction to the object, the record of the numbers and species of birds within sight of it will ensure that the result is a true negative. A trial in which it was believed that no bird was near the object under test was not counted as an experiment.

(2) The variation from experiment to experiment in the numbers and species of birds coming within range of the object.

(3) The possibility of the intrusion of a real predator upon the scene of the experiment in a position where it could not be seen by the observer. This disadvantage is a very slight one, for the focus of any strong reaction can always be detected from the behaviour of the mobbing birds.

(4) The possibility that any bird demonstrating at the experimental object may have been brought near to the threshold of reaction by a previous encounter with a real predator.

(5) The possibility that the behaviour of a mobbing bird may have stimulated other birds to similar reaction to the experimental object. It is a fact that the outcry of one bird may attract others to the scene; but in the majority of cases the new arrivals do not themselves demonstrate unless the experimental object be one which has proved to possess considerable 'enemy valence'. Rand (1941) found that the sight of one curve-billed thrasher, *Toxostoma curvirostre*, displaying to a snake did not stimulate other thrashers to display if they could not themselves see the object of hostility. In the course of one of the writer's experiments (Exp. An 30) the dried wings of a tawny owl (see Text-fig. 3) were exposed at the end of a branch, 9 ft. from the ground. Observation began at 18.17 hr. on 18 August 1947. At 18.20 hr. a female chaffinch, *Fringilla coelebs gengleri*, began to call from a branch of a walnut tree above the mounted wings, and to flit from twig to twig; at 18.22 she began to fly to and fro past the mount. Half a dozen chaffinches, one at least a male, and a few male house sparrows, *Passer d. domesticus*, assembled in the walnut, peering down at the mount, but none of them called. The calls of the mobbing hen grew fewer, but at 18.25 she flitted close to the mount. At 18.27 most of the other birds flew away. The demonstrating hen continued to call until 18.38, but there was no reaction from the other chaffinches, nor from the sparrows. Such examples might be multiplied.

In a few experiments it is possible that the behaviour of one bird did stimulate others to react. The trials in which the possibility of this form of stimulation must be considered were too few to affect the results of the whole series of experiments.

The advantages of field experiments are:

(1) Conditioned reactions to the scene of previous experiments can be more easily avoided. Nice & Ter Pelwyk (1941) found that in song sparrows, *Melospiza melodia*, 'the memory of circumstances connected with strong alarm persisted after several months'.

(2) Conditioned reactions to experimental preparations can be avoided. Lorenz (1940) found that the grey-lag goose, *Anser anser*, which had been used in work on the recognition of birds of prey, came to give response to the sight of the experimenter preparing to exhibit a test object.

(3) The birds used in the experiments are not forced into, nor retained in, the presence of a possibly alarming object.

> Such tricks hath strong imagination,
> That,...
> ...in the night imagining some fear,
> How easy is a bush supposed a bear.

In Table 1 is given a summary of the experiments to be discussed. Most of the headings need no comment. The term 'successful experiment' implies that one or more birds reacted to the experimental object within each period. It has no reference to the numbers of birds reacting nor to the duration of their reactions. 'Minutes with reaction' is the record of the number of minutes during which one or more birds were mobbing the object. 'Bird-minutes of reaction' is the record of the sum of the durations of the reactions of the individual birds. For example, if, in the minute 10.00–10.01 hr. two birds mobbed an object, the value of 'minutes with reaction' would be 1, and the value of 'bird-minutes of reaction' would be 2.

Table 1. *Summary of results of experiments*

Series	Total experiments	Positive reaction	No reaction	Total duration of experiments	Minutes with reaction	No. of species taking part	No. of birds taking part	Bird-minutes of reaction
LO	21	19	2	1084*	195*	18	117*	626*
SO	20	13	7	1075†	134†	16	80†	349†
WO I	31	28	3	1762	303	21	129	777
WO II	21	19	2	1044	194	14	85	334
V 1	20	4	16	1274	5	4	4	5
V 2	21	3	18	1335	8	4	7	8
V 3	24	5	19	1504	27	5	11	47
Sh	20	4	16	1291	12	2	4	12
Sh/Nc	20	?1	?19	1238*	?1	1	1	?1
C/T	26	3	23	1705	4	2	3	4
C/L	18	2	16	1070	3	2	2	3
An	27	7	20	1757	82	6	20	159
ON	13	9	4	720	128	6	61	279
Pr I	17	2	15	1113	2	2	2	2
Pr II	25	4	21	1640	28	6	11	71

In 19 experiments. † In 18 experiments

Table 2 shows the species which reacted in each series of experiments and the number of experiments in which one or more members of these species showed mobbing behaviour. Not the least surprising result of the investigation was the discovery that for many different species of small passerine birds (indeed, for all which figured sufficiently often in the records to justify the drawing of conclusions) the same combination of visual characters was required to give a true 'owl-valence'. The object which provoked reaction from the members of any one of the commoner species in a number of experiments called out frequent reactions from members of the other numerous species; and (with occasional exceptions) the object which provoked few or no reactions from any one of the commoner species provoked little or no reaction in the other common species. Had each species a sign stimulus, or complex of sign stimuli, different from those of other species, the values in Table 2 would be scattered far more at random. Too much importance should not be attached to the reactions of certain species to objects of relatively little 'owl-valence'. They are all

Table 2. *Number of experiments in each series in which one or more members of each species showed reaction*

	LO	SO	WO I	WO II	V 1	V 2	V 3	Sh	Sh/Nc	C/T	C/L	An	ON	Pr I	Pr II
Jackdaw, *Corvus monedula spermologus*	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
Starling, *Sturnus v. vulgaris*	2	—	—	—	—	—	—	—	—	—	—	2	—	—	—
Hawfinch, *Coccothraustes c. coccothraustes*	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
Greenfinch, *Chloris c. chloris*	2	2	1	—	—	—	—	—	—	—	—	3	1	—	—
Goldfinch, *Carduelis c. britannica*	—	2	3	1	—	—	—	—	—	—	—	—	—	—	—
Linnet, *Carduelis c. cannabina*	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Bullfinch, *Pyrrhula p. nesa*	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
Chaffinch, *Fringilla coelebs gengleri*	6	8	11	4	—	—	4	2	1	1	—	5	3	—	2
Yellowhammer, *Emberiza c. citrinella*	3	—	3	6	—	—	1	—	—	—	—	—	—	—	—
House sparrow, *Passer d. domesticus*	6	6	5	—	—	—	—	—	—	—	—	—	6	1	—
Grey wagtail, *Motacilla cinerea*	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—
Pied wagtail, *Motacilla alba yarrellii*	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Great tit, *Parus major newtoni*	2	5	3	8	—	—	—	—	—	—	—	—	5	1	2
Blue tit, *Parus caeruleus obscurus*	5	4	4	4	—	—	1	—	—	—	1	2	5	—	1
Cole tit, *Parus ater britannicus*	—	—	1	1	—	—	—	—	—	—	—	—	1	—	1
Willow tit, *Parus atricapillus kleinschmidti*	2	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Longtailed tit, *Aegithalos caudatus rosaceus*	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—
Spotted flycatcher, *Muscicapa s. striata*	1	—	—	—	1	1	—	—	—	—	—	—	—	—	—
Chiff-chaff, *Phylloscopus c. collybita*	—	—	3	1	—	—	—	—	—	—	—	—	1	—	—
Willow warbler, *Phylloscopus t. trochilus*	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Phylloscopid indet.	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Whitethroat, *Sylvia c. communis*	1	—	5	1	—	—	—	—	—	—	—	—	—	—	—
Mistle thrush, *Turdus viscivorus*	—	2	1	1	—	1	—	—	—	—	—	—	—	—	—
Song thrush, *Turdus e. ericetorum*	3	—	1	—	—	—	—	—	—	—	—	—	1	—	—
Blackbird, *Turdus m. merula*	4	5	9	8	1	—	1	—	—	—	—	—	3	—	—
Robin, *Erithacus rubecula melophilus*	9	8	11	9	1	2	1	3	—	—	—	1	4	—	2
Hedge sparrow, *Prunella modularis occidentalis*	11	5	8	4	—	—	—	—	—	—	—	—	3	—	2
Wren, *Troglodytes t. troglodytes*	11	7	4	10	—	2	—	—	—	—	—	—	4	—	—
Swallow, *Hirundo r. rustica*	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—
House martin, *Delichon u. urbica*	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Green woodpecker, *Picus viridis pluvialis*	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—

members of common species, and are thereby the subjects of most frequent experiment. It may be expected that the 'rule of heterogeneous summation' (Tinbergen, 1948) will be occasionally demonstrated in every species, and the appearance of its effects in certain species and not in others may be the expression of no more than opportunities of observation. In the discussion of results, particular species are not, normally, distinguished.

Series LO. To supply a standard of comparison, a series of twenty-one experiments was made with stuffed little owls, *Athene noctua*. Nineteen of the twenty-one experiments were positive—that is, resulted in reaction from at least one bird. In all, 117 birds of eighteen species mobbed the stuffed owls, and of a total duration of 1084 min., 195 were taken up by reactions.

Series SO. The next series of experiments was made to test the possibility that the recognition of different species of owls was specific. It might be that there was no generalized recognition of 'an owl', but rather that tawny owl, little owl and the other owls of the British list were each separately known, presumably as the result of a learning process. A 'synthetic owl' (Pl. 1, A) was made from feathers of partridge, *Perdix p. perdix*, and female pheasant, *Phasianus colchicus*, glued to a stuffed base. This object was intermediate in size between the tawny owls and little owls, which were the most numerous species of owls in the areas where the experiments were made; and although it showed a plumage of mingled light and dark brown, it did not at all closely reproduce the patterning of any known species of owl. In twenty experiments, thirteen were positive. The results of this series show a statistically significant difference from the standard both in the proportion of positive experiments and in the time taken up by reactions (134 min. out of 1075). None the less, the results, with eighty birds of sixteen species demonstrating against the object, are sufficiently striking to suggest that the 'synthetic owl' possessed considerable 'owl-valence', and that there is some generalized basis for mobbing reactions. It should, perhaps, be stressed that the patterning of the 'synthetic owl' was in tone contrasts of a single 'correct' colour.

Series WO I and WO II. In these two series of experiments wooden models of owls were used. Model WO 1, used in series WO I, is a life-size model of a little owl, painted with powder colours mixed in thin glue, which give a dull surface. Model WO 2, used in series WO II, is a generalized model, intermediate in size between a tawny owl and a little owl. In this series of experiments it was painted (Pl. 1, B, C) in a streaked and mottled patterning of browns, grey and black, not exactly resembling the plumage of any species. Oil paints were used, giving a glossy surface. In series WO I, twenty-eight experiments out of thirty-one were positive; in series WO II, nineteen out of twenty-one. There are no significant differences between the results of these two series and the results of the standard (series LO), either in the proportions of positive reactions or in the proportions of time occupied with reaction.

PLATE 1

For explanation see p. 320

The conclusion to be drawn from these two series is that a feathery texture is in no way essential to give 'owl-valence' to an object. This discovery had an important practical bearing on the rest of the investigation, for it was far easier to make reasonably well-modelled effigies from carved and painted wood than from mounted feathers. In addition, wooden models were more durable and did not have to be removed at the onset of light rain.

The strong reactions to the generalized model WO 2 confirm the suggestion of series SO that the recognition of owls rests upon some more comprehensive basis than specific identifications.

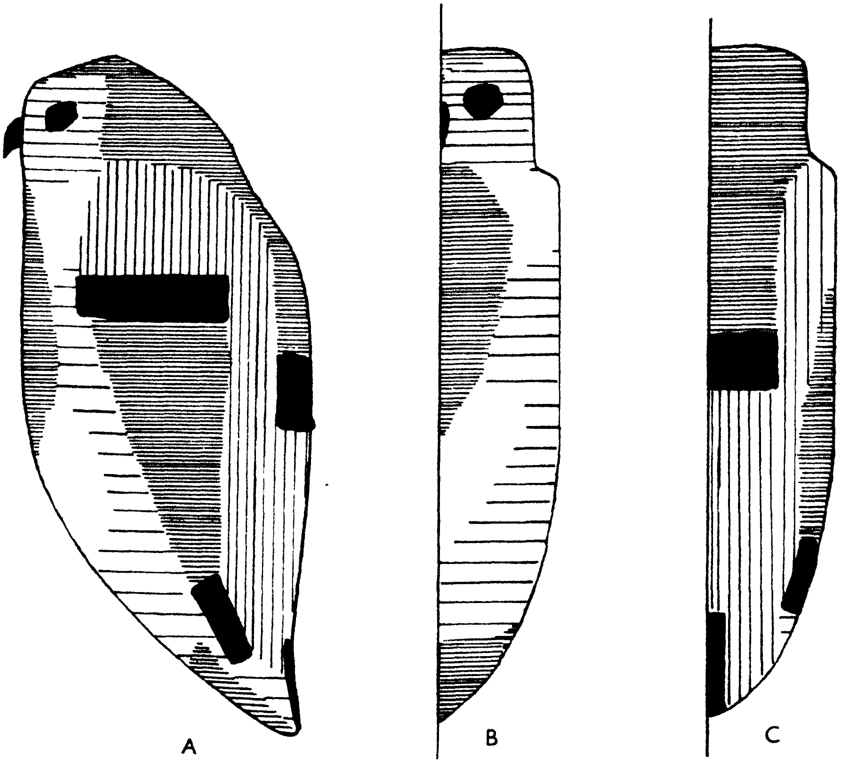
Beside possible characteristics of orientation, scale and behaviour, the two models, WO 1 and WO 2 as painted for this series had at least four visual characters in common. Both were owl-like in outlines, solid in contours and of the general colours and patterning seen in many species of owls. The next groups of experiments were designed to discover which of these four characters were essentially present in an object having 'owl-valence'.

Series V 1. Model owl WO 2 was painted bright lime green all over, save for the black spots representing the eyes. In twenty experiments only four were positive, and of 1274 min. total duration only five were occupied by reaction. The difference both from the standard and from series WO II is very great and shows that if coloration (the combination of colour and pattern) be improbable, then shape alone is not sufficient to give any marked 'owl-valence'. This series of experiments also disposed of the 'strangeness' theory (Nicholson, 1927). Model owl WO 2, in its uniform light green coloration, was far more conspicuous, even in summer, than it had been when painted in browns and greys, and was quite unlike any British wild bird. But its strange appearance was inadequate to provoke any but the briefest demonstrations of hostility. Additional evidence against the 'strangeness' theory was provided by a group of experiments (not listed in Tables 1 and 2) with stuffed aquatic and 'exotic' birds of six different species. Of twenty-nine experiments, eight were positive, with only eleven of 1909 min. total duration occupied by reaction, though the appearance of every mounted bird used was 'strange' in the scene of the experiments.

Series V 2. Model owl WO 2 was again used. The uniform light green which was the coloration in the experiments of series V 1 was used as the ground colour of a pattern of dark green spots and streaks, in which it was endeavoured to simulate the type of markings seen on many species of owl. Of the two elements which make up coloration, patterning was approximately 'correct' while colour was still 'improbable'. In twenty-one experiments, three were positive, and reaction occupied 8 min. out of a total duration of 1335 min. These results are almost identical with those of series

V 1, and establish that a 'correct' colour is a necessary component of the generalized concept 'owl'.

Series V 3. A replica of model owl WO 2 was made: this model—WO 2*a*—was painted in black, three shades of brown and an impure white. The colours were laid on in large patches so as to avoid resemblance to the mottled and streaked patterning of many owl species. Care was taken that the edges of the colour elements in the pattern should coincide with, or run generally parallel to, structural edges so as to avoid the complication of disruptive effects diverting attention from outlines and contours. The pattern is shown in Text-fig. 1.



Text-fig. 1.

In twenty-four experiments, five were positive, and of the total duration of 1504 min. 27 min. were occupied with reaction. The results are of a wholly different order from those of the standard and WO II series, and do not differ from those of series V 1 and V 2 in the proportion of positive experiments. They establish that a 'correct' patterning is a necessary component of the concept 'owl'. On the other hand, there is a significant difference between series V 3 and series V 2 in the proportions of time occupied by reaction (the χ^2 value, with one degree of freedom, is more than 8). On the basis of this difference it may be reasonable to suggest that of the two components of coloration, colour is more valent than patterning.

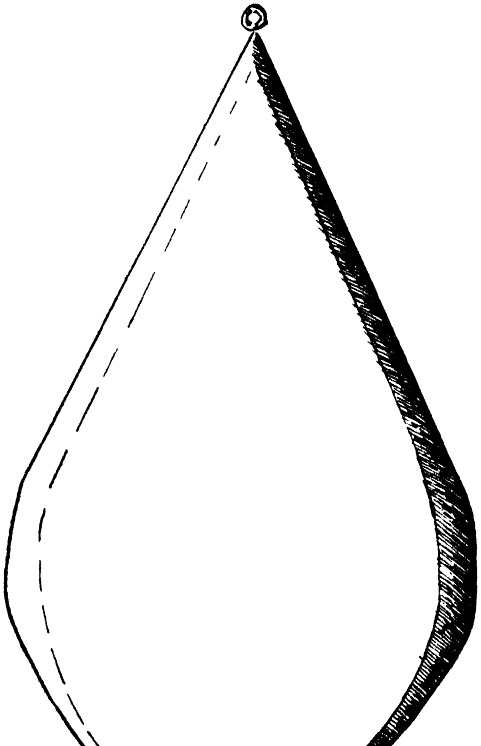
Series Sh. A home-made 'decoy' pigeon of the type used to attract wood-pigeons, *Columba p. palumbus*, for shooting (cf. Rothschild, 1947) was painted with a colour and pattern resembling as closely as possible that of the rufous phase of the tawny owl. In this group of experiments the 'improbable' element was outline; solidity, colour and pattern were all 'correct'. Of twenty experiments, four were positive, and 12 out of 1291 min. total duration were occupied with reaction. Once again, the results are of a different order from those of the standard. They differ in no way from the results of series V 2, and from those of V 3 not at all in proportion of positive experiments, and not much in proportion of time spent in reaction (χ^2 value is about 3·9).

Series Sh/Nc. In testing the valence of outline it was felt that the shape of the decoy pigeon used in series Sh might have introduced a complicating factor. It was at least possible that the pigeon outline might have been valent in some other recognition process, and so might have deflected attention from the factors of coloration. A kite-shaped piece of wood, measuring 25 × 12 × 3 cm. (Text-fig. 2) was painted in an owl-like pattern of browns, grey and black, and exhibited, point upwards, in a series of twenty experiments. There was but one doubtful reaction to it. This result showed that if the outlines of the decoy pigeon used in series Sh had any effect when compared with an object of carefully non-committal outlines, it was certainly not to detract from an 'owl-valence'.

It may, then, be concluded that series Sh establishes 'correct' outline as a necessary component of an object having a strong 'owl-valence'.

Series C/T and C/L. To test the importance of solidity of contours in the recognition of owls three flat 'silhouettes' were prepared and suitably painted—a full-face tawny owl of thin wood, used in series C/T, and full-face and profile little owls of cardboard, used in series C/L. Of the twenty-six experiments of series C/T, three were positive, with 4 min. of reaction in a total duration of 1705 min. In eighteen experiments of series C/L, two were positive, with 3 min., of a total duration of 1070 min., occupied by reaction. These results scarcely call for discussion; they establish that solidity of contours is a necessary component of the generalization 'owl'.

Series An/T and An/L. Two series of experiments were made with pairs of owl's wings, dried in an extended position and clipped together at the inner edges (Text-fig. 3). Series An/T was made with the wings of a tawny owl, An/L with wings of a little owl. Of the twenty-seven experiments of the two series, seven were positive. In these two series both the components of shape were improbable. The proportion of positive results is not significantly different from the proportion in the combined series Sh, C/T and C/L, nor from the proportions in series Sh considered alone, nor in the two C series. The value of 'minutes with reaction' is fairly high (82 min. out of a total duration of 1757). For this value two reasons may be suggested. The more probable is that the experiments were badly designed. The two characters (colour and pattern) which it was desired to test were exhibited upon a shape—the rounded wings of an owl, widely spread—which may itself have a considerable 'owl-valence'. Even so, the results of the two series are significantly different from those of the standard series, LO, and so confirm the conclusion that coloration alone is not the sufficient basis for recognition.

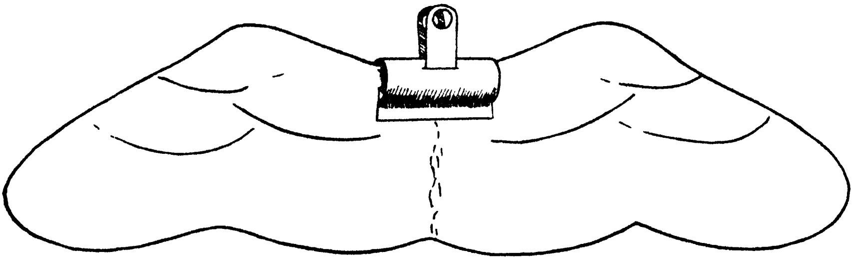


Text-fig. 2.

The second possible reason for the high value of 'minutes with reaction' is the superiority of the patterning and colour of real owl plumage over the most careful imitations, a superiority which greatly raises the value of these two characters in a summation in these two series, in comparison with their value in some of the other groups of tests.

Of the visual characters possessed by almost every animate and inanimate object, three—shape, coloration and tone—are possessed without reference to the other parts of the perceptual field in which the object is viewed. In terms of these three characters it has been shown that an object of strong 'owl-valence' must be:

Owl-like in outlines—large headed, short necked and short tailed.
Solid in contours.
Owl-like in pattern—barred, streaked or spotted.
Owl-like in colours, or in tone contrasts of one suitable colour.



Text-fig. 3.

In an occasional heterogeneous summation of visual characters one or more of these requisites may be lacking in an object which seems, from its capacity to provoke demonstration, to possess 'owl-valence'. But, in general, the presence of all four characters is required for frequent and forceful reaction. It remains to consider the characters of orientation, scale and behaviour.

Series ON. In a succession of experiments a stuffed and mounted little owl was so fixed upon a variety of perches that it projected at any angle save vertically upright. In different tests it projected horizontally, dangled head downwards by its claws or stood out at angles of less than 90° above or below the horizontal. In thirteen experiments, nine were positive, and of a total duration of 720 min., 128 were occupied with reaction. These results show no statistically significant difference from those of the standard series. It appears, therefore, that the orientation of the owl in relation to its background is of no significance in the process of recognition.

Series Pr I and Pr II. Two model owls, each 13 cm. long, were made. Model WO 6, used in series Pr I, was a model of a tawny owl, at a scale of approximately 1/3, and model WO 7, used in series Pr II was a model of a little owl, at a scale of approximately 4/7. In a total, for the two series, of forty-two experiments, six were positive, with 30 min. occupied with reaction in a total duration of 2753 min. These results suggest that there is a definite lower limit to the size range within which a combination of the four necessary visual characters is effective to bestow 'owl-valence'. Reactions have become infrequent when the experimental objects are still large enough to be conspicuous at distances greater than those which separate bird from objective at the beginning of many mobbings. This lower limit appears to be in the neighbourhood of half the linear dimensions of the smallest owl likely to be encountered. There is a statistically significant difference between the two series in the proportions of time with reaction. Model WO 7 seems to have a somewhat greater valence than model WO 6. In experiment Pr 34, model WO 7 was mobbed by three species—chaffinch, cole tit, *Parus ater britannicus*, and robin, *Erithacus rubecula melophilus*—for 12 min. In experiment Pr 20, this model was mobbed for 5 min. by a great tit, *Parus major newtoni*. It is not easy to account for this difference in valence, but a suggestion may be hazarded that the explanation is to be found in the effects of experience.

The investigation of the upper limit of size of objects possessing 'owl-valence' was a matter of technical difficulty. In a large-scale model any errors in line, proportion or patterning are exaggerated. The comparison of reactions to a stuffed eagle owl, *Bubo b. bubo*, with reactions to a wooden model only a little larger than a tawny owl, suggests that the failure of the model to provoke reaction was not to be attributed to its size, but to some other abnormality. A short series of experiments with a stuffed eagle owl suggests that the upper limit of size has not been reached in an object of at least five times the linear scale of the smallest valent object. The range of size within which the four visual characters may be combined to give a strong 'owl-valence' is, therefore, considerable.

The factor of movement can be eliminated from the study of the influence of behaviour on the recognition of owls. A living owl, discovered by birds during the hours of daylight, is usually sitting motionless, and so continues during any demonstrations against it.

Other experiments on the recognition of owls

The experiments of Nice & Ter Pelwyk (1941) on enemy recognition by the song sparrow were made with hand-reared birds. Their criteria of recognition were the calls and postures of the birds:

Stage	Note	Postures
'Alarm'	*tchunk*	Crest raised; tail raised and flipped; wings flipped; restless change of location
'Fear'	*tik*	Feathers compressed; neck elongated; body crouched
'Fright'	*tik-tik-tik*	Flies and hides; flutters in attempt to escape; pants with open bill

'These categories show "alarm", "fear" and "fright" in their extreme form; in milder cases some of the characteristics are not shown.'

In the majority of tests a series of experiments were made, each lasting 3 min. and separated from the next by a 5 min. interval. 'The sequence of models was such that strong and weak stimuli alternated, so that every test showed as much as possible the reaction to that particular model.' Results were stated in numbers of *tchunks* per experiment.

Mounted barred owls, *Strix varia*, were found to call forth strong 'alarm' reactions, mounting to 'fear' if the wings were moved; 'alarm' was also shown at a burrowing owl, *Speotyto cunicularia*, which is less than half the height of a barred owl. A series of models of barred owls were made 'cut out of cardboard and painted on one side with Indian ink and crayon. These models were shown in a series of three minute tests...'.

A model was first used (the 'best' model) which was 'as far as possible a copy of the mounted owl. Y reacted to this model as much as to the mounted owl in the same situation, showing for the most part moderate alarm (94, 115; 148, 128, 102, 124; 103, 97, 98; 121; 116 *tchunks* on five different days). The same model was shown with the eyes covered; Y gave 93 *tchunks*. A piece of plain cardboard of the same shape was shown; Y gave 16 *tchunks* in the first test and one in the second. To find out whether the size of the model was important, we made a reproduction of the "best" model at half-scale. Y showed moderate alarm with 92 *tchunks* on May 17 and weak alarm with 34 *tchunks* five days later. To a piece of cardboard with the same outline Y gave *no* reaction.'

Thereafter, the standard used was reaction to a 'head' model—'a reproduction of the head of the "best" model with a slender, unpainted body'. The outline of this body was very like that of an owl with closed wings, seen full-face. 'This model proved to be almost as effective as the "best" model, evoking mostly moderate alarm....A piece of plain cardboard of the same shape as the "head" model (the "outline") provoked *no* reaction in nine tests, and very weak alarm (14 *tchunks*) in one. So there is a remarkable difference between the results with the painted and unpainted models.'

A number of other tests were made, in an attempt 'to find the essential features in an owl'. Of these, the most interesting were upon the effects of shading. 'A model with only some shading on the head evoked 53, 27 and 0 *tchunks*, and when eyes were added no reaction was given. A model with only some shading on the breast brought 13, 66 and 0 *tchunks*. A model with a dark border around the outline evoked no reaction, but a similar model with some shading along the outline so that it seemed to be rounded brought 94 *tchunks*. A piece of cardboard of the same size as the "head" model was gradually changed and shown at intervals. Eyes, bill and disks around the eyes brought no reaction, but as soon as some shading was added that gave contour to the model, Y showed moderate alarm, uttering 85 *tchunks*.'

It is concluded that 'owls are recognized by Song Sparrows in nature largely through an inborn pattern'.

Rand (1941), working with hand-reared curve-billed thrashers, *Toxostoma curvirostre*, included the exhibition of living and mounted owls among his tests of enemy recognition. At the first sight of a great horned owl, *Bubo virginianus*, some members of a group of eight thrashers between 29 and 35 days old directed at it a display which is frequently given in the presence of snakes; when the birds of this group were 57–63 days old they were again shown a horned owl, and all 'were at once alert and alarmed'. In another group of thrashers, 56–66 days old, the birds 'kept the full width of the aviary away from the owl, watching it', though only two of them had seen an owl of this species before, and that at the age of 19 days.

On another occasion a screech owl, *Otus asio* (a small species only 22–25 cm. long), was placed with a group of thrashers 86–92 days old, 'the first screech owl they had seen'. There was not much reaction to, or interest in, the owl on the first day; but it was left in the cage overnight, and next morning the birds were found to be mobbing it as it flew about. Rand's birds were subjected to such a variety of tests that the implications of his work are not always clear, but it would seem that there is some innate standard of recognition of owls as enemies in the curve-billed thrasher.

Kelso (1940) has studied an 'instinctive' fear reaction in a non-passerine bird. Young, hand-reared screech owls, which had been taken from the nest before their eyes were open, showed fear at the sight of the skin of an American crow, *Corvus brachyrhynchos*. Experiment showed that the combination of visual characters which evoked reaction was of shape, black coloration and slight movement. The most important component of shape appeared to be that of the face, for reaction was obtained if all but the front part of the head was covered with a white cloth. The shape in white had no valence, nor had black objects in general; and if no movement was imparted to the skin the owls failed to recognize it as an object to be feared. The skin of a raven, *Corvus corax*, provoked fear reaction, but there was no apparent recognition of such other potential enemies as great horned owls and Cooper's hawks, *Accipiter cooperi*. Kelso found that at the age of 5 months the reactions of the owls to the skin of the crow became less intense. Bolles (1890) found that hand-reared barred owls showed fear of snakes in their first year and curiosity in their second.

III. DISCUSSION

Daanje (1941) found that house sparrows had two different 'alarm' calls. One was uttered at the sight of fast-moving predators, and resulted in other sparrows taking refuge; the other was used in the presence of a relatively slow-moving enemy, and was the signal for mobbing assemblies. The experiments so far discussed have been mainly concerned with reactions to stationary predators. The investigation of the reaction of birds to the more swiftly moving predators is associated with the names of Goethe (1937), Lorenz (1940) and Krätzig (1940). On *a priori* grounds it may be expected that the complex of visual characters by which a fast-moving predator is recognized will be simpler than the configuration of characters for a more slowly moving or stationary enemy. There is less time for the necessary avoiding or defensive reaction; and the most effective basis for recognition will be that which depends upon the most obvious characters. Tinbergen (1936) has pointed out that errors of interspecific identification in birds are most frequent in reaction to birds of prey 'for which swifts and pigeons are often mistaken by birds'. With a swiftly moving enemy, it is better to be hasty in decision than dead; but with the slower moving enemies, a more exact process of recognition will prevent the waste of time and energy in needless retreats or futile demonstrations of hostility. For purposes of discussion it is possible to distinguish two types of enemy recognition—the 'swift bird predator' type, where the object of fear is usually seen in silhouette, and a 'slow bird predator' type, in which it is normally viewed at or below the level of the observer, or against an opaque background.

Only experiments under controlled conditions can show that any process of recognition depends upon some inherited basis; and the work of Lorenz, Krätzig, Nice & Ter Pelwyk and others has abundantly shown that the recognition of some enemies results from innate powers. The observations of Lack (1947) that captive Geospizid finches showed fear of hawks in California, although, in the Galapagos 'selection is not maintained by fast-flying birds of prey', bears witness to the capacity of an innate power to remain latent, but effective, for an astonishing period.* Field observations can, at times, confirm the existence of latent power of enemy recognition, as when numbers of a markedly sedentary species, the red grouse, *Lagopus s. scoticus*, in the peak district of Derbyshire take wing and fly before a sea eagle, *Haliaetus albicilla*, a species which is not seen in their habitat once in a decade (Chislett, 1933). It should be mentioned that this is not a

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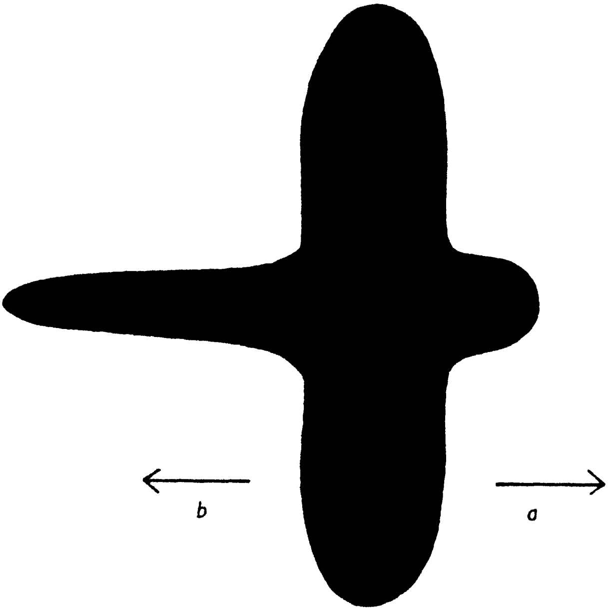
* A period only to be measured on a geological time scale.

generalized reaction to all birds of prey. Grouse lie close when a peregrine, *Falco p. peregrinus*, is overhead.

It now remains to discuss the parts which different visual characters play in the processes of recognition.

Shape. (*a*) *Outlines*. In experiments which are already classical, Lorenz and Tinbergen (Lorenz, 1940) and Krätzig (1940) have shown that in several species the recognition of a swift-moving predator of the hawk type depends entirely upon a combination of two visual characters, outline and movement. As a result of trial a generalized silhouette (Text-fig. 4) has been produced which in such birds as ptarmigan (*Lagopus l. lagopus*) causes fear reactions when moved in one direction, when it is, apparently, taken for the short-necked silhouette of a hawk, and no more than attention when moved in the other.



Text-fig. 4.

With the more slow-moving predators, the experiments of Nice & Ter Pelwyk and of Kelso in the laboratory, and of the writer in the field have all shown outline to be a factor of importance, though less dominant in the recognition process than in the fast-moving predator type of recognition. The laboratory experiments have drawn attention to the importance of the outlines of the head or face in the process of recognition. In this connexion, attention may be drawn to the results of the experiments in series SO; it was obvious that the 'synthetic owl' possessed a considerable 'owl-valence', but was less effective than some of the wooden models. It may be that this is to be traced to the lack of any attempt to model a face on the 'synthetic owl' (cf. Pl. 1A). Strausz (1938) found that plaster models of the heads of owls or hawks were capable of provoking fear in hooded crows, *Corvus cornix*, and jackdaws, *Corvus monedula*. Edwards, Hosking & Smith (1949) found that the head of a stuffed cuckoo, *Cuculus c. canorus*, is the principal point of attack by small birds, and Huxley & Fisher (1940) have drawn attention to the importance of the head in intraspecific recognition in the blackheaded gull, *Larus r. ridibundus*.

(*b*) *Contour or solidity*. The field experiments suggested that an object possessing 'owl-valence' must be solid. The results of Nice & Ter Pelwyk indicate that this statement should be modified to 'must give the impression of solidity'. In nature, of course, appearance and fact will be one, but it is interesting thus to obtain experimental proof that in birds the percept 'solidity of contour' is, or may be, an 'interpretation' of the effects of differential illumination. That birds can be induced to see the apparently solid in the flat was shown many years ago by the great zoological painter, Joseph Wolf (Palmer, 1895):

'It is not often that an artist's studio rings with the songs of nightingales and blackcaps; and it is still less often that he consults them on matters artistic; but on one occasion Wolf found them rather flattering critics. He had finished, and finished very highly, an oil picture of a peregrine. He says, "I had a large cagefull of birds at that time, and when the picture was done I thought I would try its effect upon them. So I showed it to them, and at first only one took any notice. Then all of them saw it, and there was quite a commotion among them. The Serin Finch lay all along the perch, and the Chaffinch hid himself down by the board at the bottom."'

In the 'swift-moving-predator' type of recognition, solidity is of no importance; the solidity of any object seen against the light is only perceptible at very short ranges.

Coloration. (*a*) *Colour*. In the 'swift predator' type of recognition colour—and tone contrasts—are of no importance; the object of fear is usually seen against the light.

In the recognition of owls, field experiments have shown that colour is one of the necessary visual characters; and coloration was also valent in the recognition of crows by Kelso's (1940) screech owls. Turner (1924) found that short-eared owls, *Asio flammeus*, had an antipathy against black. 'Black they abhorred, and fled in alarm...if anyone approached them in black array.'

In interspecific recognition, the perception of colour difference or tone contrast is involved in the recognition of other objects than predators.

Grey of Fallodon (1927) observed that the colour of clothing affected the behaviour of tame wild-fowl. 'But the waterfowl are perceptibly less tame if I wear dark clothes, though my whistle and gestures are familiar to them. In the long days of summer-time the sunset feed is not till after dinner, and it is desirable when visiting them to conceal evening clothes (if one has dressed for dinner) with a light-coloured overcoat.'

(*b*) *Pattern.* The field experiments have shown pattern to be a necessary visual character in the process of recognition of owls; and Rand (1941) believed pattern to be a factor in the recognition of snakes by curve-billed thrashers. Hudson (1915) considered that patterning of a tweed fishing hat 'of an obscure grey colour, striped or barred with dark brown' was the cause for which goldcrests, *Regulus r. anglorum*, and swallows, *Hirundo r. rustica*, mobbed him when he was wearing it. Hudson considered the colour and pattern to be cat-like; it is possible that the resemblance was rather to an owl. Turner (1924) found short-eared owls to be sensitive to pattern. 'If I went into the aviary in a blouse which had any kind of pattern on it, one or the other would be sure to alight on me and gently trace the pattern with its bill.'

In the discussion of the valence of colour and pattern in the recognition of owls, references to 'owl-like' colours and 'owl-like' patterns would seem to suggest that the coloration of all species of owls is some system of streaks, spots or bars in tones of brown and grey. This coloration is borne by the majority of owl species, but in the barn owls, *Tyto alba* subspp., the coloration is golden buff and white, and almost without spots of darker tone.

In Britain, barn owls are more diurnal than such species as tawny owls and long-eared owls, *Asio o. otus*, and eat considerable numbers of birds. Jourdain (1938–41) lists sixteen species of wild birds as prey of barn owls, nineteen species as prey of tawny owls, and twenty as prey of long-eared owls. Although barn owls are enemies of small birds, and are, by reason of their semi-diurnal habits, conspicuous, they are very rarely mobbed (cf. Ryves, 1943; Hosking & Newberry, 1945). If the mobbing of predators results from a system of learned recognition, this immunity of barn owls is extremely puzzling, but it is at once comprehensible if the recognition be an innate reaction to a complex of visual characters which includes a system of coloration different from that of barn owls. Barn owls are, in fact, the 'correct' shape, but the 'incorrect' colour. The occasional mobbings of barn owls which are recorded (cf. Meinertzhagen, 1942) presumably result from a heterogeneous summation in which characters of outline and contour have played a dominant part, with, perhaps, an addition of learned response.

Tone, as expressed in texture. Laboratory experiments and field experiments alike show that feathery texture is not an essential character of objects possessing 'bird enemy valence'.

Orientation, in relation to the rest of the perceptual field, seems to play no important part in the recognition of owls. Attention appears to be concentrated upon the configuration of visual characters which is the owl itself, without referring it to its background. Edwards *et al.* (1949) have published photographs of a willow warbler, *Phylloscopus t. trochilus*, and of a nightingale *Luscinia m. megarhyncha* attacking a stuffed cuckoo while it is held in a man's hand. This lack of reference to the background in which the object is viewed is characteristic of innate behaviour. 'Innate behaviour is never a reaction to the environmental situation as a whole, but only to a few parts of it' (Tinbergen, 1948).

Scale. The investigation of scale is complicated by the possibility of a change in the nature of the 'valence' of an object, without any obvious change in the reaction to it. Thorpe (1944) has written that small and defenceless animals have '...instead of, or in addition to any specific response...an instinctive equipment whereby they tend to take avoiding or self-protection action to (1). A wide range of stimuli which are likely to be signals for danger, especially any moving object....'

The increase in size of an experimental object may change it from 'enemy-valent' to 'alarmingly-large-object-valent' without the possibility of detecting the moment of change. Rand (1941) found that the larger the snake, the more intense the reaction of thrashers to it. The change of valence is more especially a source of confusion in experiments on moving objects. In work upon slow-moving or stationary predators, sufficient skill in modelling should enable the upper limit of scale of an 'owl-valent' object to be fixed. Certainly the range of size within which a combination of visual characters can bestow 'enemy valence' is large.

Behaviour. (*a*) *Pose.* In 'swift-bird-enemy' recognition, the pose of the object of fear is defined, with the widespread wings of the flying bird making a setting for the short neck and head. In 'slow bird enemy' recognition more work is needed. The results of Nice & Ter Pelwyk, and of one or two field experiments with newly dead little owls, show that owl shapes are equivalent with spread or with closed wings; but a study of some more abnormal poses might give interesting data. The results of a few experiments of the writer's (the results of which were, unfortunately, lost during the war) suggest that birds do not mob a dead brown rat, *Rattus norvegicus*, lying on the ground. Small birds will certainly mob a mounted brown rat and here the difference is one of pose. All cryptic attitudes, and aposematic and pseudaposematic displays depend for their effect upon the ability of change of pose to bestow a change of valence.

(*b*) *Movement.* In 'swift bird enemy' recognition, movement is of the highest importance; it is movement which gives orientation to the generalized shape (Text-fig. 4). Krätzig (1940) gives the opinion that in recognition of this type, there is the possibility of very marked heterogeneous summations of the two characters of movement and outline, and suggests that a sufficiently violent movement, especially a head-long descent, may give 'enemy valence' to an object of almost any outline. Here, of course, change of valence may be involved. The reactions of small birds to sparrowhawks, *Accipiter n. nisus*, vary with the flight of the hawk. When a sparrowhawk is flying high with an alternation of several flaps and a glide, it is often mobbed by small birds, especially swallows; when the hawk is in hunting flight, fast and low over the ground, it is not harried.

In recognition of owls (recognition of the 'slow bird enemy' type) movement is not an essential visual character, although Nice & Ter Pelwyk have shown that the movement of the wings of a stuffed owl increases the intensity of reaction from 'alarm' to 'fear'. Southern European bird watchers use dummy owls with movable wings to lure small birds on to limed twigs or within shot.

Recognition of predators by voice. The only method of recognition which has been discussed is recognition by visual clues. The possibility that auditory stimuli alone, or in conjunction with visual characters, may be clues to recognition cannot be dismissed.

André (1904) states that plumage-hunters in Trinidad imitate the hooting of an owl, *Glaucidium phalaenoides*, to attract humming birds and other species within shot. Smith (1946) gave an account of a threat display of a willow warbler, provoked by the imitation of a cuckoo's note; and on one occasion the writer saw an assembly of clamorous mistle thrushes, *Turdus viscivorus*, and blackbirds, *Turdis m. merula* summoned by an imitation of the 'Ke-wik' note of a tawny owl. On the other hand, Nice & Ter Pelwyk (1941) found that a hand-reared song sparrow gave no response to 'excellent imitations of the hoots of great horned, barred and barn owls and also the cry of the red-shouldered hawk'.

The recognition of predators by auditory means is a field for investigation which lies almost wholly unexplored.

IV. SUMMARY

1. Predators, by reason of the strong reactions which they evoke from their victims, are suitable subjects for the study of interspecific recognition.
2. A series of experiments was made in which model owls and other objects were put out in the open, and the reactions of wild birds were noted. The advantages and disadvantages of this method are discussed.

3. In these field experiments 'mobbing' reaction was the criterion of recognition.

4. Many species of passerine birds were found to recognize owls by the same combination of visual characters.

5. It was established that an object, to have strong 'owl-valence' must within a considerable range of size, be:

(i) Owl-like in outlines—big headed, short necked and short tailed.

(ii) Solid in contours.

(iii) Coloured in browns and/or greys, or in tone contrasts of these colours.

(iv) Patterned in a system of spots, streaks or bars.

6. Some experiments with hand-reared birds are described, and their results compared with those of the field experiments.

7. The experiments with hand-reared birds suggest that the process of recognition by a configuration of visual clues is innate.

8. The possibility of the existence of auditory clues to recognition of predators is briefly noticed.

It is a pleasant duty to acknowledge my gratitude to Dr H. B. Cott for his repeated assistance, to Prof. N. Tinbergen for valuable suggestions on method and to Mr R. E. Moreau for his helpful criticisms of the MS. of this paper.

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SPECIALIZATIONS IN ORGANS AND MOVEMENTS WITH A RELEASING FUNCTION

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Ethological observations on many different kinds of animals have led Lorenz (1940) to distinguish rather simple behaviour elements, very constant in form, which he has called 'Erbkoordinationen' or 'Instinkthandlungen', and for which we will use the term fixed (motor) patterns. As Koehler has already described in a preceding paper, the adaptation of these fixed patterns to the ever-changing environmental conditions is brought about by special steering mechanisms of a reflex-like character, the taxes, with which the fixed patterns are fused. Moreover, studies on the three-spined stickleback (Tinbergen, 1942) and on the digger wasp, *Ammophila adriaansei* (Baerends, 1941), have revealed that these motor patterns are arranged in groups (that we should like to call instincts) in the sense that a motor pattern can only be performed when certain factors have activated in the animal the instinct to which the motor pattern concerned belongs. As Tinbergen has pointed out in his contribution to this symposium, the instincts themselves are grouped under an instinct of higher order, so a hierarchical system exists.

As a rule internal and external factors together determine whether a certain motivation is activated in an animal or whether a certain motor pattern is performed. That external stimuli sent out by some object can evoke definite instincts or activities in an animal, nobody will call in question; that internal stimuli are also playing a part in arousing these behaviour elements appears from the often observed fact that an animal which has not performed a certain activity for a long time, because it did not encounter an object adequate for producing a reaction to react to, at the end may show this activity towards a completely inadequate object. As Lorenz has pointed out, this indicates that as long as an activity is not performed, an internal factor is accumulating, making the animal more sensitive to external stimulations.

We will restrict ourselves here to the external factors. When the internal factors are favourable, the animals react to a definite object by showing definite activity or by getting into a condition in which the activities belonging to a certain instinct can be released. Moreover, external stimuli release the steering mechanisms. In all three cases the stimuli (visual, chemical, tactile, acoustic or other kinds) are percepted by sense organs and transformed into impulses, that are transferred to some centre where the character of the object is judged. On this judgement, which is influenced by internal factors, depends whether the motor pattern or the instinct is released or not. The mechanism beginning at the sense organs, ending at the centre released and including the sensitivity for characteristics of the object, we will call the releasing mechanism. The releasing mechanism, therefore, is part of the responding animal; to get into action it needs the releasing stimuli sent out by the object. All characters of an object may be able to stimulate sense organs of an animal, but only when a releasing mechanism is activated we may say that these characters send out releasing stimuli with regard to this releasing mechanism. These releasing stimuli we will call sign (or key) stimuli. In some cases the action of a stimulus as a releaser is innate; in other cases a stimulus becomes a releasing stimulus by conditioning. If the releasing stimuli, representing an object associated with some reaction of an animal, are inborn, then they are small in number; when, however, the knowledge of the object is acquired by conditioning, the stimuli releasing a definite releasing mechanism are numerous. Then the object is known down to small details. One might suppose that this difference would be a consequence of greater capacities of the sense organs or sensory centres concerned. That this is not true has been shown by different authors, but probably most convincingly by Seitz (1940). He found that in the same male of the Cichlid fish, *Astatotilapia striggigena*, the fighting drive is released by only a few stimuli that are, however, very typical for a reproductively motivated male; and the courting drive by a very complex situation containing many detailed characters of the female. These female characters were learned during the youth of the male when it was swimming in a school together with its brothers and sisters, all showing the asexual colour markings which are very similar to the female reproductive markings. If a male is kept isolated from the egg stage, it appears that only a few stimuli suffice to release the courting drive. There is no period, however, in which the male could learn the male reproductive dress; for this is quite different from the asexual markings, and it is only shown by a male that dissociates itself from the school to establish a territory.

But in the following I will only ask you to consider innate releasingstimuli.

Many students have already, mainly with the help of simplified models, investigated in different kinds of animals and in different activities, which characters of the adequate object innately release the response. As an example of the analysis of the releasing mechanism of a fixed motor pattern I give here the study of the egg-rolling movement in the grey-lag goose by Lorenz & Tinbergen (1938); the releasing mechanisms of both the fixed motor pattern and the orientating taxis have been investigated on the gaping responses of young thrushes by Tinbergen & Kuenen (1939), while I had myself the opportunity to study the releasing mechanisms of the different sub-instincts of the reproductive mood in *Ammophila adriaansei* (Baerends, 1941). Thus we are rather well informed about the general characters of these releasing situations. It is desirable to summarize here these qualities shortly.

First the releasing situation contains only a very limited number out of all the features of the object, but very often it is those features that are most typical for the object and that distinguish it from similar objects which have a releasing value. Unless it is specially provided for in the innate behaviour system of the animal (for instance, in cases of imprinting), the releasing situation is not extended by conditioning. There seems to be a maximum number of features involved in the releasing of a single response; this response can, however, also be elicited by fewer stimuli. This wholly depends on the intensity of the inner factors that determine the value of the threshold for the releasing of the response. The greater the intensity of the internal factors, the lower the threshold. The total value of the releasing stimuli has to surpass this threshold. There is a good amount of evidence that each stimulus has a certain releasing value which may be different from that of another stimulus. To release a response the sum of the values of the partaking stimuli has to surpass the threshold. If the threshold is below the maximum, only part of the releasing situation will suffice to evoke a response. Provided the sum required is reached, it does not matter which of the releasing stimuli, fitting to the releasing mechanism concerned, is acting. For example, a male of *Lebistes reticulatus* will display to a freshly killed, but otherwise undamaged, and motionless female. It refuses to display to the same female when the eyes are removed. For a living free-swimming female with extirpated eyes, however, it displays vividly.

Secondly, in a great many cases the releasing stimulus is not sent out by one single feature but by a configuration of features. The red colour in males of the three-spined stickleback has only a releasing value when it is situated at the ventral side of the body (Tinbergen, 1948); the silhouette of a bird of prey only releases alarm in other birds when it is moving with the short neck forwards (Lorenz, 1943).

There is important evidence to support the conception that every releasing mechanism has its own sign stimuli. For example, the digger wasp, *Ammophila adriaansei*, that catches caterpillars and drags them to its nest as food for its larva, may respond to the perception of a caterpillar in different ways, all depending on which instinct is activated. When it is hunting, a caterpillar is caught and stung; when it is found near the nest opening, just after the wasp has opened the nest, it is drawn in; but when it lies close to the nest when the wasp is filling the nest entrance, it may be used as filling material. Finally, when we put it into the nest shaft when the wasp is digging out the nest, then it brings the caterpillar away, exactly as she would deal with another obstacle, for instance, a piece of plant root. It is, therefore the same object, that with different conditions of the animal, releases different responses. Still, in every situation the caterpillar is always sending visual as well as chemical stimuli to the sense organs of the wasp where they will be always transformed into impulses. But then it depends on the instinct activated in the wasp which of these impulses will be intercepted somewhere and which can pass along a still unknown way in the nervous system finally to stimulate the principle motoric centre of the reaction. There are indications that in each case different stimuli are working. When hunting, *Ammophila* very likely becomes aware of the presence of a caterpillar by its odour, but when it loses the caterpillar during the transport to the nest in the first place optical stimuli are used to find it (Baerends, 1941).

In many cases it is not possible to judge the adequacy of an object at once. Then it is only accepted after having passed a number of tests. One test consists of a releasing mechanism brought into action by some sign stimuli percepted from the object, and by which a new activity, a new motivation, or a combination of both, is released which brings the animal internally as well as externally in position for the next test. It seems that the releasing mechanisms of every test reacts to other combinations of sign stimuli. Such has been shown, for instance, by Tinbergen (1935) in his study of the hunting behaviour of the bee-catching digger wasp, *Philanthus triangulum*. The example I will give here is taken from the hunting behaviour of the water bug, *Notonecta glauca*.

In one of its types of hunting this insect makes use of waves that spread over the water surface when some insect falls on the water. *Notonecta* starts by taking position with the tips of its first and second pair of legs and of its abdomen against the surface film. It is able to percept the vibrations of the water surface, and vibrations which are neither too weak nor too strong are the sign stimuli that release the beginning of the attack. *Notonecta* directs itself towards the vibrating source and, led by the vibrations, swims towards it. *Notonecta* may get alarmed in this way at distances as far as 20 cm. Having arrived within about 5 cm. from the vibrating object, the behaviour changes. *Notonecta* swings the third pair of legs powerfully backwards and falls upon the prey. This sudden leap is not released by the vibrations, it does not occur when the vibrations are aroused by a hardly visible piece of iron wire. When we make the vibrations with this wire close to the glass wall of the aquarium, but move a small object a few centimeters outside the aquarium beside the wire, it is this object that releases the jump and is directed towards this object, not towards the wire. The next test takes place when the object is seized. Then it depends on its hardness where the mouthparts are introduced. The object is felt all over with the mouthparts; a solid wax ball is not pierced but a piece of cotton wool releases piercing. Sucking only follows in a piece of cotton-wool if it is impregnated with meat extract. Otherwise the object is soon dropped.

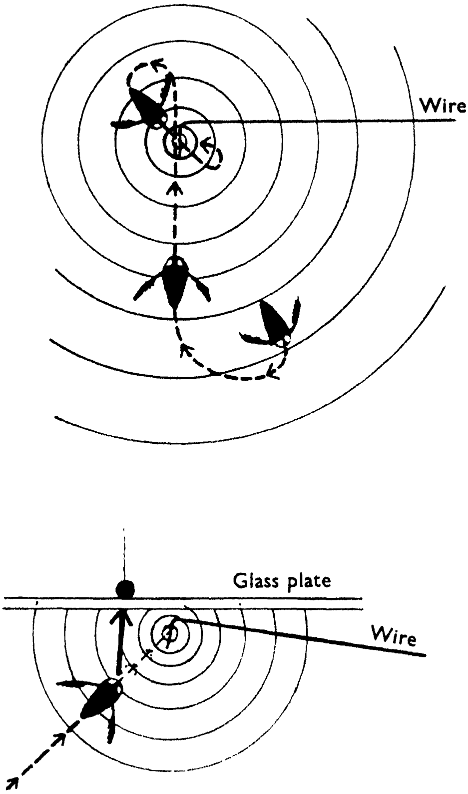

Fig. 1. Hunting behaviour of *Notonecta glauca*; explanation in text.

So the different elements of the hunting behaviour are released by different stimuli: the approach by vibrations, the leap by the visual perception of the moving object, the stinging by tactile and the sucking by chemical stimuli. It is not only the activity that is released but also the possibility of response to further key stimuli. It is a very interesting open question how this takes place.

One of the reasons why the adequacy of the object can often not be recognized at once is that not all the necessary stimuli reach the reactor at a greater distance, as in the vibration in the example of *Notonecta* given above. Another reason is that the object is often not very well defined. Objects such as nesting material or prey, even if they are adequate to one and the same animal, can be very different in shape, colour, size, odour or consistency, yet they have to release the nesting or hunting activities. This implies that the releasing mechanisms involved have to react to not very stereotyped stimuli. The final selection can only be reached after several characters of the object have passed several releasing mechanisms in succession.

Examples of this we find, for instance, in the pike and in robber-flies, where every not too big or not too small object that moves not too fast or not too slow releases the first phase of hunting behaviour.

The more particular the animal becomes about its nesting material or its prey the greater the possibility becomes that it uses typical features of a definite kind of material or prey as releasing stimuli. Then it will have survival value if the animal develops releasing mechanisms that fit closer to the object desired. Such releasing mechanisms adjusted to very specific stimuli occur, for instance, in parasitoid Hymenoptera which are often adapted to small groups of prey. They probably also occur in obligate parasites.

Having accepted that every releasing mechanism has its own combination of releasing stimuli and that in the course of evolution the releasing mechanism will develop towards a more perfect enclosure of the adequate object, we can ask whether this development trend has any influence on the object sending out the releasing stimuli if this object is alive. I think this must certainly be so, for the objects will show genotypic variations in the organs sending out sign stimuli as well as in every other part of the body. Some variations will fit better, others will fit worse to the releasing mechanism, and it must depend on the relation between the actor and the reactor which variation has a better chance of surviving.

First, we will discuss the situation in which the actor has a damaging effect on the reactor, as in a relation as predator and prey or parasite and host. In that case every mutation preventing the catching or feeding activities in the predator or parasite from being released will give the mutant a greater survival chance. In parasite-host relations we know that, for instance, some cuckoo species possess organs sending out releasing stimuli that fit just as well to the releasing mechanisms of the foster parents as the stimuli sent out by their own young (Cott, 1940). But on the whole there is not much known about this kind of relation. In predator-prey relations we know two different ways of development.

Primarily we know animals that have developed structures, colour markings or behaviour patterns that prevent the situations which would release feeding activities from stimulating the predator. We possess a great many descriptions of, at least from the point of view of *our* sense organs, protective structures, protective colour markings or protective attitudes. It is a pity that we possess only a few experiments to show sceptics that these developments really mean a protection, not towards all enemies and in all cases, but towards those enemies that use for finding their prey the sense organs to which the protective organs correspond, and in the statistical majority of cases. The kataplexy of a beetle when attacked will not protect it from being stung by a beetle-hunting digger wasp, but it may save it from animals like many reptiles that only snap at a prey when it moves. The correspondence between the protective coloration and the attitude of the animal that gives it the highest effect is rather convincing of the value of protective markings. That one cannot deny the value of protective coloration when one has seen an animal bearing such markings caught, was shown by Sumner (1935) who proved that penguins, herons and carnivorous fishes, though catching fishes with protective coloration (*Gambusia*), captured a statistically significant greater number of the specimens that had not yet adapted their colour to the background.

Secondly, we know animals that, instead of structures meant to prevent the releasing of an activity in the predator, have developed organs sending out stimuli releasing instincts or activities that counteract the original hunting drive. They suddenly show special conspicuous structures or colour markings, produce repelling odours or frightening yells. Just as the concealing structures or attitudes are means of defence not against one special type of enemy but against a greater number of potential enemies, the intimidating display too will only be of value if it can release fright responses in several predatorious species. Here, too, we possess a greater amount of descriptions of such frightening actions than of experimental evidence of its value to the actor. But the fact that the warning structures are supported by behaviour patterns that make them more conspicuous fully justifies serious attempts to study their effect on the predator. Unpublished experiments by Tinbergen and some of his pupils show the value of the eye spots on the hindwings of the Sphingid *Smerinthus ocellatus* in escaping from small birds.

It is very remarkable that in the development of frightening structures the colours red and yellow as well as dark patches surrounded by a bright ring ('eye spots') are so often used. Other characteristics of frightening actions are sudden and quick movements. Many animals appear to have responses, which are often fright responses, to structures or movements of this general type. It is probably because of the existence of these non-specific fright-releasing mechanisms that organs producing such sign stimuli could develop in the threatened prey.

As far as I know there are at present no data sufficient to decide whether the association of these responses with the sign stimuli is innate or conditioned. But even if it is conditioned, these reponses are so widely spread that we must assume that this conditioning process is an essential part of many behaviour patterns.

Warning structures are not the only developments meant to divert the attacker by releasing another instinct. We find a still more elaborate development in the phenomenon of mimicry. Here it is almost the entire body, not merely a relatively small part of it, which is specialized to transfer the attack into a harmless response. The fact that here the imitation of the dangerous or distasteful example is carried through even to small details suggests that the responses released by it are associated with the releasing stimuli by a conditioning process. Here, too, we greatly need experimental studies.

The organs developed in the animals to distract their enemies are not exclusively releasing fright or indifference. In some animals, especially in animals such as myrmecophiles that live as alien elements in societies of which the members normally attack foreigners, we find species that possess organs producing some secretion which is sucked up by the host without the development of hostile reactions, and in that way save their lives.

However, one might object to this example that it is not a pure case of a predator-prey relation. For the ant guest seeks the company of the ants where it finds a good deal of safety against potential enemies. So since it is a definite gain to the ant guest to live in the ant society we should perhaps classify it under the heading next to be discussed, namely, relations between two organisms which are of advantage to both.

While in the predator-prey or parasite-host relation a development towards each other of a releasing mechanism and the organs sending out the releasing stimuli is impossible if natural selection is the ruling principle, such a converging development is possible as soon as the activity or motivation released is of biological value not merely to the reactor, but also to the actor, the bearer of the releasing organs.

That does not mean that in cases of symbiosis we always find special organs in the actor that have only the function to send out sign stimuli.

The fresh-water mussel, *Anodonta*, for instance, that discharges its larvae over the bitterling, *Rhodeus amarus*, in order that they can attach to its head-parts when this fish approaches the mussel to place its eggs in its expiration chamber, does not show a special development of releasing organs. But from the observations by Verwey (1930) and by Gohar (1948) on the behaviour of fishes of the genus *Amphiprion* with anemones of the genus *Discosoma*, I get the impression that in this well-known symbiosis special situations have developed singly for the case of their releasing power. From Gohar's observations it is very unlikely that *Amphiprion*—that finds shelter in *Discosoma* and in return brings food to the anemone and which enables it to eat bigger prey when back in its shelter—is immune to the cnidoblasts of *Discosoma*. There are several indications that *Discosoma* can put its cnidoblasts out of action. Now before *Amphiprion* enters a new *Discosoma* it snaps cautiously at the tentacles for some time. It looks as if this particular behaviour is a sign stimulus which releases the inactivation of the cnidoblasts in the anemone. The same fish or fishes remain for a long time in the same anemone; after some time the anemone gets used to these particular individual guests; then the fish drops the snapping behaviour.

The most widespread case in which organisms have developed structures that have primarily the function to release in other species behaviour patterns that are of benefit both to the actor and to the reactor, is the symbiosis between flowers and their fertilizing visitors.

Generally, the structures of a flower are neither adjusted to every flower-visiting animal nor to one single species, but more to a special group of flower visitors. We know flowers fertilized by birds, others fertilized by bats, while fertilization by insects is the commonest. But as a rule the mechanisms of the flowers are in correspondence with still smaller groups; some insect flowers are specialized to large, others to small insects, some toward insects with relatively long tongues, others to those with short tongues.

These features of the flower, however, have not the special function of releasing the visiting behaviour in the animal. For that reason some flowers possess conspicuous visual structures or penetrating odours.

When I assert here that the flowers have developed these special structures as a result of the fact that the visiting insects possess releasing mechanisms sensitive to the stimuli sent out by these organs, I must prove that the latter is true.

In this field, too, we find incidentally only experimental researches (von Frisch, 1914, 1919; Hertz, 1929, 1930, 1931; Knoll, 1926; Kugler, 1930–41). Particularly in the older studies one did not sufficiently realize that flower visiting, just like hunting behaviour, is also built up of several elements, each element with its own releasing mechanism and key stimuli. The stimuli by which the animal becomes aware of the presence of a flower may be another stimulus than that which releases the approach to the flower, and both may be different from the factors that make the animal enter it.

Let us begin to consider the characters that first make the animal aware of the presence of the flower. Kugler (1930) found in bumble bees and Knoll (1927) found in the Sphingids *Macroglossum stellatarum* and *Deilephila livornica* that visual characters represent the first stimuli to which these insects react. Ilse (1928), however, found that many Rhopalocera are first alarmed by chemical stimuli. Several kinds of scents release in these butterflies the instinct to search for flowers. Tinbergen told me that he and some of his pupils have often observed that the Sphingid *Hyloicus pinastri* is at great distances attracted by the odour of *Lonicera* flowers; it is not unlikely that Knoll did not find a reaction to scent because he did his experiments in cages. It is, however, enough for us here to state that to some insects odour—and there is enough evidence to say special kinds of odours—means a releasing stimulus.

But also those kinds of insects that began by using olfactory stimuli react to visual stimuli in the next phase. It appears that then the insects mentioned show a distinct preference for particular colours, every group having specific preferences (Fig. 2). The Large White (*Pieris brassicae*), for instance, prefers blue over all other colours, the Large Tortoiseshell (*Vanessa polychloros*), on the other hand, prefers yellow colours, while the Small Tortoiseshell (*Vanessa urticae*), like the bumble bees and the Sphingids, directs its flight to the blue and the yellow parts of the spectrum. These different reactions to different parts of the spectrum are partly due to a colour sensitivity of the insect eye somewhat different from ours (honey bees and bumble bees are certainly less sensitive for the colours of long wave-length, more sensitive at the violet end). But that we may also certainly speak of an innate 'preference' follows from Ilse's experiments in which she taught butterflies to react to colours they did not prefer *a priori*.

Especially for the Sphingids Knoll (1927) has shown that not only certain colours are preferred over others but also brighter objects over less brighter ones. He could show that *Deilephila* judges the brightness by comparison against the background (Fig. 3).

When directing their flight towards flowers bumble bees show an innate preference for complex over simple configurations. Rhopalocera prefer bigger objects over smaller ones (Ilse, 1932, fig. 4).

Near the flower odours certainly play a role in the bumble bee, but visual characteristics are also very important. An indented outline like most flowers have is preferred over a smooth circumference. Hawk-moths and bumble bees have a distinct preference for more saturated colours and bumble bees also for patches and stripes differently coloured from the background. Finally, indents in the flower surface release intensive sucking attempts in bumble bees (Fig. 5).

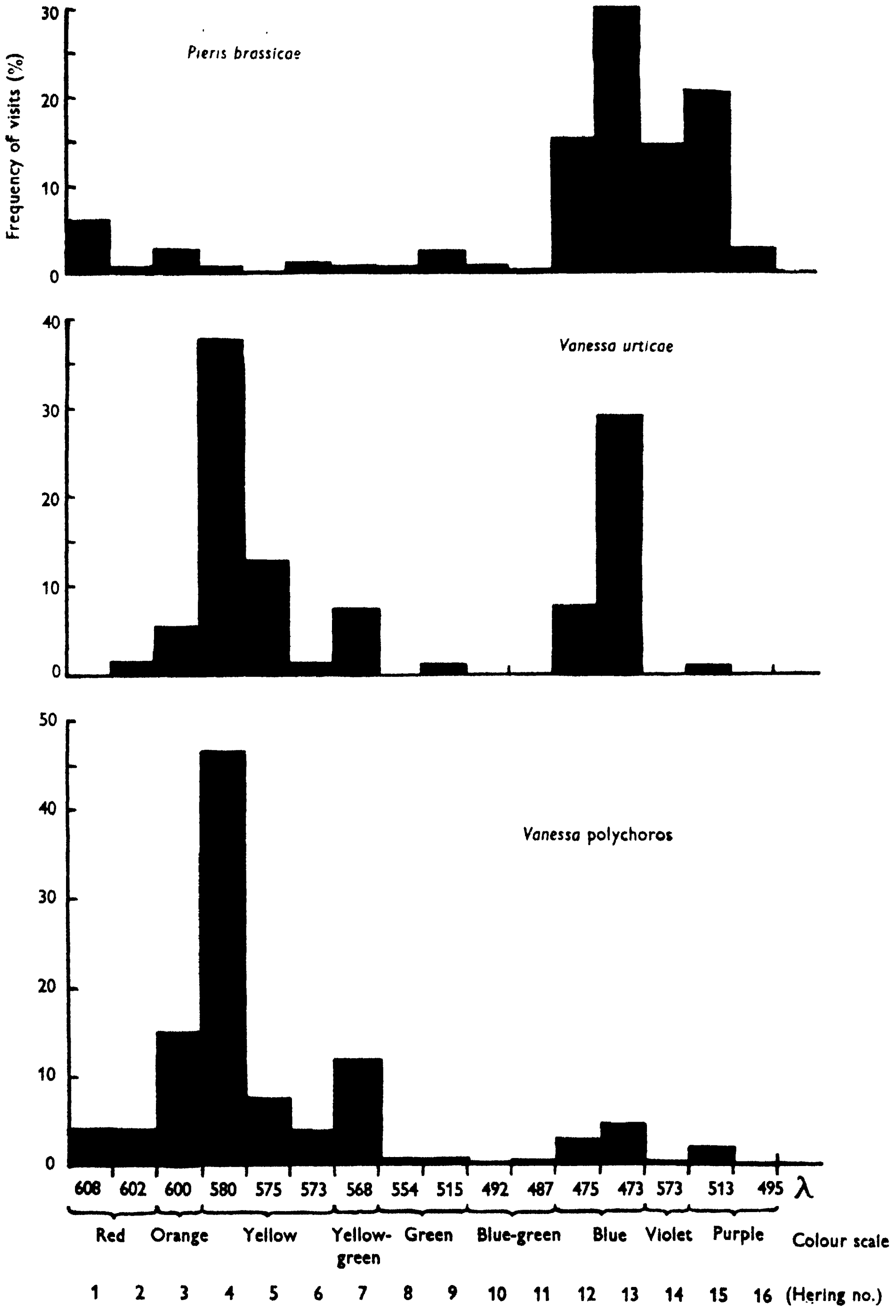

Fig. 2. Diagrammatic representation of the results of some of Miss Ilse's experiments on the colour preference of butterflies. The vertical columns show the number of visits paid to different colour papers after the butterflies had been activated by chemical stimuli.

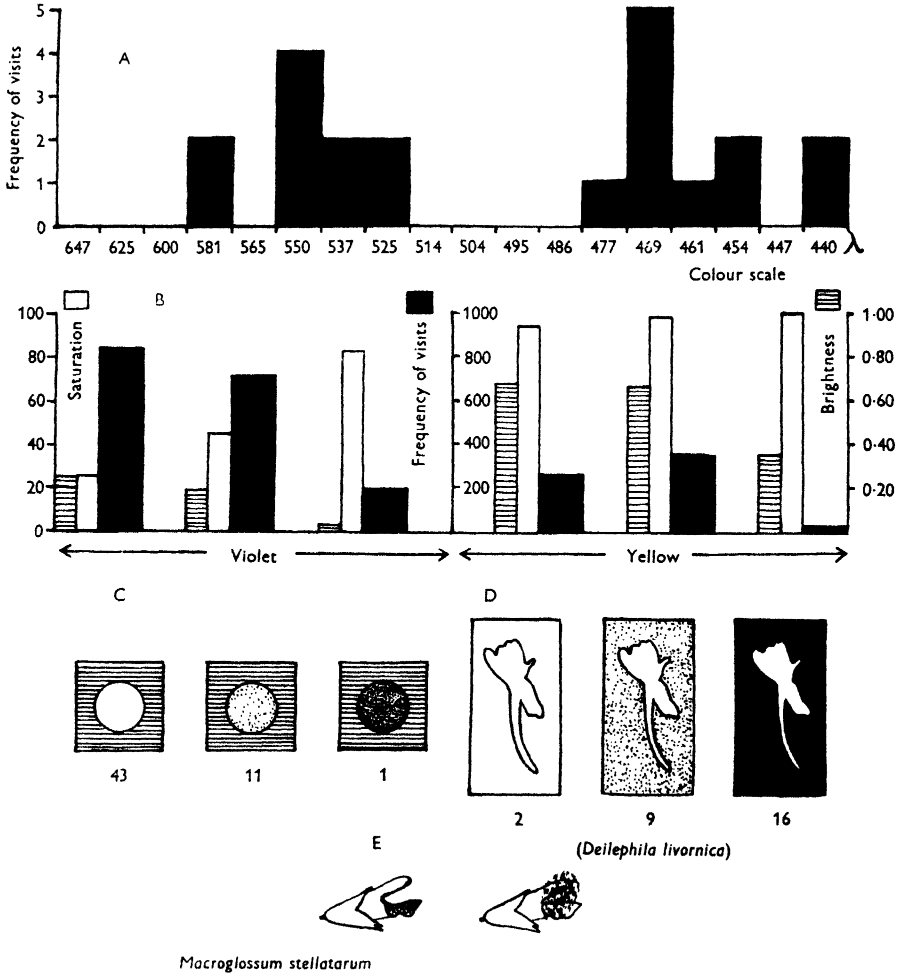

Fig. 3. Diagrammatic representation of the results of some of Knoll's experiments with hawk-moths. A. Colour preference of *Macroglossum stellatarum*. B. Violet and yellow coloured papers of high degrees of saturation are more frequently visited than less saturated ones. The difference would probably be still more conspicuous but for the fact that a low degree of saturation goes hand in hand with a high degree of brightness. For, as C shows, more visits are paid to a brighter than to a darker object when these objects are presented on the same background. Series D suggests that the degree of brightness is judged from its contrast against the background. In E the right flower shows the spots to which the hawk-moths directed their tongues when the flower was placed underneath a glass plate. It appears to be the region of the conspicuous 'nectar mark'.

A great many of these preferences are innate, they were found in butterflies recently emerged from the pupae, and in bumble bees at times they were not bound to a special flower species.

Though more experimental work of this kind is greatly wanted, it is already striking how remarkably well these innate preferences fit with the features of the insect flowers. They have mostly yellow, blue or purple colours; most bumble-bee flowers have composite inflorescences, and hawk-moth flowers, like *Lonicera*, show very bright against the dark green leaves. The outline of most flowers is indented; near the places along which the tongue of the insects has to pass to bring about fertilization there are often markings conspicuous by a coloration different from or more saturated than the background. These places are very often also the deepest places of the flowers.

Very little is known about the releasing mechanisms in flower-visiting bats and birds. Van der Pijl (1936) incidentally observed that young *Pteropus* bats, that had always been reared in captivity, showed intensive searching responses when confronted with the smell of a *Pteropus* food plant which they had never met before. So here the typical odour of bat flowers and fruits seems to be known innately. In bird flowers it is striking that the flowers possess the same colours and colour combinations as the birds. Red is a very common colour in bird flowers; we know that birds often eat red fruits, and it is likely that birds are better than most insects equipped to distinguish colours of longer wave-length.

From what is known in the literature we get the impression that there is much more interspecific variation in the characters of the flowers than in the preferences of the visiting animals. That makes it likely that the features of the flowers have developed under the directing influence of the releasing mechanisms of the animals, and not the latter under the compulsion of the widely varying flowers.

That there is not only the existence of the releasing mechanism in the flower visitor and of the organs sending out releasing stimuli in the flower, but that there is also an inclination for both to develop farther towards each other, is illustrated by cases of adaptation of small groups of plants and small groups of animals to each other. One of these examples is the symbiosis between honey-eaters and the Loranthacea (Docters van Leeuwen, 1931). Here in contrast to most other plants the flower is not accessible to a large group of animals but only to some honey-eaters in which a special activity to open the flowers can be released. In this co-operation a few species of Loranthacea and a few species of honey-eaters take part. We might expect further specialization to lead towards symbiosis between only one animal and one plant. At the moment I do not know if such cases occur.

Wherever co-operation between animals of the same species is necessary we can expect the highest level of development of the combination between releasers and releasing mechanisms, for here the sign stimuli must be specific, they can no longer—as in most cases of symbiosis—release activities in a group of species, but they must use a special code accessible to individuals of one particular species and often even to only one sex or one age class of that species.

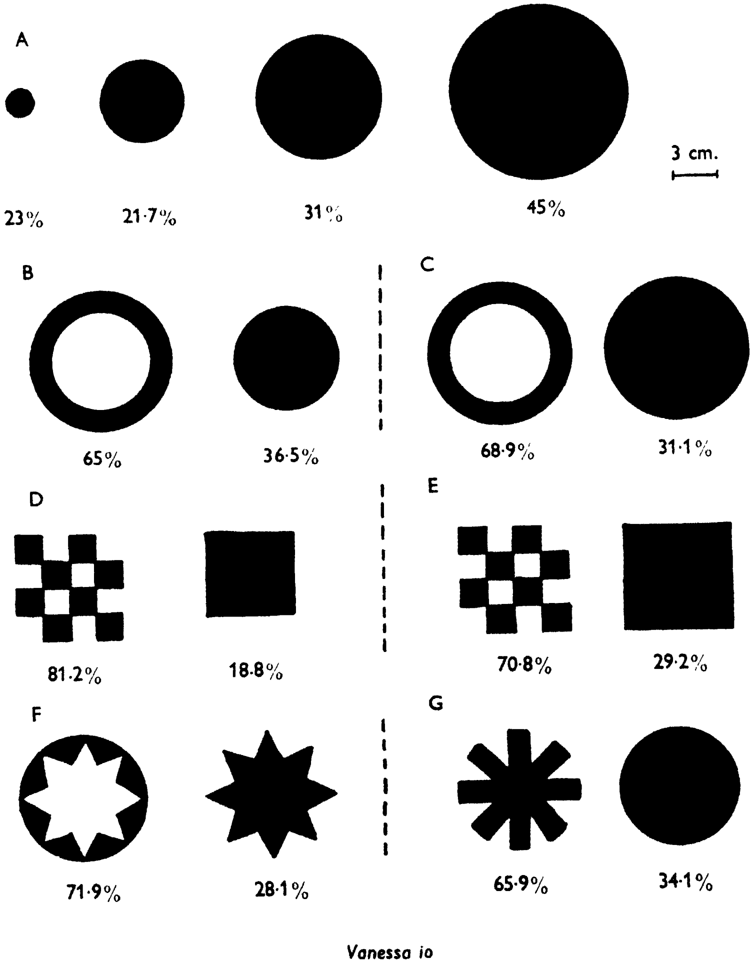

Fig. 4. Some results of Miss Ilse's experiments on the preference of the peacock for certain patterns and structures when seeking for food. The figures indicate the percentage of the total numbers of visits paid to the models of each series. Series A shows the preference of bigger objects over smaller ones; B, C, D and E of disrupted over solid ones, independently of the total surface of the coloured paper. Series F and G show the preference for more complicated circumferences.

It is in this group that the occurrence and the development of sign stimuli-producing organs have been most extensively studied, much under the influence of Lorenz's 'Kumpan'-paper (1935). On p. 377 of his paper, Lorenz defines his concept of 'Auslöser' as follows: 'Structures and instinctive actions that serve exclusively to send out sign stimuli reach a high degree of specialization, parallelling the evolution of the correlated responsive mechanisms. We have called such structures and instinctive actions, for brevity's sake, "Auslöser". From this definition all the organs sending out sign stimuli, which we discussed above, could be called "Auslöser".'*

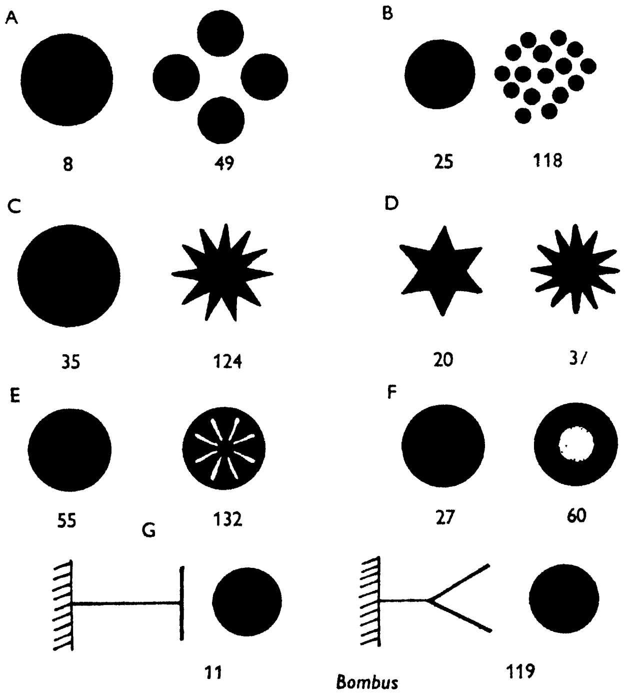

Fig. 5. Some results of Kugler's experiments with bumble bees. The figures refer to the number of visits paid to every model. Series A and B show the innate preference for composite patterns, C and D for the more complicated circumferences, E and F for conspicuous markings, G for depth.

However, Lorenz gives another definition on p. 143, and from this definition it is clear that he restricts the concept 'Auslöser' to organs sending out releasing stimuli that elicit responses in *members of the same species*: 'I have used the term releasers for characters which are peculiar to individuals of a given species and to which responsive releasing mechanisms of conspecific individuals react and thus set in motion definite chains of instinctive actions.'*

Still, I think that the most important reason to distinguish the 'Auslöser' from other types of releasing situations is that it is an organ adapted to and evolved in accordance with a definite releasing mechanism in another animal to which the first animal stands in some relation. I do not think that

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* Translations from German by N. Tinbergen (1948).

it is of so much importance whether the animals belong to the same species or stand in any other relation to each other. So I would be inclined to extend the term 'Auslöser' to every organ especially serving to send out sign stimuli, a conception in accordance with Lorenz's definition cited here first, hoping that this would stimulate research in the other relations as much as it has done in the interspecific relations. If in that case Tinbergen's (1948) translation of the German word 'Auslöser', namely, as 'social releaser', can be maintained, wholly depends on the question whether the term 'social' may be used for relations between two species.

So many studies on social releasers have appeared (see Tinbergen, 1948) that I think a few examples will suffice. First, we know of social releasers directed towards every member of the same species. Such are the nodding in Anatids, which functions as a warning signal, the alarm calls in many birds, the conspicuous wing patterns (specula) of Anatids which make it possible for a single duck to find and join a flock of its fellows.

Secondly, we find social releasers that evoke reactions from young towards their parents. Many Cichlid fishes can perform 'calling' movements that make the young swim towards them. Hens do the same by means of a special call.

Thirdly, the young can produce stimuli that release special reactions towards them in the parents. Gaping movements, such as we find in many young song birds, and pecking at the bill of the parent, as young herons do, stimulate the parents to feed; the call of chickens elicits searching behaviour in the hen.

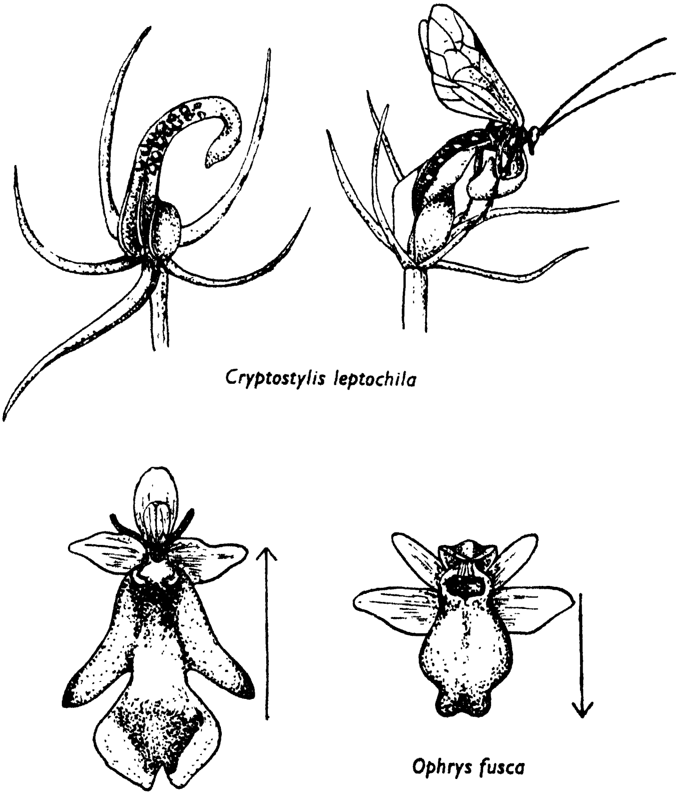
Fourthly, we know of social releasers that have a function in recognition of sex. They release the fighting drive towards their own or the courting drive towards the opposite sex. In a great many species we find that it is not merely one combination of sign stimuli with a releasing mechanism that decides whether a pair is formed or a fight ensues, but a series of several of such pairs all linked in a definite order. Such chains we have already met in the predator-prey relationship, but here we find the complication that very often the reaction of one animal on a certain sign stimulus serves as a sign stimulus to elicit a reaction in another that is again the situation necessary to release the next response in the first one, and so on. As always, the releasing situations may be structures, sounds, odours or movements; very often they are combinations of different kinds of characters; for instance, of a structure made more conspicuous by a special movement. Such chains were, for instance, found in the three-spined stickleback (ter Pelkwijk & Tinbergen, 1937) and in the Cichlid fishes of the genus *Tilapia* (Seitz, 1948; Baerends, 1950). It is very likely that they not only serve to select a female of the same species but also a female which is healthy and fully ripe; for unhealthy or not fully ripe females are often only able to respond correctly in the first couple of links, but fail somewhere further on in the series.

In other cases, for instance, in the Cichlid fishes of the genera *Hemichromis*, *Cichlasoma* and *Aequidens*, and in the herons, selection of the right partner takes place, not at the end, but at the beginning of the courtship. Then the pair is formed, but still the partners go on carrying out peculiar movements, undoubtedly having a special reproductive function. There is a good deal of evidence that the function of these actions is to synchronize the partners. Seeing a partner performing these activities stimulates the animal to start the same activities, and it is very likely that the performance of these activities accelerates the development of the gonads of the animal Aronson (1945). I think there is some difference between these special movements released by and releasing internal developments in the same animal and stimulating identical behaviour in the partner and the sign stimuli releasing a completely different reaction in the responding animal. However, I think they may still be called social releasers, particularly—as I will show later on—as they are especially developed in this context for their synchronizing function.

The last type of special developed releasing situations I want to distinguish is a most interesting one. I am inclined to call it 'sign stimuli parasitic on existing releasing mechanisms'.

As we have seen, many fishes, for instance, the pike, get their prey by means of a releasing mechanism stimulated by moving objects of medium size. This releasing mechanism is of great survival value to them, as it brings them to their food, so it will be maintained in evolution. At the most it may improve, but as long as the fish does not specialize to a special kind of food it cannot become too specific. A group of fishes, the *Lopheidae*, have, like the fishermen, used this opportunity to develop a luring apparatus. This lure releases the feeding responses in a fish; it approaches it and comes within reach of *Lophius* which snaps it up (Wilson, 1937). The relatively small mortality due to *Lophius* will never be enough to outweigh the biological value of the releasing mechanism to the fishes, some of which *Lophius* kills.

The other example I will mention here are the flowers of some orchid genera that are parasitic on the releasing mechanism of some Hymenoptera which they attract without presenting them a food source. In contrast with what I have said above every orchid species is here bound to only one or two insect species. In Europe and North Africa several students (Correvon & Pouyanne, 1916, 1923; Godferey, 1922, 1925, 1929; Faegri, 1934) have found combinations of *Ophrys muscifera* with the Sphegid, *Gorytes* *mystaceus*, of *Ophrys speculum* with the Scoliid, *Dielis ciliata* and of *Ophrys fusca*, *Ophrys lutea* and *Ophrys arachnitiformis* to solitary bees of the genera *Andrena*, *Colletes* and *Eucera*. In Australia Coleman (1929) has found a similar relation of the orchid *Cryptostylis leptochila* to the Ichneuminid *Lissopimpla semipunctata*. It is always the males that visit the flowers and



Cryptostylis leptochila

Ophrys fusca

Ophrys muscifera

Fig. 6. Orchids that are fertilized by Hymenoptera. The arrows point to the direction in which the insects alight on the *Ophrys* flowers.

fertilize them by carrying out the copulation act on the labellum. The flowers and especially the labellum resemble an insect very much, and Pouyanne could experimentally show that the sign stimuli releasing the attack of the insects are sent out by the labellum (Fig. 6). As far as I know there is not much known of the stimuli releasing copulation attempts in Hymenoptera, but I happened to have the opportunity to do some observations and experiments with males of the Sphegid *Ammophila adriaansei*. In these males motionless objects of roughly similar coloration and similar dimensions released copulation attempts, features therefore equivalent to those we find in the orchid labellum. Chemical factors do not seem to play a role. Immediately after the attack the males search for the antennae of the female; that probably accounts for the fact that in *Ophrys muscifera*, where the upper petals are imitating antennae, the insect alights with the head directed towards the pollinia, but on *Ophrys fusca*, where the upper petals have not developed in that way, with the abdomen towards the centre of the flower. So, in the first case the pollinia are attached to the head, in the second case to one of the last segments.

The orchids are especially fertilized by the insects as long as the female Hymenoptera have not yet left the pupae (the males usually hatch a week to a fortnight earlier). During that time the males are likely to suffer from threshold lowering with regards to the sexual reactions; they will therefore more easily respond to non-adequate stimuli.

The orchids need the insects to get fertilized; still they do not produce nectar or other foodstuffs, but they make use of a releasing mechanism in the hymenopteron, a mechanism that has so much biological importance to the insect that it will be retained. Their action towards the flower is of no biological value to *Gorytes*, but it does not harm it either. As the copulation action of *Gorytes* is of great importance to *Ophrys*, its releasing organ will be maintained in the flower, and we may even expect it to develop further.

Having established the fact that there exist organs or movements with the special function to send out sign stimuli which can elicit in other animals the releasing mechanisms of activities which are of benefit to the bearer of the releasing stimuli, we can ask along which way the organs and movements could have developed in the course of evolution. Are they newly built or are they derived from already existing structures, structures perhaps without any releasing value? I think that attempts to answer this question are justified.

It is a pity that we do not know anything of the behaviour of the animals that are fossils to-day in order to compare it with the behaviour of recent forms. But we still have another method of studying the possible origin of an organ, the comparison of related recent species.

Comparative studies on releasing situations have mostly been carried out in the courtship pattern, as this is most conspicuously developed. There are two groups in which interspecific comparison has been made: the Anatids among the birds by Lorenz (1941) and the Cichlid fishes by Seitz (1940, 1942, 1948) and Baerends (1950). Moreover, intraspecific comparison, comparison in one species of different activities occurring in different parts of the entire behaviour pattern, has been attempted in many forms. Such studies have revealed that movements that have a releasing function in a species may be homologous to similar movements without a releasing value occurring somewhere in the behaviour pattern of the same species or even in that of related species. We could explain this fact in the following way:

The social releasers serve to release in another animal an instinct or an activity. But, nearly always, to be able to send out sign stimuli, the bearer of the releasers has to be appropriately motivated, otherwise a potential structure is not demonstrated by the corresponding movement or is masked. The right response to the sign stimuli is only possible when in the animal the instinct concerned is activated. So the system of social releasers and releasing stimuli serves the activation of instincts in a fellow. The simplest way in which this is done is perhaps the mere imitation of the releasing activity in the other animal. We know this from flocks of birds or schools of fish where every animal usually carries out the same action. We have also met it in the Cichlid fishes like *Hemichromis*, where behaviour involved in joining the others has a definite function in courtship. In the same way nesting and fighting activities have a stimulative effect on other animals.

A little step farther brings us to the observation, that not only complete movements but also parts of movements can have a stimulative value. One group of these movements is formed by what Tinbergen (1940) has called the awakening movements, movements that are not yet complete because the intensity of the activated instinct (which, for instance, in the reproductive drive depends on the secretion of hormones) is low. Another group is formed by the preparatory movements, which, after Tinbergen's conception, occur when the proportion between the values of the internal and the external stimuli is such that a complete reaction cannot be released.

Awakening movements, like the scraping of nest holes and the uttering of the feeding call, when performed by one member of a colony, may induce the entire society to follow the example. In Anatids the beginning of the flying-off movement, a head-nodding movement, has become a warning signal to the members of the same flock. It is an example of a preparatory movement; if the danger stimulus increases, the head nodding changes into real flying off.

As soon as an activity or part of an activity stimulates similar behaviour in another animal, the possibility exists that this communicative function is still increased by developments that make the movement more conspicuous.

The movements become formalized and they are often combined with conspicuous structures. The further this development goes, the less important becomes the original function of the activity; the signal function becomes dominant and the activity can be called a social releaser. As an example of such a development in an awakening movement, I will mention the food flight in a number of terns. Here the male feeds the female on the nest. As an awakening movement this action already occurs at the beginning of pair formation, even before there is a nest. Although the female is also fishing or hunting herself, the male frequently feeds her with a ritual that has undoubtedly a place in the courtship and which resembles the corresponding activity during the period of incubation the more the sexual motivation develops in the birds.

Sometimes elements having a function as social releasers are derived from quite other behaviour patterns where they serve completely different purposes. The tendency to perform such displacement activities is great when for some reason the animal is prevented from reacting in the appropriate way. As these displacement activities will be dealt with in a separate paper a few particulars will be sufficient here. In a great many cases it is probably not determined which displacement activities are used in a given instance to unload the accumulated internal energy which cannot go at that moment along the usual path. But also it is often determined which displacement activity must occur in a certain case, and then this activity is very often somewhat different from the original example, more or less formalized and combined with conspicuous structures. It will be clear that then they have acquired a new function as social releasers.

Comparative studies show that within a group one may find in one species an activity only in its original, for instance cleaning, nest building or feeding function, in another species also irregularly as a displacement movement and in a third species as a formalized displacement movement, having releasing value. We have found such an example in the Cichlid fishes. Many of these fishes occasionally show a flickering movement of the caudal fin, a comfort movement most likely with a cleaning function, which can be seen in any behaviour pattern. In species of the genus *Aequidens* we often observed this movement as a displacement movement shortly after a female had entered a territory of a male. It did not seem to have a function in the courtship repertoire. In another species, however, *Astronotus ocellatus*, we found this same activity much more formalized as a regular part, the first part actually of the courting ritual, just after the hostile attitude in the male has been weakened. To make it still more interesting, exactly at the place on the caudalis, where the movement is most conspicuous, this species bears a big eye spot. None of the other Cichlids referred to above possesses such a well-developed spot on the tail-fin base. That brings us to the problem from where the conspicuous structures originate. The answer to this question too can be approached by comparison of related species and besides by studying the ontogenetic development of the colour pattern. Then in this case one finds that the eye spot is not entirely new, for a concentration of melanophores on that place is typical for the basic colour pattern in the Cichlids. Sometimes a somewhat brighter ring surrounds this concentration, but only in this species of all the Cichlids we have observed has a real eye spot developed from these structures. It is also very striking that during the display the flickering movement is made just in front of the eyes of the partner, the flickering tail not seldom flapping along its head.

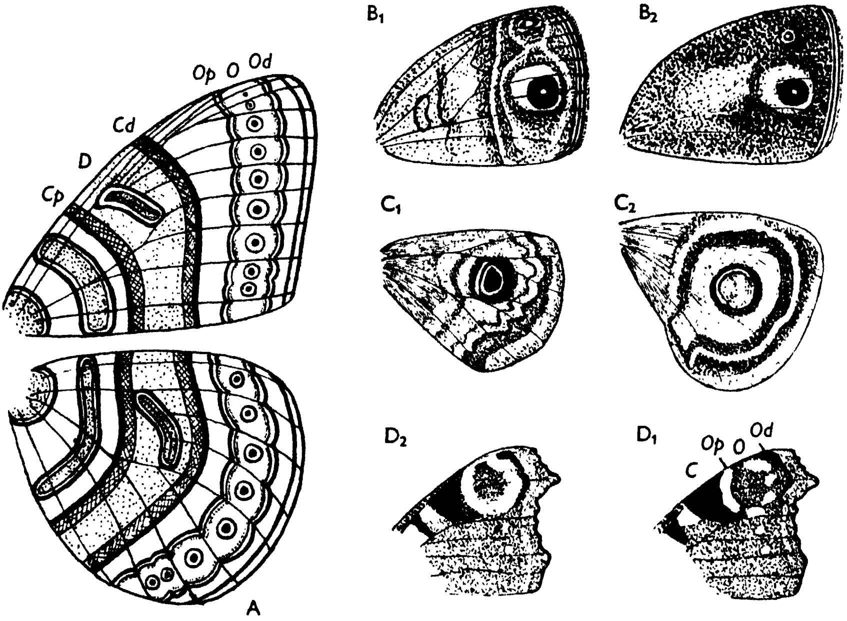


Fig. 7. Wing patterns of butterflies. A. Nymphalid pattern. B$_1$ and B$_2$. Forewing of the Satyrid *Mycalesis patnia*. C$_1$ and C$_2$. Hindwings of two Saturnids. D$_1$, normal forewing of the peacock; D$_2$, abnormal wing of a peacock kept at low temperature. A, C and D after Süffert; B, original.

There is still a quite different group of animals, the Lepidoptera, which, thanks to Süffert's (1927, 1929) studies, gives us some idea about the origin of conspicuous structures. Süffert's analysis of the wing patterns of butterflies revealed some basic pattern system underlying the superficially different looking colour markings of different species. One of these patterns is the Nymphalid pattern and Fig. 7A shows how the eye spot in the forewings of *Mycalesis patnia* is formed by hypertrophy of one ocellus of the ocelli band (*O*) of the Nymphalid system. In the peacock (*Vanessa io*) the conspicuous eye spots are built up out of elements of different systems, the ocelli band (O_p, O, O_d) and part of the symmetrical central band (*Cd*). This complex character only became clear when the pupa was kept at low temperature. Finally, Fig. 7C shows the homology between the discoidal patch and the eye spots of the wings of the Saturnids. The effect of these patches can be enlarged by the symmetrical bands bending conspicuously in correspondence with the outline of the patch.

The tendency to perform movements as displacement movements varies in different individuals; it often goes hand in hand with an easily released high intensity of the sexual instinct. The Cichlid males have adjoining territories in which they display; the females usually visit many males before they pair with one of them. So they have the opportunity to choose, and some of Noble's experiments (1939) indicate that the females do actually make a choice. So if the female is impressed by the displacement movements of the male, such a male would probably attract more females than other males do, and therefore will transfer its genes to a relatively greater offspring. The same is true for colour markings. The concentration of melanophores on the tail base of the Cichlids and the realization of the specific wing patterns in the butterflies varies individually. If the Cichlid females prefer males bearing a black spot surrounded by a bright ring; if enemies of the butterflies really get frightened by eye spots, and if the variations in these spots are genotypic, then fishes and butterflies bearing eye-spot like rings must become more numerous. We do know, as already mentioned above, that a great many animals are greatly impressed by structures resembling eyes.

If this hypothesis on the origin of the structures and movements acting as social releasers is true, there is a tendency for more links to be added to the chain of releasing stimuli within a certain behaviour pattern and for more specialization of form. This tendency will remain and improve the selection or synchronization apparatus until this becomes less favourable to the animal, perhaps too cumbersome. Then the decrease in survival value will put a stop to it. In accordance with Lorenz's concept 'Auslöser', we have as far as possible tried to restrict this survey to releasing stimuli that are innately fixed to the releasing mechanism. However, as Lorenz too has already realized, the releasing mechanism can also be combined with releasing stimuli by a conditioning process. For instance, Kugler showed that the bumble bees very quickly learn to associate the centre of a radially symmetrical flower or conspicuous markings on the petals with the presence of nectar. It will be clear that, if the formation of such an association is a rule in a certain case, conditioned combinations of releasing mechanisms with releasing stimuli will have as great a value as formative forces as innate combinations.

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THE NATURE AND FUNCTION OF DISPLACEMENT ACTIVITIES

By EDWARD A. ARMSTRONG

I. DEFINITION

Amongst birds, more than any other organisms, behaviour-patterns are, at times, performed 'out of context'. They suffer transposition from the context within which they are normally integrated and effectively functional to another behaviour-context in which they are usually incongruous and irrelevant unless they become ritualized into it. It has been suggested (Armstrong, 1947) that such activities, hitherto known as 'substitute activities' might be called 'displacement activities'.* The following definition is suggested:

'A displacement activity is the performance of a behaviour-pattern, usually in an incomplete, eccentric, or imperfectly orientated form, out of the functional context of appetites and behaviour-patterns to which it is normally related, as a consequence of tension and the resultant deflexion of energy.'

It is desirable in referring to displacement activities that instead of such terms as 'false-' or 'substitute-brooding' and 'habit-preening' the more explicit terms 'displacement-brooding' and 'displacement-preening' should be used. The term 'substitute activity' is unsuitable, as it is already in use by psychologists concerned with human behaviour, sometimes denoting behaviour related to that of 'displacement activity', but seldom or never in the sense of a transposed, overt, inborn behaviour-pattern—its chief connotation for the comparative psychologist.

II. ELICITATION

Displacement activities are wont to be manifested when impulses are obstructed so that aroused energy is prevented from attaining its appropriate functional outlet. When a displacement activity occurs it is usually due to the thwarting of a drive. This is not the whole story, however, for,

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* 'Displacement' is used in another sense in psycho-analytic literature, in connexion with the transference of emotion from one object to another, but there need be no confusion with 'displacement activity' as used in comparative psychology. The term 'Replacement activity' has been suggested and in some respects would be appropriate, denoting as it does the essential aspect of the secondary behaviour concerned—replacing a more relevant activity—whereas 'displacement' has reference to the process by which the secondary activity arises rather than to the activity itself. On the other hand, 'Replacement activity' inadequately suggests the frustration which is usually involved in the elicitation of these activities and terms such as 'replacement-nesting' lend themselves to misunderstanding.

as we shall see, reactions which can reasonably be interpreted as displacements occur as a consequence of a superfluity of drive, and these have an important bearing on our interpretation of displacement activities.

The conditions in which such activities are manifested have been discussed in a valuable review by Tinbergen (1940). The analysis below differs in some respects. A displacement activity (when unritualized) is a secondary behaviour-pattern performed: (1) when there is competition or conflict between two incompatible drives, or appetitive and aversionary behaviour, such as to stay and to go, as frequently happens with birds disturbed at the nest; (2) when a drive is thwarted, due to: abrupt deprivation of the object, as when a broody domestic fowl is removed from the eggs, or the sudden disappearance of an adversary, or, in the case of chain-sequence reactions, the absence of an external stimulus-link, as when the female stickleback, *Gasterosteus aculeatus*, does not follow the male to the nest (Tinbergen & van Iersel, 1947); (3) when, after a goal has been attained or the threshold of expression of a behaviour-pattern has been raised, another, usually non-functional, activity is elicited, as when a bird sings, displays or pecks the female after coition or attempted coition, or a mammal bites the female after coition (Antonius, 1943).

This classification will receive some qualification later. It represents an over-simplification, for there is some overlapping of types, and the relationship between drive and object is more complicated than it indicates. Moreover, it is doubtful whether some displacement situations can be described in terms of drive and perceptual field. In examining a range of types of displacement activity one finds that although many appear to be determined independently of any functional effectiveness it is doubtful whether some can be adequately described in objectivistic, non-psychological terms. For instance, the circumstances in which certain types of displacement are elicited seem to require for their full interpretation the postulate of anticipatory reference. A female Scottish crossbill, *Loxia curvirostra scotica*, will strop her bill, displacement-preen and displacement-feed during nest-site selection (Nethersole-Thompson & Nethersole-Thompson, 1943). A female East African fiscal shrike, *Lanius collaris humeralis*, with young and two addled eggs in the nest, pecked the eggs on several occasions, behaved in a 'nervous' manner, and loitered to an unusual extent after her visits with food. Once she picked a dead leaf from a twig near the nest and flew away with it. A little later she came to the nest, hopped around for a considerable time, then seized an egg and carried it away. On her next visit she removed the other egg (V. D. van Someren, *in litt.*). Howard (1940) showed that there are grounds for believing that the tempo of a bird's activities and the strength of drives can be influenced by objects outside the perceptual field, and that perception involves expectation. Human beings in situations of tension comparable with those in the above instances, when they are anticipating some exciting or unpleasant experience, perform modified displacement activities. Marples & Marples (1934) describe how a common tern, *Sterna hirundo*, seeing its eggs painted blue, pecked them and then went off to displacement-bathe and -preen. A ringed plover, *Charadrius hiaticula*, while brooding the chipping eggs, and on no other occasion during my fortnight of observation, fidgeted with the pebbles around it. Comparable human behaviour has been recorded. A common displacement activity is that in which a bird attacks its mate, an inoffensive individual of another species, or even an inanimate object. Behaviour of this kind also is known amongst human beings.

III. DISPLACEMENT AND OVERFLOW ACTIVITIES

It is important, not only for the understanding of the nature of displacement activities but for our conception of the way energy is differentiated and distributed in behaviour, to consider the relationship between displacement activities and what I suggest might be styled 'overflow activities'—in which category I include behaviour impelled by so powerful a drive that it finds expression even when the stimulus from the perceptual field is suboptimal or minimal. Although, theoretically, the difference between an overflow activity and a displacement activity might seem quite clear, one being a direct expression of energy, the other an expression of energy at second-hand, yet, as the following instances of sexual behaviour show, it is difficult to make a hard and fast distinction between the two types.

A passing boat, or aeroplane, a sudden hail-storm or an altercation with an enemy may arouse coitional behaviour between turnstones, *Arenaria interpres*, and a male will perform the display-flight after expelling another male (Bergman, 1946). In a captive flock of black-headed gulls, *Larus ridibundus*, copulations only occurred when the birds were excited by the appearance of some unusual object (M. Rothschild, *in litt.*). When a dog which was with me disturbed a dunlin, *Calidris alpina*, near where its chicks were concealed, it performed the epigamic song-flight. In all these instances an incongruous object or cognitive situation functioned as the critical stimulus in relation to the behaviour elicited.

The inference is that drive and the releaser of the behaviour-pattern associated with it are not always as rigidly connected as might at first appear to be the case. These instances show that while in what we may define as normal behaviour the adequate object or stereotyped releaser is essential to the evocation of the behaviour-pattern, there are other types of behaviour in which the specific characteristics of the object which acts as 'catalyst' for a movement-pattern or other item of behaviour have minimal significance. The situation may be compared with that in which machinery begins to move irrespective of whose finger presses the switch. The novelty of the apparition is more important than its nature; excitement 'sets off' the behaviour so long as the object is not a releaser for a specifically different type of behaviour. Thus communal copulations between pairs of avocets occur after they have been flushed by a human being, but if the intruder be their special enemy, a gull, they react with specific warning cries (Makkink, 1936).

In some other types of behaviour there is still greater independence of the object. Thus the male short-tailed shrew, *Blairina brevicauda*, will repeatedly go through the motions of copulation during sleep, but without emission (Pearson, 1944); from early times the movements of dogs during sleep, even including barking, have been alleged to show that these animals 'dream' or 're-live' experiences. Black-headed gulls will display in their sleep (M. Rothschild, *in litt.*). Lack (1939) carried out experiments with a mounted robin, *Erithacus rubecula*, to test the reactions of a wild bird. After the experiments, during which the bird had attacked the mount, he happened to turn round as he walked away and beheld the robin attacking the empty space where the mount had been. Similarly, Hinsche (1935) describes the behaviour of a toad, *Bufo bufo*, which persisted in extruding its tongue towards the place from which a mealworm had been removed. Whether or not we regard such forms of behaviour as suggesting that an image of an object, or something akin to an image, can exist in an animal's mind, they indicate that in a wide variety of organisms drive and exteroceptive object may become to a large extent, or even entirely, divorced.

It is thus evident that in animal behaviour the correlation between behaviour-pattern and releaser is not necessarily rigid. It is possible for the behaviour-pattern to achieve a large measure of independence of its 'traditional' releaser. Indeed, in the course of evolutionary adaptation a behaviour-pattern may become detached from its releaser and become associated with a completely different releasing stimulus. Such is the history of some ritualized displacements. These facts, in support of which other kinds of evidence might be cited, are of importance in regard to displacement activities, as they are usually in varying degrees irrelevant to, or incongruous with, the perceptual situation.

IV. 'LEERLAUFREAKTION'

I suggest that the concept 'Overflow activity' be substituted for that of 'Leerlaufreaktion' or 'vacuum activity'. 'Leerlaufreaktion' is described by Lorenz (1939) as the damming-up of 'reaction-specific energy' so that the 'instinctive act' goes off *in vacuo* completely independent of the animal's receptors. He also postulates the related concept 'specific exhaustibility'—the 'draining-off' of 'reaction-specific energy'. It is doubtful whether there is evidence to justify the adoption of these terms in the sense in which they are defined. Obviously proof of the 'damming-up' of 'reaction-specific energy' depends on evidence that energy specific to the reaction has been 'stored-up' prior to its expression. The manifestation of a behaviour-pattern *in vacuo* would not, in itself, be proof of this. In so far as the occupation of the behavioural field by one type of behaviour precludes the simultaneous manifestation of another there is an obstacle to its performance, but this is a different matter from 'damming-up' as used by Lorenz. Moreover, if we are to speak of action *in vacuo*, we must be in a position to prove the absence of even a minimal environmental stimulus. This is never possible. Proof of 'specific exhaustibility' requires evidence that the energy 'drained off' is strictly *ad hoc*, and that the diminution of activity is not due to some factor acting to prevent the continuation or repetition of the behaviour.

As the term 'Leerlaufreaktion' is loosely used by some writers in describing types of behaviour in which the threshold of release is low, it is necessary to point out that this use of the term does not conform to Lorenz's definition. For example, the persistent display of lek and quasi-lek birds in the absence of the female is sometimes called 'Leerlaufreaktion' (Räber, 1948), yet such behaviour is not due to an abnormal 'damming-up' of 'reaction-specific energy'—for there is no external thwarting of the energy specific to the display—unless the absence of the female be regarded as such. Phylogenetically it is the outcome of the advantage accruing to individuals of such species in which sexual selection is operative, of prolonged and conspicuous display. This type of display, however, raises important issues which can best be discussed in our consideration of the function of displacements in the evolution of song.

I am sceptical of the validity of a number of alleged instances of 'Leerlaufreaktion'. Such incidents as those cited by Lorenz (1937*a*) of ungulates dashing themselves against the bars of their enclosure can be explained as due to unnoticed olfactory or other stimuli. Dr E. Hindle, Secretary of the London Zoological Society, informs me that no instance of an animal gratuitously killing itself in this way has been recorded at the Zoo. That lowering of the threshold of an activity's release occurs there is no doubt; nor is there doubt that maturation of the expression of a behaviour-pattern may arise in default of the normal adequate perceptual situation, but that an activity of this kind goes off in entire independence of the animal's receptors empowered by 'reaction-specific energy' has not been established.

V. EXHAUSTIBILITY OF REACTION-SPECIFIC ENERGY

Proof of the 'exhaustibility' of 'instinctive acts' is crucial if we are to accept 'reaction-specific energy' as a reality. Lorenz (1939) says: 'This specific *exhaustibility* is fundamental to all instinctive acts; and it suggests the idea of a reservoir of reaction-specific energy, after the emptying of which the organism is no longer available for the behaviour-pattern in question—long before it is itself exhausted, as a whole or in its effectors.' He cites as evidence injury-simulation by a bird which on successive occasions decreased in vehemence. But this single instance does not provide a sound basis for generalization. Again and again, for hours at a time on successive days, I induced a ringed plover to simulate injury without there being any noticeable diminution in the vigour of the performance, which, indeed, increased when the eggs were hatching. I have noticed almost equally persistent injury-simulation by a little ringed plover, *Charadrius dubius curonicus*. The behaviour of the bird commented upon by Lorenz may be attributed to habituation. He has himself drawn attention to the fact that the owner of a tame bird is unable to elicit injury-simulation because he is an insufficiently terrifying object.

The problem of the exhaustion of a reaction, though not necessarily of reaction-specific energy, arises in connexion with the behaviour of the grey-lag goose, *Anser anser*, which in the experiments of Lorenz & Tinbergen (1938) picked at grass stems after abandoning the attempt to roll an egg into the nest. Kortlandt (1940) maintains that this should not be considered displacement activity, as no thwarting occurred, while Tinbergen (1940) argues that this behaviour is comparable with the performance of displacement-preening after injury-simulation, and that it shows that in both types of behaviour the secondary activity is due to the exhaustion of the prior activity. Against this view we should note that a ringed plover will perform a displacement activity after injury-simulation and yet be ready to simulate injury again. Incidents such as the behaviour of this goose considered in conjunction with that of the fiscal shrike and the tern with blue eggs suggest that an attempt to analyse such episodes on a basis of direct thwarting due to environmental factors is an undue simplification of a complex situation.

We must conclude that in so far as the concept of reaction-specific energy is dependent on the evidence of 'Leerlaufreaktion' and 'specific exhaustibility' being valid concepts it is unproven.

VI. THE DISTRIBUTION OF THE ORGANISM'S ENERGY

It is tempting to conceive the storage of energy in terms of a reservoir with valves at different levels and to think of the opening of successive valves as releasing the flow of energy, but this 'model' is misleading, though it serves to emphasize the concept of the organism as charged with pent-up energy which finds expression, once the physiological state is sufficiently mature, in specific patterns in accordance with exteroceptive and other stimuli. Even the metaphor involved in the phrase 'lowering of the threshold' may lead us unwittingly to a non-dynamic conception of the processes involved. To visualize the situation in terms of a reservoir of energy tends to conceal the importance of modes of reaction as mutually exclusive. It is a principle of wide application in physiology, ethology and psychology that the flow of energy in one channel commonly automatically precludes the flow in other related channels, and so the 'obstacles' or 'blocks' to the expression of energy in certain ways are the movements of energy or impulses in other channels. In animal behaviour 'either—or' is the rule and compromise is rare. We must, therefore, think of the organism's energy in terms of power flowing from a dynamo in such a way that the pre-empting of energy in one type of differentiation precludes its differentiation into certain other related forms until some factor operates to divert the energy into another differentiation. The living organism is the scene of shifting, flowing energies and these energies are interrelated and control each other's expression.

VII. THE LINKAGE OF DISPLACEMENT ACTIVITIES

Many, if not all, species exhibiting displacement activity manifest characteristic and comparatively readily expressed patterns, when the appropriate type of situation occurs. Mammals, such as cats, *Felis* spp., and voles, *Microtus* spp., wash and groom when thwarted, the house sparrow, *Passer domesticus*, strops its bill, lapwings, *Vanellus vanellus*, both chicks and adults, make feeding movements—and so forth. Moreover, there are often similarities between the displacement activities throughout a genus, family or even an order. Amongst the Corvidae, species belonging to different genera, such as the crows and jays, perform the same displacement activity of hammering a branch when in a state of agitation. The destruction of the nest after it has been plundered by a predator has been recorded of two species of cotinga, *Cotinga amabilis* and *C. nattereri* (Skutch, 1945), a displacement-nesting activity which cannot have survival value but is not therefore dysgenic. Displacement-nesting activities occur widely amongst the Charadriiformes and displacement-sleeping appears to be more characteristic of birds of this order than of any other (Armstrong, 1947). Some activities, such as displacement-feeding, are performed by a great variety of species throughout the Vertebrata, including birds, ungulates and primates. Possibly it occurs amongst insects. Betel-chewing, gum-chewing, tobacco-chewing, straw-sucking, smoking and like activities are so widespread amongst mankind and seem so often to be in essence or origin a means of relieving tension that they may be regarded as modified forms of displacement-feeding.

Kortlandt (1940) has demonstrated from his observations of the southern cormorant, *Phalacrocorax carbo sinensis*, and the work of Makkink (1936) on the avocet, *Recurvirostra avosetta*, that there are innately determined linkages of displacement activities in these species which react in a reciprocal way. Thus, epigamic display tends to 'spark over' or become side-tracked into fighting, and vice versa. This linkage between sex and belligerence is, of course, widespread in the animal kingdom, not excluding man, as the ancient association between Mars and Venus reminds us. It has even given rise to the extravagant theory that all epigamic display is aposematic (Hingston, 1933).

There is also some evidence of a tendency towards an ontogenetic hierarchy in displacement activities. Displacements are often regressions to behaviour which 'comes easier' to the animal than the task or predicament from which it has 'taken refuge'. As Palmer (1941) has pointed out in connexion with displacement activities of common terns during the reproductive cycle, they are usually those belonging to an earlier phase of that cycle. A common tern whose eggs have just been removed proceeds to make 'scrapes', but if the eggs are restored it ceases to do so. The displacement activity common amongst the Charadriiformes and some other birds during the change-over at the nest of picking up and throwing about material is also a recrudescence of, or regression to, nest-making behaviour. It is, as suggested earlier, and as we shall discuss later, as if an active behaviour-pattern automatically suppresses closely related or 'contiguous' patterns. However, displacements are not invariably revivals of earlier phase behaviour. A stickleback may make the displacement-movement of fanning the eggs when seeking to guide a female to his nest (Tinbergen & van Iersel, 1947).

VIII. THE OBJECT IN RELATION TO THE DRIVE

Displacement activities are of particular interest in that they are in many ways stereotyped and innately determined, bearing strong resemblance in these respects to the movement-patterns described as 'instinctive' by Lorenz, but perhaps better styled 'automatous'. We might even be tempted to suppose, on observing the imperfection of such an activity as displacement-feeding, that here we have an 'instinctive' act without associated taxes, but this would be precarious. The importance in displacement activity of the object and the perceptual field in general should not be underestimated. The innate determination of displacement activities is not as complete as might at first glance appear to be the case. Kortlandt found that a thwarted impulse to copulate would 'spark over' to display-fighting or nest-building, but in the absence of material to mandibulate a further sparking-over to displacement-brooding or displacement activities connected with tending the young might occur. Thus an obstructed impulse tends to find an outlet through increasingly indirect channels, or to put the matter in another way, to give way to increasingly 'remote' behaviour-patterns. The deviation may be occasioned by the absence from the perceptual field of an item or complex normally associated with the performance of the displacement.

The importance of the perceptual field is shown positively in other situations. When eider ducks, *Somateria mollissima*, are disturbed from the nest they perform various displacements, but do not normally displacement-drink, but in Iceland a bird which I alarmed found a stream in her way and displacement-drank repeatedly. Then she displacement-brooded in the shallow water. The incident illustrates the influence of the perceptual field in determining displacement activities as well as the imperfect co-ordination with the environment which so often occurs. A gannet, *Sula bassana*, alarmed at my presence, repeatedly picked up and swallowed scraps from the nest—behaviour not recorded of this bird by any other observer and certainly not a stereotyped activity. When I disturbed an incubating black-headed gull, *Larus ridibundus*, on an island in a marine lough, it flew a few feet to the water and displacement-bathed—quite unusual procedure in such circumstances. A little ringed plover, alarmed at the nest, displacement-bathed in sand (Creutz, 1931). When an oystercatcher, *Haematopus ostralegus*, displacement-bathed, its mate followed suit (Edwards, Hosking & Smith, 1948). Prairie falcons, *Falco mexicanus*, in a state of agitation due to the eyrie being menaced, will strike down other birds of prey, hitherto unmolested, which happen to be nesting close at hand (Bent, 1938). It would not be difficult to multiply such instances in which the importance of the perceptual field in determining the nature of the displacement is evident. Thus it would seem that there is a latent tendency for the evolution and stereotyping of new displacement-movements which might ultimately become ritualized and innately conditioned. Innate linkages are apparently not so rigid that they cannot be modified by the intrusion of new patterns mediated or determined to some extent perceptually. The absorption of maintenance movements* into display indicates that this is so (Lorenz, 1941). It is noticeable, however, that while there are displacement activities characteristic of certain situations the object releasing the activity may vary enormously.

IX. THE IMPERFECTION OF DISPLACEMENT ACTIVITIES

The incompleteness or disorientation of most displacement activities indicates the subordination of the cognitive element and its lack of co-ordination with the drive. A ringed plover when displacement-feeding pecks towards the ground, but does not pick up anything in its mandibles; a stickleback when displacement-nesting in its ritualized threat display normally does not thrust its snout into the sand; a turkey, *Meleagris gallopavo*, will go to a fountain to displacement-drink but swallows no water (Räber, 1948), bathing movements are apt to be perfunctory, and so forth. However, Kortlandt (1940) exaggerates when he states that displacements are always incomplete. A stickleback performing its threat display may actually bore hollows in the sand instead of merely pointing its snout downwards (Tinbergen & van Iersel, 1947); displacement-feeding birds may actually swallow something as did the gannet previously mentioned; the bill-stropping of various species such as the greater and lesser birds of Paradise, *Paradisea apoda* and *P. minor*, is, according to my observations, complete—apart from there being no particles to wipe from the bill. The eider duck mentioned above once pointed its bill upwards, apparently swallowing some water. Usually, however, even when the movement is complete and correctly orientated, it is performed in a rather abnormal manner—perfunctory, hurried or frenzied. The imperfection of displacements is due to the incomplete impetus of the drive and imperfect correlation with the object which appears in at least some cases to be inadequately apprehended. Thus, a southern cormorant may perform displacement epigamic display to a rival or to a stork, *Ciconia alba*, or pelican, *Pelecanus* sp., even when its mate is by its side (Kortlandt, 1940). In the light of my suggestion (1949) that displacement elements are involved in some forms of diversionary display, including injury-simulation, it is interesting to note that an injury-simulating golden plover, *Pluvialis apricaria altifrons*, has been known to display 'by mistake' to its mate instead of the intruder (Williamson, 1948*a*). Expressed psychologically the conational element is deficient in displacement activities, the volitional element in human displacement activities.

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* A distinction is made between display activities which are characterized by having signal function, and maintenance activities without such function which are employed in the maintenance of the bird's life and the lives of its progeny. As many maintenance activities have acquired signal function the distinction must not be pressed too far.

X. THE RITUALIZATION OF DISPLACEMENT MOVEMENTS IN DISPLAY

Most displacement activities are stereotyped as characteristic transposed behaviour-patterns of the species, but they may also become formalized or ritualized within their secondary context so that they become functional as releasers in epigamic or aposematic display. This integration of behaviour-patterns into novel and originally alien behaviour-contexts shows that the description of a displacement activity as a movement-pattern empowered by an allochthonous drive (Tinbergen & van Iersel, 1947) breaks down when the displacement activity becomes ritualized and appropriated to the main drive in the expression of which it has become functional. This has important implications, for it reinforces the conclusion reached earlier that there is potentially considerable 'plasticity' or looseness of connexion between drive and object. We observed in connexion with overflow activities that a drive could be activated by an incongruous object. In ritualized displacement activities a behaviour-pattern is appropriated to another drive and released in connexion with an object with which it was not originally connected. It is difficult to reconcile this instability of association between drive and object with the concept of reaction-specific energy.

The ritualization of displacements has been reviewed by Tinbergen (1940) and the present writer (1947), so that only brief mention of some aspects of it will be made here. Apparently there is no maintenance activity which may not become stereotyped into another context and ritualized as display.

It is of considerable interest that movements associated with behaviour so divorced from sexual activity as hunting for prey have become ritualized as epigamic display. Thus Verwey (1930) has shown that the posture which the male heron, *Ardea cinerea*, assumes to attract the female to his territory is similar to that which it uses in catching fish. Possibly the aerobatic displays of some of the Falconidae, such as the prairie falcon (Bent, 1938), originated as displacement-hunting. The ringed plover is one of the species which make pattering movements with its feet on the mud or sand 'dancing for its dinner'. This dance is also performed during courtship (Selous, 1901; Venables, 1948) and possibly also as a displacement-threat (Edwards, Hosking & Smith, 1947). It is an element in the pre-coitional display of the little ringed plover (Tucker, 1940), and also is performed as a displacement activity when the bird is disturbed at the nest (Creutz, 1931). Similar movements are performed when seeking food by many other waders (Portielje, 1928), some ducks, such as the sheld-duck, *Tadorna tadorna*, and various species of gull. The black-headed gull executes the dance when feeding, nest-building and about to settle on the eggs. A pair of laughing gulls, *Larus atricilla*, apparently suffering from the thwarting of the breeding impulses in confinement, displacement-danced on a hard floor (Kirkman, 1937). As this 'dancing' performance is associated with feeding in widely separated groups, we can assume that the display-dancing of the ringed plover and the little ringed plover is displacement-feeding ritualized as epigamic display, and that the black-headed gull's dances during nest-building and incubation are displacements characteristic of phases of tension, such as when the change-over at the nest occurs. The merlin, *Falco columbarius aesalon*, and kestrel, *Falco tinnunculus*, also perform 'marking time' movements when under the influence of the hunting drive. This is a displacement of the movements customary when settling on the eggs (Portielje, 1940). Thus, while the black-headed gull's movements on settling to incubate are a displacement from hunting for prey, the rather similar movements of the merlin and kestrel appear as displacement activities when the hunting drive is thwarted. The activities of birds become displaced and ritualized in as arbitrary and unpredictable a way as the stereotyping of etiquette amongst different peoples. Thus amongst cranes, *Grus grus* (Heinroth & Heinroth, 1924–33), and pigeons, *Columba livia* (Carpenter, 1933), a movement of the head towards the wing, which is evidently originally displacement-preening, functions in the one species as aposematic display, in the other as epigamic display. In some species, such as the great crested grebe, *Podiceps cristatus*, movements associated with nest-building have epigamic function (Huxley, 1914), in others, such as the raven, *Corvus corax*, as I have observed, they are used as threat display. The gadwall, *Chaulelasmus streperus*, exhibits an epigamic display-pattern in which displacement-preening and displacement-drinking follow one another, welded together in the ceremonial; the mandarin duck, *Aix galericulata*, performs similar ceremonial, but the displacement-drinking precedes the displacement-preening (Lorenz, 1941). Thus a bird's display displacement-activity equipment is attributable to displacements becoming stereotyped and ritualized through the effect of selection in maintaining those displacements which enrich and give additional effectiveness to the display. No doubt many dysgenic displacements have been eliminated with their performers in the course of evolution.

XI. THE OPERATION OF DISPLACEMENT IN THE EVOLUTION OF SONG

It would be surprising if the principle of displacement were operative only in regard to visual and not to audible display, to posturing and not to songs and calls. Undoubtedly it does apply to the latter. As I have commented on this elsewhere (1947, 1949), only a few instances of displacement-song need be mentioned. Birds will sing when flying up the beam of a lighthouse or after escaping from a bird of prey. When a male wren, *Troglodytes troglodytes*, is ringed during the breeding season it sings almost immediately on being released from the hand. A stone cast into a reed-bed will stimulate a sedge warbler, *Acrocephalus schoenobanus*, to sing. Hudson (1920) describes an occasion when a chestnut-shouldered hangnest, *Icterus pyrrhopterus*, which he had shot, sang as it lay dying in a stream. A song thrush, *Turdus ericetorum*, excited by my frightening the young from the nest, sang close by in a most unusual situation on, or within a few inches of, the ground. Observers of their own kind may have noticed that while boys whistle as a mode of sometimes rather aggressive self-assertion or sheer *joie de vivre*, when men regress to this juvenile practice it is often in situations of suspense, tension or surprise. Such whistling appears to be a modified displacement activity.

Not only may song be evoked in incongruous circumstances but thwarted, agitated or surprised birds may utter the call appropriate to one situation in quite another situation. Thus, a turkey which normally only 'gobbled' when alone uttered the call as a displacement when subject to conflicting display and aggressive impulses (Räber, 1948). The squealing notes uttered by a short-eared owl, *Asio flammeus*, when disturbed at the nest (Armstrong & Phillips, 1925), are apparently those associated with feeding the young, or, possibly, with courtship. When an avocet is particularly excited it may utter the specific cry which betokens the approach of a gull when some other bird appears, or, on the other hand, utter the normal warning cries when a gull appears. Makkink (1936) describes this as 'sparking over', that is, as displacement activity. If in the excitement of opposing a rival or predator a bird uttered calls displaced from another context, together with its threat calls, we would have a situation in which, if the association of the calls became stereotyped and then subject to modification, elaboration into song would ensue.

In the Charadriiformes not only are the display-songs of many species patently an elaboration of their maintenance call notes, but in some, such as the dunlin, as we have already noted, displacement song-flights occur when the bird is disturbed near the nest or chicks. It is not unusual for a snipe, *Capella gallinago*, to perform his bleating song-flight when a human intruder enters his territory. Temminck's stint, *Calidris temminckii*, has evolved a type of performance similar to that of the dunlin to such an extent that the birds constantly song-flight by day and night (Haviland, 1916) and hover trilling above an intruder (Seebohm, 1901). The thwarting of aroused energy in connexion with the fighting and mating impulses of the avian ancestral stock may have elicited the repetition, elaboration and accentuation of calls in other contexts than those to which they originally belonged. Thus, song may well have become associated with novel cognitive objects and been extended to topographical, and ultimately territorial, situations, instead of being restricted to a male-male or male-female situation.

The problem of making a precise distinction between normal activity, overflow activity and displacement activity arises acutely in connexion with song. The behaviour of the song-flighting dunlin disturbed by the dog may be described as an overflow activity if we argue that the alarm provided the critical stimulus to release a form of behaviour with a low threshold, or it may be considered a displacement activity on the basis of its affinity with other kinds of incongruous behaviour characteristic of birds disturbed at the nest or with small chicks. Even when un-alarmed a quetzal, *Pharomachus mocinno*, will display-flight on leaving the nesting-hole after incubation (Skutch, 1944)—behaviour comparable with the series of displacement activities, including song, performed by a broody hen on being removed from the nest. If we are to consider the coitional behaviour of avocets when disturbed as an overflow activity, how can we make a hard and fast distinction between such behaviour and that of vermilion flycatchers, *Pyrocephalus rubinus*, which perform the display-flight, sing or attempt to copulate when alarmed at the nest (Rand, 1943)?

The behaviour of lek and quasi-lek birds, referred to earlier, presents a similar problem. Is the persistent display of such birds as the turkey observed by Räber, or of an ocellated turkey, *Agriocharis ocellata*, which I have seen displaying persistently while alone in its cage, to be regarded as normal, overflow, or displacement activity? The display is normal in so far as the movements are similar to those of a bird in normal circumstances. It can be regarded as overflow activity to the extent that it finds expression when the stimulus from the perceptual field is suboptimal; and it can be considered a displacement activity if we suppose that its sustained character arose as a result of the prolonged absence of the female, as it can then be ascribed to the absence of an external stimulus-link. This is not an unreasonable supposition in view of the fact that many lek birds perform obvious and frequent displacements in their 'courts', such as displacement nest-building (removing objects) or bill-wiping, and the displays of birds such as Gould's manakin, *Manacus manacus vitellinus*, in courts not too far apart for the birds to hear each other's calls may be aposematic posturing displaced and modified to a mainly epigamic function. The stickleback being a convenient experimental animal Tinbergen & van Iersel (1947) have been able to prove that the nest-building movement of the male when a stimulus-link is missing by reason of the female not following him is a displacement activity. A male wren, leading a female to his nest, sings softly, displays, and goes in and out as he does on routine visits. He probably makes nest-building movements inside and certainly occasionally makes displacement-nesting movements outside. If it were not for what we know of the stickleback's behaviour, we would not suspect that the displacement principle might have a bearing on the interpretation of these activities.

The predicament we have reached, in which types of behaviour which seemed clear-cut dissolve into each other, is due, I believe, not to deficiencies in our observation or analysis but to basic similarities. The problem is that of the nature of the 'interference' of one behaviour-pattern with another and of what constitutes thwarting. A consideration of all the varied facts suggests a dynamic relationship between behaviour-patterns operating so that they are able to modify the energy available for each other, especially 'contiguous' patterns—those related in a 'propensity disposition'. A behaviour-pattern may achieve such independence of other patterns as to become the channel of unusual energy—an overflow activity. It may suffer obvious thwarting or deflexion when the perceptual field is exercising a noticeable degree of control—a displacement activity. Or the inter-relationship between the patterns may be so balanced that neither abnormal freedom nor abnormal restraint is apparent—normal behaviour. It must be borne in mind that evolutionary processes are continually at work tending to modify one type of behaviour into another by shifting the innate controls on the distribution of the organism's energy. This is, of course, an extreme simplification, but I need not speak here of physiological factors, exteroceptive releasers and of what is known of the hierarchical relationship of controls on behaviour, as these aspects are discussed elsewhere in this symposium.

Such conceptions as these aid us in interpreting a variety of other types of behaviour, such as the excessive autumnal fishing activity of the cormorant which Kortlandt (1940) and Tinbergen (1942) attribute to the diversion of energy expressed in sexual activities during the breeding season. It is significant that the stickleback's displacement nest-building has been found to be self-stimulatory. A fish which is not quite ready to lead the female is able to do so after such activity (Tinbergen & van Iersel, 1947). As a (secondary) displacement activity may result in the augmentation of the energy of a primary activity, it appears possible that the performance of a displacement may absorb energy from elsewhere, which by a kind of reverse displacement augments the original behaviour-pattern.

XII. THE OPERATION OF THE DISPLACEMENT PRINCIPLE IN RELATION TO NEST-BUILDING

While considerable attention has been given to the role of displacement activities in display the possibility that they may have played a part in the evolution of maintenance activities has been overlooked. Probably this is due to its being much easier to identify displacement elements in display than in maintenance activities. Maintenance components ritualized into display are often fairly readily recognizable as what they are, and we can be certain that the component has been displaced from the maintenance activity, not vice versa. It is inconceivable that, for example, preening or feeding movements were evolved as display and then adopted as maintenance movements. With such maintenance activities as nest-building the case is different. It can be argued that the fidgeting with nesting material which occurs in many forms of display is a more or less ritualized displacement from nest-building, or, as Selous maintained in a long series of publications, that nest-building originated from the 'mandibulation' of material during the frenzy of coitus.* The argument is apt to become circular, and *a priori* it is probable that there has been some reciprocity between the two tendencies, that is, that nest-building movements have been displaced and ritualized into display and that the manipulation of material during crises of excitement has become stereotyped into nest-building. I shall confine myself to certain aspects of the problem which deserve attention, not only because they give some insight into the relationship of the displacement principle to the evolution of nest-building but because they also illustrate some characteristics of displacements which are of interest in connexion with the problem of the nature of the drive involved in these movement-patterns.

A number of species, such as the black-tailed godwit, *Limosa limosa*, snipe, waterhen, *Gallinula chloropus*, water rail, *Rallus aquaticus*, little grebe, *Podiceps ruficollis*, red-head duck, *Nyroca americana*, red-throated diver, *Colymbus stellatus* and Montagu's harrier, *Circus pygargus*, add material to the nest when the contents are menaced by rising water, and in some cases the birds succeed in saving the eggs or chicks from destruction. I have seen a black-headed gull persistently carry loads of material to the nest as a spring tide engulfed it. This gull brings material to the nest as a displacement activity when the drive to brood is thwarted (Kirkman, 1937). An osprey, *Pandion haliaëtus*, will do likewise when prevented from brooding (Storer, 1943). Thus whether normal brooding is thwarted by

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* Selous was the first naturalist to realize the interest of displacement activities. He attributed them to 'the law of the interchangeability of energies' (1914).

rising water or the reluctance of the gull's mate to leave the eggs the same nest-building behaviour is elicited, but in the one type of situation the behaviour may have survival value and in the other it has not. This 'secondary' nest-building is, therefore, in one sense a displacement activity and in another the recrudescence of functional behaviour from an earlier phase. Exactly the same is true of the displacement scrape-making of the common tern after its eggs have been removed. A bird unable to brood its eggs where they had been placed on a high sod made a scrape, rolled the eggs into it, and proceeded to incubate (Palmer, 1941). The displacement nest-building of the stickleback is indistinguishable from functional nest-building and can be identified as such only by the circumstances in which it is performed (Tinbergen & van Iersel, 1947). Our interpretation of all such behaviour is apt to be coloured by the extent to which we are able to ascertain that it contributes to functional effectiveness, but we cannot deny the displacement character of secondary nest-building because it happens to be functional. The similarity between this kind of situation and the recrudescence of song and display to which reference has already been made is evident. Such facts illustrate the artificiality of the distinction between autochthonous and allochthonous behaviour.

XIII. THE DISPLACEMENT PRINCIPLE IN RELATION TO NEST LINING

The nest-lining behaviour of some birds, such as the ducks, may have had its origin in displacement activities which became stereotyped because of their efficiency in concealing the eggs and maintaining their warmth. An eider duck, disturbed from the nest, was seen plucking her belly during diversionary display activities (Williamson, 1948*b*). Birds being particularly prone to perform displacement activities when alarmed at the nest, the probability is the greater that the nest-lining impulses of ducks originated as such.

Certain species of love-bird, *Agapornis* spp., pluck their own feathers to add to the nest pad. *Agapornis taranta* not only plucks feathers from the breast and neck for this purpose, but also carries leaves to the nest in its beak or in the plumage of breast, wings or neck (Schütze, 1934; Prestwich, 1947). Other species carry material in the feathers of the rump (Moreau, 1948). Possibly this practice arose as a displacement activity, for a displacement-preening movement in which the head is drawn backwards over the shoulder or towards the wing is very common amongst birds of widely diverse families. Many species also perform displacement activities in which material is thrown over the shoulder. Common terns executing this movement pass material over the wings. In this connexion Palmer

(1941) writes: 'It seems quite obvious that when nesting material is passed along the back or wings, the "symbolic" use of this material has become interwoven with formalized preening. The result is a behavior-pattern used only at the nest.' Such interlacements are found in other movement-patterns, as in the duck displays previously mentioned. These movement-patterns are sufficiently similar to the Agapornids' method of carrying material for it to be a plausible hypothesis, that this technique originated from displacements.

XIV. DISPLACEMENT DIVERSIONARY DISPLAY

Elsewhere I have suggested (1949) that forms of diversionary display are displacement activities and that injury-simulation displays illustrate the integration of displacement-components originally associated with aposematic or epigamic display into distraction display, so the matter need not be discussed here. The fact that injury-simulation display seldom or never suffers displacement to another context supports this hypothesis, as the displacement of ritualized displacement activities is rare.

XV. GENERAL FUNCTION OF THE DISPLACEMENT PRINCIPLE IN EVOLUTION

This necessarily brief survey shows that the displacement principle operates in many different types of bird behaviour, and as, undoubtedly, comparatively elaborate patterns ritualized into a new context may become modified and further elaborated out of all recognition, it is probable that displacements are commoner than can at present be definitely proved. *A fortiori* this would be true of displacements composed of only one or two simple movement-components, such as possibly occur in injury-simulation displays. Whether or not these minor displacements occur, a species which is able to modify its behaviour to suit changed circumstances by means of displacements, rather than by the evolution of *ad hoc* modifications starting from scratch, will have an advantage over other species. Therefore, *ceteris paribus*, a displacement-prone species will be more adaptable, and consequently more successful, than a species not so equipped.

XVI. INFLUENCE OF DISPLACEMENT-MODIFICATIONS ON MORPHOLOGY

When a displacement movement becomes ritualized and acquires a function as a releaser it tends to accentuate a previously existing adornment displayed in the ceremony (Tinbergen, 1940), or it may evolve an adornment proper to itself. Lorenz (1937*b*, 1938) has shown that as the European night-heron, *Nycticorax nycticorax*, and the South American boatbill, *Cochlearius cochlearius*, have similar 'appeasing' ceremonies, although the crest feathers displayed are different in the two species, the presumption is that the ceremony is older than the adornment. In a comparative study of the head coloration and associated movements of nestling Rallidae, Boyd & Alley (1948) reach a similar conclusion. On the whole, movement seems to have the primacy over adornment and often ante-dates the structure or adornment it uses, though there is, of course, reciprocity in their evolution between movement and the adornment involved in it. I have pointed out (1946) that the conspicuous coloration of some of the Laridae, Charadriidae and a number of other groups and species serves the purpose of social signalling, enabling individuals, when they see one or more of their fellows descending to feed, to profit by a rapid realization of, and onslaught upon, a sudden plenitude of the sporadic sources of food on which so many of these birds rely. Coloration must have followed feeding habits. It is highly unlikely that birds took to feeding on sporadic sources of food in order to exploit their conspicuous coloration to best advantage; probably the conspicuous coloration evolved by reason of its effectiveness in facilitating quicker and more efficient communal exploitation of the food supply. If, on the whole, structural adaptation more readily follows movement adaptations than vice versa, there is additional reason to believe that species which are prone to displacement-modifications are likely to have an advantage over competitors not so equipped.

If this conclusion be correct, psychological and ethological factors play an important part in the adaptation of birds, so far as positive adaptation, not merely elimination of the non-adapted, is concerned; therefore, in regard to them, much of the 'directive' appearance of evolution (Russell, 1945) is explicable without recourse to Lamarckism. Moreau (1948) has suggested in his discussion of the nesting habits of Agapornids that the movement-pattern involved in the portage of material in the plumage may be determined by a single recessive genetic factor. Incidentally, there is some evidence that some displacement activities are more characteristic of one sex than the other. Prolonged displacement-preening is more commonly performed by the male than the female common tern (Palmer, 1941), and I have never noticed the peculiar crouching posture characteristic of the male ringed plover when alarmed at the nest adopted by the female.

XVII. DISPLACEMENT COMPONENTS IN HUMAN BEHAVIOUR

Probably displacement activities are commoner in some other groups besides birds than is at present known, but they have reached their highest development in birds. They play a rather less important part in the behaviour of mammals, perhaps due to the tendency in this group for maintenance activities to be more 'smoothly' ritualized into display and signal movements, though, of course, such modification of maintenance activities to serve as display also occurs amongst birds. Amongst some species of fish displacements are important, but so far as is at present known they have a comparatively insignificant role amongst insects. A thwarted solitary wasp, *Bembex rostrata*, when forced to remove pebbles repeatedly from the mouth of its burrow merely buzzed loudly and ran around in a wide arc (Nielsen, 1945). When experimenting with butterflies attracted to pieces of coloured paper Dr D. Ilse noticed movements which might have been displacement activities (personal communication). Possibly one of the factors responsible for the apparently slower speciation of insects than birds (Mayr, 1942) is the greater displacement-proneness of the latter. The high development of the *corpus striatum* in birds may have a bearing on the importance in their behaviour of ritualized movement-patterns and displacement activities.

In man displacement activities occur as learned movements, such as fidgeting with a watch-chain or other object. As scratching occurs as an innate displacement activity amongst apes the human displacement activity of scratching the head when puzzled or bewildered is possibly innate. The 'substitute activities' of children who express thwarted or pent-up energy by vigorous motor activities can be considered modified displacement activities. They take the form of easy, familiar movements and are regarded by psychologists as regressive. Children loosed from the schoolroom as readily perform displacement activities of this kind as apes escaping from the intelligence tests of the psychologist (Köhler, 1927). Domination may evoke such behaviour in children and also in apes (Yerkes, 1943). The gesture of shrugging the shoulders, performed in comparable situations to those which elicit displacement plumage-shaking amongst birds—a transition movement between anxiety and 'dismissal of concern'—is possibly a modification of a like gesture. It need hardly be pointed out that sublimation, in which energy is diverted from one channel to another, has affinities with displacement.

Perhaps the displacement principle is operative in man's behaviour on a yet deeper level. If we are correct in the inference, based on some of the instances of overflow activity cited earlier, that the object may in some measure be internalized or introjected as an image, we have a suggestion as to one of the steps in the evolution of imagination and association in the human mind—by the mental image becoming detached or emancipated from the external object. Thus we may suppose that in man the transmuted object, abetted by the development of language, has achieved greatest independence as idea, drive has become differentiated and, in part, intruded into consciousness, as emotion. Thus there is a similarity in the relationship between idea and emotion, and that which we have noted between object and drive in subhuman organisms.

Freud, who had a psycho-biological outlook, based his early theorizing on a concept of urges very similar to the 'instincts' of nineteenth-century biologists. His 'instincts' are basic psychic urges or drives, rather than the inborn automatisms of current theory. According to his view the ideational content can become separated from the instinct. Writing of hysterical states he commented: 'The ideational content of the instinct-presentation is completely withdrawn from consciousness as a substitute-formation—and concurrently as a symptom we have an excessive innervation (in typical cases a somatic innervation), sometimes of a sensory, sometimes of a motor character, either as an excitation or an inhibition' (1948). This situation resembles what happens during displacement activity. Makkink (1936) has already drawn attention to the similarity between Freud's 'symptom' and the displacement-sleeping which has been recorded of belligerent oystercatchers, avocets and turnstones, also of courting red-necked phalaropes, *Phalaropus lobatus*, possibly common sandpipers, *Actitis hypoleucos*, and great northern divers, *Colymbus immer* (according to my own observation), and also in man (Armstrong, 1947). Research on experimentally induced neuroses in mammals 'suggests similarity to the human situation where difficulties arise under social pressure' (Liddell, 1941), and the objective manifestations of neurosis in sheep and dogs bear considerable similarity to those characteristic of neurotic human beings. When waiting for experiments to begin a neurotic sheep will alternate between trembling in the straps securing it and eating ravenously (Anderson & Parmenter, 1941). This behaviour may be considered displacement-feeding.

Bird displacement activities most closely resemble the symptoms in conversion hysteria. In disorders of this type psycho-biological energy is diverted into an abnormal channel and manifests itself in the symptom, which is often a somatic disturbance, such as a manual or ocular tic. Thus, the affect is excluded from consciousness. In displacement activities and conversion hysteria alike the performance is irrelevant to conative behaviour, but is a somatic means of release from tension; in both the activity is incomplete and apparently detached from normal affective experience. Conversion hysteria is a regression to an earlier, more primitive level; displacement activities are regressions to the extent that they are maintenance forms of behaviour rather than built-up display-patterns transposed to another context, and they are often, as we have seen, the recrudescence of behaviour characteristic of earlier phases of the reproductive cycle.

Further research will reveal whether such similarities between human and animal behaviour are, as I believe, more than analogies. If so, we may be encouraged by the prospect that the explorer of the human mind and the comparative psychologist, starting from very different positions and using different techniques, may yet be found to be pursuing converging paths.

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LEARNING

THE CONCEPTS OF LEARNING AND THEIR RELATION TO THOSE OF INSTINCT

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I. INTRODUCTION

Individual self-preservation by means of accommodation to a changing and unstable environment is one of the most reliable criteria for distinguishing living from non-living. Yet there are few aspects of animal behaviour that have been more neglected by present-day zoologists than learning, which we may provisionally define as that internal process which manifests itself as *adaptive change in individual behaviour as a result of experience*, and which after all is one of the most important methods by which animals, and especially the 'higher' animals, succeed in establishing a 'conservative equilibrium to change of external conditions' (to use Humphrey's phrase). This is not to imply that there is not a great deal of work and interest devoted to the subject of learning—anyone who attempts to review the literature will soon be disabused of any such idea—but it mostly consists either of analysis of the conditioned reflex regarded as the fundamental discrete unit of modifiable behaviour, in which case it is carried out mainly by physiologists, or it consists of a study of the more elaborate behaviour of mammals (predominantly the white rat) by means of the maze and detour technique, in which case it is done chiefly by psychologists, most of whom have been trained primarily in human psychology. Zoologists have a great deal to learn from both these groups of workers, but they should also have much that is essential to contribute, for there has been a tendency in the past for work on this subject to be too exclusively concerned with a few species, studied under highly artificial conditions, ignoring the immense variety and plasticity of behaviour as seen under natural conditions.

One of the main objects of the present conference is to bring together groups of workers who are attacking the same problems from different angles. But before we can take any steps in the direction of that goal it is essential that we as members of different groups learn to speak a common tongue. It seems therefore that the first thing required of a speaker introducing this discussion is to suggest a series of definitions which can at least be used for the immediate practical purpose of discussion, however far off the participants may be from agreeing that the categories used correspond to any fundamental divisions in the enormous range of natural processes included under the general term 'Learning'. Viewed from one standpoint, learning ability appears to show an essential uniformity throughout the animal kingdom, displaying a smooth and gradual course of development from the simplest acellular animals to man himself. Seen from another angle, discontinuities appear. In the development of every science there are periods when it is profitable to emphasize similarities, and other periods when advance comes through distinguishing differences and attempting to formulate them as exactly as possible. Whichever standpoint gives us a truer picture, I believe that the science of comparative ethology is now at the stage when the second alternative is what is required. Accordingly, I shall endeavour to set forth as concisely as possible a tentative classification of the types of learning. I propose then to describe and discuss some recently investigated instances of the more elaborate kinds of learning found among invertebrates, especially the Arthropoda, and to consider their significance in relation to modern views of instinct. In this way it is hoped to relate to-day's discussion with what has gone before and to lead up to the question as to how far the concepts of instinct and learning are antithetical and how far complementary.

II. HABITUATION

To Humphrey (1933) belongs the credit for the first comprehensive discussion of the importance of habituation. In its widest sense habituation is a simple learning *not* to respond to stimuli which tend to be without significance in the life of the organism; a tendency merely to drop out responses. Behaviour of this kind is known in response to all types of stimuli (Thorpe, 1944) and in animals of all grades of organization, including Protozoa, Coelenterates and Echinoderms, and clearly it may illustrate a fundamental property of living matter. Of the anatomical site of habituation in such cases we know next to nothing. In animals with a central nervous system, however, whether or not sensory 'accommodation' or 'fatigue' on the one hand and central nervous system habituation on the other are ultimately expressions of the same fundamental property, it is obviously both interesting and important to distinguish between the relatively transient effects of sensory fatigue and the persistent effects of central habituation. Konorski (1948, pp. 78–9) evidently regards the mechanism of habituation as something absolutely *sui generis* when compared with events taking place in the receptors or in the central nervous system apart from the cortex and subcortex. He does not consider it as even analogous to the fading of spinal reflexes under too frequent repetition or any other form of fatigue. Quite obviously neither functional exhaustion nor a subnormal period can account for the process, and it is a well-established fact that extinction of the orientation reflex takes place the more rapidly with nervous systems which are in good functional condition and where the animal is one of high phylogenetic development. Some of Konorski's other reasons for making such a clear-cut distinction seem to me, however, to be less convincing, and I hope he will find opportunity to elucidate them in the course of discussion. It is clear, then, that for animals at and above the Annelid level we require a more restrictive definition from which peripheral 'adaptation' is excluded. Accordingly, modifying slightly a definition published six years ago (Thorpe, 1943–4), I would like to define habituation as *an activity of the central nervous system whereby innate responses to certain relatively simple stimuli, especially those of potential value as warning of danger, wane as the stimuli continue for a long period without unfavourable results.*

It is natural to regard habituation as the simplest of all our categories of learning, since, ideally at least, it involves stimulation from only one receptor field. The Pavlov school have, of course, studied what is essentially habituation under the term 'Extinction of the orientation reflex'—a term which, now that we understand more clearly the far-reaching importance to all animals of this method of adjustment, is seen to be clumsy, misleading and biologically inadequate and should be dropped. That term, however, receives some justification from work of recent years, for as Konorski (1948, pp. 145–6) makes clear, the processes of habituation and of extinction of the conditioned reflex under internal inhibition show so many similar properties that we seem justified in regarding them as at least analogous: in spite of the fact that habituation was originally regarded as concerning inborn mechanisms of self-preservation (reactions to mild shock and warning stimuli), and thus to be subcortical, whereas internal inhibition is of cortical origin. But as Humphrey (1933, pp. 194–5) has pointed out, the evidence that in the typical process of extinction there is included something more than habituation, is very strong indeed, and it would certainly be unjustifiable to assume them to be in all respects identical. In extinction the effects of sheer repetition are in some way complicated by the fact that repetition is taking place in connexion with a conditioned response.

I have elsewhere (Thorpe, 1944) pointed out the functional relation of habituation to instinctive avoiding reponses to certain releasers indicative of special types of danger such as the recognition of hawks, owls or snakes. Some animals have precise instinctive responses to such dangers—dangers which are so serious and so ubiquitous that an instinctive mechanism is biologically warrantable. Where such instinctive recognition exists it would be dangerous in the extreme for it to fade readily by habituation following temporary absence of attack by the predator, and the evidence (though we require much more) is that it does not. Obviously, if it were otherwise, a bird which had the misfortune on a few occasions to meet a satiated hawk or a sleepy snake would soon be doomed—though there is a good deal of evidence that animals can, either by a learning process or by the precision of the innate releasing mechanism, respond appropriately to the 'mood' of a predator and only flee when hunting behaviour commences (e.g. Hamilton, 1947).

But this instinctive response to a particular species or kind of predator is probably rather rare. Most animals, particularly small or defenceless animals, are subject to a great variety of dangers from many kinds of predator and from other causes, and for them a specific instinctive response to each kind of predator and to any and every danger is out of the question. Therefore, instead of, or in addition to, any specific response, they have an inherent equipment whereby they tend to take avoiding or self-protective action to (1) a wide range of stimuli likely to be signals for danger, especially any moving object; (2) any stimulus or situation which is strange; (3) any stimulus at an unusually high intensity. This mechanism with its wide scope ensures that they are on guard against most of the usual risks of life. But, obviously, sensitiveness to such a wide range of stimuli would, if the response was completely automatic and unvarying in intensity, make life impossible. Hence the need for some form of learning which saves the animal from wasting its energies in responses to stimuli which experience shows to be harmless or of no significance. Habituation exactly meets this need and is well-nigh universal.

The role of habituation has been emphasized in relation to 'negative reactions', i.e. avoiding and fright responses, because it is in this connexion that it must have appeared first in phylogeny, and it is here that its importance is greatest and is most clearly seen. But similar considerations presumably apply to positive reactions, i.e. those which arouse curiosity and presumably have as their ultimate goal the satisfaction of some need, such as the getting of food. In those monophagous or oligophagous animals of specialized feeding habits in which the food-getting behaviour is released by some complex or highly specific situation or set of stimuli, it is inconceivable that habituation could operate to any considerable extent without disastrous results to the animal. With polyphagous animals of generalized feeding habits, on the other hand, the environmental situations which release feeding behaviour are probably very general and non-specific (e.g. the pecking behaviour of a young chick). The animal has to learn from among a great variety of objects which are edible. This process is probably not *only* a matter of associative learning on the trial and error principle, as is usually assumed; on the contrary, there is little doubt that here, in addition to positive association, habituation also plays its negative part, causing objects and situations which fail to give any satisfactory sensation, or any advantage, to be more and more neglected.

III. CONDITIONING

Prof. Konorski has dealt so recently and in such a penetrating and thorough manner with the whole question of the nature of the conditioned reflex that it is quite unnecessary for me to do more than raise one or two points of definition which seem to me to be important, and which I hope he and others will be able to deal with in the discussion which is to follow.

Prof. Konorski includes under the heading *conditioned reflex* two very different phenomena which he calls Type I and Type II. The first of these is the classical conditioned reflex of the Pavlov school. It does not appear itself ever to constitute the whole learning process, at any rate in animals of sufficiently high grade of organization to be capable of directed movements. Rather it represents an artificially isolated part thereof, the appetitive motor behaviour normally associated with the unconditioned stimulus (e.g. the food-seeking behaviour in the alimentary response) having been purposely eliminated by the experimental conditions. As such its study is of immense interest and importance as long as its artificial limitations are kept in mind. How far it can be considered as a unit out of which the more complex learned responses of the whole animal are constructed is, however, another matter, and one which Prof. Konorski will no doubt be discussing with us shortly. In this connexion I think it important to emphasize three points. The first is that the concept of the local or partial reflex as the 'automatic response of a single organ or organ system to a simple stimulus' is an idealized concept which in fact is seldom or never realized in experimental investigation. As Sherrington made abundantly clear, the organism's response is always multiple, involving a large number of receptors, and that far from being independent of one another the responses show a great deal of mutual excitation and inhibition. Secondly, few of the stimuli which evoke even the simplest reflexes are in fact simple; for, however simple the salient feature of the stimulus situation may appear at first sight to be (e.g. the odour of food or a sudden sound), the animal is reacting not to this element alone but to a complex stimulus situation consisting of the element itself differentiated against a complex and changing background. It is of course true that with animals of low grade of receptor organization (e.g. the eye of a Planarian) the stimulus perceived is vastly simpler than that to which a dog or a human being is exposed when, say, the pupillary reflex is being elicited. In the case of the simplest of all orienting reactions, such as photokinesis, such an animal is reacting to change in intensity of stimulus, the adaptation of the sense organ itself being such that its response varies according to its past experience. It has been suggested that there is a slowly changing photochemical equilibrium in the eye which provides the animal with the rudimentary form of memory required for the reaction. But even so it is better for all purposes to omit the word 'simple' from our definition. Thirdly, there seems to be no escaping the fact that the conditioned reflex is essentially 'anticipatory' in nature (cf. Zener, 1937). This being so it cannot very well be regarded as an essentially simple physiological mechanism; for whether or not we consider the 'stimulus-trace' concepts of Hull (1937) and Guthrie (1935) as successful in overcoming this difficulty, we certainly cannot regard them as 'simple'. Since the unconditioned stimulus-response system, on which the classical conditioned reflex formation is based is usually an inborn or instinctive response, we may well recall the penetrating remark of Sherrington who speaks (1906) of 'Instinct with its germ of anticipation'.

IV. TRIAL AND ERROR LEARNING

'Conditioned Reflex Type II', however, is an entirely different matter from the classical conditioned reflex; so different that Prof. Konorski himself admits (and I agree with him) that these reflexes represent a separate kind of plasticity and thus do not come within the scheme of the Pavlovian conditioned reflexes at all. This being so, I suggest that it is quite misleading to use the term 'conditioned reflex' and that another must be found. What then are the characteristics which distinguish 'Type II' from 'Type I'? As I see it the essential differences are as follows: Type I consists essentially in connecting a stimulus (often an indifferent stimulus) with a new response which was originally the inborn or habitual response to the reward or reinforcement, associating the stimulus and the reward in time in such a manner that the stimulus terminates either immediately before the commencement of the reward, or if they overlap, well before the latter's termination. In Type II, however, the response is an independent voluntary somatic action and not originally connected necessarily with the reward, and both stimulus and response precede the reward in time. In this type of conditioning the stimulus thus becomes firmly connected to the response as the result of a kind of retroactive influence exerted by the reward. In addition to these differences Konorski & Miller (1937*a*, *b*) point out that whereas the classical conditioned reflex is always of the same pattern irrespective of the unconditioned reflex which serves for reinforcement, in the Type II reflexes the pattern of the reflex depends on whether the reinforcement is positive or negative, i.e. a 'reward' or a 'punishment'. In the former the response is the movement (e.g. leg withdrawal) provoked, in the latter it is the corresponding antagonistic movement. There is now plenty of evidence for subcortical conditioning, and it is very significant that Culler & Mettler (1934) have shown with decorticate dogs that while classical conditioned-reflex formation can be achieved the formation of Type II conditioned reflex is impossible. Similarly, Girden & Culler (1937) found that even under complete curare paralysis, which is assumed to inhibit cortical functions completely, reflex twitches of skeletal muscle can still be conditioned. Moreover (Konorski, 1948), in dogs the pyramidal system seems to be a necessity for the formation of Type II reflexes, and it is supposed that it is this feature which gives to the motor activity of the process its characteristic of 'voluntary activity'. Finally, there is the extraordinary efficacy of 'partial reinforcement' in the case of Type II. Thus Skinner (1938, p. 288) has succeeded in establishing a Type II conditioned reflex in the rat when only one in every 192 responses was reinforced—a phenomenon surely without parallel in classical conditioning, but recalling at once the persistence and relative fixity of what we ordinarily call habit formation. As Hilgard & Marquis (1940, p. 152) point out, such instances illustrate very strikingly the distinctions between the two types and the difficulty involved in bridging the gap between them. When we turn over all these differences in our minds we see at once that what we are speaking of as conditioned reflex Type II is none other than our very old friend 'Trial and Error Learning' in its simplest form, as demonstrated in the well-known experiments of Grindley (1932) on guinea-pigs. 'Trial and Error' was a term first used in animal psychology by C. Lloyd Morgan in 1894, and brought into general use by Thorndike in 1898. Thus the term from the beginning had a well-defined meaning which was made fully precise in relation to Pavlovian conditioning by the work of Grindley above referred to. 'Trial and Error Learning' has thus undisputed priority and is fully precise. 'Habit formation', which is sometimes used as a synonym, is quite vague, and in any common usage must include any and every method of acquiring automatisms. The term 'Instrumental Conditioning' recently coined by Hilgard & Marquis (1940) is obscure and misleading, and, as we have seen, the term 'Conditioned Reflex Type II' is not only cumbersome but, what is much more serious, obscures just that fundamental distinction which it is most important to emphasize. No term is perfect, and some objections can no doubt be raised against 'Trial and Error', but it seems to me that they are trivial compared with those which can be offered to the various alternatives, and that unless and until it is agreed to abandon vernacular terms altogether in favour of specially coined terms of classical origin, we cannot do better than adhere to 'Trial and Error'. *Accordingly I propose that:* (*a*) *Conditioning be retained to denote the classical conditioned reflex formation of Pavlov* and that (*b*) *Trial and Error be used instead of Conditioned Reflex Type II.*

It has already been made clear (e.g. Thorpe, 1943–4; Hull, 1934; Konorski, 1948) what widely different grades of performance in animal learning can be accounted for, at least theoretically, in terms of habituation combined with simple associative learning—performances including even the learning of quite complex maze paths. But there are many performances of animals, even among invertebrates, which suggest the existence of a higher grade of learning than trial and error. These we will now consider.

V. INSIGHT AND INSIGHT LEARNING

In attempting to outline a working set of categories of learning the next problem that arises is that of insight. In this matter it is, I believe, vitally important to make a clear distinction between insight itself and insight learning. As a practical and convenient definition I consider insight to mean *the apprehension of relations*, and insight learning is, I suggest, *the sudden adaptive reorganization of experience or the sudden production of a new adaptive response not arrived at by random trial behaviour*, this being a slight modification of a definition proposed some years ago (Thorpe, 1943–4, p. 223). Thus insight learning seems to be a kind of action by hypothesis and has often been held to be evidence of ideational processes. The concept of insight has been the subject of experiment and debate among psychologists ever since the term was brought into use by Köhler (1921), and there seems as yet no prospect of a generally agreed conclusion, though substantial progress has undoubtedly been made. Much of this discussion has centred round the question whether trial and error learning and insight learning are two fundamentally different processes, and if not which of the two reveals more clearly the fundamental nature of the learning process. Here, it seems to me, the discussion has suffered from two defects. First, it has not been sufficiently recognized among psychologists how closely bound up with form vision and spatial representation is the *traditional* concept of insight. Second, the neglect of the study of invertebrate behaviour has given the impression that insight learning is a characteristically human faculty hardly to be expected in a subprimate mammal and of course out of the question in an Arthropod (see Yerkes, 1943, p. 169). Facts given below will show, I hope, what an astonishing misconception this is.

With regard to the first point, it is no accident that the first champions of the concept of insight were the gestalt psychologists whose whole position and outlook is based upon the work of Wertheimer (1912) on visual perception of movement. We have only to ask ourselves the question 'What is the equivalent of insight among the non-visual and non-proficient senses?' to see at once how primarily visual, how completely bound up with spatial representation and cortical mapping, is this idea. What becomes of the concept if applied, let us say, to olfactory sensations? At first sight, because of the traditional restriction of the word to visual situations the suggestion that it might be applied to olfaction seems merely ridiculous, and it is significant that of the 700 pages of Koffka's *Principles of Gestalt Psychology* barely more than one page is devoted to non-visual senses. Yet is not insight merely the counterpart in form vision of that power of generalization which now seems to be characteristic, in some degree at least, of all perceptions?* If this idea is kept in mind, I believe that the phenomenon of insight is seen to be much more readily linked up with perception as a whole. And if, as seems to be the case, the response to even the simplest external stimulus is in fact based upon perception of relations in the sensory field—then insight is nothing more nor less than the very essence of form perception and has its counterpart in all other sensory fields. We thus see that the distinction between trial and error learning and insight learning, while practically convenient, is not in fact a fundamental one. The immense amount of discussion over this issue which has taken place between the 'association' psychologists (typified by Hull & Guthrie) on the one hand, and the exponents of gestalt and other field theories on the other, appears to me to be based on what we now see to be a misapprehension. The assumption that trial and error learning is strictly associational in the sense of Thorndike's 'law of effect' which, it was assumed, might imply a simple mechanism of reinforcement based on current physiological concepts can, it seems to me, no longer be maintained. Not only is expectancy or anticipation characteristic of classical conditioning, but, in addition, the attempts to explain latent learning (see below) and even other far simpler performances shown by rats in mazes, in terms of trial and error, show how far removed from strict associationism trial and error theories now are. From the very voluminous literature one may mention three quite recent papers which reveal some of the apparently insuperable difficulties which latent learning of the maze offers for association theory (Buxton, 1946; Karn & Porter, 1946; Meehl & MacCorquodale, 1948). While I greatly admire Hull's efforts to overcome difficulties which even the simplest maze-running performance creates, and readily admit that they have had valuable experimental results, I believe that some of the supplementary theories he finds necessary only serve to show how impossible it is to maintain any

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* It must be emphasized that the term 'perception' as used here does not necessarily imply and is not intended to imply consciousness.

strict association theory. Thus the concepts of 'habit family hierarchy' and of 'fractional anticipatory goal reactions' appear to be essentially as far removed from strict associationism as any tenet of Tolman's or other exponent of field theories; and it seems as if (Hilgard & Marquis, 1940, p. 254) Hull himself has gone some way towards admitting this. In my view the work of recent years has on the whole confirmed the conclusions of Adams (1931) that all learning is in some degree the manifestation of a process basically identical with insight. According to him trial and error is merely a means whereby the experimenter measures the rate of the learning process; if learning is slow, we call it trial and error, if rapid, we call it insight. In the latter case the rate is sufficiently rapid to enable us to see the true nature of the learning process of which it is an extreme instance.

Perhaps the arguments as to whether certain performances of rats in mazes represent insight or trial and error learning would have been somewhat less prolonged if the abilities of some of the 'lower animals' such as insects had been known, and it may be helpful to describe and discuss them here. But first we must consider another type of learning—latent learning—which bears very closely on the subject.

Latent learning was a term coined by Blodgett (1929) to denote learning without patent reward; as when a group of rats which have had *unrewarded* experience of a maze for 10 successive days are, on the eleventh day, presented with food in the food box and immediately show a very striking decrease both in errors and times of running as compared with a control group which has not had that previous experience. The introduction of the reward thus makes *patent* that learning of the maze which had been taking place throughout the 10 days without reward or reinforcement but which had perforce to remain *latent* until reward was provided. Moreover, the fully trained animal, once it has found food in one part of the maze can then go direct to that point from any other part of the maze in which it is placed. The difficulties of interpreting such a performance in terms of association theory have been mentioned above, and Maier & Schneirla (1935, pp. 404–6) equate latent learning with insight learning. I have previously argued (Thorpe, 1943–4) that latent learning does not *necessarily* involve insight learning in that the situation provided by the provision of a reward is not essentially a new one, but I am now of the opinion that this was a mistake, and that since the performance does undoubtedly involve simultaneous integration and reorganization of previous experience the distinction is not valid. I now therefore agree with Maier & Schneirla. However, even if we take this position and, moreover, admit that the term 'latent learning' is an unsatisfactory one in that it stresses a particular aspect of the performance which is peculiarly dependent on the artificial conditions of the experiment, there is no doubt that the latent learning experiments and the controversy which followed have fulfilled valuable functions. These experiments have not only provided something of a transition between what were thought previously to be the mutually exclusive concepts of trial and error learning and insight learning; they have also drawn attention to important capabilities of animals in the field. Thus it has been pointed out (Thorpe, 1944) that latent learning, involving as it does 'delayed response' and 'transfer of training', is essentially characteristic of animals which tend to explore their environment without the satisfaction of any immediate reward, but by their exploration secure information which may afterwards be of use to them in a number of contexts, for example, in food getting, in escape from enemies, or in finding their way home to a nest or territory. In other words, latent learning is really *exploratory learning*, and in saying that we are implying that animals which show it are on a relatively high behavioural level. Thus latent learning is the laboratory version of what is probably characteristic of all animals which show complex homing behaviour.

VI. INSIGHT LEARNING IN INVERTEBRATES

It is highly probable that exploratory learning of this kind is involved in the territorial orientation of the dragon flies Odonata with their highly developed compound eyes,* and something very similar to it has been shown experimentally to occur in a parasitic Ichneumonid, *Nemeritis canesceus* (Thorpe, 1938, 1943–4). That it occurs among many of those higher Hymenoptera (Sphegidae, Pompilidae, Vespidae, Apidae, etc.), where there is a more or less well-defined foraging area and the need to return at regular intervals to a particular nest, can now hardly be doubted. The beautiful experimental work of Baerends (1941) has shown the behaviour of the hunting wasp, *Ammophila pubescens*, to be of extraordinary complexity. The female, which digs and provisions a burrow in three stages lasting over several days with intervals in between, may have as many as three different nests under construction at one and the same time, each in a different stage of completion. Besides provisioning visits, on which she brings a paralysed caterpillar to add to the store of food for her offspring, she pays occasional visits during which no prey is brought, the function of which visits is to determine whether or not the egg has yet hatched. The further provisioning of the nest depends on what the wasp finds on this inspection visit, and thus

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* It is worth noting that compound eyes are not essential to form sight in Arthropods, but that rudimentary form sight may be achieved by means of groups of a few simple stemmata (as in lepidopterous larvae), provided that the animal performs appropriate rotary and to and fro movements of the head (Dethier, 1942, 1943).

this single experience may regulate the behaviour of the wasp for the following 24 hr. or more. Baerends' work has also shown the extraordinary ability these insects possess of learning the detailed topography of their territories and I have been able in this same species to demonstrate detour behaviour closely comparable to that which is taken as evidence of insight in the classical experiments on the subject. Thus females of *Ammophila pubescens* (Thorpe, 1949*b*), when dragging their prey towards the nest (a journey that may be as much as 150 ft. or more), will repeatedly detour around a curved metal screen, 4 ft. long and 18 in. high, placed in front of them at a distance of 3 ft. This is not simply avoidance of an area of deep shade, for the performance will take place irrespective of the direction of the sun. No one who has experimented with these insects can fail to be astonished at the appearance which they present of possessing a highly detailed knowledge of the general area around their nests. When in possession of prey they can easily be picked up and transferred in a dark box to another place, 100 ft. or more away. Yet when released they will seldom show any signs of disorientation, but will immediately set out on and maintain a true course irrespective of the innumerable obstacles on the stony heaths on which they live, and arrive without hesitation at a closed nest burrow, the entrance to which is so well camouflaged that the human eye finds it impossible to detect unaided—or even to remember when shown unless deliberate note of the position has been taken by means of intersecting sight lines on conspicuous landmarks. The use of such landmarks for direction finding has been the subject of detailed study in the wasp *Philanthus triangulum* by Tinbergen & Kruyt (1938) and van Busekom (1948). It seems difficult from such work to avoid the conclusion that there is a *fundamental* similarity between such behaviour in insects and our own use of landmarks for finding our way about. When we consider the inferiority of even the best compound eyes of Arthropods to the eyes of mammals and birds it is difficult to regard such insects as inferior to those groups in their ability to correlate and co-ordinate their visual and other impressions for purposes of orientation. That such a performance is possible for the insect brain does, indeed, provide a problem for the neurologist, for the insect brain has, of course, nothing corresponding to the highly convoluted cortex of mammals. There is good reason to think that latent learning or exploratory learning must be a major factor in the orientation of birds (Thorpe, 1943–4, 1944), but they have been omitted from discussion here because they have not so far been the subject of detailed experimental investigation. A summary of the present state of knowledge of the learning abilities of birds is in course of preparation (Thorpe, 1950).

But the insight learning ability of insects does not even end here, as all who have read the recent papers of that very eminent zoologist, Karl von Frisch (1946, 1947, 1948) on the hive bee will at once realize. He has shown that the 'waggle dance' performed by the foraging worker on her return after discovery of a rich source of food is, in fact, a method indicating both the distance and the direction of the food source to the other workers. The speed of the waggle dance is inversely proportional to the distance of the food source, and gives an accurate indication of this to the other bees in the hive, while the direction of the straight part of the dance (the 'waggle run') indicates the direction of the food source with an extraordinary degree of accuracy. When the dance is performed on a horizontal surface in the daylight the 'waggle run' of the dance gives an absolute indication of the direction of the food source. But these conditions are exceptional, and the dance is normally performed on the vertical comb in the darkness of the hive, when, of course, absolute indication of direction is impossible. Under these circumstances the waggle run of the dance indicates not the absolute direction but the direction of the food source relative to the direction of the sun, the direction vertically upward on the comb always representing the position of the sun. 'Thus a waggle dance upwards indicates that the food source lies in the direction of the sun. A waggle dance downwards indicates a feeding place in the opposite direction. A waggle dance to the right means that the food source is to be found to the right of the sun, and at such an angle to the right by which the waggle dance deviates from the vertical. A waggle dance to the left indicates a feeding place at a corresponding angle to the left of the position of the sun' (von Frisch, 1947, p. 31). *In other words, this performance of the worker hive bee is nothing more or less than elementary map making and map reading, a symbolic activity in which the direction of action of gravity is symbolic of the direction of incidence of the sun's rays.* We are forced to ask ourselves whether, apart from human faculties, there is anything comparable to this behaviour in the animal kingdom? Still more remarkable is the fact that if the foraging bee is forced by an obstacle such as high rocks or steep mountain walls to make a detour in order to reach a food source, the direction indicated by the dance is the true straight line direction over the obstacle, while the distance indicated is that actually flown around the detour. Von Frisch's work leads to a conclusion apparently so revolutionary that I am much indebted to him for his kindness in arranging for me to perform a number of the crucial experiments with him at the University of Graz Experimental Station at St Gilgen near Salzburg last summer, and thus confirm for myself some of these astonishing results (Thorpe 1949*a*). Speculation upon this work is in some ways premature; for we as yet know little about the development of this extraordinary faculty in the life of the individual. Such hypotheses as present knowledge justifies our making will be considered below in connexion with another type of learning, namely, imprinting.

VII. THE NATURE OF INSIGHT AND ITS ROLE IN LEARNING

But before we can come to imprinting, some further consideration must be given to the intrinsic nature and role of insight as distinct from insight learning.

If we grant that something of the nature of insight is at the very basis of the perception of relations and is therefore involved in the very act of recognition itself (for probably all the external stimuli to which higher metazoan sense organs react are in some degree patterned (for odour see Adrian, 1947*b*))—what then becomes of the distinction between inborn and acquired responses? Have we not thereby abolished the distinction between instinct and learning? Not, I think, if viewed in the right light. We must, I think, in view of present knowledge of the mechanism of nerve action, regard all animals as having in some perhaps infinitesimal measure at least one, probably two, elementary inborn faculties inherent in the very nature of behaviour—perception of temporal and spatial relations* at the base of all receptor activity and all responses. If Adrian's (1947) conjecture ultimately turns out to be correct, it may be possible one day to express both of these in terms of one fundamental activity of nervous tissue, whether central or peripheral, namely, temporal adaptation; though that day seems so far away as to be hardly worth worrying about just now. Looked at in this way the difference between inborn and acquired behaviour is simply one of degrees of rigidity and plasticity, both in perception and response. Thus the striking work of Hebb (1937) on the behaviour of rats reared to maturity in complete darkness when using their eyes for the first time, suggests that for at least some animals with binocular vision, depth perception, figure background relation and elementary form sight are inborn, and the animal can, as soon as its organs are functional and on its very first experience of visual sensations, cope with spatial phenomena (see also Woodworth, 1938, chap. 26).† Moreover, they persist in the rat (Hebb, 1938) after total destruction of the striate cortex, from which it seems that they must be as primitive as discrimination itself. Similarly with colour and brightness constancy in birds and mammals the work of both Köhler & Katz (see Katz, 1937, p. 75) indicates that the ability is inborn. But individual learning alone, coupled with the inborn faculties of depth perception and constancy

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* Or, as McDougall would say, 'insight' and 'foresight'.

† Woodworth (1938, pp. 674, 680) comes to the conclusion, after detailed discussion of experiments, that perception of distance is primarily a matter of visual, not oculo-kinaesthetic, cues.

relation will not, for an animal of very limited brain size, be a very efficient means of ordering life in the complex world in which it must survive. Accordingly, the more that responses to oft-recurring stimuli and situations can be stereotyped, the more the limited neural equipment for plasticity can be reserved for situations where it is indispensable. This is done by specializing the innate perceptory mechanism so as to provide inborn mechanisms for immediate recognition of more specialized stimuli which are unlikely to be encountered except in the appropriate biological situation, namely, sign-stimuli and releasers (specific odours or sounds, forms or colour patterns or movements characteristic of the species partner or the prey). Concomitantly we have the development of increasingly specialized moods and behaviour patterns associated therewith to form kineses, taxes and instincts. It is hard to avoid the conclusion that this elemental form of insight inherent in all perception, this primary learning ability, is in some way the primary *drive* of the animal itself. Indeed, a very similar view, namely, that an animal is *primarily* something which perceives, has been developed by Agar (1943), backed by a wide zoological and philosophical knowledge. This primitive conative faculty of insight inherent then in the very nature of perception of pattern has developed in two directions. On the one hand, in the less specialized conative form of mood and drive it has developed its learning powers capable, on both the receptor and effector sides, of coping with an increasingly wide variety of situations expressing itself in the well-known categories of learning that we have been discussing. On the other hand, it has become, so to speak, canalized and specialized on both the receptor and effector side to produce stereotyped instinctive behaviour where little is left of the original learning element except that which is involved in the recognition of a few particular patterns of environmental stimulation and in the perfection of certain specialized combinations of movement. In doing so it appears to have travelled as far in the direction of innate recognition of complex visual pattern as it has been possible for the hereditary mechanism to transmit, the animal showing a hereditary bias to recognize one kind of pattern rather than another.* It seems from much of the work of Lorenz

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* This is not, of course, to deny that many examples of complex instinctive behaviour may have been brought about by selection of random germinal variations controlling behaviour. Obviously in many cases it must have been so. What I am pointing out here is the fact that over and above the ability to recognize temporal (and in perhaps all but the very lowest animals spatial) relations animals are also endowed in varying degrees with the ability to learn and to act. This ability to learn may be largely unspecialized so that, within the limits set by its bodily structure, relatively very wide possibilities, both of perception and action lie open to it. Or it may be so specialized and restricted that only certain patterns, out of the many that its sense organs must be capable of registering, can be recognized and attended to, and learning can only proceed in certain restricted directions. Similarly, out of the many possible actions which appear mechanically feasible for it, only certain ones can be performed and improved by practice in certain directions only.

and others on bird behaviour that if it is biologically essential for the recognition of a species pattern to be entirely inborn, then the pattern to be recognized must be kept relatively simple or the hereditary mechanism will be unable to cope with its transmission. At the same time, of course, it must be sufficiently complex to ensure that there is little chance of the behaviour patterns concerned being set off in the biologically wrong situation. So the pattern (for instance, the specific plumage pattern of the male) must be a compromise between two conflicting requirements—simplicity and improbability. It follows that we must expect there to be innumerable examples among birds and other animals of intermediate situations where hereditary recognition can cope with the situation in part only, thus providing a more or less well-developed *tendency* to recognize a given pattern (form, colour or movement or sound) of stimulation, leaving the details to be filled in and the recognition process to be completed by individual learning. In such a situation the ordinary methods of learning may be inadequate, and it is not perhaps surprising that we do in fact find a very special type of learning occurring in just such situations. This is called *imprinting* by Lorenz (1935, 1937).

VIII. IMPRINTING

The first observations on this subject were those of Heinroth (1911), who found that young geese reared in isolation from the egg react to their human keepers (or to the first relatively large moving object that they see) by following them as they would their parents. This need happen for only a few hours (possibly only for a few minutes in some cases (Lorenz)) for the young bird to accept a human as its proper associate and to retain for the rest of its life a tendency to take to human beings as the parent companion, the fellow-member of the species to which later the sexual behaviour will become attached. At this early stage the attachment is not to an individual human (though that will often come with longer association) but to 'humans'. Geese probably show this behaviour in its most extreme form, but it appears from the work of Heinroth, Lorenz and others that imprinting is peculiar in the following respects:

(1) The process is confined to a very definite and very brief period of the individual life, and possibly also to a particular set of environmental circumstances.

(2) Once accomplished the process is very stable—in some cases perhaps totally irreversible.

(3) It is often completed long before the various specific reactions to which the imprinted pattern will ultimately become linked are established.

(4) It is supra-individual learning—a learning of the broad characteristics of the *species*—for if this were not so and the bird at this stage learnt (as it can easily do later) the individual characteristics of its companion, the biological effect would be frustrated.

Imprinting of various degrees of intensity is now known to occur in many birds (Portielje, 1921; Bierens de Haan, 1926; Goodwin, 1948), in fishes (Seitz, 1940–2), and something similar is apparent in insects (see Thorpe, 1944). Probably the process of acquiring the song by example from the parents, which the Heinroths (1924–33) and others have shown to be taking place in so many birds, and which may be brought about (as in nightingale and blackcap song) by an exposure for 1 week only, 6 or 8 months before, is also of this nature. Baerends & Baerends (1949), confirming the earlier work of Noble & Curtis, have shown that the parent Cichlid fish may become imprinted to the young as well as the young to the parent, and Lorenz notes that a young jackdaw may become imprinted to a human if kept away from its own kind, but not if in a flock of more than two or three. But as yet it is only the fringes of the subject that have been touched, and there is not a single instance of imprinting which has been adequately investigated. While it is clear that imprinting does not fit neatly into any of the categories of learning already discussed, it seems to have some affinities with both habituation and insight learning. Moreover, if it is permissible, as I have suggested elsewhere (Thorpe, 1944), to extend the concept to cover the possibility of attachment not to a fellow-member of the species but to the type of immediate environment first perceived by a newly emerged organism so that this becomes the future breeding quarters of the individual, then there are also obvious affinities with exploratory learning. But the extreme interest of imprinting lies above all in the fact that its study seems to be more promising than that of any other kind of learning for the understanding of the nature of the perceptual side of instinct and its relationship to plastic processes in general. It needs and would repay full and precise experimental investigation more almost than any other aspect of animal behaviour. If we are right in considering instinctive recognition of patterned stimuli as representing a special stereotyped form of the more fundamental organizing activity at the base of all perception tending to build up and respond to more and more complex 'gestalts'—then in imprinting we seem to see in ontogeny just that process of complex form recognition and organization which has taken place in phylogeny. Thus, where the innate powers of recognition can only carry the animal a part of the way towards its goal, the process is completed and adjusted by a tendency to attend to certain aspects of a situation and learn in certain restricted times and directions (as in the tendency of a bird to learn and copy the song of its own species in preference to the song of another) so that experience completes for the individual the process commenced for him by his inherited constitution.

IX. METHODS OF BEE COMMUNICATION IN THE LIGHT OF IMPRINTING

Possibly this concept of a tendency to learn in certain directions and in certain situations only can now take us a little way in accounting for the astonishing results of von Frisch described above. The difficulties are enormous, but several points already seem clear enough.

(1) The main orienting stimulus outside the hive is the direction of the sun as perceived by the compound eyes.

(2) The main orienting stimulus inside the hive is the pull of gravity on the body presumably perceived by the proprioceptive sense organs at the limb articulations.

(3) There must be an inherent instinctive association of these two stimuli so that one replaces the other, according to whether the bee is inside or outside the hive. (If there is, as seems likely, an inherent tendency among young foraging bees to fly, other things being equal, in the direction of the sun rather than away from it, then we can see how it might be that since the abdomen is the heaviest part of the body, gravity will tend to make the bee on the comb face upwards, and so the upward, rather than the downward direction will 'stand for' the direction of the sun.)

(4) There must be an inherited recognition of the characteristic movement pattern of the waggle run as equivalent inside the hive to the activity of the foraging flight outside it.

These are big assumptions, but they seem to me to be the minimum ones required in any attempt to solve this problem; for the opportunities which the individual bee can have for perfecting, still less for learning, this astonishing behaviour appear inadequate in the extreme. Thus, although correct *perception* and *interpretation* of the dance is undoubtedly rewarded by finding the food source, the time available to the short-lived worker bee for improving such an elaborate performance by practice seems hopelessly short. Moreover, even if interpretation of the dance is rewarded, *correct performance* can hardly be so—unless, indeed, companionship of other bees at the feeding place is itself an adequate reward for such sociable creatures! Faced with such a problem all theories seem as yet trivial.

X. IMITATION

There remains the whole question of *imitation* which requires much more intensive and critical work than it has received. Much so-called 'imitation' among animals is either social facilitation or local enhancement and probably need not involve any high form of insight learning. Nor, for reasons which need not now be discussed, is there any necessary reason for regarding the vocal imitation of birds as above the trial-and-error level. True imitation in the sense of the copying of a novel or otherwise improbable act, some act for which there is clearly no instinctive tendency, is another matter in that it seems to involve self-consciousness and realization of another individual as resembling oneself. Such true visual imitation has been searched for in chimpanzees by Yerkes (1943) with uncertain results, and I do not find this author quite clear on the point (see p. 142). For the present, then, I do not think we can regard it as firmly established even in the apes. There are a few records suggestive of it in birds (Porter, 1921; Lorenz, 1935; Morley, 1942; Swynnerton, 1942), but none of these cases has been adequately investigated, and Lorenz (1935) suggests that flocking birds (e.g. Corvidae) tend to follow as leaders those individuals which show the most direct, determined and purposive behaviour—namely, the older and more experienced members of the flock.

XI. SUMMARY

Thus, omitting true imitation, as not yet demonstrated in animals, we arrive at five grades of the animal learning process which seem to me to have sufficient distinctness to have practical utility in classification, description and investigation. They are: (1) *Habituation*; (2) *Conditioning*; (3) *Trial and error*; (4) *Insight learning*; (5) *Imprinting*. Probably all of them can be found in one form or another among the insects. Of these the first three appear to show tangible differences from one another. No. 4 is a rapid form of learning which shows in a particularly clear manner something of the true nature of the process which is the basis of the other types. Its separation from no. 3 is possibly a question of degree and convenience rather than of kind. It is suggested that something conative and of the fundamental nature of learning is inherent in the very perception of all patterned stimuli, since the very recognition of pattern involves comparison usually in both time and space. This comparison, which may be either peripheral or central, is by definition a process essentially equivalent to insight though, of course, it is not thought of as necessarily involving any consciousness. Learning involved in perception must therefore be phylogenetically prior to anything which could be classified as instinct and must indeed be an essential component, on the perceptory side at least, of even the most rigid instinct. Thus the two concepts are very closely connected, and it is particularly from the intensive study of the at present rather anomalous form of learning known as *imprinting* that we may expect further light on the relation between fixity and plasticity in behaviour. It may be that the tendency to perceive one pattern in preference to others and the tendency to learn in one direction rather than another are in the last resort the same thing.

I am much indebted to Dr J. H. Woodger for a critical reading of the proof of this article which led to several improvements in consistency of definition.

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MECHANISMS OF LEARNING

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I. INTRODUCTION

Before we proceed to the main topic of this paper it will be useful precisely to determine the scope of problems we shall deal with and the method of their analysis.

First and foremost let us explain the concept of learning. It seems that according to the intentions of the organizers of this symposium learning is to be understood in its broadest sense, including, among others, the simple Pavlovian conditioning. Although we shall show later that perhaps it would be better to restrict somewhat this term and to apply it only to those phenomena which are *commonly* called learning, we shall give here a general definition embracing all the phenomena with which we shall be concerned.

*By learning we shall denote a process leading to the lasting changes in the manner in which an organism reacts to a stimulus which are due to the application of this stimulus in definite combinations with other stimuli,** *and which are not caused by any destructive effects which the applied stimulus might produce.* Such changes we shall also call *plastic changes*, and the property of the system responsible for their formation *plasticity*.

This definition requires some comments. The first concerns the term 'stimulus'. By this term we shall understand any compound of agents acting on the receptive parts of the nervous system (i.e. on receptors, afferent pathways, or directly on nervous centres) and evoking their excitation. Thus the direct stimulation of dorsal roots or of a sensory area of the cortex *is* a stimulus, while the direct stimulation of the motor cortex or of ventral roots will not be called a stimulus within the above meaning. We shall see later that the term stimulus defined in this manner is perfectly adequate for the description of the various forms of learning discussed in this paper.

Further, the lasting character of plastic changes needs some comment. The point is that in many cases the repetition of a stimulus may lead to such a change in the manner in which an organism reacts to that stimulus which is only transitory. As examples may serve: a diminution of the magnitude of a conditioned alimentary reflex in successive trials as the animal grows more and more satiated; an increase of defensive conditioned reflexes in

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* The application of a stimulus alone is also considered as a definite combination.

successive trials due to facilitation; an increase of a motor reaction elicited by direct stimulation of the motor cortex at brief intervals, etc. Such changes are generally based on transitory alterations in the excitability of corresponding centres and, as we assume, they have nothing in common with the learning process. On the other hand, it can be proved that the changes occurring in 'genuine' learning are always lasting. Indeed, if a combination of stimuli (leading to some particular plastic change) is applied even at very long intervals, after a sufficiently great number of trials the change in an animal's reaction will become manifest, which means that previous trials *were* effective in its formation. Similarly, if after the establishment of a definite plastic change the training has been discontinued for a long time and the animal seems to have fully forgotten what it had been taught, it can be proved that the reversibility of the process was only apparent, as the second training necessary for the re-establishment of the plastic change will be shorter than the first.

Finally, the non-destructive character of the applied stimuli must be explained. It is clear that if a stimulus has a destructive effect, the way in which an organism reacts to such a stimulus will change on its repetitive applications, and this change may be, in dependence on the degree of damage, more or less lasting. The most common example of this kind of change is the fatiguability of nervous centres as a result of their repetitive stimulation. In this case the change in the animal's response is usually transitory. On the other hand, if the applied stimulus is a drug (e.g. morphia), the progressive destruction of the stimulated centres may be permanent. Although there are cases in which it is difficult to say whether the given change of animal's reaction arose owing to the true learning process or to such a 'pseudolearning' caused by damage, we think that these two processes must be clearly distinguished.

While accepting this rather wide definition of learning, we must, however, point out that only a small group of phenomena included within it will be discussed in this paper. First, we shall be concerned only with the simplest types of learning, and secondly, we shall trace them only in higher animals.

We pass now to the second term which requires explanation, viz. the term 'mechanism'. It must be stressed that we shall be concerned here only with the *physiological* mechanism of learning. Such a viewpoint is rather unpopular among psychologists concerned with those problems. Although psychologists, especially in America, make abundant use of the Pavlovian conditioned reflex, they tend to deal only with its behaviouristic content, and usually they reject *in toto* Pavlov's physiological theory, regarding it as a needless speculation.

Undoubtedly the reluctance to accept Pavlov's theory is partly due to its unintelligibility and to defects which have often been emphasized and criticized. But it would seem that the inadequacy of Pavlov's theory does not mean that the physiological approach to the learning processes is in itself unsound or impossible. On the contrary, we think that in the study of conditioned reflexes, just as in the study of innate reflexes, the description of their properties and interactions is not the aim of the investigations, but rather a method by which to understand their central mechanisms; in other words, we think that the hypothetical central mechanisms with which we operate here play the same role as the structural formulae in biochemistry, i.e. that of systematizing, integrating and controlling experimental work.

In my recent monograph (Konorski, 1948) I have made an attempt to present the main data of the physiology of higher nervous activity in a form more intelligible to the contemporary neurophysiologist, and thus to bridge the gap between physiologies of the lower and the higher nervous functions. In the present paper, basing myself partly on the evidence given in that book, I shall try to separate and to define different types of learning, to present their chief properties, and to discuss some problems connected with their structure.

II. MODIFIABILITY OF UNCONDITIONED REFLEXES

One must assume that the simplest form of a plastic change should be the modifiability of innate reflexes due to the mere repetition of the corresponding stimuli. Unfortunately, this type of plastic change is as yet very poorly investigated, and therefore we can give here only fragmentary evidence which may serve as its illustration.

To begin with, there are unconditioned reflexes which tend with their repetition to diminish in strength or, as it is said, to be extinguished. The orientation reflex may serve as a classic example of these reflexes; it is evoked by new and unusual stimuli which in themselves possess no specific significance for the organism.

It is easy to see that even with very rarely spaced repetitions, an orientation reflex gradually diminishes, which means that this process is not due to the fatigue of the centres involved.

In the Pavlov school the opinion prevails that the extinction of the orientation reflex is a cortical process, and that in decorticate animals this reflex is as stable as other unconditioned reflexes. The experiments of Lebedinskaia & Rosenthal (1935) seem to refute this opinion. In their dog, which was almost completely decorticated, the orientation reaction to an auditory stimulus was totally extinguished after eighty-eight applications of the stimulus at brief intervals. Of course this effect could be ascribed to fatigue. But the next day the reflex disappeared after only twelve repetitions, which fact, if it is not accidental, must be ascribed to the learning process. Unfortunately, this series of experiments has been discontinued and we do not know what would have been the further course of the extinction.

The problem arises whether the orientation reflex is the only unconditioned reflex possessing the property of being extinguished on its simple repetitions, and especially whether this property is manifested also in some specific reflexes, such as, for example, the defensive reflex of rats to the smell of a cat (Griffith, 1920). As yet we have no evidence on which to base an answer to this question.

The next question, also so far unsolved, is whether unconditioned reflexes exist which on repetition undergo a lasting increase in strength. It is well known, for instance, that when the introduction of acid into the mouth of a dog is repeated day after day, the salivary reflex gradually grows stronger and its latent period diminishes. But it may be that this procedure, being obviously very unusual for the animal, evokes a strong orientation reflex which at first inhibits the specific reaction to the acid and then gradually subsides. So this whole problem too awaits its more extensive elaboration.

To end this section it must once more be emphasized that the problem discussed here concerns only the modifiability of a reflex caused by its repetitive elicitation and not by its being combined with other reflexes. It is clear that if a stimulus evoking an unconditioned reflex is conditioned to another reflex, then its own response can be either increased or diminished according to whether the two reflexes are allied or antagonistic. So in this sense every reflex can be said to be modifiable, but such modifiability depends on quite a different central mechanism.

III. CONDITIONED REFLEX OF THE FIRST TYPE

While, as we have seen, the problem of the modifiability of unconditioned reflexes as the effect of their repetition has, as yet, been worked out rather unsatisfactorily, another plastic phenomenon commonly called the conditioned reflex (and which we shall call here conditioned reflex of the first type) has been studied far more thoroughly. This is because the great physiological school of Pavlov was engaged in its study during nearly 40 years, and to-day it is being investigated in many other laboratories.

One great merit of Pavlov is that from the immense chaos and complexity of the acquired activity of the organism he separated out some simple and, maybe, elementary phenomenon, reproduced it in a pure form in laboratory conditions, and made it a basis for further extensive investigation. If Pavlov's idea was really sound and his conditioned reflex *is* actually an elementary phenomenon of acquired behaviour, then his method should be accepted as a most valuable instrument for the analysis of animal behaviour. But if it is not so, and if the principle of reflex does not show the proper way to the understanding of cortical activity, then a great deal of the vast experimental material accumulated in this field may appear to be useless, and the science of conditioned reflexes will lose much of its value and significance.

Taking into consideration the vast experimental evidence accumulated in this field both by Russian and American authors we can formulate the general principle of first-type conditioning in the following way:

If two stimuli s_1 and s_2 are applied in overlapping sequence, the stimulus s_1 being antecedent, then, with repetition of such combination, a plastic change in the nervous system is formed, consisting in the stimulus s_1 acquiring the ability to elicit the response of the same kind as the stimulus s_2. Bearing in mind the general meaning given to the term 'stimulus' in §1, we may apply this definition not only to the typical cases of conditioning, in which stimuli s_1 and s_2 act on receptors, but also to all other cases, in which one of these stimuli (or both) acts with the omission of receptors. For instance, stimulus s_1 may be applied directly to a receptive area of the cortex (Loucks, 1938), or it may be not an actual external agent but its 'trace' left in the nervous system after this agent has been removed (cf. Pavlov, 1927, p. 39); similarly, stimulus s_2 may be applied to the dorsal roots (Loucks & Gannt, 1938), or it may be a drug affecting directly nervous centres, etc.

The above definition gives only the necessary but not the sufficient condition for the establishment of the conditioned reflex. The actual course of conditioning greatly depends on physiological relations between stimuli s_1 and s_2 and their relative physiological 'strength'. If the two stimuli give rise to allied responses, the conditioned reflex is set up promptly and is strong; when they are antagonistic, the conditioned reflex is established with difficulty and is rather weak (Konorski, 1948, chapter VII, §3). When stimulus s_2 elicits a very weak response which is, moreover, antagonistic to the one evoked by stimulus s_1, the conditioned reflex may fail to be established at all, since the response to s_2 is fully inhibited by the reflex evoked by s_1. This is the reason why in conditioned reflex practice it is the rule to use stimuli evoking a strong reaction (such as presentation of food, introduction of acid into the mouth of the animal, electric shock, etc.) as reinforcing stimuli (s_2), while the so-called 'neutral' stimuli (auditory, visual and tactile) usually serve as conditioned stimuli (s_1), as they produce a very feeble proper reaction and are neither antagonistic nor allied to other reflexes. An alternative explanation of why this is the best way of establishing conditioned reflexes will be given in the last section.

In our definition we have introduced two statements which need a more detailed examination.

The first is the assumption that the 'direction' of conditioning is determined by the sequence of the stimuli applied, i.e. that the antecedent stimulus is always conditioned and the subsequent stimulus is conditioning. This assumption is based on the vast experimental evidence collected both in Russia (cf. Konorski, 1948, p. 19) and in America (cf. Hilgard & Marquis, 1940, p. 174). It goes to show that if a 'neutral' stimulus is preceded by an unconditioned stimulus the conditioned reflex to the neutral stimulus either fails to be established at all or is insignificant and evanescent. It has been claimed that 'backward conditioning' (as it is called) *can* be successfully elaborated (Shnirman, 1925; Switzer, 1930; Neždanova, 1940), but as the experiments yielding the negative result are abundant and unequivocal while those yielding the positive result contain some possibilities of error,* we deem that the hypothesis concerning the sequence of stimuli in the process of conditioning is well substantiated.

The second assumption put forward in our definition is that, in order that conditioning might be set up, the reinforcing stimulus (s_2) must be a stimulus in the proper sense (see §1). In other words, according to this assumption it is impossible to form a conditioned reflex, if a 'reinforcing agent' acts directly on efferent parts of the nervous system and produces a reaction which is not mediated by nervous centres.

This assumption is based both on theoretical considerations and on experimental evidence.

As to the former, we have many reasons for believing that the process of conditioning takes place in the midst of the central nervous system between its 'entrance gate' and its 'way out', where various factors reaching the system from outside meet to interact and associate. If a reaction is produced by the stimulation of efferent parts of the nervous system in or beyond its 'way out', it cannot become a conditioned reaction, since it does not interact with other incoming stimulations. Speaking freely, we can say that the 'creative' part of the nervous system lies somewhere between the receptive and the executive sets of neurons.

This standpoint is also well substantiated by many experimental data. In particular, Gannt and his associates were greatly concerned with the

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* One of these possibilities consists in the fact that application of an unconditioned stimulus not preceded by a conditioned 'signal' leads to the elaboration of a strong conditioned reflex to the experimental environment and 'to time'. Therefore in these conditions the apprising of the conditioned effect of a tested stimulus is very uncertain.

problem of which parts of the nervous system are essential for conditioning (cf. Gannt, 1937). Loucks (1935) has shown that conditioning was impossible when the 'reinforcing' agent directly stimulated the motor cortex. Similarly, it has been found that such reactions as gastric secretion to histamine, or adrenaline hyperglycaemia, cannot become conditioned reactions (Katzenelbogen, Loucks & Gannt, 1939; Gannt, Katzenelbogen & Loucks, 1937), since they are produced by the direct action of these drugs on peripheral organs. On the contrary, the effect of morphia (consisting in salivation, vomiting, etc.) can be easily made a conditioned reaction, since it is mediated by nervous centres.

The above general principle, according to which only those activities can become conditioned which occur through the mediation of the central nervous system, may be very useful in determining the mechanism of action on the organism of various agents. Suppose we have an agent *A* (which may be the peroral or parenteral application of a drug or a chemical, the direct stimulation of a nervous structure, etc.) that produces a number of effects a_1, a_2, a_3, etc. In order to establish which of these effects have peripheral and which central origin we attempt to set up a conditioned reflex using the agent *A* as reinforcement. Those effects which will enter into the conditioned reaction are undoubtedly mediated by the centres, while those which will be missing are probably peripheral. Thus the conditioning procedure may serve as a 'sieve' to select reactions of different origin.

To take an example let us turn to the experiments by Masserman (1943). This author has demonstrated that the 'sham rage' which is produced in cats by the direct stimulation of the hypothalamus by means of chronically implanted electrodes cannot become a conditioned reaction; in other words, we can hundreds of times 'reinforce' an indifferent stimulus by the stimulation of the hypothalamus, and the indifferent stimulus will not evoke the corresponding response. Similarly, the author observed that 'sham rage' does not in the least interfere with other, antagonistic activities of the animal; the cat can simultaneously continue to lap milk, clean its fur, respond to petting, etc., in spite of vigorous outward manifestation of rage. All this goes to show that stimulation here affects only the purely executive centres and not the structures involved in the production of the rage itself. It is worth pointing out, however, that the general conclusion of the author, according to which 'there is little or no basis for the thesis that the hypothalamus governs or even mediates the emotional experiences themselves' (p. 56), is not convincing. According to the evidence recently provided by Hess (1947), we can obtain a 'genuine' rage in the animal if, not the efferent fibres emerging from, but the afferent fibres leading to, the hypothalamus are stimulated. It would be extremely interesting to examine whether in the latter case conditioning of the rage reaction could be more successful than in Masserman's experiments.

In the light of these considerations rather unexpected results seem to have been obtained by Bykov (1944), who claims to have obtained a conditioned acceleration of the heart rate (p. 47) and a conditioned contraction of the spleen (p. 60), using as reinforcing agent an adrenaline injection. We have hitherto believed that both these reactions to adrenaline are of peripheral origin, and consequently their conditioning should be impossible. Bykov's results seem to indicate that our belief has been erroneous and that the mechanism of these effects must be quite different. Unfortunately, the author stating the above facts leaves them without any further analysis.

To end this section we should like to discuss one further question which very often causes misunderstandings. According to our definition the conditioned response of the first type comprises only those elements which are present in the corresponding unconditioned reflex. It is not necessary that *all* elements of the unconditioned reflex should be represented in the conditioned reflex and that their intensity should be the same. It is, however, essential that the conditioned response should not contain any foreign elements. We mention this because many authors stress the fact that very often a conditioned response is *qualitatively* different from the unconditioned reaction. A commonplace example of this is a motor behaviour which accompanies the conditioned alimentary reaction. It consists in an attentive fixation on the place whence the food appears and in 'expectation pose', while the unconditioned response consists in the seizing of food, in biting it, chewing and swallowing. Of course, there is nothing in common between these two reactions.

From our standpoint such facts do not in the least testify against the existence of Pavlovian conditioned reflexes, nor do they refute our definition, but they indicate that in the repertory of acquired animal reactions there are responses which do not occur according to the classic Pavlovian scheme. With such responses we shall be concerned in later sections.

IV. INHIBITORY CONDITIONED REFLEX OF THE FIRST TYPE

If after the elaboration of a conditioned reflex we cease to reinforce it by the unconditioned stimulus, the conditioned response gradually disappears. As is well known, Pavlov demonstrated that this process is due to a special kind of inhibition which he called internal inhibition.

In the above-quoted monograph (Konorski, 1948, chapter IX, §I), on the basis of our own experimental data as well as on data of other authors, we came to the conclusion that if a neutral stimulus s_1 is applied in the reverse overlapping sequence with an unconditioned stimulus s_2, i.e. when it precedes and signals the end rather than the beginning of the action of this stimulus, then an inhibitory conditioned reflex to stimulus s_1 is established, and this kind of inhibition is a typical Pavlovian internal inhibition. It is easy to grasp that this experimental situation is exactly reverse to that which takes place when stimulus s_1 signals the beginning of the stimulus s_2 and which gives rise to the formation of an excitatory conditioned reflex to stimulus s_1. So we see that the inhibitory conditioned reflex of the first type has exactly the same general 'formula' as the excitatory reflex, the only difference between them being that in the case of the excitatory reflex the reinforcement consists in the onset of the unconditioned stimulus, while in the case of the inhibitory reflex it consists in the cessation of that stimulus.

This new kind of internal inhibition may be called *simple* or *original* inhibition, since other kinds of internal inhibition (extinction, differentiation, etc.) can be easily derived from it. Indeed, when a conditioned stimulus s_1 is applied without reinforcement it evokes an excitation of the unconditioned centre which immediately ceases, when this centre is not subsequently excited by its proper stimulus. In consequence, stimulus s_1 becomes now a signal of the cessation of excitation in the unconditioned centre, and as a result the inhibitory conditioned reflex is formed to it.

V. CONDITIONED REFLEXES OF THE SECOND TYPE

If we assumed for the moment that Pavlovian conditioned reflexes (both excitatory and inhibitory) were the basis of *all* acquired behaviour of the animal, then this behaviour should be described in the following way.

The foundation of all behaviour would consist of a limited number of unconditioned responses, which could be elicited not only by their specific stimuli, but also, thanks to conditioning, by their 'signals', i.e. by neutral stimuli which happened to coincide in time with the former ones. Thus the plasticity would be ascribed only to the receptive side of the nervous system, while the executive side would be constant and unmodifiable and would comprise only such responses as are founded in the unconditioned reflex arcs.

If we take into consideration the whole of animal behaviour and especially the motor activity, we shall observe at once that it cannot be confined in this scheme. For we know very well that the motor activity is not less modifiable than the receptive activity, that it also changes as the effect of the animal's individual experience, and cannot in the least be reduced to the mere compounds of unconditioned responses. Therefore, besides the

Pavlovian conditioned reflexes there must be other mechanisms of plasticity which would account for these other forms of acquired behaviour.

In 1928 we succeeded in separating out a new form of conditioned reflex, different from the Pavlovian conditioned reflex, which we called the 'conditioned reflex of the second type' (Miller & Konorski, 1928). On the basis of our experimental work concerning this type of reflex (vide Konorski, 1948, chapter XI) the principles of its elaboration can be generally formulated as follows:

If we subject to conditioning procedure of the first type (*i.e. reinforce by an unconditioned stimulus*) *a compound of stimuli consisting of an exteroceptive and a proprioceptive stimulus, in which the proprioceptive stimulus constitutes an indispensable complement to the conditioned compound,** *then the exteroceptive stimulus begins to evoke either the movement generating the proprioceptive stimulus or the movement antagonistic to it, which depends* (1) *on whether the conditioned reflex, first type, to the compound is excitatory or inhibitory, and* (2) *on whether the reinforcing stimulus is positive or negative. By positive unconditioned stimuli we denote such agents as food, an individual of other sex, etc., and by negative unconditioned stimuli we denote such agents as the introduction of acid into the animal's mouth, the electric shock, etc.*

Thus we obtain four varieties of conditioned reflexes, second type. They are as follows (*s denotes an exteroceptive stimulus, s_r proprioceptive stimulus, r corresponding movement, $\sim r$ antagonistic movement, $\rightarrow$ evokes*)*:*

(1) *If the compound $s+s_r$ is reinforced by a positive unconditioned stimulus, stimulus s alone not being reinforced, then stimulus s begins to evoke the movement r ($s \rightarrow r$).*

(2) *If the compound $s+s_r$ is not reinforced by a positive unconditioned stimulus, while stimulus s alone is reinforced, then stimulus s begins to evoke the movement antagonistic to r ($s \rightarrow \sim r$).*

(3) *If the compound $s+s_r$ is not reinforced by a negative unconditioned stimulus, while stimulus s alone is reinforced, then stimulus s begins to evoke the movement r ($s \rightarrow r$).*

(4) *If the compound $s+s_r$ is reinforced by a negative unconditioned stimulus, while stimulus s alone is not reinforced, then stimulus s begins to evoke the movement antagonistic to r ($s \rightarrow \sim r$).*

For the investigation of conditioned reflexes of the second type a method had to be devised in which:

(1) both the exteroceptive stimuli and the reinforcing agents are easily applicable and discernible,

(2) the motor responses are simple, easily elicitable, observable and measurable,

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* I.e. the exteroceptive stimulus alone is differentiated from the compound (see below).

(3) and in addition to the registering of the conditioned reflexes of the second type the registering of the reflexes of the first type is possible.

It seems that an appropriate method which fulfils the above conditions is as follows: (1) as the experimental animal we take a dog with the Pavlovian salivary fistula; (2) as exteroceptive stimuli we use the so-called 'neutral' stimuli commonly applied in conditioning technique; (3) proprioceptive stimuli are supplied by the lifting of one of the dog's limbs; (4) the presentation of food is used as a positive unconditioned stimulus, while the introduction of acid into the mouth or air-puff into the ear is used as negative unconditioned stimuli; (5) both the flexion movements and the extension movements are recorded on the kymograph; (6) raising the limb can be produced either mechanically (passive flexion), or by electric shock applied to the dog's foot, or even through electric stimulation of the motor cortex by means of chronically implanted electrodes (Loucks, 1935; Konorski & Lubińska, 1939).

The above definition requires several comments. The most important concerns the proprioception.

According to the definition, in order that any movement may become the effect of a conditioned reflex, second type, the proprioceptive stimulus generated by its performance must become a conditioned signal of a certain unconditioned stimulus. Therefore, if a given movement is not accompanied by any reception, as happens, for instance, in the case of de-afferentation of the limb, the flexion of this limb cannot become a conditioned stimulus of the first type, and consequently the animal is unable to learn to perform this movement as the effect of the second type conditioning, unless the proprioception can be substituted by other stimuli, e.g. visual, as is the case with people suffering from tabes dorsalis. Similarly, if in producing a passive movement we exercise too strong a pressure on the dog's limb (or in a reflex flexion we use too strong a current), then the weak proprioceptive stimuli are overshadowed by the strong exteroceptive ones (cf. Pavlov, 1927, p. 141); consequently the conditioned reflex, first type, cannot be established to the proprioceptive stimuli, and as the result the conditioned reflex of the second type, consisting in raising the leg, also cannot be formed.

On the other hand, the problem arises whether all the movements accompanied by proprioception, or, more generally, all activities which are 'felt' can become conditioned responses of the second type. As to the autonomic activities there is no doubt whatever that they cannot. If we evoke the erection in a dog (or for that matter in man) and reinforce it, say, by food, we shall not teach the animal to 'perform' erection, as we should teach him to perform a movement. We are not able to turn pale or to blush purposely (i.e. in order to reach some positive aim or to avoid some negative result) in the same way as we are able to move our limbs, although both these effects are accompanied by sensation.

But when we turn to the motor activity the matter is not so clear. If, for instance, we try in a dog to set up a conditioned reflex of the second type consisting in raising the foreleg, the training is easy and prompt. But to teach dogs in the same way to lift their hindlegs is more difficult, and I have seen dogs (though not many) which were not able to perform this movement as the effect of second type conditioning. Instead, they performed some indefinite reaction with their rump, lifted both hindlegs, etc., but there was no isolated flexion of one leg, which movement was taught to them. Whether this inability is due to the lack of exact proprioception connected with this movement (the animal does not 'know' which movement is to be performed), or to the imperfection of the central motor apparatus, is difficult to say. It seems that this problem deserves a detailed comparative investigation, in which the elaboration of various conditioned reflexes of the second type in different species should be accompanied by corresponding histological and direct physiological studies of the motor cortex.

The second comment to our definition of the conditioned reflex, second type, concerns its reinforcement. According to some authors (first and foremost Pavlov, 1941; and Guthrie, 1935), the motor behaviour of animals is based simply on the 'association' set up between an exteroceptive stimulus and a movement. As an example the usual teaching of a dog to raise the foreleg to the command, or to come to a call, is given. It is said that no reinforcement is required to teach the animal these tricks.

Such conclusions are based on inexact observations. When we teach a dog to 'give his paw' we usually apply positive reinforcement, e.g. petting when the movement is performed, as well as negative reinforcement, e.g. light strokes when it is not performed. We have been able to prove over and over again that if such an experiment is conducted in proper conditions (the dog on a stand, the experimenter outside the room) the simple combination of a stimulus with a passive flexion repeated hundreds of times leads to no 'association' of the stimulus with the movement (the problem of the so-called latent learning will be discussed later). The same negative result was obtained by Loucks (1935) who combined an exteroceptive stimulus with a movement elicited by stimulation of the motor cortex. Moreover, one needs only to extinguish a conditioned reflex of the second type (first variety) by not reinforcing it by food to see that the 'association' between the stimulus and the movement does not depend at all on their simple coincidence.

Finally, our third comment concerns the role played by the proprioceptive component in the conditioned compound stimulus. We have said that for a conditioned reflex, second type, to be established a proprioceptive stimulus must be a necessary complement to the conditioned compound, i.e. it must be an indispensable condition (in the given situation) to obtain food or to avoid a noxious stimulus.

When an alimentary conditioned reflex of the second type is elaborated to the experimental environment, i.e. when we simply raise the dog's leg in a given situation and reinforce this by food, then the above condition is obviously fulfilled; for the external stimulus (the experimental environment) alone is not reinforced, while the raising of the leg in this environment is. But if we wish to elaborate a conditioned reflex of the second type to a sporadic stimulus, it is not sufficient simply to combine the stimulus with the passive flexion and to reinforce this compound by food, for in this case the movement is not made a necessary condition for obtaining food. To achieve our aim we must teach the dog that the external stimulus alone does not lead to food, which we can do either by applying this stimulus alone without reinforcement, or by protracting its duration till the dog performs the movement trained. Generally speaking, a conditioned reflex of the second type comes into being only when the compound of external and proprioceptive stimuli is *differentiated* from the external stimulus alone. According to whether the compound is reinforced and the exteroceptive stimulus alone is not or vice versa, and whether the reinforcing agent is positive or negative, we obtain the four varieties of these reflexes, as above specified.

It is evident that the mechanism of the second type conditioning accounts for a great part of animal motor behaviour, viz. for that type of behaviour which arises when the animal learns to *perform* some action if this action is rewarded (first variety), or if it leads to avoiding or escaping the punishment (third variety), or to *refrain* from an action if it is punished (fourth variety), or leads to deprivation of or missing a reward (second variety). This is precisely that type of behaviour which was first subjected to scientific analysis by Thorndike and now forms the foundation for the great majority of behaviourist studies. It is commonly called 'habit', and its acquisition is called 'learning' in a narrower and more usual sense of the word. Indeed, the sentence 'a dog has learnt to raise his leg to metronome' sounds quite natural, but the sentence 'a dog has learnt to salivate to metronome' makes a rather awkward impression.

It is beyond the scope of this paper to show how the common methods of learning used in animal psychology, such as maze learning, trial-and-error learning, and so on, can be explained by the principle of the second type conditioning, as this task would involve a more detailed discussion of the properties of this type. But we ought to summarize briefly the views of certain American psychologists concerning the idea of the diversity of the two types of conditioning.

It seems that as soon as Pavlov's work had penetrated to America the first reaction was to identify the Pavlovian conditioned reflexes with habits. One representative of this view was Watson (1924), who believed that conditioned reflexes are elements of habits, and that a complex habit, if analysed, can be shown to consist of conditioned reflexes. As a matter of fact the views of Pavlov and Guthrie quoted above are not very far from this standpoint.

However, approximately since the 1930's more and more authors have been disposed to believe that there *is* a profound difference between the 'Pavlovian type of response' consisting in stimulus substitution and the 'Thorndikian type of response' based on the 'law of effect' (Thorndike, 1932, chapter XVI; Grindley, 1932; Skinner, 1935, 1937; Schlosberg, 1937; Kellog, 1938; Youtz, 1938*a*, *b*, 1939; Hilgard & Marquis, 1940; Mowrer, 1947, etc.).

Owing to lack of space we cannot enter here into a detailed analysis of the views of the above authors nor discuss the concepts of other authors as, for instance, Hull (1943), who, on the contrary, attempt to base both types of conditioning on one and the same principle. We shall undertake this task elsewhere.

VI. SOME OTHER FORMS OF LEARNING

In the preceding section we put the question whether the Pavlovian conditioned reflex exhausts the whole of acquired animal behaviour, and we demonstrated that there exists another mechanism of learning which we called conditioned reflex of the second type. Now we may ask again whether these two types of conditioning cover all animal behaviour, or whether there are other elementary mechanisms of learning not reducible to these two.

We have a good deal of psychological evidence indicating that there is a special kind of behaviour based on 'reasoning' or 'insight' and called 'intelligent behaviour' which is claimed to be distinct from habit behaviour and is often contrasted with it. In this section we shall attempt to examine this kind of behaviour and inquire into its specific character.

On the basis of the experimental evidence provided by the authors who have been particularly concerned with the subject, especially by Köhler, Maier and Tolman, we can present the following definition of intelligent behaviour:

If, owing to previous training or experience, the animal 'knows' (see below) *that in situation s_1 the movement r leads to situation s_2 (the latter being neither positive nor negative), and after the acquisition of this knowledge, to situation s_2 a conditioned reflex (either of the first or of the second type) is established, then when placed in situation s_1 the animal will perform the movement r if the reinforcing stimulus is positive and avoid the performing of this movement if the reinforcing stimulus is negative.*

Here are some examples to illustrate this type of behaviour:

(*a*) Köhler's experiment (1925):

(1) An ape 'knows' how to carry objects from one place to another; i.e. he 'knows' that if an object is in place s_1, then the movement r (taking and carrying it) transfers it to a new place s_2.

(2) The ape 'knows' that if an attractive goal is hung high above the ground and beneath it there is an elevated object (say a box), then he can climb the object and reach the goal. In other words, the animal has established the following reflex of the second type: the sight of the goal hung high and an object beneath it elicits the movement of climbing which is followed by a positive reinforcement.

Both these things are learnt through everyday experience.

(3) In the crucial experiment the box is placed some distance from the hanging goal. If the animal displays 'insight' he seizes the box, carries it beneath the goal, climbs it and reaches the goal.

(*b*) Maier's experiment (1929):

(1) A rat has become acquainted with a given environment and knows that from place s_1 he can reach place s_2 by means of the movement r (say leaping through a barrier).

(2) The rat has been taught to run from place s_2 to place s_3 where it finds food, i.e. a conditioned reflex of the second type to the stimulus s_2 has been established.

(3) Put in situation s_1, the rat runs to s_2 and thence to food.

(*c*) Unpublished experiments by Spence and Lippitt (Tolman, 1948):

A *Y*-maze contains two goal-boxes, one with food the other with water. Rats which are neither hungry nor thirsty are made to run through the maze and thus become acquainted with the location of the two goals. After several days of such training the rats are tested, when hungry or thirsty. If the hungry animals run towards food and the thirsty animals towards water, it signifies that the animals have displayed insight.

All these experiments possess one particular element which was not met with in the previous types of learning. It is that the animal acquires the 'knowledge' that (to put it in Tolman's words) 'a given spatially and temporarily stimulus-object (sign) is going to lead, as the result of a particular type of behaviour (or lack of behaviour) on the part of the animal, to a spatially and temporally more distant stimulus-object (significate)' (Tolman, 1937). What is essential in this is that not only the antecedent stimulus (sign) but also the subsequent stimulus (significate) are neutral stimuli.

So the question is bound to arise how does the animal learn 'what leads to what', if the subsequent stimulus is neither positive nor negative, and consequently the animal's behaviour is not reinforced and therefore cannot be fixated according to the principles of conditioning? In the above-cited experiments (similarly as in the majority of experiments concerned with this problem) such a type of learning occurred as the result of the investigatory behaviour of animals. The apes of Köhler had undoubtedly been long used to carry various objects from one place to another without any particular purpose; similarly, in Maier's experiments the thorough exploration of the environment explicitly constituted the first part of his experimental series.

We can also arrange the experiments in such a way that the learning process of 'what leads to what' is even more regular and observable. Let us imagine a dog in a stand (situation s_1), which is compelled from time to time to raise his leg (the movement r) by various means, each of these movements being followed by the sounding of a tone (stimulus s_2). This is the first part of the experiments. In the second part we apply the tone separately and reinforce it by food. If the animal did 'associate' the raising of the leg in situation s_1 with the tone he would now raise the leg 'spontaneously' to secure himself the conditioned stimulus that signals the food.

As is seen from these examples, in this type of learning the animal acquires 'knowledge' of the external world, which knowledge does not manifest itself until it is necessary, i.e. until stimulus s_2 becomes a signal of some positive or negative agent. For this reason psychologists often call this type of learning 'latent learning'. Clearly it can be detected in animals only by introducing a special final test which should, so to say, 'develop' the plate impressed in the animal's brain, i.e. make manifest the hidden associations established between stimuli.

The wider the scope of the stimuli which the animal is able to associate in this way, in other words, the greater his capacity for acquiring such a 'knowledge' of the external world, the greater is the possibility that he will display 'insight'. Scarce as is the experimental evidence concerning this subject, it seems very probable that the above-described capacity to form associations between neutral stimuli does not extend equally to all their kinds, but is, within a given species, highly selective. Thus, according to the vast experimental evidence, the rat possesses a highly developed spatial orientation (which is undoubtedly connected with its mode of life), i.e. it learns very easily 'what leads to what' in spatial situations, and hence in this field it is capable of displaying a great deal of 'intelligence'. However, in a somewhat modified experimental arrangement when stimulus s_2 is not a spatial situation but an 'object' (such as food for a satiated animal), the 'intelligence' of the rat fails more often (cf. the experiments of Spence & Lippitt (1946), Kendler & Mencher (1948), Grice (1948), in which the test of latent learning gave negative results). Probably, if stimulus s_2 were an auditory stimulus, no latent learning could be detected in the rat at all.

The ape has a highly developed (in comparison with other animals) 'practical intelligence', i.e. the knowledge of 'what leads to what' in the field of manipulation with objects. But the highest level of capacity to form associations between neutral stimuli is, of course, achieved in man, where this kind of association constitutes a greater part of his higher nervous activity far surpassing the two discussed mechanisms of conditioning.

The problem of the selective capacity to form associations between various categories of stimuli still awaits its thorough and detailed investigation.

However, when speaking of intelligent behaviour we must keep in mind that the knowledge of 'what leads to what' is only its prerequisite. Another no less important moment concerns the way in which the individual makes use of this knowledge.

To explain this point let us suppose that an animal finds itself in situation s, and that it 'knows' (owing to previous training) that particular motor reactions $r_1, r_2, \ldots, r_n$ may lead to particular new situations $s_1, s_2, \ldots, s_n$ respectively. Suppose that one of these situations s_k is a conditioned stimulus and signals a positive reinforcement. To reach the goal the animal must, among various possible reactions, *choose* that one which will lead to s_k. It is clear that the possibility of making an appropriate choice may not be an easy matter for the animal and may depend on very many factors, such as: the total number of reactions among which the animal has to choose, the relative degree of 'knowledge' which reactions lead to which particular situations $s_1 \ldots s_n$, the character of and the differences between these situations, the existence of some facilitating or misleading cues which may make the choice more easy or more difficult, etc.

So the problem of how and when the latent knowledge is *utilized* in particular situations is quite distinct from that of how such knowledge is acquired, and its analysis raises many interesting difficulties. This problem, however, does not belong to the topic of the present paper.

VII. ANALYSIS OF THE MECHANISMS OF PLASTIC CHANGES

So far, when discussing various types of plasticity, we have been trying to keep closely to the experimental facts, and any generalizations made were of a purely empirical character. In this section we shall attempt to formulate some hypotheses which would enable us to explain the above facts from the point of view of their central mechanisms.

As this subject has been extensively discussed in my recent monograph, and it is needless to repeat here previous arguments, I shall confine myself only to a brief account of main statements and shall deal a little more fully only with those questions which were not discussed in that monograph.

So far as the conditioned reflex of the first type is concerned the elaboration of its physiological theory does not involve great difficulties. Taking into account that this reflex, when established, has many properties in common with innate reflexes (the laws of summation, facilitation, occlusion, antagonism, etc.), we can reasonably assume that the conditioned reflex, similarly to the unconditioned, has its 'reflex arc' (with all the reservations connected with this term), the only difference being that it is formed during the animal's life through its individual experience, while the unconditioned reflex arc is formed according to the developmental pattern where the individual experience plays a lesser role. In other words, we assume that if two stimuli are applied in overlapping sequence the excitatory-inhibitory pattern elicited in the central nervous system by the antecedent stimulus changes in such a way that it partially reproduces the excitatory-inhibitory pattern specific to the subsequent stimulus. How such a transformation of excitatory patterns occurs is still unknown, although we believe that the problem is not very far from being solved. In the quoted monograph (chapter v, §4) certain simple hypotheses concerning this subject have been put forward, and though I make no claim to their being strictly adequate, I have shown their usefulness in explaining experimental facts. It has been assumed that: (1) a prerequisite for the establishment of a conditioned reflex is that the 'centre' of the stimulus to be conditioned (the 'emitting centre') and the 'centre' of the unconditioned stimulus (the 'receiving centre') must be joined by potential nervous connexions directed from the first centre to the second; (2) when excitation of the first centre coincides in time with the rise of excitation in the second centre, potential connexions between these centres are transformed into actual excitatory connexions; (3) the substratum of conditioning is a morphological process consisting in the growing and multiplication of contacts (synapses) between the axon-endings of neurons of the emitting centre and neurons of the receiving centre.

So far as the inhibitory conditioned reflex is concerned we must recall (§IV) that its original form arises when the two stimuli in question are applied in reverse overlapping sequence, the reinforcing stimulus coming first. This leads us to our fourth assumption, according to which, when the excitation of an emitting centre coincides in time with the fall of excitation in a receiving centre (the excitability of this centre remaining constant), inhibitory connexions are formed between these centres. As we have pointed out, the same relation between the centres is present in ordinary cases of inhibitory conditioning, e.g. in extinction and differentiation.

More complicated is the mechanism of the second-type conditioning, and we are not in a position to deal here with this problem in detail. To put it briefly we have shown in our experiments that a conditioned reflex of the second type arises against the background of more or less manifested general motor agitation of the animal, which we have denoted as 'a state of exaltation of the motor cortex'. This state comes into being (1) during the action of a conditioned stimulus which signals a negative reinforcement (i.e. when the animal is awaiting for some nociceptive agent), and (2) when a conditioned stimulus which usually signals a positive reinforcement *is not* reinforced (i.e. when the expected positive agent was not presented). In other words, the state of motor exaltation arises when there is a rise of excitation in the centre of a negative stimulus, or a fall of excitation in the centre of a positive stimulus. If in such a state the animal performs a movement which leads to avoiding a negative reinforcement or to getting a positive reinforcement, i.e. to a removal of exaltation of the motor cortex, then excitatory connexions are formed between the centre of the conditioned stimulus and the centre of the movement. If, however, a movement does not lead to the achievement of these 'goals', i.e. if it does not abolish the exaltation of the motor cortex but instead causes its increase, then inhibitory connexions arise between the two centres, and this leads to the performance of the antagonistic movement.

Although this interpretation of the second-type conditioning cannot be regarded as exhaustive and faultless, it satisfactorily accounts for the elaboration of the four varieties of conditioned reflexes, second type, as well as for their inhibition and other properties.

We pass now to an attempt at the interpretation of the next type of learning, which forms the basis of intelligent behaviour. As we said in the previous section, it consists in the capacity to form associations between 'neutral' stimuli. These stimuli can be associated by a mechanism analogous either to that of the first-type conditioning (the animal acquires the knowledge that stimulus s_1 is followed by stimulus s_2) or to that of the second-type conditioning (the animal acquires the knowledge that in the presence of stimulus s_1 the movement r will lead to stimulus s_2). Now, the cardinal question arises: what is the difference between this type of learning —in which the subsequent stimulus is 'neutral'—and the simple conditioning of the first or second type—in which stimulus s_2 is an unconditioned stimulus, positive or negative?

The problem which we are considering now is completely obscure and unexplored, and therefore we can only propose certain alternative hypotheses which would facilitate its further examination.

The first hypothesis would be that the mechanism of association of neutral stimuli is exactly the same as that of simple conditioning of the first or of the second type. While discussing the mechanism of conditioning we pointed out that when two centres are concurrently excited they can form actual connexions only if there exist innate potential connexions directed from one of these centres to the other. Now, we may assume that the higher the developmental level of the animal's brain, the more far-reaching and many-sided is its system of innate potential connexions. Therefore the so-called higher animals have the capacity to form associations between categories of stimuli which cannot be associated by the lower animals, because they lack the appropriate morphological connexions. In other words, the whole stock of potential connexions between nervous centres of any given animal would delimit its learning capacity.

On the other hand, however, we are in possession of some experimental evidence which would suggest a more profound difference between the process of conditioning and the associating of neutral stimuli.

Let us adduce some of our experiments performed in 1939 just before the war, which we were unable to publish because relevant materials were destroyed.

We established conditioned defensive reflexes of the second type (third variety) in two dogs. This was done in such a way that the sounding of a tone was reinforced by an air-puff into the ear, while the tone accompanied with passive flexion of the leg was not reinforced. Very soon in both dogs the tone began to evoke a vigorous flexion of the leg, a movement by which the animals avoided the air-puff. When this reflex had been firmly established we began to apply the air-puff (without any signalling stimulus) in overlapping sequence with the presentation of food. Thus we transformed the air-puff into a pure alimentary conditioned stimulus. The movement of shaking off, a characteristic response to the air-puff, disappeared, and the dog instead contorted its head slightly and pricked up its ear, while salivating copiously. This done, we returned to the application of the tone. It appeared that in both dogs this stimulus continued to provoke a vigorous defensive response in the form of a flexion of the leg without any trace of the alimentary reaction. It was very easy in one and the same experiment to show alternately both reflexes: the air-puff itself produced a pure alimentary reflex, but the tone, which was the signal of the air-puff, gave only a defensive reaction. In spite of many days of such procedure the dogs displayed no tendency to change their behaviour.

How is this fact to be interpreted? If the dog was no longer 'afraid' of the air-puff (which could be judged from his behaviour), the defensive reaction to the tone should have automatically disappeared, just as for instance, an alimentary conditioned reflex disappears when the dog is satiated.

It seems that this fact may be explained, if we assume that 'the centre of the air-puff into the ear' in the combination *tone : air-puff*, and 'the centre of the air-puff' in the combination *air-puff : food* are two different centres. We may suppose that in the first case, when the air-puff is a reinforcement, we have to do with the centre of 'protopathic' sensations (to extend Head's terminology) or the 'affective' centre, while in the second case, when the air-puff is a conditioned stimulus, the 'gnostic' or 'epicritic' centre of the stimulus is involved. Thus, in these two cases the air-puff represents two different experiences for the dog, and so it is not surprising that he fails to identify them and consequently reacts in a manner inadequate to the situation.

So we dare to formulate a hypothesis asserting, first, that the stimuli evoking unconditioned responses possess two different aspects, which might be called the protopathic or affective aspect, and the epicritic or gnostic aspect, and secondly, that the 'true' conditioning consists exclusively in the formation of connexions between the gnostic centre of the stimulus to be conditioned and the affective centre of the reinforcing stimulus. Since the so-called unconditioned stimuli (such as pain, food, other sex, etc.) have their gnostic aspect poorly developed while their affective aspect is very strong (which is manifested by their strong autonomic effects), whereas the so-called neutral stimuli have, on the contrary, a strong gnostic side and a very poor affective side (hence the name 'neutral'), it is not surprising that in the laboratory practice (as well as in everyday experience) the first are always applied as reinforcing agents and the second serve as conditioned stimuli.

Now, intelligent behaviour is based on a new mechanism according to which mutual connexions can be formed between the gnostic centres. This property is very poorly developed in such animals as the dog or cat, is more strongly expressed in apes, and represents a chief feature of the higher nervous activity of man.

These considerations may throw some light on certain types of neurotic behaviour in which a patient reacts with anxiety (or other feeling) to particular neutral stimuli, not realizing whence this feeling comes and why it appears. If in childhood a neutral stimulus had been conditioned to some defensive reaction, the gnostic aspect of the reinforcing stimulus, being rather weak, could become forgotten, while the affective side has remained intact. Now in presence of the conditioned stimulus the subject experiences fear without knowing of what, perhaps in the same way as in the discussed experiments our dogs displayed fear to the sounding of the tone. The essence of psycho-analytical method may consist in the fact that owing to the strenuous efforts of the patient to recall the original conditioning situation, the unconditioned stimulus is gnostically reproduced, and can be submitted to the control of the mechanism of intelligent behaviour. Similarly, if we were able to render our dogs conscious of the fact that the stimulus which is signalled by the tone of which they are so afraid is the same stimulus which heralds food and which is not to be feared at all, they undoubtedly would stop displaying a defensive reaction to the tone, and the flexion of the leg to this stimulus would disappear.

VIII. SUMMARY

In this paper an attempt has been made to separate and to define certain simple types of learning, and to some degree to analyse their physiological mechanism. The following types have been discussed: (1) the modifiability of unconditioned reflexes, and especially the extinction of the orientation reflex; (2) classic (first-type) conditioning, both excitatory and inhibitory; (3) motor (second-type) conditioning; (4) latent learning, i.e. association of 'neutral' stimuli. Some applications of this analysis to the phenomena of everyday practice and animal experimentation are discussed.

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THE COMPARATIVE STUDY OF LEARNING

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I. THE COMPARATIVE METHOD IN STUDY OF THE HIGHER NERVOUS ACTIVITIES

It is curious that the comparative method has been so little used in the study of the higher activities of the nervous system. In dealing with any living tissue the biologist can exercise only a very limited degree of control in making his experiments; he cannot synthesize new organisms and new tissues for his purposes, as the physicist or chemist can synthesize their systems. Fortunately, nature has already made many experiments for him, and a great part of our success in solving fundamental biological problems depends on the skill with which we use and interpret the natural experimental material.

In the case of the higher nervous centres it is particularly difficult for the investigator to alter the material to suit his needs; he cannot make up various arrangements of nerve cells in order to test particular theories. There is, therefore, a special incentive to make use of the great variety of networks that is found in the different parts of any one nervous system and to compare the arrangements present in the nervous systems of animals that have different powers. In spite of the vast numbers of experiments conducted by physiologists and psychologists, however, it cannot be said that this method has even yet been seriously exploited. Perhaps this is because there has been little attempt so far to correlate the behaviour observed with the visible structure and other features of the part of the nervous system concerned. It is anomalous that we have no systematic account of the types of nervous structure that are associated with the various sorts of activity mediated by the nervous system. Is there a particular arrangement of neurons associated with simple reflex action, another with the performance of elaborate motor action, another with complex actions set off by a 'releaser', still another with modification of behaviour with experience? A prolonged study throughout the animal kingdom on these lines might yield very interesting information. It would require, however, great care in the selection of the appropriate categories, rigid criteria in the definition of types of behaviour, and an appreciation of the sorts of information that histological study can and cannot obtain in view of the technical limitations of methods of fixation and staining. It is highly desirable that such a study should also include investigations of the distribution of other properties in the various types of nervous tissue, particularly electrical properties, but also others, such as chemical requirements and output and heat production.

II. THE PROBLEM OF THE NATURE OF HIGHER NERVOUS ACTIVITY

The problem of central nervous activity that particularly claims attention is to discover the nature of the modification that occurs when an animal learns. What is it that gives to some nervous systems this quality of modifiability, of plasticity as it has been called? (see Konorski, 1948). It is probably not wise to look at this problem too narrowly. The difficulty of defining what is meant by 'learning' is part of the general weakness of our concepts for expressing the actions of the nervous system. We shall not get very far by saying that our problem is to study the activity or function 'learning', and that we anticipate that this occurs in such and such a tissue. In the case of peripheral nerve we can specify a 'function', namely, conduction, and the visible characters of the tissue are not too complicated for us to discover those that are significant for this function. In our present problem the 'function' can only be obscurely defined and the tissue is extremely complicated. Yet the analogy may carry us a little way. Certain parts of the nervous system of some animals are probably especially connected with making provision for the plasticity that allows animals to modify their behaviour as a result of experience. We may derive some information by comparing the cerebral cortex of mammals, the tectum opticum of lower vertebrates, the corpora pedunculata of insects, and the lobus verticalis of cephalopods, all of them regions that may have much to do with actions definable as learned. However, before we can expect to know how the action capacity of an organism undergoes change we must first try to understand how it operates at all, in fact to find a conception with which we can operate to describe the nature of the whole acting system.

The current conception, on which most discussions of learning, as of other nervous functions, still concentrate, is that the nervous system consists essentially of an aggregate of chains of conductors, linked at key points by synapses. This reflex conception, springing probably from Cartesian theory and method, has no doubt proved of outstanding value in helping us to analyse the actions of the spinal cord, but it can be argued that it has actually obstructed the development of understanding of cerebral function. In many cases where the brain is involved the 'response' that an animal gives to a 'stimulus' is elaborate and prolonged. The 'stimulus' does not bear the same relation to the result that a pin prick has in the flexor reflex. The internal system of the animal gives the power to maintain and prolong action, and the most interesting problems for the study of behaviour are of this system of internal activation. Presumably animal activities are usually set off in the first instance by external stimuli, and proprioceptive and other impulses generated during the action no doubt help with its maintenance, but it is nevertheless very clear that the course of action taken by animals and men is largely controlled from within the system. We have therefore to recognize what may be called internal initiators or internal drives. These internal factors include several separate categories, such as proprioceptors, visceral enteroceptors, hormonal influences and perhaps most interesting of all, those influences that may be called neural drives (Young, 1938). Undoubtedly for considerable periods of time during the life of higher animals the behaviour is controlled by trains of activity coming from within the central nervous system. During his lecture Prof. Gray showed us a film of a toad walking on a moving drum, and the experiment helps greatly in understandin the mechanism of walking. But still more interesting is the fact that toads often walk when the ground beneath them stays still! The part of behaviour about which we know least is maintained and prolonged *without* continual change in the outside world, and we may hope that sooner or later it may be possible to understand something of the changes in the central nervous system that produce such behaviour.

III. THE NERVOUS SYSTEM OF CEPHALOPODS

We are therefore in need of proper means of conceiving the actions of the central nervous system and are not likely suddenly to reach an entirely satisfactory concept. It may be of some help to examine at as many levels as possible the activities of a nervous system very different from that of vertebrates. We have begun with the cephalopods, because they have an elaborate, accessible nervous system, organized very differently from those mostly studied previously, but showing considerable and interesting variations between one cephalopod and another.

The central nervous system of cephalopods has evolved independently since the Cambrian, presumably from some amphineuran ancestor. During this time of about 500 million years it has departed so widely from that of other molluscs that it is only possible to make the vaguest comparisons with the plan of ganglia found, for instance, in gasteropods. The attempt to make such comparison is a fascinating morphological exercise, but has so far helped little in providing a nomenclature suitable for daily use. In a modern cephalopod the brain is divided into a number of rather distinct lobes, each with its characteristic neuropil structure and connexions. Various means of classifying these lobes have been suggested; the work of Thore (1939) summarizes these and adds much. We have not been able to follow Thore's nomenclature in every way, but have kept in the main to the older one of Dietl (1878) which, with amplifications, is very convenient. Fourteen main lobes can be recognized (Pl. 1), and for many purposes we can group these into three divisions, the suboesophageal ganglia with four lobes, supra-oesophageal ganglia with eight and optic lobes with two. However, the lobes are closely aggregated around the oesophagus, and some of them lie at the sides and can therefore only arbitrarily be classed as supra- or suboesophageal. The three main suboesophageal lobes are those usually called brachial, pedal and palliovisceral (Pl. 1), and the fourth is a lobe lying round the sides of the central nervous system and known as the lobus magnocellularis, because in the squid and other decapods it contains the large cells of the giant nerve fibre system (Young, 1939). In the octopus the giant fibre system is completely absent, the quick movements having been given up when the animals adopted a bottom-living habit; however, the lobus magnocellularis is still present.

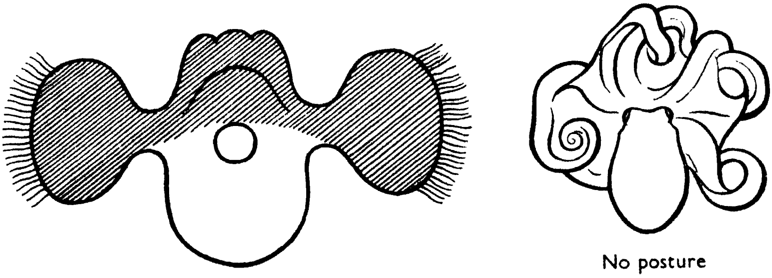
IV. ANALYSIS OF THE FUNCTIONS OF THE LOBES

Investigation of the various lobes shows that they mediate very different sets of functions. The parts of the system that are 'lower' in the anatomical sense are capable by themselves only of rather simple activities, often of reflex type. Lying above these are centres responsible for more complex movements, whose cells probably usually act in groups, providing the patterns of ratios of activity that allow elaborate and sustained acts of behaviour. These higher motor centres receive impulses from the special sensory centres, especially from the very large optic lobes, which are presumably responsible for performing analysis and discrimination of changes in the surrounding situation and for activating the motor system accordingly. Then on top (literally) of all these are certain lobes that have a regulating influence on the whole system, particularly in the sense of providing inhibition of action by other parts when experience has shown it to be undesirable.

Even this greatly simplified account will show that we are not likely to find easily any formulation that enables us to understand the whole action system of an octopus. Indeed, we should be on our guard against attempting to do so. An octopus does many different things, and it will certainly be very difficult to analyse the actions of its brain. However, we may gain some insight into the types of function performed by the various parts by describing the results of quite simple experiments of extirpation and stimulation.

V. ACTION OF THE ISOLATED SUBOESOPHAGEAL GANGLIA

It is possible to remove the entire supra-oesophageal and optic lobes from an octopus (Text-fig. 1). The remaining suboesophageal preparation is capable of respiration, but of no organized behaviour whatsoever, either for locomotion or feeding. It lies passively on the bottom, with the arms in disorder; in fact, there is no sign of the posture that is adopted by a normal octopus at rest. Under no circumstances can the operated animal make integrated movements. Even when vigorously stimulated by prodding it never makes any sustained movements of escape by walking, or by means of the funnel. Turned upside down it is unable to right itself. An arm will attach itself to an object that touches it, and other arms may be brought over to join in this grasping. Proprioceptive reflexes are present; when an arm is pulled back strongly the arms of the opposite side grip the bottom and often become alined along the direction of pull. Arms may also bend over, carrying an object towards the mouth, but the preparation is unable to kill or bite its food. A very specific reflex is elicited when the back of the mantle is scratched; several arms are brought over to touch the touched spot.

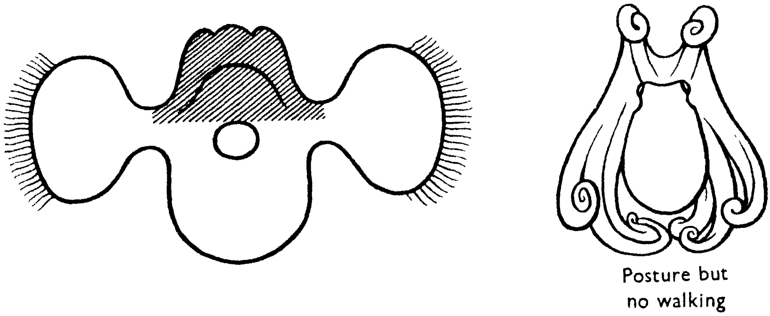


No posture

Text-fig. 1. Diagram of complete removal of supra-oesophageal lobes and section of optic tracts of *Octopus*. In this and subsequent diagrams the lobes are shown very schematically in transverse section as seen from behind. The suboesophageal centres are below, optic lobes at the sides. Above the oesophagus the line is used to show the separation between the higher motor centres (such as the basalis anterior) and the verticalis complex.

Evidently these suboesophageal ganglia contain neurons that are able to set the muscular systems in action and to mediate simple reflex actions, but not, by themselves, to allow the performance of any elaborate movements. Such behaviour might be described as that of lower motor centres. In many ways it is similar to that of the vertebrate spinal cord; an octopus without supra-oesophageal and optic ganglia has some similarity to a spinal mammal.

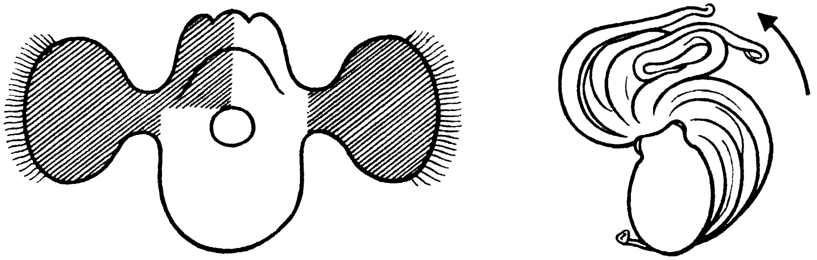
These lower motor centres of the octopus contain large nerve cells, whose processes run out into the peripheral nerves either direct to the muscles or through a further peripheral synapse, as on the pathways to the arms and mantle musculature. The motor neurons are unipolar, the process of each cell runs into a neuropil, where it gives off abundant collaterals and then passes into a peripheral nerve trunk. The collaterals presumably serve to make contact with the afferent fibres that end in the lobes, mediating the reflex actions described above, but the details of synaptic structure are not known. Terminal boutons have been described in the neuropil (Sereni & Young, 1932), but it is not by any means to be assumed that they constitute the only means of interaction between the nerve fibres. The neuropil of these motor lobes is an elaborate arrangement of interlacing fibres in which no obvious regularity appears, except in certain regions, such as those that control the chromatophores. It is impossible to say what processes go on within the neuropil. Not all of the suboesophageal cells are large; smaller ones are found, both mingled with the large cells and in separate small-celled regions. The axons of some of these small cells are confined to the lobes; their significance is unknown.



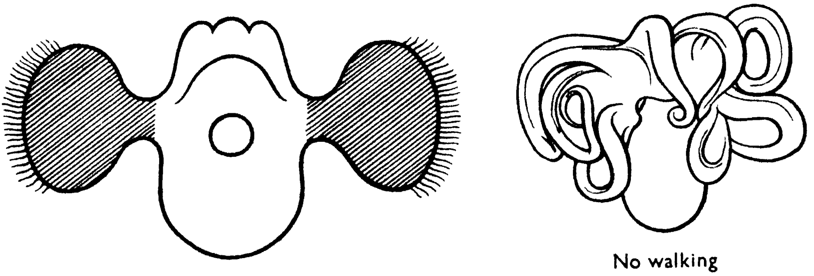
Text-fig. 2. Complete removal of supra-oesophageal lobes from *Octopus*, leaving the optico-suboesophageal connexions intact.

Evidently the suboesophageal centres alone do not suffice for the production of the normal patterns of activity of the animal, and we may seek for the source of these elsewhere in the brain. After removal of the supra-oesophageal lobes, leaving the optico-suboesophageal connexions intact (Text-fig. 2), the animal maintains a definite posture. The arms are held in a fixed and diagrammatic position, curving outwards and backwards. The animal is unable to walk when prodded, except for a few peculiar 'stepping' movements of the arms on the side opposite to that stimulated. In fact the posture is so fixed that a comparison with the decerebrate rigidity obtainable in mammals springs to mind. Changes in the visual field, produced by a crab or some other object, result in a depression of the head and its drawing away from the object. There are no attempts to move away, such as a normal octopus might make, nor are there any attempts to seize a crab as if it were a food object. Evidently, therefore, the optic lobes exert directly an important influence on the lower motor centres, but some part of the supra-oesophageal region is necessary for normal walking.

Some information about the supra-oesophageal centres has been obtained by removing large parts of the supra-oesophageal mass. Thus an octopus in which both optic tracts have been cut, and one-half of the supra-oesophageal lobes removed (Text-fig. 3) begins to walk when prodded and moves in circles, with the side that has the intact supra-oesophageal lobe on the outside. The movement may continue for many minutes after stimulation; evidently the half supra-oesophageal lobe is able to act with the suboesophageal ganglia to maintain this action. But an animal with both optic tracts cut (Text-fig. 4) is unable to make any walking movements, however it is stimulated; apparently the supra-oesophageal lobes of the two sides inhibit each other.



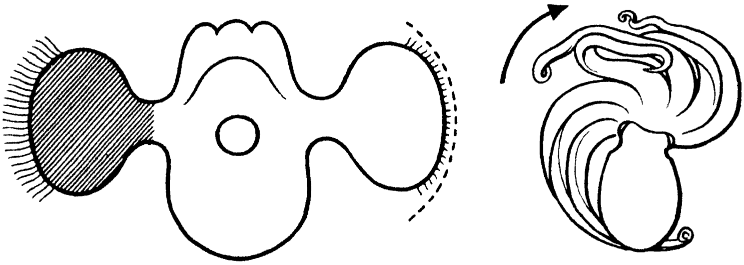
Text-fig. 3. Severance of optic tracts and removal of half of the supra-oesophageal ganglia.



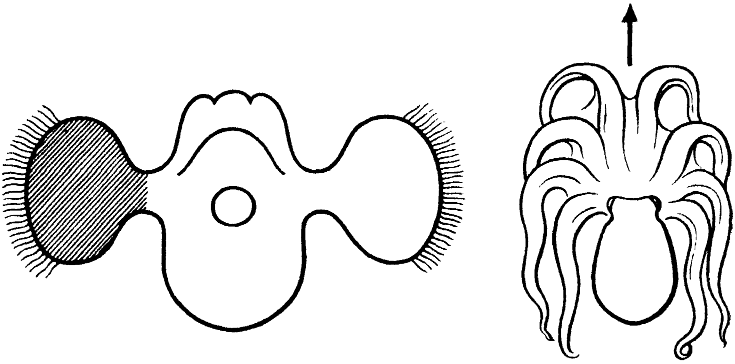
Text-fig. 4. Severance of both optic tracts.

Probably the balance of activity in these higher motor centres is normally controlled by the flow of impulses in the many fibres that reach them from the optic lobes. Signs of these influences have been obtained after various operations. Thus, if the optic tract of one side and the optic nerves of the other are cut, the animal will walk well, the side *without* the optic lobe being on the outer edge of the circle (Text-fig. 5); it seems that the intact optic lobe inhibits the activity of its own side. The effect is very marked directly after this operation, the animal moving in tight circles, almost on its own axis; later the circles become wider and the animal often comes to walk almost straight, though temporary reversion to circling may occur.

Presumably the optic lobe in controlling the movements in this way is itself controlled by the influences brought to it from the retina by the optic nerves. If the last experiment is made without cutting the optic nerves, the animal never circles (Text-fig. 6). It may well be that the retina sets up a continuous discharge of impulses that act to inhibit the inhibitory effect of the optic lobe. This sounds complicated, but actually the situation is no doubt even more involved, because of the variety of effects of differing patterns of retinal stimulation. We have as yet no detailed picture of the way in which impulses in the optic nerves influence the optic lobes and enable them to control the motor centres.



Text-fig. 5. Severance of one optic tract and the opposite optic nerves.



Text-fig. 6. Severance of one optic tract.

VI. FUNCTIONS OF THE VARIOUS SUPRA-OESOPHAGEAL LOBES

So far we have been dealing with the supra-oesophageal centres as if they were a single unit, but they are anatomically subdivided into eight lobes, differing greatly in structure, connexions and, as we shall see, in function

(Pl. 1). The terminology that we have found it convenient to adopt recognizes in the supra-oesophageal complex three basal lobes, basalis anterior, posterior and lateralis, and five centres that are 'higher' anatomically and in function, the lobus olfactorius, lobus frontalis inferior, frontalis superior, verticalis and subverticalis. Experiments in which these various lobes are removed separately show that the motor centres we have been speaking about are located in the three basal lobes. Removal of the five upper centres is not followed by any gross abnormalities of posture or movement; such an animal can only be distinguished from normal when presented with special situations that we shall discuss later. On the other hand, cuts that interfere with the three basal lobes produce asymmetries and abnormalities of movement such as those we have been discussing. Detailed analysis of the parts played by these three lobes is proving complicated, but the basalis anterior is concerned with the production of movement of the head and arms, the basalis posterior with those of the mantle, funnel chromatophores and certain movements of the arms, and the basalis lateralis chiefly with the control of chromatophores.

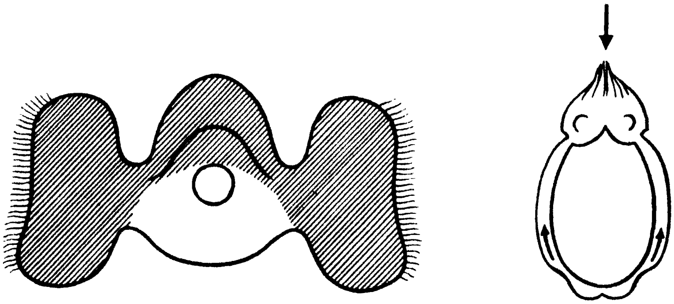
It has been known since the work of v. Uexkull (1891) that electrical stimulation of the basalis posterior region in the lightly anaesthetized octopus produces movements of inspiration and expiration, and we have confirmed that mantle movements are produced in this way. Stimulation of the basalis anterior produces a complex set of movements; the head of the side stimulated is turned forwards and there may be quite well coordinated movements of the arms, usually such as to push the body forward and away from the side stimulated, though pulling movements in the opposite direction have been observed. Perhaps it is a vain attempt to try to analyse the actions of such a complicated system by stimulation of the anaesthetized brain with single electrical pulses. We shall need finer and more complex methods before we can understand the workings of these higher motor centres, which are probably so built as to allow their efferent fibres to be excited in elaborate patterns, with ratios that can be varied widely both in grouping and timing. We cannot even say that we are much helped by study of the structure of these regions. The cells of the walls of the basal supra-oesophageal lobes include numbers of neurons of moderate size (10μ diameter) and also many minute ones. The neuropil of the basalis posterior is rather like that of the lower motor centres in its tangled arrangement, but in the basalis anterior there is a very orderly and elaborate distribution of the optic tract fibres.

It is not possible at present to produce a single consistent scheme to describe all the behaviour of such a complicated system. We should hardly expect any simple scheme to do so. There is, however, enough evidence to give some idea of the way the activities of these masses of cells and the afferent impulses that pour into them initiate and control complicated activities of movement towards or away from change in the world around.

Although we can only very dimly imagine what goes on in these higher motor centres, we at least get a glimpse from these experiments of activities that somehow interact with those of the lower motor centres and the afferent impulses to give movement towards food and away from enemies. Similar higher motor centres are to be found in vertebrates. Thus the neurons of the tegmentum and other parts of the mid-brain base of mammals act in a somewhat similar way. After lesion in that region symptoms of persistent locomotion may appear. Unfortunately, in no cases do we properly understand how such centres act, and this absence of a clear picture of the daily action system of the animal is one of the factors that makes it difficult to formulate the changes in behaviour that constitute learning. We have almost no information as to whether these centres themselves are modifiable in their action, but it is perhaps an interesting fact that in both cephalopods and vertebrates we can recognize them as to some extent separate and distinct both from lower centres and from the centres commonly regarded as the highest region of the brain, which are chiefly responsible for the more elaborate sorts of learning. Certainly the action of the higher motor centres is closely linked up with what we may call the springs of action of the individual. Lesions or other abnormalities here produce more than the simple paralysis which is characteristic of removal of a lower motor neuron.

VII. REMOVAL OF SUPRA-OESOPHAGEAL LOBES OF *SEPIA*

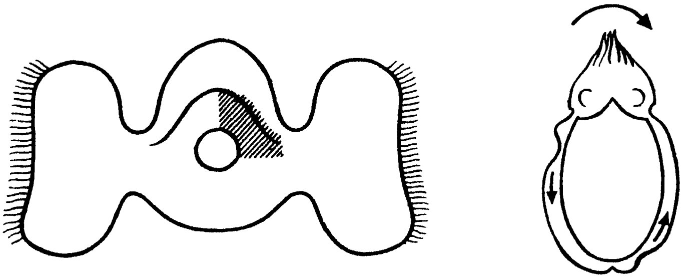
The complexity of these effects is well shown by some experiments on these lobes in *Sepia*, the cuttlefish. *Octopus* is an animal that passes much of its time hidden among the rocks for long periods; perhaps it moves only a few times a day, when food appears. Though able to hunt actively, it is often passive. *Sepia*, on the other hand, is a more continuously active animal. It moves mainly by means of its fins, lateral folds along the sides of the body, which are raised and lowered by upper and under muscles in such a way that waves pass along them. These waves may begin either in front or behind, or at opposite ends in the two fins, allowing a very delicate steering, including turning without progression, no doubt very convenient in the rocky and weedy places where *Sepia* lives and hunts for its food. In addition, *Sepia* makes frequent use of movement by the expulsion of a jet of water through the funnel, under the control of its system of giant nerve fibres. The movements of the fin are controlled by a special lobe on the upper anterior face of the palliovisceral ganglion. The cells of this lobe include the motoneurons of the fin muscles, and in this case, unlike *Octopus*, the suboesophageal centre by itself is able to produce movement. When all supra-oesophageal and optic influences have been removed by excision the fin becomes continuously active (Text-fig. 7). As soon as the animal recovers from the operation it begins to move continually across the tank by means of its fins, waves beginning at the hind end of these and travelling forwards, thus driving the animal backwards. This movement continued for the three days, which was the maximum survival after the operation. It could be stopped, however, by a light touch on the skin of the back, or especially of the underside of the mantle. An animal gently lifted by the hand remains motionless for many minutes, but fin activity begins again as soon as the hand is removed. Shaking or tapping the tank also produced momentary inhibition, and this agrees with the fact we have observed histologically, that fibres of the macula statica nerve end in the suboesophageal lobes.



Text-fig. 7. *Sepia*. Severance of both optic tracts and removal of supra-oesophageal lobes.

In *Sepia*, then, the suboesophageal centres, when isolated, can produce well-co-ordinated motor activity. The higher motor centres in this case therefore act by modifying and restraining this activity. The *Octopus* is more highly centralized, and no activity can go on without these higher motor centres. It would be interesting to find out whether this action of the fin centre of *Sepia* depends on a flow of afferent impulses. Certainly there are reflexes that affect the fin; touching its edge causes it to turn downwards and may produce a reversal of the beat of the opposite fin. It is impossible at present to say whether the continuous activity is the product of such reflexes or of some rhythmic action of the motoneurons themselves. The reflexes produced by touch usually stop the fin rather than promote its movement.

In life this movement of the fin is regulated by the action of the basal supra-oesophageal lobes, as is the walking of *Octopus*, but their action is inhibitory rather than excitatory. It has been possible in one or two cases to remove the lobus basalis anterior of *Sepia* on one side; the fins then begin to work continuously, in such a manner as to produce circling of the animal on its own axis (Text-fig. 8). The beats of the fin began on the operated side, thus driving the cuttlefish so that the intact side was at the periphery of the circle. We may regard this condition as the asymmetrical removal of the inhibition which the basalis anterior normally exercises over the fin beats. Removal of the lobe has the effect normally produced by impulses arriving from the optic lobe of one side, which may be presumed to remove the inhibition unilaterally, causing the animal to spin. Obviously we know too little at present to specify the details of the actions of the retinal and optic lobe influences. No doubt this explanation is very much too simple, for instance, in its assumptions about the nature of the discharges from the retina, but other operations in which the optic nerves and tracts were severed confirm that some balance of inhibition of the anterior basal lobes is maintained by the action of the optic lobes.



Text-fig. 8. *Sepia*. Removal of lobus basalis anterior of one side.

From such experiments we get the impression that an animal, whether it is *Octopus*, *Sepia* or any other, is provided with a delicate system of springs or drives that very readily set it into motion. The effect of a 'stimulus' is to allow a complicated set of nervous actions to begin, so that the movement which results continues for a considerable time, even after cessation of the original stimulus. During this time, therefore, the action is being produced, as it were, from within the organism. It is the function of the more elaborate nervous systems to allow such behaviour to be long and complicated. The large masses of nervous tissue found in higher animals have in part this very function of allowing sustained action under internal control. It is the purpose of studies of higher nervous centres to discover how this is achieved, and in particular how the patterns of sustained action come to have in a marked degree the quality of modifiability as a result of experience.

VIII. THE HIGHEST CENTRES OF CEPHALOPODS

In the case of the cephalopods the centres that control persistent action lie largely in the optic lobes and the uppermost of the supra-oesophageal centres. These include centres for the special receptor systems, optic, olfactory and tactile, and at the very top of the brain the lobus verticalis and lobus frontalis superior, which seem to be concerned jointly with several senses. The 'olfactory' lobes are very small centres on the optic stalk, the chemical sense seems to have little importance in *Octopus* and *Sepia*, at least as a distance receptor. The lobus frontalis inferior is the end-station of tactile and perhaps other skin receptors, especially those from the arms. It is larger in *Octopus* than in the decapods, and has an elaborately arranged structure, whose significance is obscure.

The optic lobes are enormous and of the greatest importance in behaviour, but will not be further considered here. Our information is mostly about the lobus verticalis and frontalis superior, which occupy the top of the supra-oesophageal mass and are readily accessible for experiment (Pl. 1). They do not respond to any form of electrical stimulation that we have been able to apply, including square waves of varied strength, duration and frequency. After their removal there are no obvious motor defects, but close study has shown that the animals then lose certain powers that they normally possess. Thus Sanders & Young (1940) showed that a *Sepia* without either lobus verticalis or frontalis superior is only able to attack prawns that remain within its field of vision. If the prey disappears out of sight, the operated animal no longer follows and hunts it, as a normal one will do. This suggests that these lobes can be in some way concerned with providing a system of action other than that dictated at the moment by the surrounding receptor situation. Without such an apparatus the animal cannot maintain action from within itself.

This influence of events of the past on those of the present is evidently the basis of much of what is commonly called learned behaviour, and we have therefore been interested to examine the influence of these uppermost parts of the cephalopod brain on the power of the animals to form associations. Past work on conditioning of these animals has been scarce, perhaps because of the difficulty of so arranging tanks as to allow properly controlled experiments. Most of the work is of little more than anecdotal value and none is quantitative. Ten Cate & ten Cate (1938) claimed that *Octopus* can learn to discriminate between plates of various shapes if these are associated positively or negatively with food.

IX. PROCEDURE

Each octopus was kept alone in a rectangular tank, with two or three bricks at one end, among which the animal usually lived, returning after attacking a crab. Crabs were lowered at the opposite end of the tank, attached to a black thread, the crab being kept moving gently. This movement is absolutely necessary; a crab which remains still, even in full view of an octopus, is not attacked. As soon as the moving crab appears, the octopus darkens, swims or walks swiftly down the tank, throws itself over the crab with arms and interbrachial membrane outspread, gathers up the prey and returns 'home'. The whole operation usually takes from 1 to 10 sec. With an octopus well habituated to the aquarium six and even more small crabs may be taken in a day.

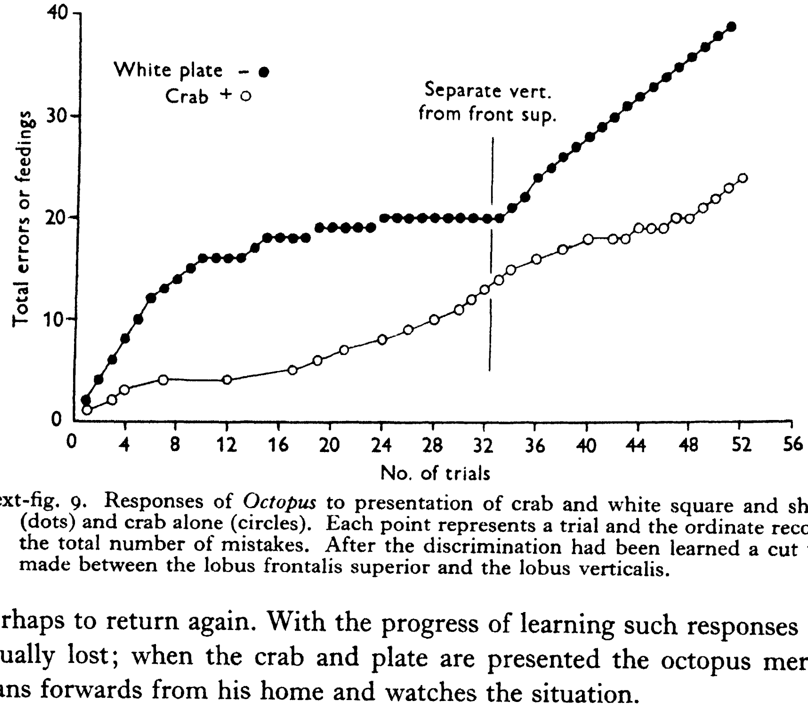
Training consists in presenting behind the crab some object to which a pair of electrodes is fixed. The electrodes are connected to a transformer, with a circuit so arranged that immediately the octopus grasps the crab an alternating current of 8 V. can be switched on. Switching off after a few seconds is necessary, since the animal is sometimes unable to release its hold on the electrified plate. After receiving such a shock the animal usually pales and moves quickly back to the bricks at the other end of the tank, often blowing jets of water over his arms and drawing the most affected ones across the oral region.

The procedure is to expose the octopus to the noxious situation three times a day and to allow it to take food an equal number of times. These negative and positive trials are systematized + − − + + − one day; the next − + − − + +, then + − + − − + and so on, so that only once in 7 days is the animal exposed to the same combination of trials. Trials are at about 2-hourly intervals, and the animal is exposed to each situation for 2 min.

It would be possible to use this method to test the powers of discrimination in many situations, but for the present we have mostly preferred to train the animals to distinguish between a white square of 5 cm. plus a crab and a crab alone, the former being the negative situation. We have also formed discriminations between plates painted red and white.

With this technique the octopus quickly learns that one situation is noxious and that another is not (Text-fig. 9). The plate in itself does not act as a deterrent; indeed, most of the experiments were begun by allowing the animal to feed a few times, without shock, from the plate. When the first shock is received the animal drops the crab and returns to its home. Sometimes there may be a second and third attack during the 2 min. of the trial, but in succeeding trials the number of attacks decreases rapidly (Text-fig. 9).

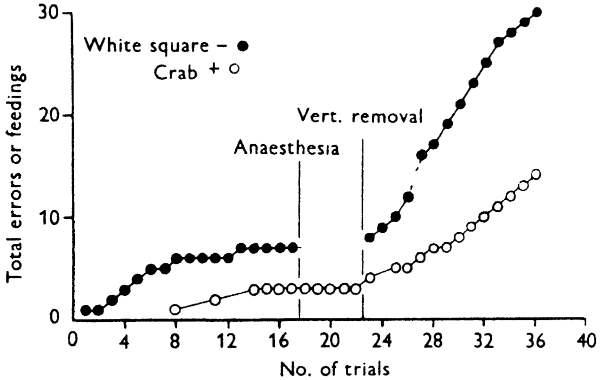
In the trials after receiving the shock the octopus usually advances down the tank with arms outstretched and half encircling the crab and the plate, presenting a picture of an intense internal strain; one force drives the animal to seize the food, while a second force, deriving in some way from previous experience of the situation, holds it back. The octopus may stay swaying a little backwards and forwards for many seconds, sometimes putting out an arm as if to pick the crab off the plate, sometimes retiring, perhaps to return again. With the progress of learning such responses are usually lost; when the crab and plate are presented the octopus merely leans forwards from his home and watches the situation.



Text-fig. 9. Responses of *Octopus* to presentation of crab and white square and shock (dots) and crab alone (circles). Each point represents a trial and the ordinate records the total number of mistakes. After the discrimination had been learned a cut was made between the lobus frontalis superior and the lobus verticalis.

The discrimination between the positive and negative situation is usually made very readily, and there is little or no disturbance of the normal feeding reaction to the crab presented alone, though attacks may show 'caution' for the first trials after a shock has been received; sometimes there is for an initial period a generalized inhibition of feeding, lasting for a shorter (Text-fig. 9) or longer time (Text-fig. 10). The great rapidity with which the conditioning is established may perhaps be an indication that the situation is not very remote from those normally occurring in the life of the animal. The stings of anemones associated with hermit crabs produce in the octopus a reaction very similar to that given by the electric shock. An octopus that has been stung in this way afterwards reacts to the hermit crab and anemone by a cautious approach similar to that we have seen to the white plate.

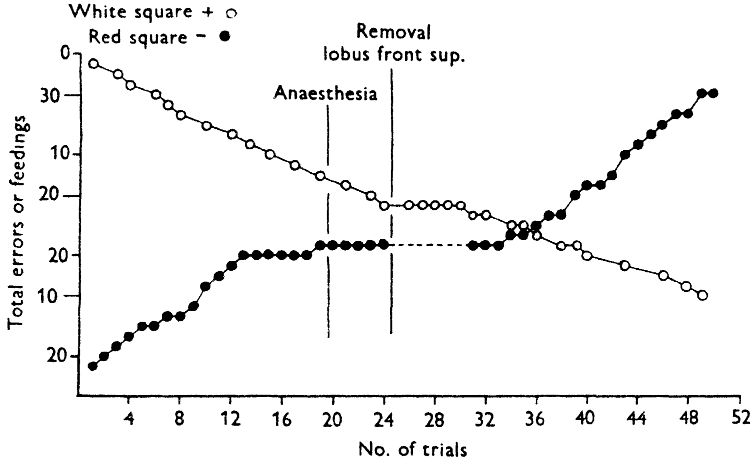
We have not yet made systematic studies of the time for which the learning is retained. Anaesthesia with 2% urethane does not produce a loss of learning, nor does the shock of falling a metre and a half to the ground. The most that occurs in either case is a disturbance of the speed of attack in the positive situation for an hour or two, or perhaps a refusal to attack for one or two trials. After removal of the lobus verticalis (Text-fig. 10) or severance of its connexions with the lobus frontalis superior (Text-fig. 9), the inhibition to attacking the crab and the white plate completely disappears. One hour after the operation an animal that had not attacked the white plate for many trials did so within a few seconds of presentation, and afterwards proved quite unable to learn not to do so, often attacking two, three and even four times during the 2 min. period.



Text-fig. 10. Situation as for Text-fig. 9. The shock produces a generalized inhibition, which is not affected by urethane anaesthesia, but disappears after removal of the lobus verticalis.

The operated animal therefore attacks the crab and plate, which when normal he had learned to leave alone; for the first attack in each trial he does not show any signs of 'caution' in his approach. Further attacks in the *same* trial may show suggestions of a rather more cautious approach, such as touching the plate with outstretched arms instead of embracing it. In other cases only one attack was made in each trial, the condition set up by the shock being able to hold the animal inhibited for most or all of the 2 min. period, though the inhibition did not last over the 2 hr. until the next trial. The fact that the operated animals did not persistently attack throughout the 2 min. period shows that some powers of learning are found in the parts of the nervous system left intact, and this residual plasticity is worth careful investigation. However, the experiments show decisively that the power to retain the inhibition for long periods depends in some way on the action of the lobus verticalis and frontalis superior, perhaps on the interactions between them. It is not, of course, possible to specify the effect of the removal exactly, since two factors are involved: (1) discrimination of the two situations and (2) inhibition of reaction to one of them. The experimental results do not exclude the possibility that the lobes of the verticalis complex are necessary for (1) and not for (2).

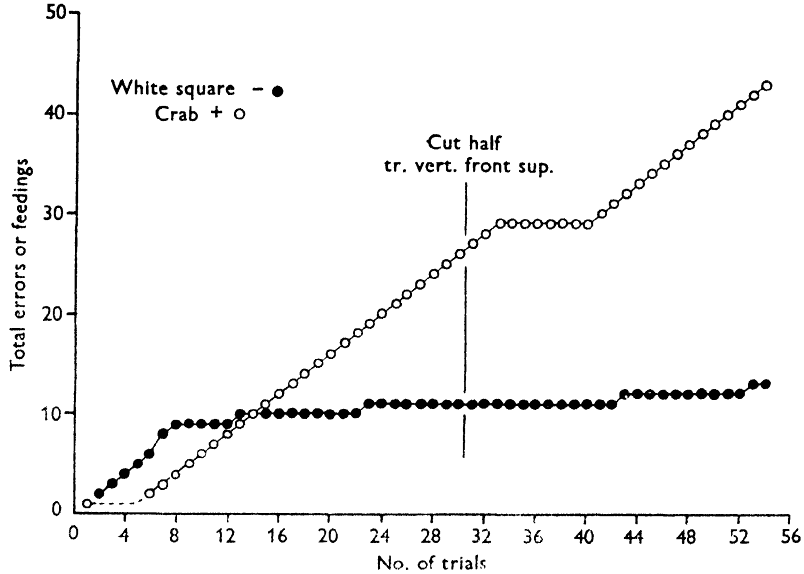
A lesion in which the lobus frontalis superior alone was removed abolished the learned inhibition to the crab and white plate (Text-fig. 11), but in some cases a new factor enters here. For a period of about 36 hr. after operation some of the octopuses would not attack, though sufficiently active to climb out of the tank. After this period the animal began to attack both positive and negative situations regularly, proving unable to learn the discrimination. In another preparation, where the frontalis superior had been removed, the octopus only attacked 5 times (2 – and 3 +) in forty-eight trials, although 8 days after operation it appeared as strong and healthy as a normal animal. Evidently interference with these highest lobes may produce a variety of changes in the drives that actuate the animal.



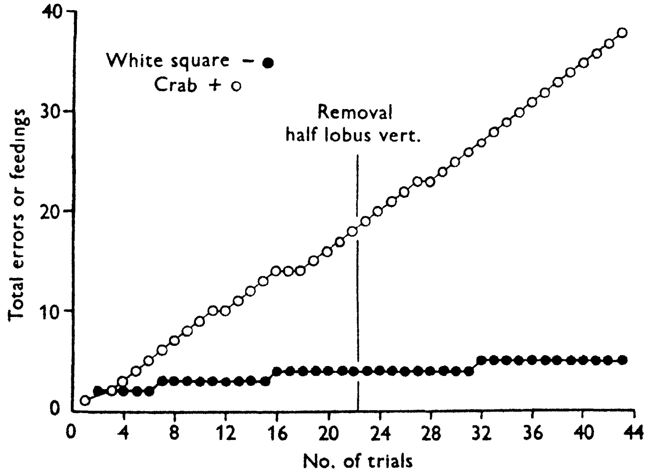
Text-fig. 11. Responses of *Octopus* to presentation of crab and white square (dots) and crab, red square and shock (circles). The animal learns the discrimination, which is not affected by anaesthesia. After removal of the lobus frontalis superior there is at first a generalized lack of response and then failure of discrimination. Total mistakes are shown on the ordinate as scales running in opposite directions.

Operations in which other lobes were removed did not produce interference with the learned inhibition. For instance, there was no loss after removal of the lobus frontalis inferior, which is probably the main centre for tactile impulses from the arms. Interruption of about half of the connexions between the frontalis superior and verticalis lobes does not destroy the learned inhibition (Text-fig. 12), which also remains after removal of half of the lobus verticalis (Text-fig. 13), but exact studies of the effects of partial removal have not been completed.

It is not possible to say much at present about the way in which the system may act to enable learning to take place. The cells and fibres of these two highest centres of the nervous system are very different from those of any other part, and the two lobes differ from each other. The neuropil of



Text-fig. 12. Effect of severance of half of tract between lobus frontalis superior and lobus verticalis. Discrimination between crab and white square and shock (dots) and crab alone (circles). After operation there was some generalized interference with response, but the power to perform the discrimination was retained. Plotting as Text-fig. 9.



Text-fig. 13. Absence of effect of removal of half of lobus verticalis. Discrimination between white square and crab and shock (dots) and crab alone (circles). Plotting as Text-fig. 9.

frontalis superior consists of interlacing bundles of fibres, running in a very regular manner in layers (Pl. 2). Some of these layers include the optic fibres, others those from the tactile centres, and in *Sepia* there is certainly a recurrent bundle of fibres from the verticalis to the frontalis superior. We cannot say how these closely woven bundles of nerve fibres act upon each other, but it seems clear that the frontalis superior provides in some way for the interaction of impulses from various receptor sources.

The verticalis neuropil differs even more widely from that of other parts of the central nervous system (Pl. 2). It is a relatively very large mass of tissue, filled with the processes of the cell bodies that lie round the edge and their collaterals. Intermingled with these are fibres coming from the frontalis superior. In *Octopus* the surface of the lobus verticalis is folded, increasing the number of cells and the amount of neuropil, but no differences have yet been discovered between the structure and connexions in the various subdivisions produced by these folds. There are interesting differences in the structure of the neuropil of these lobes in different cephalopods, and we hope to obtain further information by correlating these with differences in behaviour.

The experiments suggest that in some way this system of cells and fibres is able to produce the restraint that prevents the primary effect of influence coming from the eyes through the optic lobe. These influences would normally throw the animal into action by their effect on the lobus basalis anterior and other centres. After training, this action is restrained by the verticalis complex, by an action either on the optic lobes or on the underlying basal lobes.

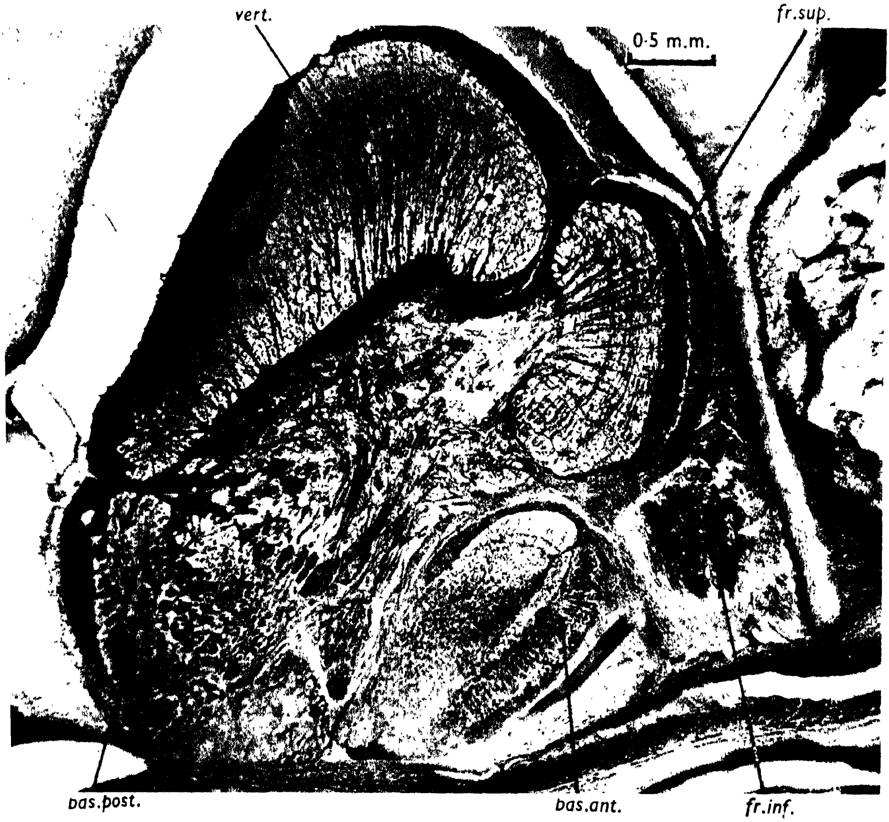
It is possible that these verticalis lobes are involved in many further types of action, perhaps not only inhibitory, and it is too early yet to be able to make any more detailed analysis. Evidently very complicated mutual interactions and balanced systems are involved in the operation of the nervous system. It is interesting to notice the way in which increasing complexity of behaviour accompanies the emergence of anatomically distinct regions of the brain, literally above the lower motor centres that produce the simpler reflex behaviour.

In the simpler types of nervous system motor centres produce the actions of the animal by the interplay of afferent impulses on the motor cells, which may perhaps themselves have the power to produce certain rhythmic actions such as those of respiration and swimming. The appearance of more elaborate behaviour depends on the development of the controlling element of such systems to form separate higher centres, which thus come to guide and inhibit the lower motor centres, producing elaborate patterns of action. In cephalopods, as in vertebrates, there has been increasing assumption of higher control. Thus in *Sepia* the higher motor centres seem to be mainly inhibitory, whereas in *Octopus* they are responsible for elaborating the whole pattern of action; the lowest centres can do little without them. Presumably these higher nervous centres are produced by exaggeration of sets of cells that were already there before. When we know more about the action as well as the evolution of the parts of the cephalopod nervous system, we may be able to follow how each higher level has arisen out of that below it. Thus the basal supra-oesophageal centres seem to act, in *Sepia* at least, by inhibiting the tendencies of the lowest motor centres. Action then results when this inhibition is removed by impulses arriving from the retina through the optic lobes. But this removal of inhibition, letting the motor system go into action, may itself have to be restrained, and to do this is the function of the still higher centres of the verticalis complex. It may well be that their action is to inhibit tendencies set up in the optic lobes to disinhibit the motor system. Such a complicated analysis may seem fantastic, but there is enough evidence to suggest that it is approximately correct. The balance of tendencies within the nervous system is certainly very complicated. It is based on simple receptor and reflex motor systems (perhaps sometimes giving 'spontaneous' action) that go into action readily. Co-ordinating or higher motor centres restrain the lower reflexes individually and allow their organization into elaborate patterns of action under the influence of higher receptor systems, such as are often associated with the eyes. Still higher systems then enable the animal to restrain such of those reactions as may have been associated with 'undesirable' consequences in the past, for instance, the attack on a crab plus a white plate. These highest centres are therefore the part of the nervous system that allows the animal to learn in this way, and if our analysis is correct we may justifiably look to them when we are seeking for the nature of the changes that constitute learning. But it does not by any means follow that we should expect to find the characteristic tissue *only* in these centres. If it is true that they have evolved out of parts less specialized, we may find that similar powers of learning are quite widely dispersed in the nervous system, and, indeed, that individual types of learning can involve action at several levels. Thus, an octopus from which the verticalis complex has been removed is not totally unable to learn. It does not attack a crab persistently and continually after receiving a shock. If the mechanism provided by the optic lobes were completely rigid, it would lead to the situation 'seizure of crab' whenever a suitable configuration occupied the visual field. What actually happens is that after a shock the operated octopus retreats to its home. It may advance again one or several times within the 2 min. we have studied it, but obviously it still possesses some power of modification of behaviour in the light of experience. It will clearly be worth while to study this residual learning power closely and to find out whether it differs from that which is associated with the verticalis complex only in that it is retained for a shorter time, or also in other ways.

X. THE CHANGES RESPONSIBLE FOR LEARNING

The highest centres in the octopus, as in vertebrates and arthropods, contain many small neurons. This finding is such a commonplace, that we have perhaps failed in the past to make the fullest inquiry into its implications. Many of these small cells possess numerous processes, but no axon. It is difficult to see, therefore, that their function can be conductive in the ordinary sense. Most of our ideas about nervous functioning are based on the assumption that each neuron acts essentially as a link in some chain of conduction, but there is really no warrant for this in the case of cells with many short branches. Until we know more of the relations of these processes to each other in the neuropil it would be unwise to say more. It is possible that the effective part of the discharge of such cells is not, as it is in conduction in long pathways, the internal circuit that returns through the same fibre, but the external circuit that enters other processes, like or unlike (Libet & Gerard, 1941; Brooks & Eccles, 1947). The fact that such small neurons are characteristic of the higher centres, whose activity is such as to be modified by experience, suggests that in some way the groups of these small cells, or the fibrous networks made up by their processes, are able to be modified by the action taking place in them. It would, of course, be a great step forward if we could discover the nature of this modification—it must be some change that can happen readily—learning may take place with one or a few repetitions—and which lasts for a considerable but not indefinite time. The requirements would be formally met by a system in which some pattern of activity is dynamically maintained. In 1938 it was suggested tentatively that cyclical re-excitation, such as is allowed for by the connexions of the verticalis and the frontalis superior of cephalopods, might provide the necessary basis (Young, 1938). It is perhaps difficult to believe that such simple reverberating circuits would continue in phase for anything like the necessary length of time. It is still an open question whether any similar dynamic process is involved, or whether the learning depends on some more definitely structural change, some modification of the orientation of the elements of the system. Thus the clue that these centres contain large numbers of small fibres does not take us very far at present. It may be that something can be learned from the distribution of similar small-celled formations in the lower centres. Comparative study at least provides us with a set of variants of learning capacity and structure as natural experimental material, by means of which the problem can be attacked.

For explanation see p. 453



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EXPLANATION OF PLATES

PLATE 1

Sagittal section of whole central nervous system of *Octopus vulgaris*, stained with Cajal's method. *bas. ant.* basalis anterior; *bas. post.* basalis posterior; *br.* brachialis; *bucc.* buccalis; *fr. inf.* frontalis inferior; *fr. sup.* frontalis superior; *oes.* oesophagus; *pall.-v.* pallioviscerali s; *ped.* pedalis; *vert.* verticalis.

PLATE 2

Lobus verticalis and frontalis superior of *Sepia*. Abbreviations as for Pl. 1.

IN SEARCH OF THE ENGRAM

By K. S. LASHLEY

Harvard University and the Yerkes Laboratories of Primate Biology

I. INTRODUCTION

'When the mind wills to recall something, this volition causes the little [pineal] gland, by inclining successively to different sides, to impel the animal spirits toward different parts of the brain, until they come upon that part where the traces are left of the thing which it wishes to remember; for these traces are nothing else than the circumstance that the pores of the brain through which the spirits have already taken their course on presentation of the object, have thereby acquired a greater facility than the rest to be opened again the same way by the spirits which come to them; so that these spirits coming upon the pores enter therein more readily than into the others.'

So wrote Descartes just three hundred years ago in perhaps the earliest attempt to explain memory in terms of the action of the brain. In the intervening centuries much has been learned concerning the nature of the impulses transmitted by nerves. Innumerable studies have defined conditions under which learning is facilitated or retarded, but, in spite of such progress, we seem little nearer to an understanding of the nature of the memory trace than was Descartes. His theory has in fact a remarkably modern sound. Substitute nerve impulse for animal spirits, synapse for pore and the result is the doctrine of learning as change in resistance of synapses. There is even a theory of scanning which is at least more definite as to the scanning agent and the source of the scanning beam than is its modern counterpart.

As interest developed in the functions of the brain the doctrine of the separate localization of mental functions gradually took form, even while the ventricles of the brain were still regarded as the active part. From Prochaska and Gall through the nineteenth century, students of clinical neurology sought the localization of specific memories. Flechsig defined the association areas as distinct from the sensory and motor. Aphasia, agnosia and apraxia were interpreted as the result of the loss of memory images, either of objects or of kinaesthetic sensations of movements to be made. The theory that memory traces are stored in association areas adjacent to the corresponding primary sensory areas seemed reasonable and was supported by some clinical evidence. The extreme position was that of Henschen, who speculated concerning the location of single ideas or memories in single cells. In spite of the fact that more critical analytic studies of clinical symptoms, such as those of Henry Head and of Kurt Goldstein, have shown that aphasia and agnosia are primarily defects in the organization of ideas rather than the result of amnesia, the conception of the localized storing of memories is still widely prevalent (Nielsen, 1936).

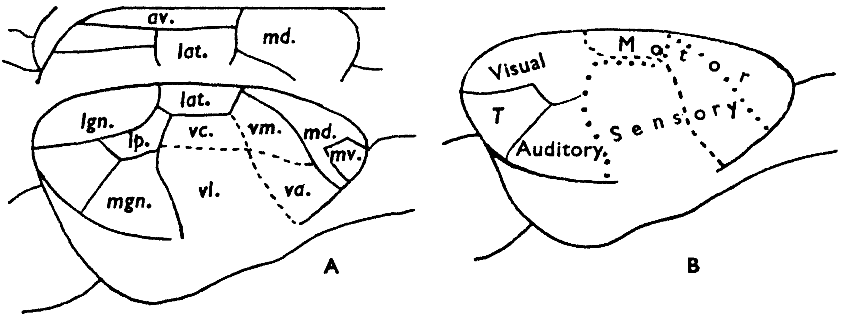
While clinical students were developing theories of localization, physiologists were analysing the reflex arc and extending the concept of the reflex to include all activity. Bechterew, Pavlov and the behaviourist school in America attempted to reduce all psychological activity to simple associations or chains of conditioned reflexes. The path of these conditioned reflex circuits was described as from sense organ to cerebral sensory area, thence through associative areas to the motor cortex and by way of the pyramidal paths to the final motor cells of the medulla and cord. The discussions of this path were entirely theoretical, and no evidence on the actual course of the conditioned reflex arc was presented.

In experiments extending over the past 30 years I have been trying to trace conditioned reflex paths through the brain or to find the locus of specific memory traces. The results for different types of learning have been inconsistent and often mutually contradictory, in spite of confirmation by repeated tests. I shall summarize to-day a number of experimental findings. Perhaps they obscure rather than illuminate the nature of the engram, but they may serve at least to illustrate the complexity of the problem and to reveal the superficial nature of many of the physiological theories of memory that have been proposed.

I shall have occasion to refer to training of animals in a variety of tasks, so shall give a very brief description of the methods used. The animals studied have been rats and monkeys with, recently, a few chimpanzees. Two lines of approach to the problem have been followed. One is purely behavioural and consists in the analysis of the sensory excitations which are actually associated with reactions in learning and which are effective in eliciting the learned reactions. The associated reactions are similarly analysed. These studies define the patterns of nervous activity at receptor and effector levels and specify certain characteristics which the memory trace must have. The second approach is by surgical destruction of parts of the brain. Animals are trained in various tasks ranging from direct sensori-motor associations to the solution of difficult problems. Before or after training, associative tracts are cut or portions of the brain removed and effects of these operations on initial learning or postoperative retention are measured. At the termination of the experiments the brains are sectioned and the extent of damage reconstructed from serial sections. The brains are also analysed for secondary degeneration, so far as available histological methods permit.

II. ELIMINATION OF THE MOTOR CORTEX

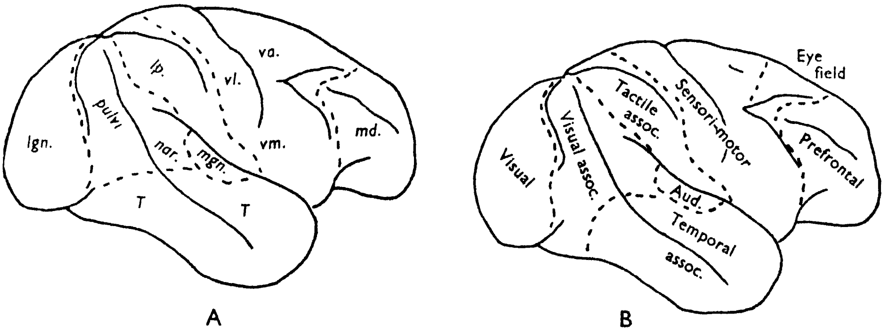
I first became sceptical of the supposed path of the conditioned reflex when I found that rats, trained in a differential reaction to light, showed no reduction in accuracy of performance when almost the entire motor cortex, along with the frontal poles of the brain, was removed. This observation led to a series of experiments designed to test the part played by the motor cortex or Betz cell area in the retention of various habits. The matter can be tested either by removing the motor cortex or by severing its connexions with the sensory areas of the brain. Both methods have been used with the rat and the monkey.



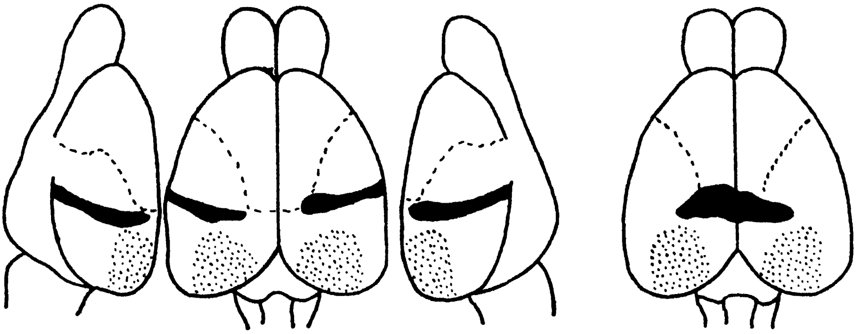
Text-fig. 1. Functional divisions of the rat's brain. A. The projection fields of the principal thalamic nuclei. *av.* anteroventral; *lat.* lateral; *lgn.* lateral geniculate; *lp.* lateral, pars posterior; *md.* median dorsal; *mgn.* median geniculate; *mv.* median ventral; *v.* the various divisions of the ventral nucleus. The projection fields of the median nuclei (*md.*, *mv.*) correspond to the prefrontal areas of primates. B. Location of visual, auditory, and overlapping sensori-motor areas (after Lashley, 1944). The region marked T is probably homologous with the temporal association area of primates.

The sensory and motor areas of the brains of these animals have been mapped by anatomic methods and by electric stimulation. Text-fig. 1 shows the principal areas of the rat's brain, the separate auditory and visual areas and the overlapping sensory and motor areas. Text-fig. 2 is a composite from several sources of the chief sensory and motor areas of the brain of the macaque monkey.

Incisions were made through the cortex and underlying fibres of the rat's brain such as to sever the visual areas more or less completely from the motor regions of the brain. The rats were then trained in what I have called the conditional reaction. They are taught to jump to a white triangle and to avoid a white × when both figures are on a black background, but to choose the × and avoid the triangle, if the background is striped; the direction of choice is conditional upon the character of the background. This is the most difficult visual generalization that we have been able to teach the rat. Animals with incisions like those shown in Text-fig. 3, which practically separate the motor regions from the visual, were able to learn this reaction as quickly as did normal controls (Lashley, 1942*b*).



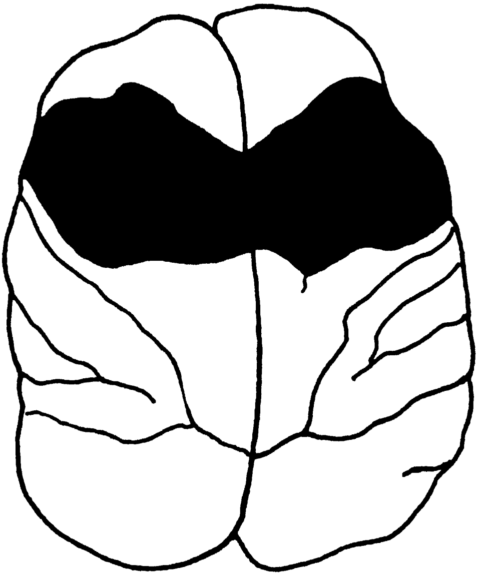
Text-fig. 2. Functional divisions of the monkey's brain. A. The projection of the principa thalamic nuclei. Abbreviations as in Text-fig. 1. The homologies between the divisions of the ventral and lateral nuclei are uncertain. B. Location of functional areas.



Text-fig. 3. Lesions partially separating the visual area (stippled) from the motor areas (outlined by dashes) of the rat's brain without disturbing visual learning.

Monkeys were trained to open various latch-boxes. The motor areas were then removed, as shown in Text-fig. 4. Note that these lesions involved both the Betz cell area and the premotor area, including parts of the eye fields around the arcuate sulcus. This operation produces a temporary paralysis, but after 8–12 weeks this paralysis recovers to such an extent that the animals are capable of the movements required to open the boxes. During this recovery period they did not have access to the training boxes. When sufficiently recovered, they were tested and opened the boxes promptly without random exploratory movements. The tasks require both a visual recognition of the latches and semi-skilled movements, such as turning a crank. Removal of the motor areas did not produce a loss of memory for the movements (Lashley, 1924). Jacobsen has since confirmed these observations with a chimpanzee from which the motor cortex was removed (Jacobsen, 1932).

These experiments seem to rule out the motor cortex or Betz cell area as containing any part of the conditioned reflex arc. The traditional view of the function of this area regards it as the region of final integration of skilled voluntary movements. My own interpretation, to which few neurologists would subscribe, is that it has no direct concern with voluntary movement, but is a part of the vast reflex postural system which includes the basal nuclei, cerebellar and vestibular systems. Certainly there is no evidence that it forms a part of the conditioned reflex circuit.



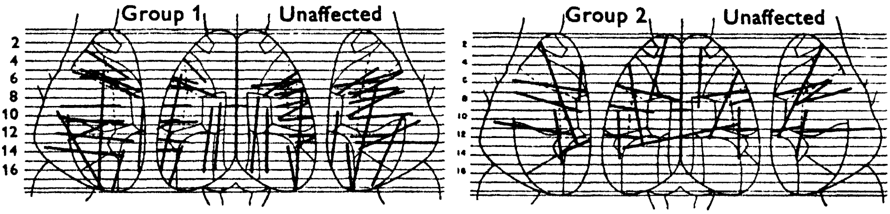
Text-fig. 4. Extent of cortical lesion which did not abolish latch-box habits. The lesion is bounded caudally by the central fissure and extends forward to include the arcuate sulcus.

For the rat the experiments rule out the whole frontal region of the brain from participation in visual habits. In the monkey there remains another possibility. The so-called visual associative area (area 18) has direct connexion with the cortex of the arcuate sulcus (area 8), and this in turn with the premotor cortex (area 6). This last area is also motor and perhaps equivalent in function with the Betz cell area (Bucy, 1934). The cortex of the arcuate sulcus and of a considerable surrounding area was removed from five monkeys that had been trained in a variety of visual discriminative reactions. After the operations they showed perfect retention of all their visual habits (Lashley, 1948). Jacobsen (1932) has reported loss of certain latch-box habits in monkeys after removal of area 6, but there are indications that this may be a kinaesthetic-sensory area (Walker, 1938; Gay & Gelhorn, 1948), and the loss cannot be ascribed to disturbance of its function as a final common motor path. I have removed it in combination with area 4 without disrupting motor habits (Lashley, 1924).

I have occasionally seen the type of defect reported by Jacobsen after prefrontal lobe lesions, as also reported by Kennard (1939), but it has not occurred consistently and its occurrence remains unexplained. I did not find it after removal of area 6 in conjunction with the Betz cell area.

III. TRANSCORTICAL CONDUCTION

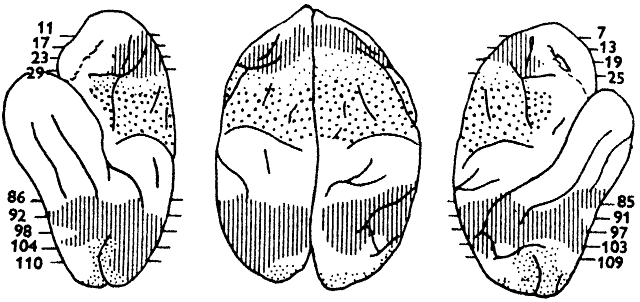
There is evidence, not only that the motor cortex does not participate in the transmission of the conditioned reflex pattern, but also that the transmission of impulses over well-defined, isolated paths from one part of the cortex to another is inessential for performance of complicated habits. The maze habit of the rat almost certainly involves the utilization of several sensory modalities, visual, tactile and kinaesthetic. In a rather complicated set of experiments I attempted to test the importance of connexions across the cortex for maze performance. Rats were trained on the maze, then knife cuts were made through the cortex and underlying fibres, separating different functional areas or cutting through functional areas. The incisions were long, averaging half of the entire length of the cerebral hemispheres. After recovery the animals were tested in retention of the maze habit. In other experiments the incisions were made before training and their effect upon the rate of initial learning was tested. In neither initial learning nor in retention could any certain effect of separating the various parts of the cortex be demonstrated. If the incisions interrupted sensory tracts to the cortex, there was loss of the habit, but uncomplicated separation of cortical areas produced no effect on performance. Text-fig. 5 gives composite



Text-fig. 5. Composite of incisions through the cortex of the rat which did not disturb maze learning (Group 1) or retention (Group 2). One pair of lines, roughly symmetrical in the two hemispheres, represents the lesion in each animal studied (after Lashley, 1944).

diagrams of incisions which were without effect on maze performance (Lashley, 1944).

Both the anatomic evidence of Le Gros Clark (1941) and the physiological evidence from strychninization of the cortex (Bonin, Garol & McCulloch, 1942) shows that the primary visual area has direct axon connexions only with the immediately adjacent cortex. In experiments which I shall report in more detail in considering the function of associative areas, I removed the greater part of this band of cortex surrounding the visual areas from five monkeys that had been trained in a variety of visual habits (Text-fig. 6). This operation almost certainly destroyed all the relay connexions across the cortex from the macular fields. It produced no loss of visual habits based on discrimination of the colour, brightness, or form of objects (Lashley, 1948).

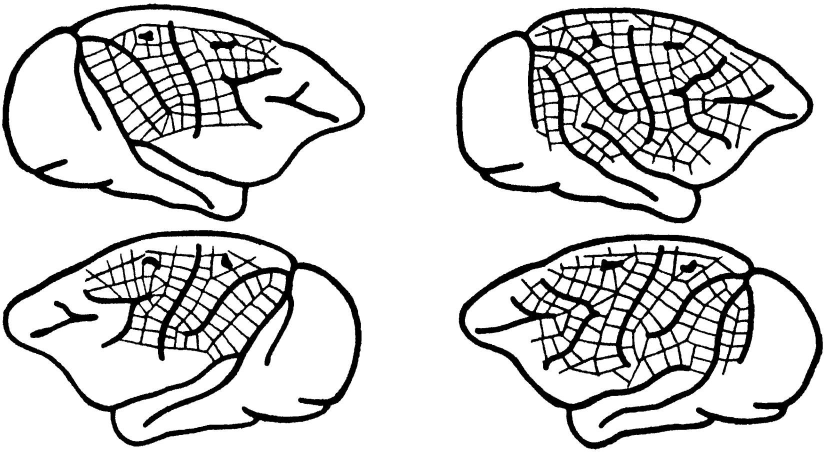


Text-fig. 6. Lesions, marked by hatching, which destroyed the greater part of the so-called visual associative areas in a monkey without affecting visual functions.

Miss Wade trained monkeys in habits which are abolished by destruction of the frontal lobes and which require visual, tactile and kinaesthetic adjustments. I cut the transcortical fibres of the frontal lobes in these animals, leaving only the projection fibres for the area. There was no disturbance of performance after the operations (unpublished experiments).

Such results are certainly puzzling. They leave us with almost no understanding of the function of the associative fibres which extend across from one part of the cortex to another. The results are difficult to accept, yet they are supported by various other lines of evidence. Smith (1947) and Akelaitis (1944) have reported careful studies of human patients in whom the corpus callosum (the great commissure of fibres connecting the two hemispheres) had been severed in an effort to stop the spread of Jacksonian epilepsy. These investigators were not able to demonstrate any effects of the operation except a slight slowing of reaction time, which was equally great, whether the reaction was on the same or opposite side of the body to that stimulated. Sperry (1947) has divided the arm motor and sensory areas of the monkey's brain into a number of small square divisions (Text-fig. 7) by careful subpial section. Although the operations were intended to sever only the intrinsic fibres of the cortex, they actually destroyed most of the longer loop fibres as well. Such animals do not show any postoperative inco-ordination of the movements of the different segments of the arm and use the arm efficiently in the performance of habitual movements.

It is difficult to interpret such findings, but I think that they point to the conclusion that the associative connexions or memory traces of the conditioned reflex do not extend across the cortex as well-defined arcs or paths. Such arcs are either diffused through all parts of the cortex, pass by relay through lower centres, or do not exist.



Text-fig. 7. Pattern of incisions in the motor and sensory areas of two monkeys which did not produce inco-ordination of movements (after Sperry, 1947).

There is the possibility that the chief associative connexions between functional areas of the cortex are by connexions through the thalamus. I doubt this for two reasons. The techniques that have been used to demonstrate cortical efferents to the thalamus, the Marchi stain and strychninization of the cortex, are unreliable indices of the direction of fibres. The supposed cortico-thalamic fibres follow the paths of the afferent fibres and may not be efferent. Secondly, in the rat at least there is little evidence of an elaborate system of intrathalamic association fibres. After a cortical injury thalamic nuclei degenerate completely without leaving a residue of internuncial cells. The question of the importance of intrathalamic association is not settled, and none of the available anatomic or physiological techniques is capable of giving conclusive evidence.

A few experiments by Ingebritsen (1933) on the spinal cord suggest that the essential pattern of a learned reaction can be transmitted by a diffuse nervous network. Ingebritsen made double hemisections of the spinal cord of rats, severing one-half at the second, the other at the fifth cervical level. These lesions cut all long fibres connecting the brain with the spinal motor centres of the limbs. Nevertheless, such rats retained maze-habits and were able to learn to operate latch-boxes requiring that they rise on the hindfeet and depress a lever with the forepaws (Pl. 1). There are no long fibres, either sensory or motor, crossing over between the two levels of these sections. Habit patterns cannot be acquired by the isolated spinal cord (Kellogg, Deese, Pronko & Feinberg, 1947). Somehow, the control of the motor pattern essential for the performance of the complex acts traverses the network of short internuncial cells of the spinal cord.

IV. THE PROBLEM OF THE 'ASSOCIATION AREAS'

In anatomic theories of the memory trace the association areas of the cortex have played a major part. Frontal, parietal, occipital and temporal associative areas have been distinguished as regions of the cortex, relatively lacking in massive connexions with the lower centres of the brain. On the basis of some clinical evidence, but chiefly because of their anatomic relations, these areas have been considered as associative and as the storehouses of memory images of sensations derived from the adjacent sensory areas. Thus areas 18 and 19 of Brodmann's questionable divisions have been called the visual associative areas, areas 5 and 7 tactile associative, and areas 20, 21 and 22 of the temporal lobe the auditory association areas. The prefrontal area was considered by Hitzig to be a higher integrative region because he believed that it showed the greatest evolutionary growth in the primate brain. Special memory functions were also ascribed to it, however.

S. I. Franz reported that the removal of the frontal association areas of cats destroyed recently formed habits but left old, well-established habits unaffected (Franz, 1907). The actual observation was that the cats lost their habits of opening latch-boxes but would still come when called. His operations destroyed much of the motor areas as well as the prefrontal cortex. I later trained monkeys on latch-boxes and removed the prefrontal cortex, in an experiment designed to test the influence of the operation on learning ability. During the period allowed for recovery one of the animals found the experimental boxes piled in the corner of the room and promptly opened them. Tests of the other animals showed perfect retention of the manipulative habits. There was no indication that the recently acquired habits had been lost. Jacobsen took up the problem at this point and carried it further. He found that visual discriminative habits and simple habits of latch-box manipulation are unaffected by loss of the prefrontal association areas. Habits requiring a series of acts, such as opening a box with several independent latches, may be lost. This is not, however, a simple removal of memory traces. The animals are incapable of relearning the functions which they have lost. They fail because of a difficulty in going on from one task to the next, not from loss of memory of the individual items of the task (Jacobsen, 1936).

Loss of the delayed reaction after removal of the prefrontal lobes of the monkey has been interpreted as a loss of immediate memory. However, this task and others, which are affected by prefrontal injury, all involve a series of conflicting actions. Difficulty in maintaining a constant set or attitude is the real basis of the loss. Such an interpretation fits better with clinical findings than does the hypothesis of memory defect.

We have recently been testing the relation of other associative areas to memory functions in the monkey. Five spider monkeys were trained on a variety of visual tasks. A band of cortex surrounding the primary visual areas and including the visual associative areas of Campbell and Brodmann was then removed (Text-fig. 7), and the animals were tested for retention of habits based on discrimination of colours, of geometric forms, and of a number of familiar objects, such as visual recognition of their home cages, of the caretaker, and the like. No loss of any visual memories could be demonstrated (Lashley, 1948).

Similar experiments with habits of tactile discrimination are now being completed. The monkeys are required to reach through a hole in a partition and to distinguish variously shaped covers of food dishes by touch alone. They learn readily such tasks as to choose a cylinder and reject a prism, if both are smooth, but to choose the prism, if both are coated with sandpaper. When they had reached a standard criterion of accuracy, the parietal associative areas (Brodmann's areas 5 and 7) were removed. No animal has shown significant loss of the habits based on tactile discrimination after removal of these areas alone (Dr Josephine Blum).

Removal of the lateral surfaces of the temporal lobes alone has also not affected visual or tactile habits.

A number of experiments with the rat have shown that habits of visual discrimination survive the destruction of any part of the cerebral cortex except the primary visual projection area. Similarly for auditory habits and the auditory cortex. There is no indication of specialized memory areas outside the primary sensory fields. Although there are not clearly distinguished associative areas in the rat's cortex, I have become somewhat sceptical of the existence of any great difference in the extent of associative areas, as between the rat and monkey. The best anatomic index that we have of the functional differentiation of a cortical area is its connexions with the thalamus. The prefrontal cortex of man is the projection field of the dorsomedial and ventromedial nuclei. The corresponding nuclei in the rat's thalamus project to a large frontal region, perhaps proportionately as large as the prefrontal lobes of man (Lashley, 1941). This region also includes the electrically excitable points for the head and part of that for the forelegs. It has therefore been classed as motor, but it is equally justifiable to class it as corresponding to the human prefrontal cortex.

It has been claimed that the differentiation of a number of cerebral areas contributes to man's superior intelligence by avoiding confusion of functions, but, if the anatomic relations in man and the rat were reversed, it would be concluded with equal assurance that, because intellectual activity requires close integration of different functions, the advantage lies with the brain in which functional areas are not sharply set off. Such *post hoc* arguments based on anatomic grounds alone have little value for functional interpretations. Many current conceptions of cerebral physiology are based upon just such dubious inferences from anatomic data.

The outcome of the experiments involving removal of the associative areas of the monkey was unexpected, in spite of the fact that it confirms the earlier results with the rat. The conclusion, which seems to be forced by the accumulated data, runs counter to the accepted tradition concerning the organization of the cerebral cortex. Memory traces, at least of simple sensori-motor associations, are not laid down and stored within the associative areas; at least not within the restricted associative area supposedly concerned with each sense modality. Memory disturbances of simple sensory habits follow only upon very extensive experimental destruction, including almost the entire associative cortex. Even combined destruction of the prefrontal, parietal, occipital and temporal areas, exclusive of the primary sensory cortex, does not prevent the animal from forming such habits, although pre-existing habits are lost and their reformation is greatly retarded.

These results, showing that the so-called associative areas are not essential to preservation of memory traces, have been obtained with rats and monkeys. Is there a greater cortical differentiation in anthropoid apes and man? We have experimental data only on the prefrontal associative cortex of the chimpanzee and of man. Bilateral removal of the entire prefrontal granular cortex in five chimpanzees in our laboratory has not resulted in any memory defect. One two-year-old animal, lacking prefrontal and parietal areas, removed in early infancy, falls well within the normal range in all aspects of development. Adult chimpanzees, trained in such complicated habits as choosing an object, like a model shown, retain the habits after removal of the entire prefrontal cortex. We have not been able to demonstrate loss of any memory or, in fact, of any function after such operations.

Clinical data, with amnesias following apparently small lesions, seem to contradict such experimental findings. However, lesions in the human brain are mostly the result either of tumor growth or of severe traumatism, both of which probably produce widespread changes in addition to the local injury. The surgical removal of parts of the frontal lobes in the recent topectomy studies has not produced such severe defects as usually result from traumatic destruction of the lobes (Mettler, 1949).

V. THE ROLE OF SUBCORTICAL STRUCTURES

Perhaps we have been looking in the wrong place for the conditioned reflex arcs or memory traces. Are they formed somewhere else than in the cortex? Experiments on the thalamus and other subcortical structures are technically difficult, and there is little direct evidence on this question. Since the classical experiments of Goltz a number of investigators have studied the capacity of the totally decorticate animal to learn. The outcome of these experiments is that such animals can form simple sensori-motor associations, although with extreme slowness in comparison with the rate of the normal animal (Polterew & Zeliony, 1930; Girden, Mettler, Finch & Culler, 1936). We must ask, however, whether such learning occurs when the cortex is intact.

When the sensory or associative areas of the cerebral cortex are destroyed, the corresponding nuclei of the neo-thalamus degenerate, so this portion of the subcortex is eliminated from consideration by the same experiments which rule out the cortical association areas. The only experiments bearing upon the participation of other subcortical centres suggest that subcortical learning does not occur when the cortex is functioning.

Fischel (1948) has maintained, solely from comparative psychological studies, that the basal ganglia are the seat of the space-co-ordinate elements of motor habits. I have destroyed the greater part of these structures in rats, trained in the discrimination box, without producing loss of orientation. The animals may perform forced circus movements but, in spite of this, they maintain their orientation in the problem box (Lashley, 1921*b*). The basal ganglia in man are subject to various degenerative diseases. The symptoms of such diseases are, in general, tremors and other disturbances of co-ordination at a primitive level, but without evidence of apraxia or other disorder of the learned patterns of motor co-ordination. The evidence seems conclusive that in mammals the basal nuclei are not an essential link in the patterning of learned activities.

It has been widely held that although memory traces are at first formed in the cerebral cortex, they are finally reduced or transferred by long practice to subcortical levels. The evidence for this has been the apparently greater fragility of recently formed habits than of old habits; the supposedly greater resistance of the latter to brain injuries. The amnesias following electroshock therapy indicate that it is the age of the trace and not the amount of practice that has built it up which determines its survival, and a difference of a few minutes in the age of memories may suffice to determine their loss or survival. This is scarcely evidence for reduction to lower levels of the nervous system. The chief argument for the dropping out of memory traces from the cortex has seemingly run somewhat as follows: Consciousness is a function of the cerebral cortex; long-practised habits become automatic and are performed without conscious control; therefore they are no longer mediated by the cerebral cortex. Both premises of this syllogism are probably false, and the conclusion would not follow if they were true.

When rats are trained in a habit based upon the discrimination of intensities of light, to choose a brightly lighted alley and avoid a dimly lighted one, the removal of the striate cortex completely abolishes the habit. The animals are able to relearn the reaction and require as much practice as they did for initial learning. One group of animals was trained in this habit and given 1200 trials of overtraining, daily practice for a period of 3 months. Their behaviour strongly suggested automatization of the habit. The striate areas were then removed. The habit was lost, just as in the case of animals which are operated as soon as they give evidence of the presence of the habit. The long overtraining did not eliminate the participation of the cortex (Lashley, 1921 *a*).

This visual habit can be formed in the absence of the visual cortex, and the rates of learning with and without the visual area are exactly the same. The average for 100 normal animals is 125 trials; for nearly 100 without the visual areas it is 123 trials. After such animals, lacking the visual cortex, have learned the brightness reaction, any other part of the cerebral cortex may be destroyed without disturbing the habit. Apparently no other part of the cortex takes over the learning function (Lashley, 1922). If, in addition to removal of the striate areas, the pretectile region of the thalamus and the optic tectum are destroyed, the animals cannot learn the discrimination reaction (Lashley, 1935 *b*). These facts indicate that, in the absence of the visual cortex, the learning of the brightness reaction is carried out by the optic tectum. However, so long as the visual cortex is intact, removal of the tectum has no effect whatever upon the performance of visual habits. The tectum apparently does not participate in visual learning so long as the cortex is intact (Lashley, 1935*b*).

Dunlap (1927) has advanced the hypothesis that complex serial habits such as that of maze-running, playing a musical passage, or speaking a sentence, are at first chains of sensori-motor reactions in which excitations from muscular contractions in one movement of the series serve as stimuli to elicit the next. He holds that, with continued practice, there is a short-circuiting of these conditioned reflex pathways through the cerebellum and that the peripheral elements drop out. McCarthy and I (1926) attempted to test this hypothesis by training rats in the maze, removing the cerebellum, and testing for retention. The operations greatly disturbed the motor co-ordination of these animals. Some of them practically rolled through the maze, but they rolled without entering the blind alleys. There was no loss of memory of the sequence of turns in the maze.

These few experiments are, of course, by no means conclusive. They constitute, however, the only direct evidence available, and they definitely point to the conclusion that, if the cerebral cortex is intact, the associative connexions of simple conditioned reflexes are not formed in the subcortical structures of the brain.

The studies which I have reported thus far point to the conclusion that habits based upon visual discrimination are mediated by the striate areas, by the primary visual cortex, and do not involve the activity of any other part of the cerebral cortex. The conduction of impulses is from the retina to the lateral geniculate nuclei, thence to the striate areas, and from them down to some subcortical nervous mechanism. The path beyond the striate cortex is unknown. It may be direct to the spinal cord. There is some evidence that the pyramidal paths contain many fibres from all parts of the cerebral cortex, not from the Betz cell area only.

It seems probable that the same restriction of simple discriminative habits to the primary sensory areas holds also for other sensory modalities. The evidence is less complete, but what there is is consistent with the data on the visual system.

The evidence thus indicates that in sensori-motor habits of the conditioned reflex type no part of the cerebral cortex is essential except the primary sensory area. There is no transcortical conduction from the sensory areas to the motor cortex, and the major subcortical nuclear masses, thalamus, striatum, colliculi and cerebellum do not play a part in the recognition of sensory stimuli or in the habit patterning of motor reactions.

VI. THE ENGRAM WITHIN SENSORY AREAS (EQUIPOTENTIAL REGIONS)

The experiments reported indicate that performance of habits of the conditioned reflex type is dependent upon the sensory areas and upon no other part of the cerebral cortex. What of localization within the sensory areas? Direct data upon this question are limited, but point to the conclusion that so long as some part of the sensory field remains intact and there is not a total loss of primary sensitivity, the habit mechanism can still function. Thus, in a series of experiments attempting to locate accurately the visual cortex of the rat, parts of the occipital lobes were destroyed in a variety of combinations. In these experiments it appeared that, so long as some part of the anterolateral surface of the striate cortex (the projection field of the temporal retina corresponding to the macula of primates) remained intact, there was no loss of habit. Any small part of the region was capable of maintaining the habits based on discrimination of intensities of light (Lashley, 1935*b*).

In a later experiment an attempt was made to determine the smallest amount of visual cortex which is capable of mediating habits based upon detail vision. The extent of visual cortex remaining after operation was determined by counting undegenerated cells in the lateral geniculate nucleus. Discrimination of visual figures could be learned when only one-sixtieth of the visual cortex remained (Lashley, 1939). No comparable data are available on postoperative retention, but from incidental observations in other experiments I am confident that retention would be possible with the same amount of tissue.

In an early study by Franz (1911) the lateral surfaces of the occipital lobes of the monkey were destroyed after the animals had been trained in pattern and colour discrimination. These operations involved the greater part of what is now known to be the projection field of the macula. There was no loss of the habits. I have destroyed the cortex of the retrocalcarine fissure (the perimacular field) without destroying visual memories. The results with monkeys thus support the more ample data for the rat; the visual memory traces survive any cortical lesion, provided some portion of the field of acute vision remains intact.

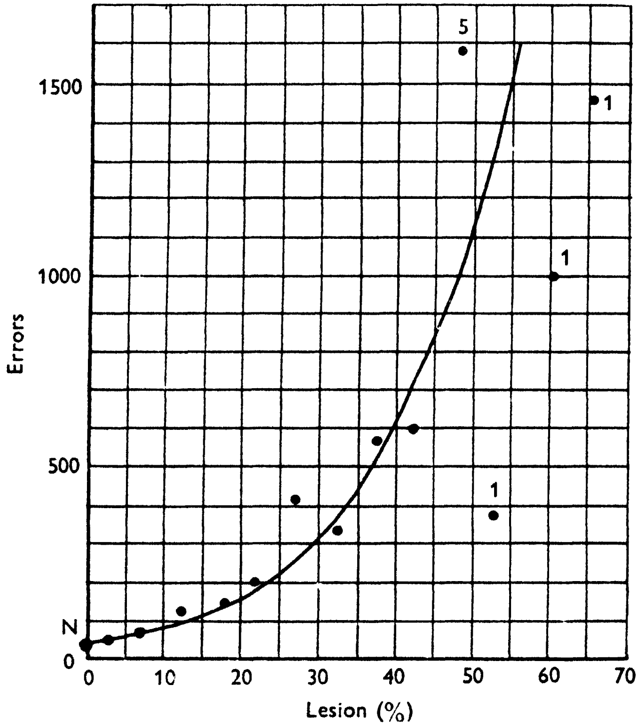
This lack of definite habit localization might really have been predicted from psychological data alone. Analysis of the effective stimuli in discriminative learning reveals that the association is independent of particular sensory nerve fibres. It is a response to a pattern of excitation which may vary widely in position on the sensory surface and consequently in cortical projection. The reactions involved in motor habits show the same sort of functional equivalence; a motor habit is not a predetermined set of muscular contractions but is a series of movements in relation to bodily posture and to the complex pattern of the environment. The writing of one's name, for example, is not a stereotyped series of contractions of particular muscles but is a series of movements in relation to the body planes which can be performed with any motor organ and with any degree of amplitude.

I have not time here to report in detail the experiments which justify the conclusion that neither the afferent path nor the efferent is fixed by habit. The mass of evidence accumulated by gestalt psychologists shows conclusively that it is the pattern and not the localization of energy on the sense organ that determines its functional effect. Similar motor equivalence is demonstrated by a variety of less systematic evidence. The psychological studies, like the more limited direct experiments on the brain, point to the conclusion that the memory trace is located in all parts of the functional area; that various parts are equipotential for its maintenance and activation.

VII. FACILITATIVE FUNCTIONS IN LEARNING AND RETENTION (MASS ACTION)

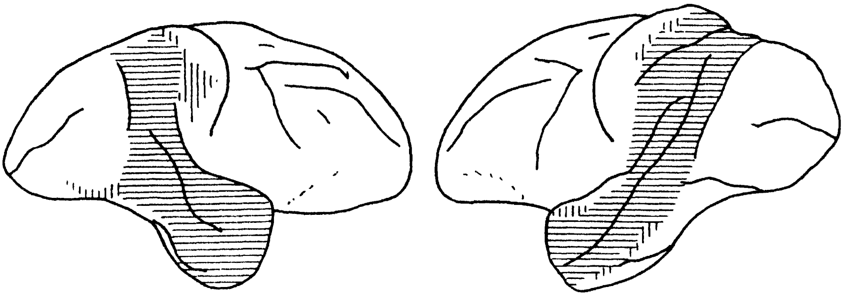
The experiments thus far reported have been concerned almost entirely with discriminative habits requiring only an association between a single sensory stimulus and a motor response. A very different picture develops in experiments with other types of learning. If rats are trained in the maze and then have portions of the cortex removed, they show more or less loss of the habit. If a small amount of cortex is destroyed, 5–10%, the loss may be scarcely detectable. If large amounts, say 50% or more, are destroyed, the habit is completely lost, and relearning may require many times as much practice as did initial learning. The amount of loss, measured in terms of the practice required for relearning, is, on the average, closely proportional to the amount of cortex destroyed. Text-fig. 8 shows the relation for one group of rats on a relatively difficult maze with eight *culs de sac*. There is some evidence that the more difficult the task, the greater the relative effect of the larger lesions (Lashley, 1929; Lashley & Wiley, 1933). Similar results have been obtained with latch-box learning and retention (Lashley, 1935*a*). So far as it is possible to analyse the data from more than 200 diverse operations, the amount of loss from a given extent of cortical destruction is about the same, no matter what part of the cerebral hemispheres is destroyed, provided that the destruction is roughly similar in both hemispheres.

The explanation of this quantitative relationship is difficult. In learning the maze the rat certainly employs a variety of sensory cues, visual, tactile, kinaesthetic, olfactory, possibly auditory. Brain injuries destroy various sensory fields and the larger the lesion the greater the reduction in available sense data. The production of different amounts of sensory deficit would thus appear to be the most reasonable explanation of the quantitative relation between habit loss and extent of lesion (Hunter, 1930; Finley, 1941). Sensory deficit certainly plays a role in it. In the experiment on effects of incisions through the cortex, which was described earlier, the severity of loss of the maze habit correlated highly with the interruption of sensory pathways, as determined from degeneration of the thalamus.



Text-fig. 8. The relation of errors in maze learning to extent of cerebral damage in the rat. The extent of brain injury is expressed as the percentage of the surface area of the isocortex destroyed. Data from 60 normal and 127 brain-operated animals are averaged by class intervals of 5 % destruction. The curve is the best fitting one of logarithmic form. For lesions above 45 % the number of cases (indicated by numerals on the graph) is too small for reliability. (After Lashley & Wiley, 1933.)

However, sensory loss will not account for all of the habit deterioration. There is evidence which shows that another more mysterious effect is involved. In the first place, destruction of a single sensory area of the cortex produces a far greater deficit in maze or latch-box performance than does loss of the corresponding sense modality. A comparison was made of the effects on retention of the latch-box habits of combined loss of vision, vibrissae touch, and the anaesthesia to touch and movement produced by sectioning the dorsal half of the spinal cord at the third cervical level. This latter operation severs the columns of Gall and Burdoch, which convey tactile and kinaesthetic impulses, and also severs the pyramidal tracts which have a dorsal position in the rat. The combined peripheral sense privation and section of the pyramids produced less loss of the latch-box habits than did destruction of a single sensory area of the cortex (Lashley, 1935*a*). Secondly, when blind animals are trained in the maze, the removal of the primary visual cortex produces a severe loss of the habit with serious difficulty in relearning, although the animals could have used no visual cues during the initial learning (Lashley, 1943).



Text-fig. 9. Minimal lesion which produces disturbances in tactile or visual memory in the monkey.

A possible explanation of this curious effect was that the rat forms concepts of spatial relations in visual terms, as man seems to do, and that the space concepts are integrated in the visual cortex. The visual cortex might then function in the formation of spatial habits, even when the animal loses its sight. To test this Tsang (1934) reared rats blind from birth, trained them as adults in the maze, then destroyed the visual cortex. The resultant loss of the maze habit by these animals was as severe as in animals which had been reared with vision. The hypothesis concerning the formation of visual space concepts was not confirmed.

Our recent studies of the associative areas of the monkey are giving similar results to those gained with rats. Visual and tactile habits are not disturbed by the destruction singly, either of the occipital, parietal, or lateral temporal regions, so long as the primary sensory fields remain. However, combined destruction of these regions, as shown in Text-fig. 9, does produce a loss of the habits with retarded relearning. Higher level functions, such as the conditional reaction, delayed reaction, or solution of the multiple stick problem, show deterioration after extensive damage in any part of the cortex. The capacity for delayed reaction in monkeys, for example (to remember in which of two boxes food was placed), may be seriously reduced or abolished by removal either of the prefrontal lobes or of the occipital associative cortex or of the temporal lobes. That is, small lesions, embracing no more than a single associative area, do not produce loss of any habit; large lesions produce a deterioration which affects a variety of habits, irrespective of the sensori-motor elements involved.

Results such as these have led me to formulate a theory of mass action or mass facilitation. It is, essentially, that performance of any function depends upon two variables in nervous activity. The reaction mechanism, whether of instinctive or of learned activity, is a definite pattern of integrated neurons with a variable threshold of excitability. The availability of such patterns, the ease with which they can be activated, is dependent upon less specific facilitative effects. This facilitation can come from a variety of sources. Some instinctive behaviour seems to require hormonal activation, probably a direct chemical effect upon specific nervous elements. Emotional facilitation may produce a temporary activation. Continued activity of related mechanisms may facilitate the whole group of associated reactions; a sort of warming-up effect.

There are indications (Krechevsky, 1936), although little systematic evidence, that the severity of postoperative amnesia varies with the intensity of motivation. Rats trained in a discrimination without punishment with electric shock for errors may show loss of the habit after lesions which do not produce loss in animals which were trained with punishment. The greater effects of cortical lesions in monkeys than in rats may be in part a result of the greater difficulty in getting consistent motivation in the higher animals. In man an amnesia often seems to be a difficulty rather than impossibility of recall; recall may be possible but only with extreme effort and fatigue. I believe that the evidence strongly favours the view that amnesia from brain injury rarely, if ever, is due to the destruction of specific memory traces. Rather, the amnesias represent a lowered level of vigilance, a greater difficulty in activating the organized patterns of traces, or a disturbance of some broader system of organized functions.

In interpreting apparent loss of memory after cerebral damage, extreme caution is necessary. The poor performance in tasks may be due to the destruction of specific associative connexions, but is instead generally, I believe always, the result rather of interference with a higher level functional patterning. Some experiments of Dr Klüver's (personal communication) illustrate this point. Monkeys were trained in a variety of discriminative reactions calling for use of different sense modalities by a method that required them to pull in the stimulus objects by attached strings. Extensive lesions in different cortical areas all caused loss of these habits. The monkeys simply pulled the strings at random. They were retrained in the discrimination of weights. When this was learned, the habits based on other sense modalities (reactions to intensities of light, for example) returned spontaneously. What had been disturbed by all the operations was the set or attitude to compare stimuli, not the specific memory of which one was correct.

This example perhaps illustrates at a primitive level the characteristic of amnesias as seen clinically. Apparent loss of memory is secondary to a disorder in the structuring of concepts. Some physiological mode of organizing or integrating activity is affected rather than specific associative bonds.

VIII. THE COMPLEXITY OF THE MEMORY TRACE

The experiments that I have reviewed deal with only a small part of the whole problem of the memory trace; with those aspects which can most readily be studied in experiments with animals. Immediate memory presents a different type of problem. It is highly probable that immediate memory is maintained by some sort of after-discharge of the originally excited neurons. Such persistent activity can scarcely be the basis of more permanent memory, although Ebbecke (1919) and Edgell (1924) have formulated theories of memory in terms of persistent states of excitation. It is by no means certain that all memory is mediated by a single type of mechanism; that motor skills and eidetic images, for example, have any physiological properties in common. The attempt to account for all memory by any single theory involves assumptions which are not supported by any evidence now available.

Much of learning theory has been based upon supposedly isolated and simple instances of association, on the assumption that these represent a primitive prototype of all memory. However, an analysis of even the conditioned reflex indicates that it is not the simple, direct association of stimulus and response that it has been thought to be. I served as experimenter and subject for several years in experiments employing both the salivary method of Pavlov and the motor reactions of Bechterev. The experience convinced me that, far from being a simple sensori-motor reaction, the conditioned reflex is very complicated (Lashley, 1916). The *S-R* diagram is misleadingly schematic. The effective stimulus is not only the object which the experimenter designates as *S*, but a whole background of other objects constituting the situation in which the experiment is conducted. Every stimulus has a space setting. When, for example, the rat is trained to react to a triangle, he fails to respond, if the figure is rotated through more than 10–15° (Fields, 1932). This means that the memory trace of the figure is tied in with the space co-ordinates of the animal's postural system. This system of space co-ordinates is a part of the postural reflex system which pervades every aspect of behaviour. There is scarcely a memory which does not have spatial orientation, either with reference to the planes of the body or to external space in addition.

Most skilled acts, from running a maze to playing a musical phrase or speaking a sentence, involve a timed series of actions which cannot be accounted for as a simple chain of conditioned reflexes (Lashley, 1949). The serial timing of actions is among the most important and least studied of behavioural problems. Almost all memories except those of automatized motor habits are dated, as Bergson (1896) has emphasized; that is, they have a temporal position in the series of memories which constitutes the individual's past. The memory trace is associated with this series as well as with the particular objects which make up its central core.

The conditioned reflex also includes an element of affective reinforcement. Corresponding to the nature of the conditioning stimulus, there is fear of electric shock, objectively demonstrable by cardiac and respiratory changes, anticipation of acid in the mouth with slight nausea, or expectation of food (Lashley, 1916). Unless this affective element is aroused, the conditioned reflex does not occur. So-called extinction of the conditioned reflex is not a weakening of the specific association, but a waning of this affective reinforcement. Other types of association also have dynamic aspects. The amnesic aphasias seem to be due less to a weakening of specific associations than to a reduction in some general form of facilitation. Henry Head has expressed this as a reduction of 'vigilance', without attempting to define further the nature of the function which is disturbed.

A variety of evidence (McGeoch, 1942) shows that, in a memorized series of nonsense syllables, associations are formed, not only between adjacent words but also between words remote from each other in the series. This, I believe, is an illustration at a primitive level of the fact that every memory becomes part of a more or less extensive organization. When I read a scientific paper, the new facts presented become associated with the field of knowledge of which it is a part. Later availability of the specific items of the paper depends upon a partial activation of the whole body of associations. If one has not thought of a topic for some time, it is difficult to recall details. With review or discussion of the subject, however, names, dates, references which seemed to be forgotten, rapidly become available to memory. Head (1926) has given instances of such recall by multiple reinforcement in his studies of aphasia. Although there are no systematic experiments upon this 'warming-up' effect, it is a matter of common experience and is evidence, I believe, that recall involves the subthreshold activation of a whole system of associations which exert some sort of mutual facilitation.

All this is by way of indicating the probable complexity of the memory trace of even the simplest associations. The engram of a new association, far from consisting of a single bond or neuron connexion, is probably a reorganization of a vast system of associations involving the interrelations of hundreds of thousands or millions of neurons.

IX. SOME QUANTITATIVE CONSIDERATIONS

It has been customary to assume that, since the nervous system contains so many millions of neurons, there must be a large reservoir of cells or of synaptic connexions which can be modified and reserved for specific memory functions. Dunlap (1930) has expressed the view that every individual has far more brain cells than he is ever called upon to use, and has urged this as an argument against any congenital restriction of ability. A similar view has been implied in the identification of intelligence as the individual's number of unpreempted and available memory bonds. However, only the vaguest sort of anatomic data have been available to support such theories. Analysis of actual cell numbers involved in a reaction system gives little indication of a reserve of unused connexions and raises a very difficult question as to the way in which the same system can mediate different functions.

I have counted or estimated the number of cells at different levels in the visual system of the rat. The numbers, which I believe are correct within approximately 10%, are given in Table 1. You will note that there is

Table 1. *The number of neurons at each level in the visual system of the rat (unilateral)*

Level	Total no. of neurons	Ratio to fibres in radiation
Retinal cells		
Rods	9,180,000	273·0
Cones	120,000	
Bipolar	3,530,000	104·0
Ganglion	260,000	13·1
Lateral geniculate	34,000	1·0
Cortical cells		
Lamina vii	68,800	2·0
Lamina vi	135,400	4·0
Lamina v	147,700	4·3
Lamina iv (granular)	127,000	3·7
Laminae ii–iii	176,000	5·2
Total cortical	654,900	19·2

a marked concentration of paths from the retinal myoids to the lateral geniculate nucleus, such that an average of nearly 300 myoids feed into each thalamo-cortical path. At the cortical level there is some dispersion, but it is not great. In the receptive layer (lamina iv) there are fewer than four neurons for each afferent fibre, and in the whole visual cortex there are only nineteen neurons for each afferent fibre.

The rat's maximal visual acuity is about 30 min. of arc, as determined by behavioural tests and from the resolving power of the lens system. Because of the extreme curvature of the cornea and lens the visual field of one eye subtends about 210°. If acuity were uniform throughout the retina, it would require more than 80,000 fibres to represent each acuity unit of the retina by one central fibre. The concentration of ganglion cells falls off from 130 per hundredth square millimetre at the fixation point to 65 at the ora serrata (Lashley, 1932). Assuming that acuity decreases proportionately, some 40,000 separate paths are required to represent each acuity unit at the cortex by a single afferent fibre. This corresponds fairly well to the 34,000 geniculo-striate paths actually counted. Since acute vision is continuous under light stimulation, it follows that all of the geniculo-striate cells must be firing constantly when the eye is stimulated by the usual lighted environment. Further, since there are not more than nineteen neurons in the visual area for each afferent fibre, it is almost certain that every cell in the striate cortex is firing during light stimulation. Certainly there is no large reserve of cells which can be set aside for excitation only in specific habits.

Corresponding counts of cells in the visual system of the monkey have recently been made by Chow & Blum (personal communication). The number of neurons in the lateral geniculate nucleus and visual cortex is enormously greater than in the rat, about 1 and 140 millions respectively, but the ratio of cortical cells to central pathways is only 140 to 1, so again there is no great reserve of cells for mnemonic purposes.

The rat is capable of retaining scores, probably hundreds, of visual habits involving discrimination of complex figures (Lashley, 1938), and retention may sometimes be demonstrated a year after training. As I reported earlier, there is good evidence that visual habits are dependent upon the striate cortex and upon no other part of the cerebral cortex. The efferent path from the striate cortex is not known. It is not via cortico-tectile fibres. If by cortico-thalamic fibres, there are far fewer neurons within the thalamic nuclei than in the corresponding cortical areas, and there is certainly no reserve of cells there for the storing of memories. There seems to be no justification for assuming that the specific shunting of nervous impulses constituting various memories occurs at some level beyond the visual cortex or that memory traces are stored elsewhere than in the cortex.

If the data on the restriction of visual memory to the striate cortex are correct, and they are supported by a variety of experiments, the conclusion seems inevitable that the same cells which bear the memory traces are also excited and play a part in every other visual reaction of the animal. In all probability, the same sort of quantitative relations holds for the other sense modalities.

Even if the associative areas are functional in memory, they do not provide the supposed excess of cells. The visual cortex is directly connected only to a band of cortex directly adjacent, the visuo-psychic area of Campbell. The boundaries of this are indeterminate, but it certainly contains no more cells than does the striate area, probably fewer. There is no geometrical multiplication of cells and pathways. Many millions of cells of the striate cortex must be firing constantly into the adjacent area, so that its cells also must be constantly bombarded with nervous impulses and constantly firing. The conclusion is justified, I believe, by such considerations and is supported by electrical studies, that all of the cells of the brain are constantly active and are participating, by a sort of algebraic summation, in every activity. There are no special cells reserved for special memories.

Lorente (1934) has shown that each neuron may bear a hundred or more end-feet or separate synapses. However, considering the enormous complexity of the nervous activity involved in performance of even the simplest habit, it is doubtful that even the multiplication of cell number by a hundredfold will provide separate connexions that function only for single specific memories.

The alternative to the theory of preservation of memories by some local synaptic change is the postulate that the neurons are somehow sensitized to react to patterns or combinations of excitation. It is only by such permutations that the limited number of neurons can produce the variety of functions that they carry out. Local changes in the cell membrane, such that combined excitation by several synapses excite the cell, would provide a possible mechanism for such response to patterns, but speculation about this mechanism without direct evidence is likely to be as futile as speculation concerning changes in resistance in the synapse has been.

X. SUMMARY

This series of experiments has yielded a good bit of information about what and where the memory trace is not. It has discovered nothing directly of the real nature of the engram. I sometimes feel, in reviewing the evidence on the localization of the memory trace, that the necessary conclusion is that learning just is not possible. It is difficult to conceive of a mechanism which can satisfy the conditions set for it. Nevertheless, in spite of such evidence against it, learning does sometimes occur. Although the negative data do not provide a clear picture of the nature of the engram, they do establish limits within which concepts of its nature must be confined, and thus indirectly define somewhat more clearly the nature of the nervous mechanisms which must be responsible for learning and retention. Some general conclusions are, I believe, justified by the evidence.

(1) It seems certain that the theory of well-defined conditioned reflex paths from sense organ via association areas to the motor cortex is false. The motor areas are not necessary for the retention of sensori-motor habits or even of skilled manipulative patterns.

(2) It is not possible to demonstrate the isolated localization of a memory trace anywhere within the nervous system. Limited regions may be essential for learning or retention of a particular activity, but within such regions the parts are functionally equivalent. The engram is represented throughout the region.

(3) The so-called associative areas are not storehouses for specific memories. They seem to be concerned with modes of organization and with general facilitation or maintenance of the level of vigilance. The defects which occur after their destruction are not amnesias but difficulties in the performance of tasks which involve abstraction and generalization, or conflict of purposes. It is not possible as yet to describe these defects in the present psychological terminology. Goldstein (1940) has expressed them in part as a shift from the abstract to the concrete attitude, but this characterization is too vague and general to give a picture of the functional disturbance. For our present purpose the important point is that the defects are not fundamentally those of memory.

(4) The trace of any activity is not an isolated connexion between sensory and motor elements. It is tied in with the whole complex of spatial and temporal axes of nervous activity which forms a constant substratum of behaviour. Each association is oriented with respect to space and time. Only by long practice under varying conditions does it become generalized or dissociated from these specific co-ordinates. The space and time co-ordinates in orientation can, I believe, only be maintained by some sort of polarization of activity and by rhythmic discharges which pervade the entire brain, influencing the organization of activity everywhere. The position and direction of motion in the visual field, for example, continuously modifies the spinal postural adjustments, but, a fact which is more frequently overlooked, the postural adjustments also determine the orientation of the visual field, so that upright objects continue to appear

upright, in spite of changes in the inclination of the head. This substratum of postural and tonic activity is constantly present and is integrated with the memory trace (Lashley, 1949).

I have mentioned briefly evidence that new associations are tied in spontaneously with a great mass of related associations. This conception is fundamental to the problems of attention and interest. There are no neurological data bearing directly upon these problems, but a good guess is that the phenomena which we designate as attention and interest are the result of partial, subthreshold activation of systems of related associations which have a mutual facilitative action. It seems impossible to account for many of the characters of organic amnesias except in such general terms as reduced vigilance or reduced facilitation.

(5) The equivalence of different regions of the cortex for retention of memories points to multiple representation. Somehow, equivalent traces are established throughout the functional area. Analysis of the sensory and motor aspects of habits shows that they are reducible only to relations among components which have no constant position with respect to structural elements. This means, I believe, that within a functional area the cells throughout the area acquire the capacity to react in certain definite patterns, which may have any distribution within the area. I have elsewhere proposed a possible mechanism to account for this multiple representation. Briefly, the characteristics of the nervous network are such that, when it is subject to any pattern of excitation, it may develop a pattern of activity, reduplicated throughout an entire functional area by spread of excitations, much as the surface of a liquid develops an interference pattern of spreading waves when it is disturbed at several points (Lashley, 1942*a*). This means that, within a functional area, the neurons must be sensitized to react in certain combinations, perhaps in complex patterns of reverberatory circuits, reduplicated throughout the area.

(6) Consideration of the numerical relations of sensory and other cells in the brain makes it certain, I believe, that all of the cells of the brain must be in almost constant activity, either firing or actively inhibited. There is no great excess of cells which can be reserved as the seat of special memories. The complexity of the functions involved in reproductive memory implies that every instance of recall requires the activity of literally millions of neurons. The same neurons which retain the memory traces of one experience must also participate in countless other activities.

Recall involves the synergic action or some sort of resonance among a very large number of neurons. The learning process must consist of the attunement of the elements of a complex system in such a way that a particular combination or pattern of cells responds more readily than before the experience. The particular mechanism by which this is brought about remains unknown. From the numerical relations involved, I believe that even the reservation of individual synapses for special associative reactions is impossible. The alternative is, perhaps, that the dendrites and cell body may be locally modified in such a manner that the cell responds differentially, at least in the timing of its firing, according to the pattern of combination of axon feet through which excitation is received.

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EXPLANATION OF PLATE

Plate 1. Rat opening latch-box after double hemisection of the cervical cord.

For explanation see p. 482