THE BEHAVIOUR OF ANIMALS

" History shows that throughout the centuries, from Aristotle and Pliny to the present day, natural history constitutes the perennial root-stock or stolon of biological science, and that it retains this character because it satisfies some of our most fundamental and vital interests in organisms as living individuals more or less like ourselves."

WILLIAM MORTON WHEELER, 1928.

THE BEHAVIOUR OF ANIMALS

An Introduction to its Study

BY

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PREFACE

This book is based upon lectures delivered in the Department of Zoology and Comparative Anatomy at University College, London, in 1933. The treatment has been expanded, but the lecture form is to some extent retained.

Obviously the book is little more than a sketch, and its object is, quite simply, to interest students and other people in the problems of animal behaviour. References to literature have been given freely to serve as a guide to anyone desirous of pursuing the subject further. Emphasis has been laid on the ecological and "natural history" aspect of behaviour, which is apt to be overlooked by the laboratory worker. Much valuable knowledge which does not appear in the textbooks is possessed by field naturalists, gamekeepers, shepherds, dog-breeders, fishermen and sportsmen, and there has been a tendency among professional students to discount such knowledge as inexact and unscientific, no doubt with some justification. We must distinguish between fact and interpretation ; any straightforward and accurate description of animal behaviour is of value in the present undeveloped state of the science, but the observer must be careful to state only the facts and avoid reading human motives, human ways of thought, into the behaviour of his animal. The animal anecdote has deservedly acquired a bad reputation among professional workers, simply because a kernel of accurate fact has been wrapped up in a bundle of faulty interpretation.

I would, however, strongly emphasize the value of recording as fully and accurately as possible not only what appear to be exceptional cases of animal "intelligence" but, what is even more important, the normal everyday activities of animals, especially in a wild state. Here is a field where the amateur naturalist and the sportsman can help. Much has of course been done, but the field is unlimited, and there is still a great deal to be learned, especially about the lower forms. It is far more important nowadays to work out the life-history and habits of a beetle or a caddis-fly than to form extensive collections or make new " records."

I hope that this book, which has been kept as simple and straightforward as possible, will be of service not only to the student commencing the study of animal behaviour but also to the great number of people who are interested in what animals do and how they live.

There is one obvious omission to which I should like to refer in order to forestall criticism. I have left out any detailed reference to the behaviour of social insects, partly because the subject is so vast, but mainly because it has been treated fully in many excellent books of recent date, by W. M. Wheeler, Forel, K. von Frisch, Imms and others.

I am indebted to my wife for the preparation of several of the illustrations.

E. S. R.

December, 1933.

PREFACE TO SECOND EDITION

A few errors have been corrected, a number of references added, but the first nine chapters remain essentially unaltered, and the book retains its original character of an introduction, What I have wished to add to, and modify in, the original presentation is contained in a supplementary chapter (X), which gives an outline of certain new concepts which I have worked out since the publication of the first edition. I am indebted to my friend, Mr. F. B. Kirkman, for reading this through and checking the statements about the black-headed gull.

E. S. R.

May, 1938.

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THE BEHAVIOUR OF ANIMALS

CHAPTER I

METHOD OF APPROACH

By way of introduction I shall describe in the simplest possible terms a number of examples of animal behaviour, keeping deliberately to the standpoint of the naïve observer.

A terrier is playing in a room with its ball; the ball rolls out of sight under a chest of drawers; the dog follows it, pushes its head under the chest but cannot reach the ball; then lies down on its side and scrabbles with its feet, trying now in this attitude, now in that, to reach the ball. After a while, if its efforts are fruitless it desists, and, if it is experienced in the art, waits expectantly till I fetch a stick and push the ball out, while it lies in wait and pounces on the ball as it appears.

That is a simple but accurate description of the behaviour, expressed in ordinary language—the " plain tale," as Lloyd Morgan would call it; it can be verified by any observer present at the time. We note that the salient feature of the behaviour is the continued, persistent and varied effort of the dog to reach the ball, whether the ball is in sight or not. We say that the dog is *trying* in different ways to get at the ball; in more technical language, the dog is exhibiting *conative* or *directive behaviour*.

Take another example from a much lower zoological level. While walking on the beach between tide marks I observe a good-sized shore-crab and I try to catch it. How does the crab respond to this attack? It may scuttle away as fast as it can, holding up its big claws in such a way that it can clash them together and nip the incautious finger. It may skulk out of sight under a stone or sink gently into the sand by burying itself; if I seize it and pull it out, it will resist with all its might by extending its legs stiffly in an attempt to anchor itself to the ground. If I grasp it by a leg instead of gripping it properly across the back it will certainly bite me, and if I hold the leg very tightly and pinch it, the crab will, as a last resort, autotomize the leg and make its escape.

Here again we have directive activity, persistent and varied. All these diverse actions are directed to one main end—escape from danger.

I want you to note particularly that in this straightforward description I am making no assumptions about the crab's feelings or desires nor am I ascribing forethought to it; I am merely describing the objective facts in the simplest and most comprehensive way. We know nothing, and can know nothing, about the quality of the crab's "experience"; we do not even know whether it has any; on the other hand, we certainly cannot assert that it has none.

That is a fundamental point about the study of animal behaviour. All we can study directly are the overt and visible actions of animals; their inner life cannot be known directly, and must be a matter of inference.

My third example illustrative of directive activity relates to a familiar insect larva, the caddis worm, in this case of the genus *Limnophilus*, which lives in a tube constructed of little pieces of leaf and stalk of aquatic plants. Ejected from its tube it wanders vaguely round until it touches the empty tube, then fastens on to it and crawls all over it till it finds the front entrance and goes in head first. The hind entrance is too narrow to permit of its entry. When it is inside it enlarges the narrower hind entrance until it gets its head and legs free, but then retracts and turns right round inside the tube so that its head and legs emerge at the front end; then all is well and it carries on with the main business of its life, which is eating.

If however the empty tube is not available the caddis larva will, after wandering around for some time, construct a new one out of any suitable material it finds, building first a collar or zone round its thorax and pushing this further back as it adds bits on to the anterior edge.

The important thing to note is that if the first effort to cover its nakedness fails, that is, if it cannot find the old tube, it adopts a totally different line of action and constructs a new tube.

Let us take now some cases of persistent striving where the immediate object is not so obvious.

Major Hingston [1], in his excellent book entitled *Problems of Instinct and Intelligence*, gives a vivid account of the persistent trek of butterflies, mostly Pierids, up the southern slopes of the Himalayas.

> "All were going north-west", he writes; "and all steadily up the slope. There was no hesitation, no deviation; all struggled up the face of the range. . . . For two months the stream continued. . . . The height of the range was 17,000 feet. Beyond and behind it were far loftier ranges, an impassable barrier of rock and ice, standing right across their course. . . . In my efforts to find out the purpose of this flow, I followed it up to the snow-line, which then lay at 10,000 feet. There the stream still continued, thinner certainly, but still the same stream, pushing outward on to the snow" (p. 27).

Think, too, of the persistent and steady ascent of elvers in their millions in a river like the Severn, or the salmon swimming up a turbulent stream, breasting the swift current and leaping the falls. An elver confined in a small pond will respond to the merest trickle of water running into it and will wriggle painfully and persistently up a vertical bank if there is any water at all coming down it.

These are a few observations, selected at random over the wide field of animal behaviour, and described in the simplest way. They serve to illustrate what is the most characteristic feature of behaviour as directly observed, namely that the animal tries or strives to do something specific, that it seeks to achieve some end, to satisfy some need. It is not in the least necessary to assume that it is conscious of the end pursued, that it represents to itself the goal and the means of reaching it; we may be fairly certain, for instance, that Hingston's migrating butterflies were acting blindly and without foresight. We need make no hypothesis at all about the animal's inner experience, but we must accept the direct observational evidence that, in the examples quoted and in thousands of others, behaviour is, objectively considered, directed towards an end. We can further see that behaviour is to a considerable extent determined by its result. Thus the dog tries all ways of getting at its ball; the crab tries one method of escape after another; if one method does not work, another is adopted. So too the caddis larva's activity is satisfied and ceases only when, by one method or the other, it manages to clothe its nakedness in a suitable tube. In general we find that the action goes on until the goal is reached; it may be a stereotyped and unvarying action like the relentless flight of the butterflies, or it may be varied and altered to suit the circumstances. Always it persists, until the goal is reached, or the animal is exhausted, or turns its attention to some other line of activity.

Let us turn now to another characteristic of animal behaviour that impresses the naïve observer, namely the apparent spontaneity of many actions. The most obvious example is the play of young animals. Except in its frequent periods of sleep, the young kitten or puppy is constantly active, constantly doing something, shifting from one activity to another, now chasing a ball or a leaf, now stalking or fighting with its companions. This constant activity, so varied and changeable, appears the very antithesis of forced movement, of mechanical response to stimulation, of reflex action. Let me recount one seemingly trivial little incident. A six-weeks'-old kitten, an hour or so after being introduced into a house new to him, walked up to the tray supplied for his use, hooked out a cinder with his paw and began playing with it on the floor. The tray was some two inches deep and had steep sides. The action was, on the face of it, entirely spontaneous—the march up to the tray, the selection of a suitable plaything.

Like all other kittens brought into a strange place, this one carried out the usual thorough exploration of the room, specially investigating all holes and crevices and corners. This locality study also had all the appearance of being a spontaneous action, one carried out on the animal's own initiative.

Naturally one can hardly imagine that the spontaneous actions of animals are completely uncaused or unmotivated; often indeed one can guess at an internal state or internal stimulus which touches them off. Thus the hunting animal is no doubt moved by hunger; the bird that starts to build a nest is probably stimulated to this action by some particular state of the gonad. But what I wish to convey is that there is in much behaviour an active *seeking* of means or ends, a going out to look for food, or a plaything or a mate—an active effort to satisfy some need, not merely a response to some *present* external stimulus. The animal is in such behaviour essentially active—the springs of its activity are in some sense within. One sees this clearly not only in the intelligent behaviour of some of the higher animals—as when a chimpanzee goes and looks for a stick or other tool with which to draw a banana into its cage—but also in purely instinctive behaviour, where we have no grounds for thinking that the action is consciously planned. To quote Koffka [2]—

> " While reflexes are typically ' passive ' modes of behaviour, which depend upon the fact that some stimulation has taken place, instinctive behaviour is, by contrast, significantly ' active ' in its search for stimuli. The bird *seeks* the material for its nest, and the predatory animal *stalks* its game. In other words, the stimulating environment is not a sufficient cause for these activities. Every movement requires forces which produce it ; but the forces that produce instinctive activities are not in the stimulus-situation—they are within the organism itself. The *needs* of the organism are the ultimate causes of its action ; and when these needs have been satisfied, the action comes to an end " (p. 103).

Let us add then to our conception of behaviour as directive [3] this further datum that behaviour is often active or " spontaneous," in the sense that it is not a reaction to *present* external stimuli.

Let us go a step further. There is abundant evidence that many animals perceive, however dimly and imperfectly, an external world of their own. The domestic dog and cat know their own homes inside out and much of the surrounding territory. Bees know their own hive, and can find their way back to it. Birds live in a visual world, whose spatial relations must be clearly articulated and thoroughly well known to them. The worlds of other animals may be predominantly olfactory or tactile. Thus the spider and the caddis larva live by feel, the dogfish largely by smell. It is unnecessary to labour the point ; to the naïve observer nothing is more certain than the fact that the animals of his acquaintance perceive and react to their surroundings. A little reflection shows him that each animal must live in a world of its own perceiving.

From the simple objective standpoint which we have provisionally adopted, there is no great difficulty in thinking of animals as perceiving their surroundings, just as we ourselves live in worlds of our own perception.

Many animals too give evidence of profiting by experience, and of remembering significant features in their perceived environment. Here are two quite simple cases, relating to cats. A saucer of milk was placed in a particular spot, not being the spot where the kitten was usually fed. After one experience the kitten returned to the spot later on to look for the saucer, which had meanwhile been removed. An older cat was fed once on the top of a six-foot trellis near the back door. The next day it climbed up the trellis to look for food, and on several subsequent occasions it did the same thing, though no food was there. In both cases one experience was sufficient, and there could be no question of the establishment of a motor habit. Here is another case, also of my own observation, relating this time to topographical memory in a dog. While out for a walk with me my terrier bitch Gina found a chunk of brown bread and buried it under a hedge in sandy soil, covering it completely with straw and debris. I disinterred this to see what it was, whereupon Gina picked it up and wandered about in the adjacent field, finally burying the bread rather inefficiently in an overgrown furrow. The next day we went for the same walk, but skirting the hedge in the opposite direction. When we got near, Gina suddenly turned off, without preliminary search, and went straight to the spot under the hedge where she had originally buried the bread. I had taken the precaution to mark the spot with a match stub, otherwise I should not have been able to recognize it in the somewhat featureless ground. Gina failing to find the bread we went on some twenty yards, Gina hunting in the furrows ; then we came back, whereupon Gina searched the furrows thoroughly and soon found the bread ; she then dug a hole in the sand by the side of the path and covered it up completely.

This observation shows that she remembered quite definitely the spot where she had first buried the bread, and then that she had re-buried it in the adjacent field. The area was not well known to her ; it was about a mile from her (temporary) home. What cue she used to find the spot is not certain—whether olfactory or visual or both—but my strong impression was that she recognized the place by sight.

Memory for localities is, as everyone knows, well developed in bees and hunting wasps and many other nesting insects. Take again the well-authenticated cases of the return of house-martins or swallows to the old nest after wintering in the south. Or the return of salmon to the river in which they were bred. From the standpoint of direct observation, then, many animals appear to show memory or retentiveness.

I turn now to a very important characteristic of much behaviour, the significance of which is apt to escape the sophisticated observer, intent on analysis. This is the fact that behaviour is often part of a long-range cycle of events, in which one action prepares for and leads on to the next until the end term is reached. Each stage in the chain or cycle is unintelligible to us except in its relation to what has gone before, and, more particularly, to what is yet to come. Such cycles have a temporal unity, extending often over months of time, just as a simple conative action has unity of short temporal range.

The best example is perhaps the breeding cycle in birds. Here we have in many cases selection of territory by the male, warding off of intruders, the attraction of a mate, courtship, sexual union, the building of a nest, egg-laying, brooding, the feeding of the young until they can fend for themselves ; parallel with these events are cyclical changes in the reproductive organs. To go into more detail, take as an example the chaffinch.

> " Here the male must leave the flock, if he has belonged to one, and establish himself in a territory which may at the time be incapable of sustaining him alone, but must later in the season supply a satisfactory food-supply for himself, his mate and family, and for as many birds of other species as overlap his sphere of influence. He must then sing loudly and incessantly for several months, since, however soon he secures a mate, trespassers must be warned off the territory, or, if they ignore his warning, driven out. His mate must help with the defence of the territory when she is needed ; pairing must be accomplished ; a suitable site must be found for the nest ; materials must be collected and put together securely

enough to hold five bulky young birds ; eggs must be laid in the nest and continuously brooded for a fortnight till they hatch, often in very adverse weather ; the young are at first so delicate that they have to be brooded and encouraged to sleep a great part of the time, yet they must have their own weight of food in a day, and in proportion as the need of brooding them decreases their appetites grow, until in the end the parents are feeding four or five helpless birds equal to themselves in size and appetite but incapable of digesting nearly such a wide diet. Enemies must be watched for and the nest defended and kept clean. When the young scatter, often before they can fly properly, they need even greater vigilance, but within a few days of the fledging of the first brood a second nest will (in many cases) be ready and the process in full swing over again. All this has to be done in face of great practical difficulties by two creatures, with little strength and not much intelligence, both of whom may have been hatched only the season before" ([4], pp. 63–5).

The remarkable thing about the whole intricate cycle is that each step is anticipatory or *proleptic* of the stages yet to come. Territory is selected with a view to the needs of the young that are to be born a month or two later. The nest is built in readiness for the eggs to be laid, and of a size sufficient to accommodate the fledglings. All goes on *as if* the pair of birds planned their course of action with foresight of its end. It is of course extremely doubtful whether they do foresee the ultimate end or aim of their actions ; their behaviour is mainly instinctive, independent of previous experience, and to a considerable extent stereotyped and invariable.

Take another case—the spawning migration of the eel. In the autumn the mature eels take upon themselves a "breeding dress," as C. G. Joh. Petersen called it [5] ; their colour becomes silvery, their eyes enlarge, as it were in preparation for their ocean journey to the Sargasso Sea. These preparations, this urge to go down to the sea, are *to us* meaningless save as related to the end that is striven for ; but we cannot suppose that the eel is aware of what it is doing or has the ultimate end in view. Nor can we imagine that the salmon deliberately stores up fat whilst in the sea for the purpose of ripening its gonads in fresh water ; yet here again is a long chain of behaviour acts and physiological processes all related with one another and all essentially directed towards one end, the reproduction of the species in a certain definite environment suitable for the upbringing of the young. There is a temporal unity, continuity, and directness of the whole chain of events which we must accept and recognize if we are to make sense of it at all.

We have now considered in a very general way some of the more obvious characteristics of animal behaviour as they appear to the ordinary observer. Our point of view has been that of simple direct observation, without theory and without analysis.

I believe that we can get a very long way in the study of the behaviour of animals by the use of this simple objective method, combined with simple experiment. Endless difficulties arise if we try to explain behaviour partly in physiological and partly in psychological terms ; let us try therefore to keep to the unitary point of view suggested by common observation ; let us think of behaviour as one of the forms of response shown by the organism as a whole (see [3 and 3A]), and let us leave the question of the relation of " matter " and " mind " to the philosophers.

This method which I suggest is definitely opposed to the mechanistic interpretation of animal behaviour which derives from Descartes, and it proceeds on different lines from the causal-analytic method which is usual in physical, and to a great extent, in physiological investigations. The ordinary method of physical science, whether it is applied to inorganic substances or to living things, is to seek out the causes of events, and to get at these causes it is necessary to analyse complex events into their simpler constituents. This causal-analytical method is of immense practical value, even when applied to such extraordinarily complex objects as living things. To it are due the triumphs of physiological research, with which we are all familiar.

So powerful and fruitful in results is the causal-analytical method that many people regard it as the only possible method for science. They would say then that it is the only scientific method of studying animal behaviour, and that our tentative direct method is doomed to failure.

You get this point of view very clearly expressed by Loeb and by Pavlov. To the former is due the theory of tropisms and forced movements, according to which the organism is passively actuated by the physical and chemical stimuli impinging upon it. If it is asymmetrically disposed with respect to a directed stimulus, like light, the theory requires that the stimulus shall act upon the neuro-muscular system in such a way as to force the animal to orientate itself either directly towards or directly away from the source of stimulation. Actually the facts of observation do not fit in very well with this schema, and the original theory of tropisms is not now widely accepted. The modern theory of tropisms however, which we owe to Kühn [6], still holds fast to the physiological or causal-analytical point of view.

Pavlov's standpoint is quite definitely mechanistic. He has no understanding whatsoever of the psychological attitude, which he regards as totally unscientific [7], and he adheres strictly to the physiological point of view, investigating and systematizing the whole subject of animal behaviour by physiological methods alone.

> " Our starting point," he writes [8], " has been Descartes' idea of the nervous reflex. This is a genuine scientific conception, since it implies necessity. It may be summed up as follows : an external or internal stimulus falls on some one or other nervous receptor and gives rise to a nervous impulse ; this nervous impulse is transmitted along nerve fibres to the central nervous system, and here, on account of the existing nervous connections, it gives rise to a fresh impulse which passes along outgoing nerve fibres to the active organ, where it excites a special activity of the cellular structures. Thus a stimulus appears to be connected of necessity with a definite response as cause with effect " (p. 7).

He applies this conception to the inborn or " unconditioned " reflexes which form the basis of animal behaviour, as well as to the " conditioned " reflexes which may be written in to the nervous system by training. Instincts also are regarded from this mechanistic point of view. " These also," he writes, " take place in the nervous system, and they are the inevitable reactions to perfectly definite stimuli. They have to do with reactions of the organism as a whole, and comprise that general behaviour of the animal which has been termed ' instinctive ' " (p. 9). Instincts according to Pavlov are merely chain-reflexes, and instincts and reflexes alike are the inevitable responses of the organism to definite internal and external stimuli. Now all this sounds very impressive and scientific—much more so than the simple objective method I suggest.

Do not, however, be led astray into thinking that the mechanistic method, and it alone, can give us absolute and final truth. No one nowadays can seriously hold that the mechanistic conception is anything but a working hypothesis or useful fiction, a method of interpretation which can be applied to the facts of experience, a method which has proved itself of practical worth for the purposes of physical and physiological science [9].

There is no sound philosophical reason why we should accept *a priori* the mechanistic formulation of behaviour problems. If we find that the direct method renders to begin with a more adequate account of the facts we are fully justified in preferring it.

Applied to the study of behaviour the mechanistic method obviously implies certain definite restrictions on interpretation. It regards behaviour as being directly determined by the physical and chemical stimuli impinging upon the sense organs of the animal. It excludes the possibility that the animal exhibits directive activity in relation to its needs, and that it responds to its own perceptual field, rather than to the separate physical and chemical stimuli which we discern as acting upon it.

The implications of the mechanistic or reflex theory of behaviour are vividly and amusingly illustrated by Raymond Pearl in the following passage from his paper on the behaviour of Planarians [10]. Their behaviour is in the main

" what may be characterized as reflex. It is very simple to say that an animal's activity is composed of a series of invariable reflex acts in response to stimuli, but I doubt whether the full significance of such a condition is always realized. It implies that the animal as an individual ' does ' nothing in the sense that a man ' does ' things. It is moved about from place to place by its locomotor organs ; it is put into certain definite and invariable relations to its surroundings by its reflex mechanisms. Considered as a whole, such an organism is a sort of shell to hold a series of mechanisms, each of which is independently capable of doing a certain thing, and in the doing produces some effect on the shell as a whole. We may perhaps get a clearer picture of what such a reflex existence means by considering for a moment what would be the effect if all a man's activities were composed of invariable reflexes, to be set off by the appropriate stimuli. Under such circumstances, whenever a man saw or smelled food he would have to go to it and eat it. . . . Whenever he touched water he would have to take a bath, and perhaps drink till he could hold no more. During the day he would have to move always in a definite direction with reference to the sun, and so on *ad infinitum* " (pp. 703–4).

As it happens, pure reflex action of this kind *has* been described in *Planaria* [11]—but only in an organ divorced from its association with the rest of the animal.

> " When we examine the reflex conduct of an incomplete organism or organ the suggestion of choice in the conduct becomes nil," writes Kepner. " Dr. Arnold Rich and I observed that, by destroying certain neural centres of *Planaria albissima*, its proboscis would undergo auto-amputation. The proboscis thus freed would swim about as an independent organism ingesting or swallowing every small object that it would encounter. But in this reflex conduct it displayed no choice. Swallow it had to ; so that if we placed small particles of glass in its path, these would be taken in. The proboscis would even turn upon the body of which it had formed an organized part and eat its way through from one side to the other. When this organ is under the normal inhibitory control of the animal, as a whole, it displays a very evident faculty of choice in that it nicely chooses between food and non-food. In normal life, therefore, we have the proboscis of *Planaria* displaying choice, whereas it is only when it is detached from its body proper that it shows a purely mechanical reflex in which no choice is apparent" (pp. 176–7).

In the intact animal, as is now generally recognized, there is no such thing as pure reflex action in normal behaviour ; all so-called reflexes are parts of co-ordinated, and generally " purposive " or directive actions, and they cannot be understood until their relation to the objective aim of the whole action is known.

Here is a simple observation (which anyone can make) which is quite sufficient to demonstrate the inadequacy of the reflex theory. A blackbird picks up a worm in its beak, and if it is feeding itself swallows it. This *might* be a purely reflex train of events. But if it is foraging for its family it does not swallow the worm, though on the reflex theory swallowing ought to follow automatically from the stimulus of the worm in the mouth. It keeps the worm in its beak and perhaps hunts for more before taking them back to the nest. The objective aim or " purpose " of the activity controls its detailed course, inhibits the normal swallowing reflex, if reflex it be.

But it is not my intention here to confute the mechanistic reflex theory by the accumulation of examples—easy though this would be. All I am concerned with at the moment is to point out that the causal-analytic method does not allow for the possibility that animals are more than mere machines, and that neither their actions nor their perceptions can be satisfactorily analysed in physiological terms alone (see [12]).

We should be very unwise, in beginning the study of animal behaviour, to ignore these possibilities. All we have got to go upon is the observed, objective behaviour of animals. We are not in the least bound to accept *a priori* the mechanistic or causal-analytic method ; the direct method is at least equally possible, and on the face of it more adequate, at least as a first approach to the problems. (I am in no way concerned to deny that physiological analysis of a behaviour-complex may yield valuable results and enrich our knowledge of behaviour, but I do deny that the results of analytical study are the equivalent of, or can be substituted for, the broad facts of behaviour, the main responses and activities of the animal as a whole. My point of view is " organismal " or " holistic.") It should be possible to determine by direct observation, preferably of animals in their natural surroundings, exactly to what they do respond. We should not assume *a priori* that single physical or chemical stimuli are the controlling factors ; we should investigate with an open mind whether animals do not in fact respond to somewhat complex situations and relations, rather than to simple stimuli.

Let me illustrate this by an example. I had a Toy Yorkshire terrier, which towards the end of his life developed a rather high level of intelligence. This dog had a special towel kept for drying him after a bath or a clean down. Like many dogs he did not relish being bathed, and in normal circumstances it was sufficient to show him the towel to elicit a very characteristic negative reaction. He crouched down, " made himself small," and crept slowly away. To turn on the tap at the same time made the reaction more pronounced. The same negative reaction could be elicited by showing him the bottle of shampoo mixture which was a usual accompaniment of his bath. The reaction in both cases was to a definite percept. Of course one cannot be certain that the percept was as detailed and complex to the dog as it was to us—very probably it was not. But the reaction was to specific objects or percepts—not to simple stimuli. Even more remarkable was the following behaviour. He came in from a long country walk very wet and muddy, and we wanted to rub him down with warm water. On this occasion the sight of the towel brought out, not the negative reaction, but a positive one. He made no attempt to slink away, but on the contrary came up to us and lent himself readily to the bath. Here was a complex situation, differing from the usual one in that the dog was wet and uncomfortable; his needs were different, and his response accordingly was different.

This is a piece of behaviour which seems to show clearly that the response is to the situation as a whole, including the dog's own needs, and not to simple physical stimuli.

We ought to approach the study of animal behaviour with circumspection, discarding all preconceived notions, and observing exactly what happens—not an easy task. There is, at the present time, great scope for simple naïve observation of animal behaviour. We know surprising little about the normal behaviour even of our dogs and cats ; we have been in too great a hurry to hustle them off into physiological and psychological laboratories and subject them to experiments, many of which from the animal's point of view are ridiculously complicated and show no appreciation of what the animal might reasonably be expected to grasp. There is an interesting illustration of the truth of this view to which attention may be called. The greatest stimulus which the study of animal behaviour has received during the last fifteen years undoubtedly came from Köhler's celebrated observations of the behaviour of chimpanzees [13]. He kept these animals in out-of-door cages in Teneriffe, in fairly natural conditions, good enough at least to let them display much of their normal behaviour. He took the trouble to get to know their ways intimately—he even took part in their round dances—and he has described exactly what they do in the different circumstances of their normal life. His book is a treasure house of exact, unbiassed and sympathetic observation. And when he experimented with them he was careful to give them problems within their capacity—quite simple problems like climbing for a banana suspended out of reach, or raking in a banana placed outside the cage just beyond arm's length.

These simple observations and simple experiments have given a new turn to animal psychology, which is bringing it into much closer contact with the facts. I do not mean that other people did not use this method before him—the late Professor Hobhouse [14], for example, carried out many simple yet significant experiments—but it was certainly Köhler's simple method and the important deductions he drew from his work that gave the new and healthy orientation to these studies. We shall have occasion to refer to his work more fully later (see pp. 154–9).

There is another point which I wish to get clear before we go on to study more closely the observed facts of behaviour, and that is the nature of the explanations which the direct method provides. In the physical sciences and to a large extent in physiology we are concerned primarily with causal explanations, with tracing out the action of laws or invariable sequences. We do not get this sort of knowledge by using the direct or descriptive method. What we get may be better described as an understanding of behaviour. When you see a wasp, for example, standing on a gate post and busily chewing at the wood, you do not understand this action until you follow the wasp up and find out that it uses this material to construct its nest; you go on then to discover what the nest is used for—the care and upbringing of the young. In a word, to understand the action of the wasp on the gate post you have to integrate this action into the whole directive cycle of activity [12]. You have to find out the objective purpose of the whole train of action.

This is the sort of knowledge which we get by studying animals from the objective point of view, and it is extremely valuable knowledge too. Without this knowledge we simply cannot make sense of behaviour; even the most extreme believer in mechanism must use this sort of knowledge to make behaviour intelligible at all.

When we study behaviour from this point of view we must ask first of all, *what is the animal doing, or trying to do?* This means that we must investigate the objective intention of its acts, the end to which they are leading, the end which satisfies them and brings them to a conclusion. This we can do without making any assumptions about the animal's feelings or desires or intentions. To understand the acts we must put them in relation with the life of the animal, discover how they further one or other of the main purposes of its life—maintenance or reproduction. We must sort them out or classify them according to the proximate end pursued; thus many actions are concerned with food-finding, others with protection from enemies, others with resisting unfavourable environmental conditions or finding suitable ones: all these activities link on to, and form part of, the main drive towards self-maintenance. Similarly, other trains of activity become intelligible only when their relation to the master function of reproduction is discovered. It is obvious that we must make a full study of the animal's normal life, in its normal surroundings, before we can hope to understand what it is driving at (see Chapter II).

In the second place we must ask, *to what exactly does the animal respond?* Or, in other words, what does it perceive? We must inquire then how an animal becomes aware of its food, of its enemies, of favourable or unfavourable environmental conditions. How does it become aware of its mate, how does it find a suitable spot in which to lay its eggs? I have already pointed out that every animal, if it has perceptions at all, must have *its own* perceptual world, and this perceptual world may be very different from ours. I am not thinking so much of the obvious point that its sensory capacities may be very different from ours, that, for instance, it may be colour blind, or have no sight at all, depending on smell or perception of vibration to guide it through life. I mean rather that even if its sense organs are similar in capacity to ours the focal points of interest in its perceptual world may be quite different from ours, and it may perceive and attend to these alone. Thus, to take a very simple case, it is probable that a dog entering a familiar room does not perceive chairs, tables, couches, pictures, and so on, *as such*; he perceives (i.e. responds to) places where he can lie comfortably, spots where he can bask in the heat of the fire, the ball he plays with, and generally only those places or objects that have a functional significance in relation to his own needs; other objects he perceives only as indifferent masses. We can judge of an animal's perceptions only by studying its behaviour, and we must take care, in investigating the perceptions of animals, to avoid the pitfall of assuming that they are similar to our own. We must try in a sense to look at the situation from the animal's point of view, not from our own. I do not mean that we should try to imagine in detail how the world appears to the animal, but we should ascertain very carefully just what it is that elicits significant behavioural response, and we should be prepared to find that the animal reacts to wholes, or to relations, or to some feature which is representative or proleptic of a normal situation, and that it may be quite indifferent to many things that we perceive in the situation. And of course we must expect to find that an animal's perceptual world is much simpler, less differentiated, less articulated, than our own ; objects which appear to us extremely complex will probably appear in much simpler form to the animal (see Chapter X).

This perceptual aspect of behaviour is a difficult one to study and a great deal of patience and an open mind are required if we are to make anything of it ; the only way to achieve results is to spend a lot of time observing exactly what the animal does in a variety of situations, starting with those which correspond fairly closely to the situation it meets with in its normal life. In this connection a wise remark of Pearl's is worth quoting.

> " It is almost an absolute necessity," he wrote in his Planarian paper [10], " that one should become familiar, or perhaps better, intimate with an organism, so that he *knows* it in somewhat the same way that he knows a person, before he can hope to get at even an approximation of the truth regarding its behaviour " (p. 582).

A third thing which we must do if we are to understand behaviour is to observe our animal throughout the course of its life, with the object particularly of discovering *how its behaviour develops through maturation and experience.* Anyone who has brought up a pup must know how rapidly and subtly its behaviour changes and develops ; the pup of to-day has made an advance on the pup of yesterday, and the pup of to-morrow will have learnt some new thing. Particularly in animals that can learn it is impossible to understand behaviour thoroughly without a knowledge of their history and past experience or training. Finally, there is the interesting task of discovering *whether the animal's behaviour is modifiable or adaptable*, whether when confronted with a new or unusual situation it can adapt its behaviour accordingly. This line of investigation has the additional attraction of involving experimental work, and of disclosing capabilities which do not normally find scope to reveal themselves. In this experimental investigation we have of course to bear in mind the limitations of the animal and devise experiments which are simple, adapted to its capacity and means of action, and within its powers of perception. We must bear in mind, here as always, that the animal's perceptual world (i.e. the world to which it responds) is likely to be simpler and less differentiated than our own, and that the focal points of interest may be different.

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CHAPTER II

BEHAVIOUR AND ECOLOGY

One of the great practical difficulties about the study of animal behaviour is that it does not lend itself readily to laboratory work ; it is necessary first of all to study the animal in its natural surroundings, to become acquainted with its normal mode of life. Without such knowledge we may easily go astray in our interpretation of behaviour in the unnatural conditions of a laboratory experiment ; we may easily devise experiments which are meaningless, and, from the animal's point of view, stupid.

Work in the field then—good old-fashioned natural history observation—should precede experimental work in the laboratory. This is often a difficult task, requiring the expenditure of much time and energy.

The common eel kept in an aquarium tank is rather a dull animal, exhibiting no particularly interesting behaviour. No one would imagine that it was capable of carrying out those extraordinary migrations which have been revealed by the work of the late Dr. Johannes Schmidt. It has taken years of labour to piece together this story, and the data have had to be collected in the open sea by means of extended and costly oceanographical expeditions. The same holds good of the study of fish migration generally ; if we now know the main migrations of sea fish in North European waters, this is due to thirty years' hard work at sea on the part of the nations interested in sea fisheries. Think too of the immense amount of labour in the field that has gone to establishing the main facts about the migration of birds.

To take another case—most of our knowledge of the remarkable phenomena of instinct has been derived from the life-long study of insects and spiders in the field by such observers as Fabre, the Peckhams, Rau, Ferton, Hingston and many others.

The experimental study of behaviour requires to be based upon a sound knowledge of life-history and ecology.

It is the merest commonplace to say that animals are adapted both in structure and in behaviour to their surroundings, but this bald statement is not very illuminating. Let us substitute for it the following proposition ; that there is for each species a definite *ecological norm*, and often what we may best describe as an *ecological niche*. Let me illustrate this by reference to the animals of the seashore.

If you are an experienced shore-collector, you know almost exactly where to lay your hand upon the species you want. Some forms are limited to sandy beaches, others to mud, others again to rocky shores. Many species occur only near low-water mark of spring tides, others are found only at or near high-water mark. Some are most abundant where there is an infiltration of fresh water coming down from the land ; many avoid any such contact with fresh water.

Sandy and muddy shores are inhabited mainly by burrowing forms like the lug worm, the cockle, the razor fish, and so on ; when the tide is up there are of course a number of predatory forms to be found roaming over the bottom, like small plaice and dabs, shore crabs and shrimps. Sessile animals, like sea anemones and hydroids, barnacles and sponges, require a solid substratum, and are hence to be found only where rocks or stones or weeds provide the necessary foothold. Many creeping animals, like gastropods, also require a solid substratum, and many crustacea lurk by preference in crevices of the rock or among boulders. Zonation of species according to depth or time of exposure is one of the most striking features of distribution on a rocky shore [1]. On our coasts it is very clearly and obviously displayed by the larger sea-weeds ; near high-water mark we get *Pelvetia canaliculata*, and then *Fucus spiralis* ; the next zone is characterized by the bladder wrack, *Ascophyllum nodosum* ; below that *Fucus serratus* becomes dominant, and near low-water springs *Laminaria* and *Chondrus* appear (see Fig. 1). The zonation of the animals is not so conspicuous, but is readily revealed by even a cursory examination. The fauna becomes much richer the nearer we get to low-water mark, and many forms are exposed only at low spring tides. A few forms are limited to the neighbourhood of high-water mark, like sandhoppers, the small winkle, *Littorina neritoides*, and dwarf forms of *Littorina saxatilis*; further down the beach we get larger *L. saxatilis*, then the common periwinkle *L. littorea*, and, almost exclusively on sea-weeds, *L. obtusata*; the ordinary barnacle (*Balanus balanoides*), which extends high up on the shore, is replaced by other species, e.g. *B. perforatus*; there is also a zonation of the species of top-shells (*Gibbula* and *Calliostoma*). Many other examples could be given (see Fig. 1). Specialization of habitat may go even further. There are, for instance, several species which one almost always finds on the holdfasts or fronds of *Laminaria*, the little blue-striped limpet, *Patina pellucida* for instance, and the polyzoan *Membranipora*. In the same way one would expect to find the hydroid *Clava* on certain sea-weeds occurring further up the beach.

One could further illustrate the point that most marine (and fresh-water) animals have a very definite habitat, strictly limited by the nature of the substratum, the depth and other factors, but enough has perhaps been said to establish the principle, which is a very general one.

Now this fact that every species has its own habitat, or ecological niche, raises some interesting problems of behaviour, and also gives us a key to their behaviour in laboratory conditions. How does it come about that shore animals find their ecological niche to begin with, especially when they start life as planktonic larvæ? There is surprisingly little known about this, and there is a good opening here for experimental work in the field and in the laboratory, on the behaviour of free-swimming larval forms and of the early bottom stages. I do not propose to go further into this problem at the moment, except to mention that Franz [2] interprets the wide-spread positive phototropism of young pelagic larvæ as an adaptation to bring them near the surface and ensure their wide distribution by the currents. The question will be discussed further in the next chapter (pp. 59–62).

A problem which is more readily accessible to study is this: suppose you take an animal out of its ecological niche, how does it find its way back, how does it restore the ecological norm? This problem takes several forms, according as we are dealing with sessile, or sedentary, or mobile species. If

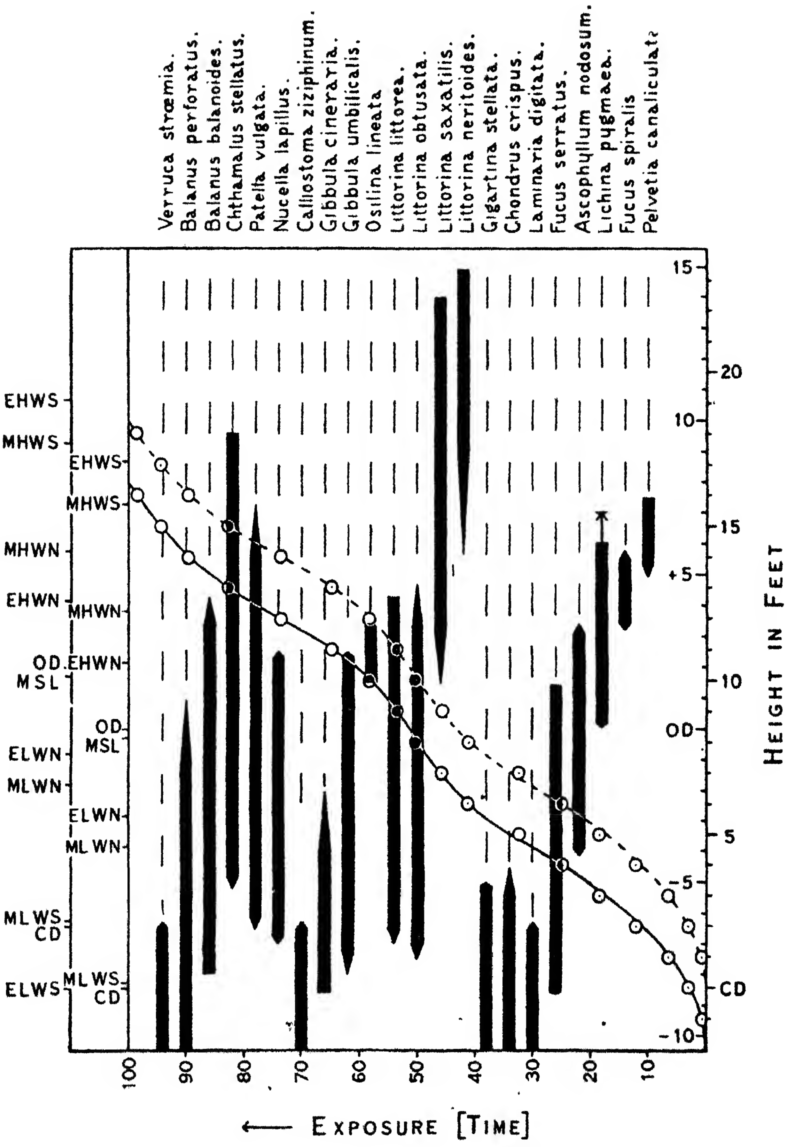

FIG. 1.—Zonation of Animals and Plants on the Seashore (from Colman, 1933, by courtesy of the Marine Biological Association of the United Kingdom)

a piece is cut from the stem of the rooted hydroid *Antennularia* and suspended freely in the water, it will send out shoots which feel their way down in response to gravity and attach themselves to the bottom. Mobile and some sedentary forms carry out exploratory movements until the ecological norm, or part of it, is restored. To take a very simple case, if you dig up an earthworm and place it in a glass dish, keeping it sufficiently damp, it will crawl steadily around, usually in the angle of the dish where maximum contact is possible. If you place in the dish a little heap of earth, as soon as it touches it the worm will creep into the earth until it is completely covered and will then come to rest—the ecological norm has been restored. You can get the same effect if you supply a piece of rubber tubing of suitable bore ; the worm will crawl into it and come to rest. You may also get the same result with a glass tube, though here the restoration of the ecological norm is very incomplete, the worm being still exposed to light.

It is of interest to note that the earthworm *Allolobophora fœtida*, which lives by preference in manure heaps, will not burrow into a heap of filter paper or sawdust moistened with water, but if a decoction of manure is added the worms bury themselves in the heap at once [3]. Here the ecological norm includes specific chemical factors.

Some people would account for these actions by saying that the worm exhibits specific chemotropism, positive stereotropism, positive geotropism and negative phototropism, and much time and energy has been spent in studying these supposed simple tropisms. But to my mind it seems simpler and more illuminating to think of the worm's action as being an effort, an attempt, to get back to its normal environment ; the various " tropisms " come in as parts of this effort, and they seem to me meaningless, except in relation to the aim of the whole train of activity. This interpretation seems to me more comprehensive, more adequate, than the physiological interpretation in terms of tropisms.

Let us go on to a very interesting case, which has recently been fully studied by Fraenkel [4] from the point of view of tropisms and reflexes, the burying reaction in the razor-fish, *Solen*.

Solen normally lives buried in the sand at a slight angle to the vertical, with the dorsal edge uppermost, and at such a depth that the siphons just reach the surface of the sand. If it is dug up, or washed out of the sand by wave-action, it will proceed to bury itself, to restore its normal position. The foot is protruded in a point and bent down into the sand; there it works its way deeper in, as far as it can go. When the foot has reached its maximum extension the tip is suddenly swollen out by injection of blood into a flattened bulb or disc. This acts like a mushroom anchor, so that when the retractor muscles come into play the foot contracts and pulls the shell down into the sand. While the foot is next extended the shell margins gape, thus holding the animal firmly in the sand, but they are tightly closed when the foot contracts, and drive the water out from between the foot and the mantle, softening or washing away the sand and thus facilitating the burying moment. There is a collar round the foot which prevents the sand entering the mantle cavity. The whole process is repeated a few times, till the animal is completely buried.

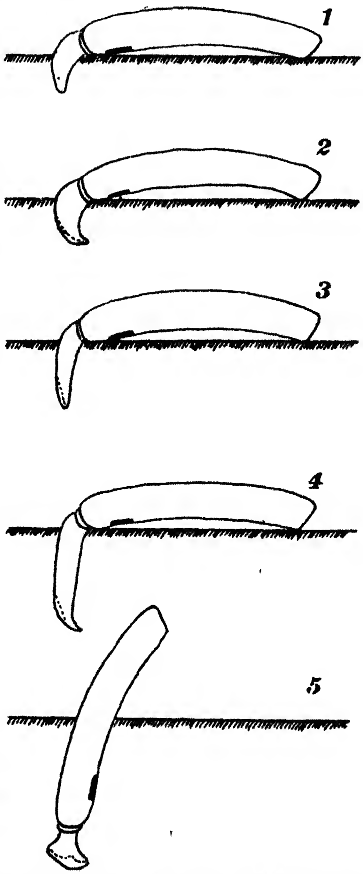

FIG. 2.—The Burying Response in *Solen* (after Fraenkel, by courtesy of Julius Springer)

The burying reaction always occurs when the animal is uncovered. It is not due to the immediate effects of being dug up, for the burying response can be elicited hours after this. It is not solely due to the absence of contact-stimulation from the sand, for if the animal is pulled half-way out and held till it is quiet, it will begin to re-bury itself; if it is inserted into the sand in the normal position it still continues to bury; if when lying on the surface it is covered with sand it will still bury. It is not its abnormal position when lying on the sand which causes it to bury, for if it is held suspended in the water in its normal position it goes through the typical motions of burying. Fraenkel sought in vain for any one definite stimulus to account for its burying response. He concluded that it was the whole complex of stimuli—as we should say the situatiön as a whole—affecting the *Solen*, when removed from its ecological niche, that brought about the burying response. He summed up his findings as follows: "Burying movements always occur when a *Solen* finds itself in a different situation from that which it has dug for itself by its own activity."

We could not wish for a better example of a general directive activity aiming at a restoration of the normal position. It is to be noted further that if the ground is unsuitable, *Solen* soon desists from burying movements, and moves away by various means, by jerking itself backwards or forwards, or even swimming away by lashing its foot from side to side. When it is suspended in the air and the siphon is stimulated it will go through the motions of burying, but only so long as the stimulus is repeated. When it has successfully buried itself, that is when the end or aim of the action is reached, it becomes quiescent.

Fraenkel is inclined to regard the whole process as a chain of reflexes. Certainly it is to a large extent stereotyped, but it is also modifiable according to circumstance, and if ineffective it is stopped and replaced by another type of activity. Note too that the so-called reflexes involved can occur in a different order, when the objective aim of the action is a different one. This is the case when the deeply buried *Solen* rises towards the surface. Here the muscles of the foot act in quite a different way. The tip is swelled up while the foot is contracted, and remains swollen while the foot is extended, thus pushing the shell upwards; then the swelling disappears as the foot is retracted,—a quite different succession of movements from that involved in the burying response.

Both when the animal buries itself and when it rises towards the surface we have to do with a continuous directive activity having a definite objective aim, rather than with a number of separate tropisms and reflexes. The *post hoc* analysis of the action artificially separates out a number of simple elements, but fails to account for their sequence and aim, and the adaptability of the behaviour.

It is interesting to note that the animal responds not so much to the abnormal stimuli present, as to the absence of the normal stimuli, and, as it were, goes to look for them; we may express this most simply and adequately by saying that the *needs* of the animal are the real source of its exploratory or restorative movements. One sees this clearly in the "righting reaction" of many animals where the need is simple, consisting merely in the re-establishment of effective contact with a surface on which they can progress (see pp. 46 ff., below).

Let me take now a simple case of the maintenance and restoration of a particular environmental position, which appears to involve two simple tropisms. You are probably familiar with the little American catfish *Ameiurus*, which is a favourite aquarium exhibit. This fish is nocturnal in its habits, and during the day lies hidden in an ecological niche, which it finds or even makes for itself. In an aquarium with a natural bottom of sand and stones each catfish selects a hole or crevice in which to live; this according to Schiche [5] may be merely a circular depression in the sand which the fish makes for itself; more often it is a niche under a stone so chosen that the fish is sheltered from light and is wedged up against the surrounding objects. If no stone is available it will wedge itself under a strip of glass or into a glass tube. If there is no shelter available at all, it will squeeze itself into a corner of the aquarium. It exhibits then a need to have its body in contact with something solid; in terms of the tropism theory, it manifests a positive thigmotaxis. In my reading of the facts this so-called thigmotaxis is merely a part of the effort to find its ecological niche; if it cannot find exactly what it wants it takes the next best thing; if it cannot have both contact and protection from light it accepts one of them—just like the earthworm. Experiment shows, as one would expect, that the catfish chooses shade rather than light—if it is placed in a dish half of which is cut off from the light it will come to rest in the shaded half.

By experiment we can thus separate out the two factors of contact and light and find out that the fish reacts to either of them. But we should not overlook the artificial nature of such experiments. A substance like glass, which satisfies the need for contact but lets the light through, is practically unknown in Nature and certainly the fish has never before come across it. What wonder then if it reacts to glass as it normally does to a stone. What it is really seeking is the normal combination of contact and darkness—quite simply, a dark hole or crevice. I very much question whether we gain anything at all by thus splitting up the situation or perceptual field into its constituent stimuli ; the animal is not exposed in Nature to the action of isolated stimuli, but to definite and rather constant complexes of stimuli. We should try to see the effort from the animal's point of view, not from our own sophisticated standpoint.

When the catfish is sitting in its crevice it faces towards the outlet and remains watchful and alert, constantly moving its eyes backwards and forwards, presumably on the look out for possible enemies. This attitude, I think, explains what happens when its so-called phototaxis is tested. Placed in a dish with the light coming from one side, it faces towards the light ; if one half of the dish is now shaded it moves into the shaded half, but faces towards the lighted half (see Fig. 3). This seems the natural behaviour for an animal that spends its days looking out from its dark corner into the open water.

I turn now to some interesting observations made by Herter [6] on the behaviour of certain small species of freshwater leeches, observations which can be interpreted only in terms of the normal ecological peculiarities of the species concerned.

Herter collected many examples of the following genera—*Piscicola*, *Hemiclepsis*, *Protoclepsis*, *Glossosiphonia* (2 species), *Helobdella*, and *Herpobdella*—and placed them in a tall glass tube measuring 2·5 cm. in diameter and 130 cm. in height, leaving them there for some weeks. They arranged themselves as follows : *Helobdella* and the two species of *Glossosi-*

phonia (which used to be called *Clepsine*) lay at the bottom tucked into the angles of the glass ; of the *Piscicola* 80 per cent collected within 5 cm. of the bottom, mostly at 2–4 cm., hanging just clear of the bottom in their usual lurking position ; about half of the *Hemiclepsis* also occurred within 5 cm. of the bottom and the rest were scattered right up the tube ; the *Protoclepsis* individuals settled down mostly at or near the surface, especially the small and hungry specimens ; finally the *Herpobdella* remained near the bottom for the first five or six days, then moved upwards, for the bottom water became somewhat foul, and this species is more sensitive to such conditions than the other bottom loving kinds. Experiments with various intensities of light showed that all except *Hemiclepsis* and *Protoclepsis* preferred a dim light, especially *Glossosiphonia*. *Protoclepsis* was positively phototactic when hungry, and *Hemiclepsis* partially so.

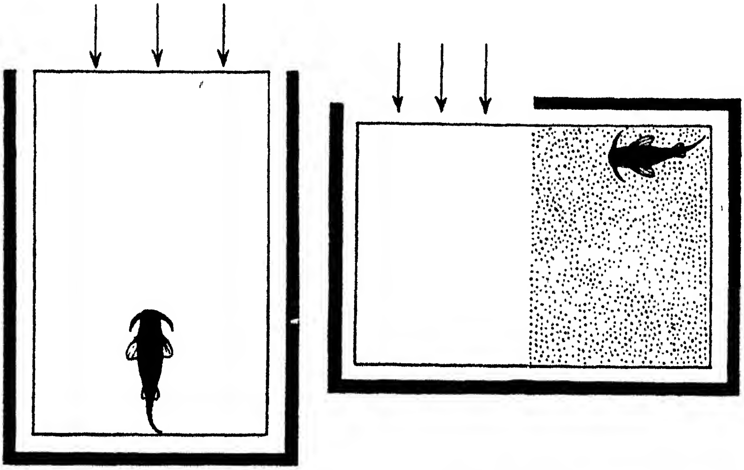

Fig. 3.—" Phototaxis " in the Catfish *Ameiurus* (after Schiche, by courtesy of Gustav Fischer)

Now these reactions, these varied choices of a special lurking place, are in close relation with the normal feeding habits of the animals. *Protoclepsis*, which when hungry settles near the surface and seeks the light, attaches itself to water-birds ; when full fed it seeks the obscurity of the bottom layers. *Hemiclepsis* is a fish parasite, with a partiality for the youngest fish, and lives in the middle depths. *Piscicola*, which is also a temporary parasite on fish, normally lurks near the bottom in dim light, attached to plants. The species of *Glossosiphonia* are snail eaters, which they find mainly on the bottom. *Helobdella* is also a bottom feeder on various invertebrates, while *Herpobdella* is a rover, swims freely and is not limited to any one level.

We see clearly in this example how each species in experimental conditions takes up the position which most nearly represents its ecological norm—that position in which it can best find its normal food, or rest after feeding.

We have now considered, by means of a few casual examples, one of the main activities of living animals—their tendency to seek out, to maintain, and to restore their ecological norm. We have seen too that one of the first things they do when brought into experimental, usually abnormal, surroundings, is to try to find conditions resembling the normal. If they cannot find their true ecological norm, they take the nearest thing to it.

Another activity which animals exhibit when brought into unfamiliar surroundings is an attempt to escape from disturbing conditions. The earthworm tries to get away from light; the *Solen* from the unaccustomed exposure to water or air. The constant uneasy exploratory movements which many newly captured animals show is no doubt a combination of a flight reaction and a search for the ecological norm.

Here also we encounter what seems at first sight to be tropisms. In many cases flying, creeping or swimming towards the light—so-called positive phototaxis—is clearly an escape reaction. The flies in a room, if undisturbed and not seeking food, circle round and round in the air; if you begin to chase them, they make for the window. So too, a bee or a wasp that has blundered into the room tries to escape towards the light, through the window-pane.

This relation between positive phototaxis and the attempt to escape from unusual or threatening conditions has been carefully studied by V. Franz [2] in plankton crustacea, young fish, tadpoles and many other forms. In general he finds that freshly caught animals, especially if placed in confined quarters, make for the light. After they have settled down and got accustomed to their surroundings, this phototaxis disappears, but can often be revived by disturbing the animals. Thus the larvæ of the fish *Centronotus* placed in a large aquarium are at first positively phototactic ; after about twenty-four hours this reaction fades away ; the least jarring of the tank will, however, send them flying to the lighted side. This reaction is the more marked the more numerous the individuals in the aquarium. Tadpoles living in a large aquarium to which they have become accustomed show no orientation to light, but swim about in all directions. If, however, a few are caught and confined in a small glass dish floating on the water they orientate themselves towards the light (see Fig. 4) ; the disturbance caused by capture and close quarters brings out the flight reaction towards the open.

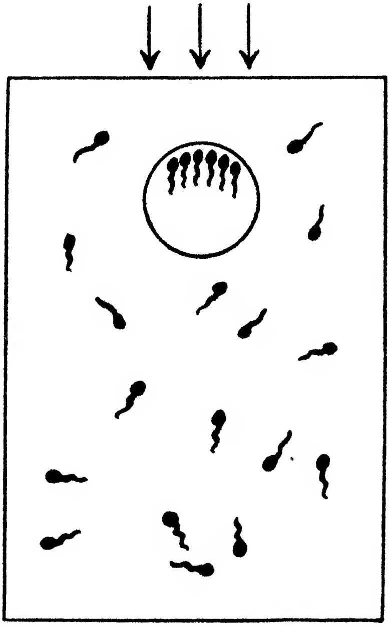

FIG. 4.—" Phototaxis " in Tadpoles (after Franz)

It is interesting to note that the flight reaction in captivity is not always towards the light—this depends upon the normal behaviour of the animal in its natural habitat. Thus the young sucker fish or lumpsuckers (*Cyclopterus*) seek the bottom of the tank when alarmed; young horse mackerel (*Caranx*) take shelter under large medusæ if these are present; the larvæ of the pogge (*Agonus cataphractus*) show negative phototaxis and sink to the bottom. Curiously enough, if the aquarium is lighted from below they still seek the bottom; the normal habit is strong enough to overcome their negative phototaxis. This shows clearly that the flight reaction is the primary thing; it is not a forced movement controlled by the direction of the rays of light. The normal flight response of the common stickleback is to dart under the cover of floating weeds or otherwise out of sight. It shows also a specific defence reaction, sinking to the bottom and remaining motionless, with its spines stiffly erected and its pectoral fins spread out. This reaction can be elicited in three ways—(1) by frightening it, (2) by confining it in a small dish, and (3) when it is in the dark, by suddenly illuminating it [7].

The fact of the matter is that all mobile animals have their own particular way of escaping from danger or from unsuitable conditions. The most usual method is to escape towards the open—this gives the appearance of positive phototaxis; others attempt to hide, to get out of sight, and this usually entails so-called negative phototaxis. Arboreal animals like squirrels naturally seek the tree-tops when alarmed; burrowing animals like rabbits make for the underground. The essential thing is the effort to escape, which depends upon the perception of danger or uncomfortable conditions; the animal seeks the light or the dark as indicative respectively of a way of escape to the open or a possibility of hiding. In this interpretation, external stimuli such as light do not act with directive force upon a passive organism, as the theory of tropisms assumes; the stimuli reacted to by the organism are those representative or indicative of coming situations, or of situations which may be sought or avoided by the organism. Thus agitation of the water is commonly a sign of approaching danger, and elicits an escape response; light is generally indicative of a way of escape for those animals that make for the open, hence they flee towards the light. This interpretation seems to me to be more illuminating and to correspond more closely to the observed facts than the alternative physiological interpretation.

The principle of representative stimuli, or *sign stimuli* as we may call them for short, is illustrated not only in the flight reactions of animals which we have just considered, but even more clearly in the other great group of maintenance activities which we may describe as food-finding behaviour. I said above that water disturbance is very generally treated by aquatic animals as a sign of approaching danger and usually elicits an escape response. But there are cases in which it acts as a sign of food. The following case came under my own observation.

The little fish leech *Piscicola* spends most of its time attached by the hind sucker with its body held stiffly extended. Sometimes it shows waving movements of its body. If you gently agitate the water, say with the end of a metal seeker, some 5 mm. away, the leech will immediately swing towards it, touch it and then jerk its head away. To water disturbance 10 mm. distant it will also respond, but not so accurately in direction. A similar reaction is given to a stream of water directed towards it by a pipette. Similar behaviour has been described by Herter [8] in the fish leech *Hemiclepsis*. Other leeches such as *Glossosiphonia* and *Herpobdella* react to a water jet by retraction. There can be little doubt that the fish leeches respond to water disturbance as normally indicative of the approach of their host, a little fish.

As Wunder [9] has shown, some fish, when deprived of the use of their eyes, will use water disturbance as an indication of food. Thus a blinded pike, if hungry, will follow and snap at the end of a pencil which is moved backwards and forwards in the water. It will respond to this vibration up to 5–10 cm. distant. It will pay no attention to motionless food. A blinded eel will behave in a similar way, though it does not go so far as to snap at the pencil. There is also a well-developed positive response to vibration shown by the burbot (*Lota vulgaris*) even when the eyes are intact. It is probable in all these cases that the vibrations are perceived through the lateral line system of sensory canals. Further cases of response to water-vibration as a sign of food are given later (pp. 74, 78).

The usual response to the casting of a sudden shadow is in many animals a retraction or a flight reaction. This is strikingly shown, for instance, by tubicolous annelids, like *Serpula* or *Sabella,* where the response to a shadow is a lightning quick retraction of the crown of tentacles. So, too, mosquito larvæ in a water-butt wriggle down if a shadow is cast upon them.

But at least one case is known where a positive response is made to a shadow, which here is clearly indicative of food. The marine leech *Branchellion* sucks the blood of the fish *Torpedo.* When it is attached to the fish the casting of a shadow upon it has no effect, but when it is lying quiet on the bottom the least shadow thrown upon it will cause it to erect its body and stand up vertically, ready to attach itself to a passing fish [10].

I shall take one more example of a sign stimulus indicative of food. A careful study has been made by Rivnay [11] of the way in which the common bed bug finds its prey. It is not specially attracted by the smell of blood or muscle or washed skin; sebum and cerumen have some attractive power; but the bug appears to be guided primarily by its temperature sense. Here is one of Rivnay's experiments.

> "A test-tube 10 mm. in diameter, containing an adult female bug, was placed over the metal shade of a desk lamp so that the tube was slightly heated at one end. The bug, which had been in a quiescent state, soon reacted, directing her antennæ toward the source of heat. After stroking the antennæ with the forelegs for a moment, she moved toward the source of heat with proboscis extended, ready for piercing. Such reactions were shown also when a dissecting needle was slightly heated over a lamp and placed near a bug. Upon reaching the needle, the bug followed it in every direction, but when the same needle was cooled and the procedure repeated, none of the above reactions occurred."

A bug will respond to the heat of the human body 3–4 cm. away. A difference of 2° C. will bring about the reaction. It is influenced in its actual attack by the character of the surface; thus it will not attempt to pierce any smooth surface like nail or horn or glass, but will do so if these substances are roughened. Similar results have been obtained by Wigglesworth and Gillett [11A] for the blood-sucking bug *Rhodnius.*

There is some evidence that, for mosquitoes and lice also, heat acts as a sign stimulus for food just as it does for the bed bug [12].

An interesting parallel is afforded by the behaviour of the medicinal leech (*Hirudo medicinalis* L.), which when adult attaches itself only to warm-blooded animals. Clear evidence has been adduced by Löhner and by I. van Baal that it is attracted to its prey by temperature. The latter has shown [13] that the leech will approach a heated tube and climb upon it, carrying out exploratory movements with its head. Kept in water at 19° C. it would respond positively to the tube at 22° C., being thus sensitive to a temperature difference of 3°. Several other smaller species of leeches were tested, none of which attack warm-blooded animals ; none of them showed a positive response to increased temperature.

The examples we have considered of the restoration of the ecological norm, and of the methods and clues employed in the search for food and escape from enemies—all give point to the statement made at the beginning of this chapter, that a full knowledge of an animal's normal life, of its normal ecological relationships, is necessary before we can hope to interpret in an intelligible way its behaviour in experimental conditions. These conditions are generally abnormal and unusual from the animal's point of view, and its first impulse is to escape or, if this effort fails, to take up the position most nearly corresponding to the norm. We can understand these efforts only if we know what that norm is, and what is the animal's normal method of flight. So too the meaning of the clues or sign stimuli which it uses as indicators of danger or of food becomes clear to us only in the light of our knowledge of the animal's behaviour in nature.

As might be expected, an animal's behaviour in quite abnormal surroundings is often itself abnormal. A *Paramæcium* exposed to a constant electrical current of low intensity experiences something which it has never before encountered, and the galvanotaxis which it exhibits has no obvious meaning or significance *qua* behaviour. So, too, bright and localized sources of light are practically unknown in nature and the apparently forced phototaxis which many nocturnal insects exhibit towards a bright lamp has something abnormal, meaningless and pathological about it. It is mainly when exposed to such unnatural conditions that the animal shows that forced and automatic response to simple physical stimuli, which according to the theory of tropisms is the basis of all behaviour. Tropisms are in fact very largely laboratory products—the outcome of exposure to artificial and unnatural stimuli.

The theory of tropisms or forced movements is of course the offspring of the causal-analytic view which we discussed in the first chapter. Quite different is the point of view which we have illustrated in the examples we have just been considering.

From this point of view the animal is regarded as essentially active, not as acted upon, as exhibiting directive activity in relation to its needs, and under the guidance of perception, not as an automaton moved this way and that by the direct action of impinging stimuli.

I referred at the beginning of this chapter to some of the extensive work which has been done in the last twenty or thirty years on the migrations of fish. The facts of fish migration are extremely interesting, and form a good example of a large-scale study of behaviour in relation to ecological conditions.

The migratory movements of fish fall mostly into two main groups—feeding migrations and spawning migrations. There are also, in addition, movements which are connected directly with environmental changes, particularly changes of temperature. A striking instance of this occurred as a result of the abnormally cold weather which was experienced in the early months of 1929, when most of the soles in the southern part of the North Sea moved out from the icy waters of the Continental coasts to seek deeper and warmer water offshore more suited to their needs [14]. Most species of sea fish have quite definite habitats or areas of distribution, which are determined by environmental factors, such as temperature, salinity, depth and nature of the bottom [15]. Where the environmental norm moves or extends with change of season the fish may migrate with it ; thus the large tunny moves north as the sea gets warmer, and some find their way regularly into the North Sea in the autumn to provide sport for ambitious anglers.

But it is the spawning migrations of fish that are the most interesting from the point of view of behaviour. Feeding migrations are also important, and sometimes they are quite well defined, but they are rather in the nature of nomadic and irregular wanderings in direct search of food, and are comparatively easy to understand and explain.

This is not the case with the reproductive migrations, which still remain in large measure mysterious. Let us take as a simple example the spawning migration of the plaice in the southern North Sea. This has been studied in great detail in the course of the international fishery investigations; thousands of plaice have been marked with little vulcanite buttons [see Plate I (i), p. 50], and a good percentage of them recovered from the catches of fishing vessels; the spawning area has been accurately delimited by fishing for the planktonic eggs; the hydrographical conditions of the area are also well known.

In the beginning of winter the mature plaice, which are scattered about, as far north as the Dogger Bank and the Danish coast, start moving southwards and collect in the deepish water between the East Anglian coast and the coast of Belgium. There is here a tongue of comparatively warm and salt water which extends up from the English Channel and it is in this water that the plaice spawn in December and January. At this time of year the current which flows through the Straits of Dover towards the north-east is usually well developed, and carries the floating eggs towards the coasts of Holland, Germany and Denmark, where the tiny fish settle down on the sandy flats which are favourable to their growth (see Fig. 5). There they live, moving further out from the coast as they grow older, until some five years later they are ready to complete the circle by themselves repairing to the spawning ground where they were born. After spawning, the adult fish disperse in search of food, mainly towards the north.

The adaptive nature of this spawning migration is clear; the eggs are spawned up-current, in such a position that most of the larvæ will be passively drifted to the areas in which they can best develop; they find thus their ecological norm. The spawning fish seek, not the habitat of the young, but an area from which the eggs and larvæ will be carried to that habitat.

It is a general though not invariable rule that fish spawn up-current so that their young are distributed down-current

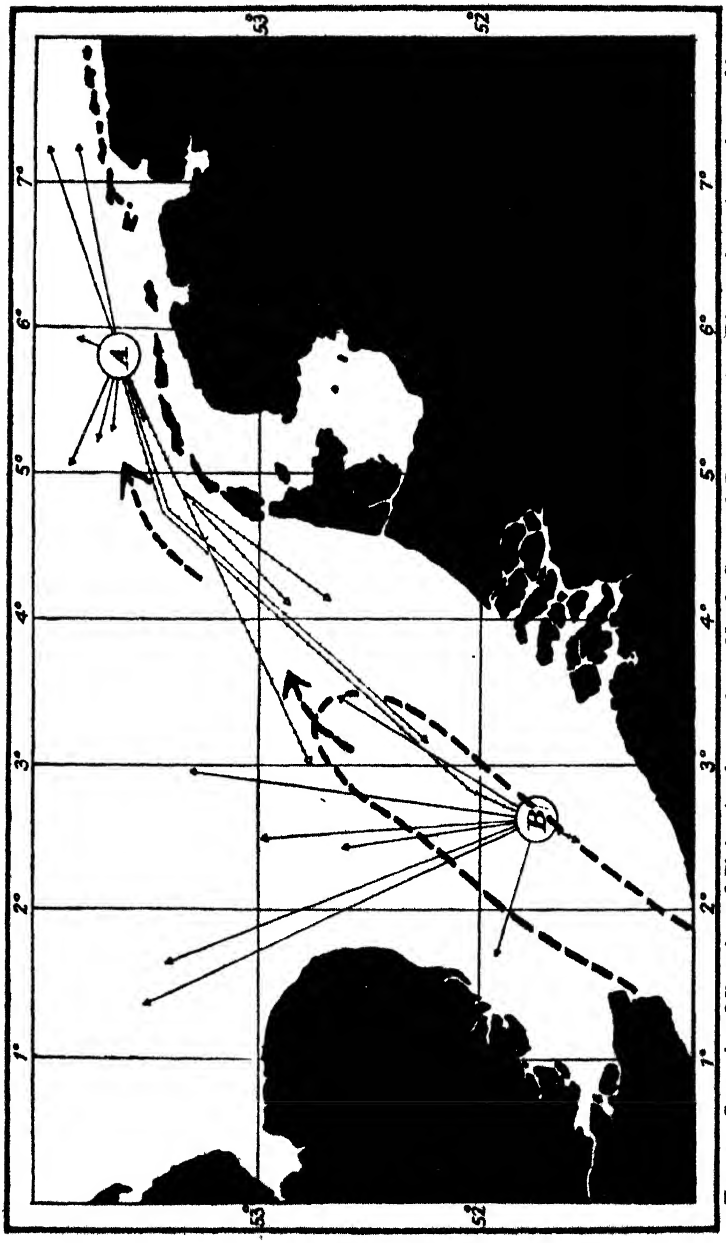

FIG. 5.—Spawning Migration of Plaice in the southern North Sea and Post-spawning Dispersal, as shown by marking experiments carried out at *A* and *B*.

The area enclosed by the broken line is the spawning area; the arrows indicate the prevalent drift towards the grounds on which they live and grow. The spawning place of the European eel, in the deep water south of the Bermudas, is so situated that the larval eels or leptocephali are carried slowly by the prevailing easterly drift towards the coasts of Europe, where they run up the rivers as elvers (see Fig. 6). After several years of river life the mature fish descend to the sea in the autumn, and complete the cycle by migrating out all these thousands of miles to their place of birth.

The reverse migration is shown by the salmon and other anadromous fish, which move up the rivers to spawn, returning again to the sea where the greater part of their feeding and growing life is spent [16].

Now there is much that is puzzling and unexplained about these spawning migrations. We may perhaps assume that the immediate stimulus to the migratory movement is some particular physiological condition associated with a certain state of development of the gonads. But why does the fish make for some special locality and how does it find its way? We know that salmon return, as a rule, to the river in which they were born or somewhere near it, and there is strong evidence that individual memory must play the dominant part in this so-called homing instinct. The extensive and thorough marking experiments of Rich and Holmes [17] have demonstrated for the Chinook salmon of the Pacific coast of North America that the return to the stream of origin must be due mainly to individually acquired experience. Eggs were taken from one branch of the great Columbia River system and reared in another branch hundreds of miles away; after a year or so of river life the young fish went down to the sea and travelled probably great distances therein. When they returned three to four years later they made straight for the branch system in which they were reared, not that in which they were spawned, some returning to the actual tributary in which they had spent their early life. The fish then must get to know their own river, its estuary and the approaches to it. But they may travel hundreds of miles in the sea; how do they find their way back to the neighbourhood of their river? Can they guide themselves by the prevailing currents, or do they become acquainted with the somewhat featureless topography of the sea-bottom? No one knows.

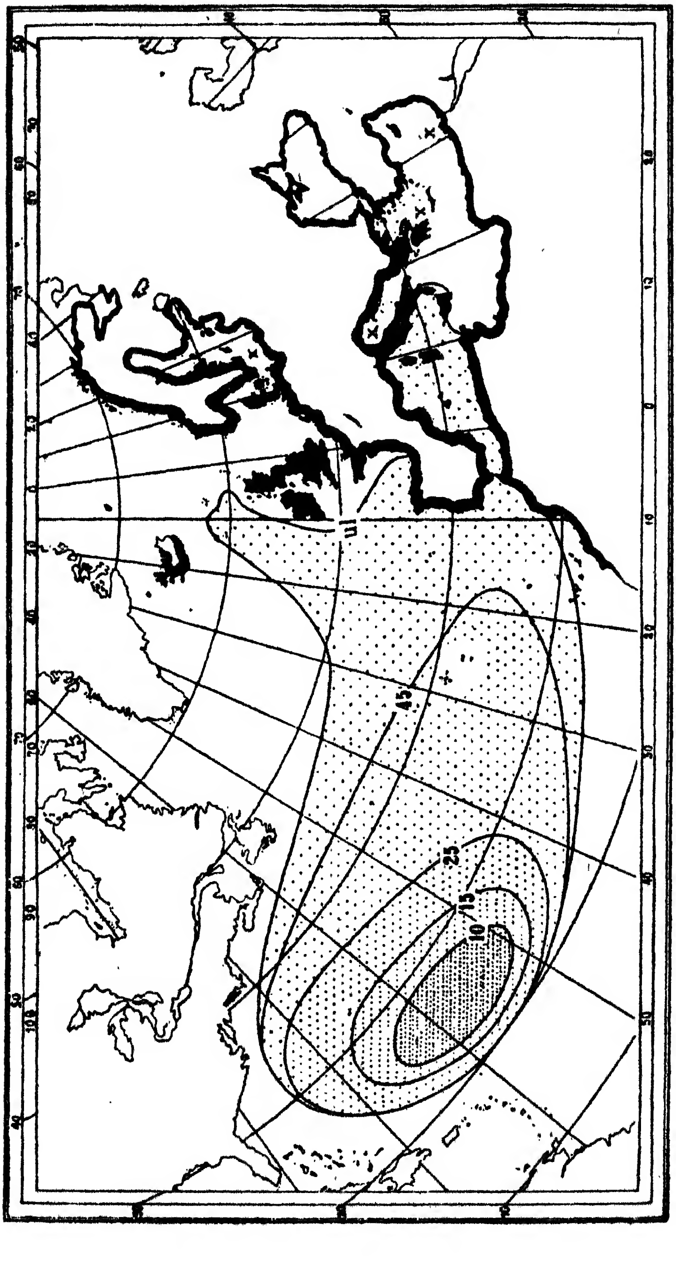

FIG. 6.—Spawning Area and Distribution of the European Eel (by courtesy of the Director of the Natural History Museum)

Eels occur in the countries outlined in black; eel larvæ in the dotted area, those less than 10 mm. in the centre, spreading to the east as they grow bigger

The return of mature plaice to the spawning area is more mysterious still. They left the spawning area as eggs transported by the current, and they cannot possibly have learnt anything about the topography of the grounds over which they drifted as larvæ. Yet when the time comes they find their way to the right spot. Probably they are guided by the current, and swim persistently against it on their spawning migration ; even so, how do they know when they have arrived, why do they not continue onwards down the Channel ?

These spawning migrations have all the appearance of being long-range directive activities. They are activities directed towards the future ; the fish actively seeks a set of conditions which are not yet there. It seems highly unlikely that its behaviour in setting out on its spawning migration can be explained in terms of reaction to immediate or present stimuli.

A distinguished French ichthyologist [18] has suggested that the ascent of the salmon is due to what he calls " Branchiotropism "—a response (mediated by the gills) to increased quantities of dissolved oxygen in the water. He considers that the salmon, when it is ready to run up to spawn, is attracted to estuaries by the higher content of oxygen in the fresh water coming down, and that it swims right up the river because in general the oxygen content increases towards the upper reaches, owing to increased turbulence. He holds that the main determining cause of the up-river migration consists in this direct action of increased oxygen content on the gills of the fish.

But clearly an active seeking for this particular stimulus when it is absent is a very different thing from reacting to it when it is present, and the theory does not in the least explain why the fish in the sea sets out to look for increased oxygen at all—we have to fall back upon *needs*. Still less does it explain why the salmon seeks a particular estuary—that leading to the river system in which it was born.

Furthermore, many facts show that in the mouth of the river increased oxygen content is *not* the factor that determines ascent. Thus, in the lower reaches of some of our salmon rivers, like the Tees and the Tyne, there is a long stretch of heavily polluted water, in which the oxygen content may fall very low indeed; directly poisonous substances may also be present; in spite of this the salmon try hard to penetrate this polluted zone and a proportion manage to get up. The directive impulse to ascend is then not determined or controlled by environmental conditions, but if these are unfavourable it continues and persists in spite of them.

It is clear that no theory of the reproductive migration of the salmon can be adequate which does not take cognizance of this active seeking out of a particular locality, and the persistence of the effort to reach it, even in the face of difficulties. The up-stream migration is essentially a long-range and persistent directive effort to reach the right place for spawning, that is to say, a place favourable for the development and growth of the young fish.

This is true also of the spawning migrations of the plaice and the eel and of thousands of other cases.

I shall not attempt here to work out any theory of the migrations of fish—I doubt whether it is yet possible, but it seems certain that a purely physiological theory must be inadequate. A review of recent work on the subject will be found in [19].

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CHAPTER III

MAINTENANCE ACTIVITIES

If we take the broadest possible view of organic activities we see at once that they can be grouped under three heads, according to the ends to which they are directed. There are the activities aiming at the maintenance of the individual ; there are the activities directed towards reproduction ; there are the activities whose end is the development of adult form and capacities. In these master-activities, maintenance, reproduction, development, behaviour plays a considerable part, at least in animals, and it is accordingly convenient and illuminating to classify the behaviour activities of animals with reference to these three main ends.

I propose in this and the following chapter to consider some examples of the maintenance behaviour of animals, in order to expand and illustrate further the conclusions we reached in a tentative way in the last chapter. Reproductive and developmental behaviour will be dealt with to some extent later (Chapter VI), apropos of the problems of instinct.

A very great part of the life of all animals is concerned with self-preservation and the wresting of a livelihood from an oft-times hostile environment. The " conatus in suo esse perseverandi," as Spinoza phrased it, is one of the most potent springs of all action. It lies deeper than thought or deliberation, deeper than consciousness—as we realize when we react " instinctively " in the presence of great and sudden danger. We do not need then to assume that the animal is consciously aware of the aim or end of its self-preservative activities or thinks out how to achieve it. Its actions take place at an altogether lower level, where the relation between perception and action is immediate and unhesitating.

We can most conveniently classify the maintenance behaviour of animals by considering the *needs* which they seek to satisfy—needs for food, water, shelter, protection from enemies, and so on. The first and simplest of these is the need to achieve and maintain an effective position or orientation with respect to gravity and the substratum. Animals that walk or creep upon the earth must maintain contact with it if they are to carry out their life-activities effectively; we find accordingly that if the normal relation to the substratum is disturbed they try to restore it. Animals that move freely through the air or the water are faced with the problem of balance or equilibrium; those that live buried in the earth must as a rule maintain a particular orientation to the surface of the soil, and to gravity, as we saw when we considered the burying response in *Solen.*

Closely linked with the need to maintain a particular position or orientation, is the need, which we have already considered, to find and remain in the appropriate ecological surroundings, the proper ecological niche. This includes the problem of finding the niche to begin with, emigrating from it when through seasonal or other changes it becomes unsuitable, or otherwise countering unfavourable modifications of it, e.g. by hibernation or æstivation.

A third group of maintenance activities arises from the need to obtain the means of life and growth, namely suitable food, water and oxygen. Finally we have the behaviour which is directed towards escape from enemies, whether by passive defence or by flight or by fighting.

We get then the following simple scheme of maintenance responses in relation to particular needs:

1. Position responses.
2. Finding and maintaining the ecological norm.
3. Food-finding activities.
4. Escape from enemies.

I propose in what follows to consider some examples of these different types of maintenance behaviour, with particular reference to the nature of the perceptions involved. Naturally I shall be able to give only a few such cases, for to cover the ground systematically would mean writing a natural history of animals in many volumes.

1. Position Responses

Let us begin with the simplest of position responses—those arising out of the need of creeping animals to maintain foothold. When this foothold is lost through accident or interference there follows in almost all cases a definite "righting reaction," or, putting it more generally, an effort to re-establish adequate contact with the substratum. Take, for example, one of the least differentiated of all animal forms—*Amœba.* An Amœba will creep on the surface film or on the underside of a cover-slip as well as on the slide itself. If suspended freely in the water it sends out long slender pseudopodia in all directions, the body being reduced to little more than the nodal point of these outstretched arms (see Fig. 7). If the tip of any process comes in contact with a solid surface it spreads out and attaches; the other pseudopodia are withdrawn into the body and the Amœba glides on to the surface

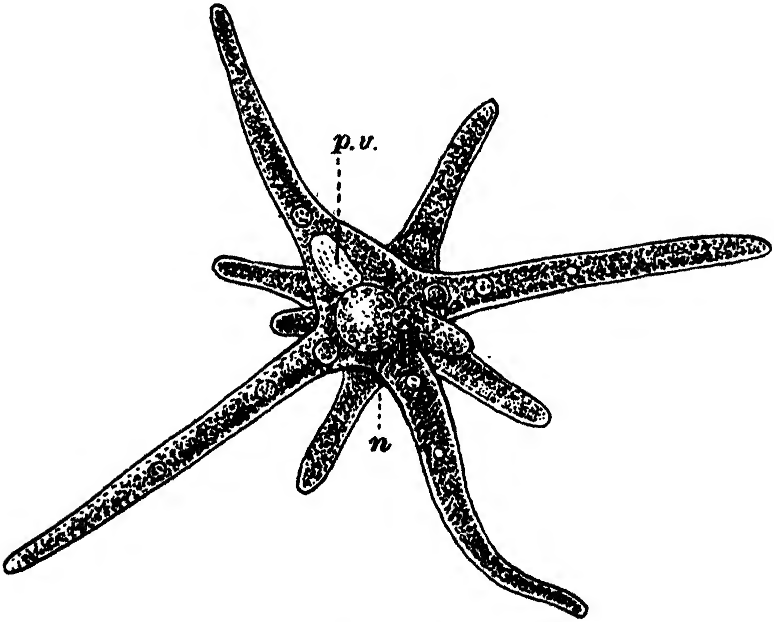

Fig. 7.—Amœba suspended in Water and reaching out for Foothold (after Leidy)
p.v. Vacuole. *n.* Nucleus.

and resumes its normal shape [1]. As the Amœba has neither dorsal nor ventral surfaces there is, naturally, no "righting reaction" in the strict sense.

This reaction is shown very clearly in the Rhizopod *Arcella*, which has a low limpet-like test with the edges tucked in to form a plane surface surrounding a large foramen through which the pseudopodia are exserted. The animal creeps about on this physiologically ventral surface, and if it is reversed it rights itself. Much interest attaches to the method of righting. Engelmann, who studied the question in 1869, noticed that gas bubbles were almost invariably formed in the peripheral protoplasm when the Arcella was overturned, and disappeared again when the animal regained its footing. Sometimes the bubbles formed on one side only, and so raised the edge of the test, thus greatly facilitating the righting movement. Engelmann regarded this one-sided formation of bubbles as a definite means employed by Arcella for the purpose of righting itself, and he thought also that Arcella could so regulate the appearance and disappearance of the bubbles as to regain its attachment, with, of course, the assistance of its pseudopodia. Thus he wrote :

> "An analogous phenomenon is seen in some of the *Arcella* which have been floated up to the top of the drop, dorsal side uppermost. After they have exhausted themselves for some time in useless efforts to attach themselves by their pseudopodia, the gas-bubbles diminish in volume on one side. Consequently, this side sinks, the *Arcella* takes up an inclined position, then a vertical one and finally turns over completely as soon as one of its pseudopodia has fixed itself. Then the gas-bubbles disappear rapidly" (Quoted from Bles, 1929, p. 535).

The late Dr. Bles, who made an extremely careful and detailed study of gas production in *Arcella* [2], came to the conclusion that while gas bubbles were usually formed whenever an Arcella was reversed, and undoubtedly facilitated the righting movement, this reaction could take place without them and was primarily due to the activity of the pseudopodia.

He describes the normal righting process as follows (see Fig. 8). The pseudopodia, which are withdrawn on reversal, are protruded after one or two minutes and vigorously waved about in the water "as though they were groping for a solid object above the animal." One of them, bending downwards, comes in contact with the substratum, attaches itself, shortens and thickens and pulls down the edge of the test. By this time, 5–20 minutes after reversal, gas bubbles may or may not have been formed, but in any case the test is up-ended so that it stands vertically and then tips over, to fall with the flat ventral side downwards. The actual righting movement after the pseudopod has taken a grip occupies only one and a half to two minutes.

Bles definitely formed the opinion that " the gas-vacuoles are formed, not as an adaptation to be used in facilitating the righting of a reversed *Arcella*, but as a by-product resulting from the main activity of the organism for the time being, which consists in the struggle to turn over into the crawling position " (p. 551). The vacuoles disappear after the righting process is completed, just as Engelmann said. They appear to consist of pure oxygen. They have also a hydrostatic function, enabling the animal to rise from the bottom when the water is poor in oxygen and reach better oxygenated layers.

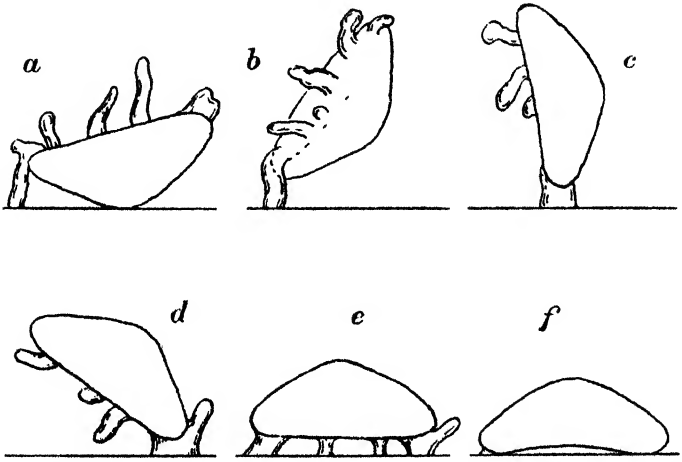

FIG. 8.—The Righting Response in *Arcella* (after Bles, by courtesy of the Oxford University Press)

Loxophyllum is a Ciliate which habitually moves about with its right side in contact with some solid object. When turned over on its left side, it adopts various methods of righting itself; it may raise either end of its body and wave it about until the right side touches ground, when it twists over and rights itself; sometimes it raises the anterior end straight up in the water and topples over; one was observed to curl up both ends, forming a hoop, then to roll over, attach its right side and glide away. If cut in two, the front half can right itself just as the whole does. These observations we owe to Holmes [3]. The attraction which a surface has for creeping Ciliates is amusingly illustrated by an observation which Marie Goldsmith [4] quotes from Verworn. The latter watched an *Oxytricha* running for hours on the surface of the spherical egg of the fresh-water bivalve *Anodonta.*

If *Hydra* is detached from its hold and placed on a horizontal surface with the tentacles downwards, it reattaches with its foot and raises its body up. This is not a reaction to gravity, for Hydra may be found attached to the surface film, hanging downwards, or to the bottom spreading its tentacles upwards, or to a perpendicular surface, hanging as a rule with the body obliquely directed downwards. The righting reaction is clearly a contact response, an effort to re-establish the normal contact relation between the foot and its support. The response of the animal to the abnormal situation goes further, as Jennings [1] points out; mere foothold is not sufficient, the Hydra must have space in which to spread its tentacles, so as to be in a position to catch its prey. Accordingly, it shifts about till this condition is fulfilled, and it reaches a fully " normal " position with respect to the environment. It is noteworthy that when it moves from place to place, as it may do under the influence of hunger, it will spontaneously detach its foot after taking hold with its head and progress in the manner of a leech or a looper caterpillar. Contact between foot and substratum is therefore not a " forced " taxis; it is in this case a constituent in a train of directive behaviour.

Fresh-water planarians, as everyone knows, readily glide along under the surface film, and their righting reaction, which is well developed, has no relation to gravity. The following (original) observations on *Dendrocoelum lacteum* illustrate this. The animal sticks rather firmly to the bottom of the dish in which it is crawling and is difficult to overturn.

When it is turned over, it writhes a little, twists its head until the under surface touches ground, takes hold, and starts strong muscular contractions of the body which soon pull it round ventral surface downwards. (The movements referred to are typical of its progression when disturbed. Fixing itself by the head it carries out an energetic contraction of the body, pulling along the hind part; this in its turn fixes and the fore part extends, and so on alternately.) If, while it is reversed, a flat object is presented to the head, it will creep upon this, back downwards, and from this to the surface film; if the water is shallow, it will reach down till its head touches bottom, then twist ventral surface downwards and flow along the bottom.

The righting reaction of planarians, which as we have seen is a pure contact reaction, has been very fully studied by Pearl [5] in *Planaria dorotocephala.* Normally the reaction takes place very simply, the overturned flatworm twisting itself spirally so that the ventral surface of the head touches ground and the rest of the body follows rapidly. Isolated pieces of the worm will also strive to right themselves, even though they are not big enough to carry out the usual twisting movements. Thus small strips cut from the front end and reversed will fold back their posterior ends till they make contact with the surface, then pull the rest of the strip over backwards. In a triangular piece cut out as shown in Fig. 9, the method of righting is even more remarkable. The long side begins to roll or curl its edge backwards to make contact, the movement taking place first in the middle, then extending to the ends.

> "As soon as a considerable portion of the edge had so folded under and become attached, the piece gave a series of strong contractions and literally 'flopped' over the attached edge and came down right side up. . . . This behaviour was so peculiar, and at the same time precise, that the experiment was repeated many times on this piece and on others cut in the same way. The same method of righting was always observed. After the first few times the turn is made in this way; it is done more quickly at each successive trial" (Pearl, p. 682).

In this case, where the normal mechanism of righting has been destroyed, the crippled piece uses an entirely novel method—one which has probably never been used by any of

PLATE I

(i) MARKED PLAICE

(ii) THE RIGHTING RESPONSE IN THE STARFISH *ASTERIAS FORRERI*

Left.—Uncoordinated movements, starfish beginning to turn back tips of arms on the right.

Right.—The unified impulse has set in to turn on arms to the right.

(After Jennings, Publications of the University of California)

its ancestors. The end is more constant than the means of attaining it. As Jennings says : " The essential point seems to be, to get some portion of the ventral surface, by any means whatever, into contact with the substratum, then by working out from this point, to bring the whole ventral surface into attachment " (p. 246).

Much work has been done on the righting reaction in starfish and brittlestars ; outstanding contributions are those by Preyer [6] and Jennings [7]. The interesting point about it is that it is not a simple and stereotyped reflex, but a definitely directive action, showing much variation in the method of turning adopted. Jennings describes seven different modes of righting in *Asterias forreri*. Generally one or more of the arms curl back and attach themselves ; the simplest method is when two adjacent arms take hold and pull the rest of the body over. If more arms attach, the turning becomes more difficult, and one or more may have to relinquish their hold. At first the action lacks co-ordination, but sooner or later there sets in what Jennings calls a unified impulse towards a particular type of solution [Plate I (ii)]. Preyer also called attention to this unification of effort. Occasionally the righting may take place without the help of the tube-feet,

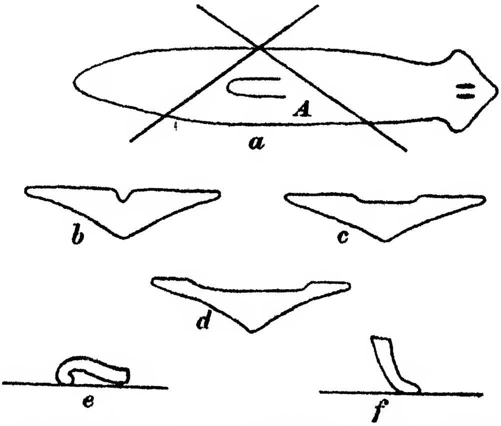

FIG. 9.—The Righting Response in Triangular pieces of *Planaria* (after Pearl, by courtesy of the Oxford University Press)

b, c and *d* show the rolling over of the edge ; *e* and *f* show the turning piece in profile especially if these are prevented from taking hold. In this case, the starfish raises its disc by standing on the tips of all five rays and then swings one or more rays over or under until it topples over right side up. I have observed most of these methods of turning in the starfish *Asterina gibbosa* [8], but not the last, the rays being too short and stubby in this form to permit of it raising itself on their tips. In about 90 per cent of the cases observed, the *Asterina* turned neatly and quickly (often in 30 secs. or less) on two adjacent rays. Sometimes when three rays were employed, the starfish got " tied up " and the righting was greatly delayed. Sooner or later, however, the unified impulse set in, and the bad start was retrieved.

The question as to the initiating " stimulus " of the righting reaction has been much discussed. It has been held that the stimulation of the dorsal integument produced by the inverted position is the initiating cause, but this seems to be definitely disproved by the work of Preyer and of Fraenkel [9], who have shown that if the skin of the back is completely removed the inverted starfish will still right itself. The theory of Wolf [10] that the stomach acts as a static organ by reason of its drag on the mesenteries has also been disproved by Fraenkel.

It is very doubtful whether response to gravity comes into the story. Preyer found that starfish suspended in the water with the ventral surface uppermost would try to turn, but Fraenkel showed that turning took place just as readily if the starfish was suspended right way up. It is well known too that in natural conditions starfish are often found adhering to the under surface of stones or to a vertical wall of rock. Placed in a wide horizontal tube, a starfish will crawl round in any position, quite irrespective of gravity (Preyer). As Loeb has shown [11], if a starfish is fixed to the under side of a floating piece of cork with its ventral surface downwards it will turn over and attach itself to the cork (p. 64). I obtained a similar result in *Asterina.*

There can be little doubt that, as maintained by Fraenkel and myself, the initiating stimulus or perception is the lack of contact between the tube-feet and something solid on which the starfish can creep—in other words, it is the *need* to establish contact, the *need* to re-establish the normal relation to the substratum, that sets the reaction going. I found that if a piece of slate were held just above an inverted *Asterina* it would attach itself to the slate and could be lifted away; if the slate was kept in the same position, the starfish usually crawled off it, on to the bottom, and there turned. If a piece of *Fucus* was placed on the ventral surface, this, giving no firm foothold, was carried right off the starfish by the walking movements of the tube-feet, and the animal then proceeded to right itself. From my experiments I drew the conclusion

> " that the primary aim of the righting reaction is to bring the tube-feet into contact with a solid and resistent surface. The first thing *Asterina* does when detached from its hold is to stretch out its tube-feet and feel round in all directions. Mere tactile contact is, however, not sufficient . . . the surface must resist a pull. The perception involved in the contact reaction is not so much tactile as kinæsthetic. It does not seem to matter very much whether the surface of adhesion lies below the starfish, as in the normal righting reaction, or above it,"

as in the experiment with the slate. Space to the starfish must be mainly a " kinæsthetic space." It is probable that it can dimly distinguish between a level and a steeply inclined plane, though it shows no pronounced tendency to take up any particular orientation to gravity. When it is crawling at peace over a level surface the tube-feet do not attach themselves by suction to the bottom, but act rather as legs or levers pushing the starfish along. But when the starfish ascends a steep slope or crawls along an inverted surface it must attach itself more firmly by means of the suckers on its tube-feet. So we may presume that it is probably able to distinguish in a vague way, by kinæsthetic sense, between a surface on which it may walk and a surface to which it must cling.

This may perhaps also be the case with ants and other small insects. I refer later on (p. 99) to an observation by Hingston from which it appears that the ant *Messor barbarus* will persist in attempting to establish a rubbish dump on a vertical bank. I use this as an example of the inflexibility of instinct, but it perhaps indicates also that this species has little if any perception of gravity. The same conclusion is suggested by an observation recorded by Remy de Gourmont, in his *Promenades Philosophiques* (1st series).

An ant-hill is situated near the foot of a wall; the ants returning to it along the foot of the wall do not travel in a direct line, but deviate to right and left considerably, following an irregular and sinuous path. They turn as readily up the wall as out from it across the level. It seems to make no difference to their divagations whether they move up the wall or over the ground. Gourmont concluded that the ants believed themselves to be always on a horizontal plane, and had no perception of verticality. Being very small and very light, and having immense muscular strength, they need exert very little extra effort to climb, and it is possible, as Gourmont suggests, that they do not distinguish in practice between a horizontal and a vertical surface, so that, in a sense, space appears to them as a level, if irregular, plane.

Animals that live buried in sand or mud, like the lug-worm (*Arenicola*) and others, the heart-urchin (*Echinocardium*), and many bivalves, such as the cockle, take up and maintain a particular position with respect to the surface of the sand and often a particular orientation with respect to gravity. We have studied this particular position-response in *Solen* (pp. 25–7, above) and there is no need to consider further instances. I append, however, one or two references [12].

Animals that swim or fly, and to a less extent those that walk or run, have to maintain and constantly adjust their equilibrium, and their orientation to gravity. Much attention has been paid, especially in Vertebrates, to the physiology of equilibration, to the complex interaction of visual, kinæsthetic and labyrinth functions which ensure an automatic maintenance of balance [13]. But this question belongs rather to physiology than to behaviour and need not detain us further. I should, however, like to mention one set of observations—those by W. von Buddenbrock [14] on a peculiar reaction to light shown by many Crustacea. Most species have statolith organs, which subserve equilibration, but some have not. Now Buddenbrock found that species without statoliths very generally orientated themselves to unidirectional light by turning their backs to it, whether the light came from above, or from the side or from below, and he found the same to be true of many species possessing statoliths, when these organs were removed. It is clear then that the direction of light, which normally falls from above, is used in taking up and maintaining the normal back-upwards orientation, in addition to the stimuli originating in the statolith organs, in those species that are provided with them. Light coming from above and the pull of gravity from below is the normal perceived "situation," but we see that the response may in experimental conditions be to light alone, i.e. to a part of the normal situation. Similar results have been obtained for *Planaria* by Bock [14A].

Another interesting position-response shown by many aquatic animals is that which has received the imposing name of *rheotropism* (response to currents). Everyone knows that trout in a stream spend much of their time head on to the current, keeping station in a particular spot. But of course this is not a fixed tropism ; the fish may dart upstream, or turn and shoot downwards after food, or in order to take cover. And at the spawning time keeping station gives place to a persistent and active migration towards the spawning grounds. " Rheotropism " is conspicuously shown also by the long-legged water-skaters (*Gerris*) which can be observed in almost any stream. The animals, such as insect larvæ and snails, which creep about on the bottom of the stream, must also resist the current, if they are not to be gradually washed downstream.

In the case of creeping animals there is no great difficulty in understanding how they manage to sense the direction of flow ; the pressure of water on the upstream side of the body must be greater than on the downstream side, and we find in fact that many of these forms orientate themselves along the line of flow, with the head end upstream.

It is not so clear how fish and other free-swimming animals manage to sense the direction of the current. In a wide and deep stream of uniform velocity, for instance, it is difficult to see how fish can orientate themselves at all. They are by hypothesis moving with the current, so that there can be no difference of pressure exerted by the stream on the different parts of the body. Without some point of reference which is at rest relatively to the stream, it seems impossible for the fish to react to the current in any way. Such points of reference could be supplied by tactile or visual perception of the banks or bottom of the stream.

That such perceptions do in fact account for rheotropism in certain fish has been shown by Lyon [15] in a series of ingenious experiments, principally with the American mud-minnow *Fundulus*. Here are some of his experiments, together with some observations of my own on the stickleback (*Gasterosteus aculeatus*).

(*a*) The fish are in a glass-bottomed aquarium slightly raised from the ground. A cloth painted with black stripes is drawn slowly along under the aquarium. The mud-minnows, especially the young ones, as a rule swim in the direction of movement of the striped cloth. I have been unable to obtain this response in the stickleback.

(*b*) Inside a galvanized-iron dish there is placed a beaker filled with some opaque fluid; the intervening circular channel is filled with water, and it has gravel on the bottom and weeds on the side. The fish are introduced and the dish rotated. The fish follow the direction of rotation, although this means that they move *with* the current that is slowly generated by the movement of the dish. If the rotation is now stopped, the circular motion of the water continues, and the *Fundulus* turn round and head into the current, trying to keep position relative to the now stationary side and bottom of the dish. It is clear that the perception leading to the so-called rheotactic response is that of a slipping visual field, and the aim of the response is to maintain the visual field constant, i.e. to keep station relative to a moving or apparently moving surface. As Lyon expresses it, " the stimulus is the moving or apparently moving optical field, and the current is only indirectly responsible " (p. 154).

I have repeated this crucial experiment several times with the stickleback, and can fully confirm Lyon's observations. The apparatus used is shown in Fig. 10.

Instead of a galvanized-iron dish supplied with weeds and gravel I used a circular glass dish, with a striped band fixed round it. Vigorous sticklebacks almost invariably swim with the rotating dish, keeping pace with the stripes so far as they can. When, after 10–12 slow revolutions, the dish is stopped, the sticklebacks turn and head against the stream. Sometimes in a slow current, when they are facing downstream, the sticklebacks will back against the current instead of turning to face it.

(*c*) A long bottle, holding 10 litres, is filled with water containing young *Fundulus* and corked. When it is moved along the tank wall to the right, the fish swim to the left. When it is floated downstream in a tide-way the fish swim to the upstream end, though of course there is no current in the bottle itself.

(*d*) The *Fundulus* are placed in a box 1·25 metres long and 50 cm. wide, with ends made of coarse wire netting. The bottom is covered with gravel and the sides with weeds. If the box is held stationary in a tidal stream the fish head into the current ; if the box is allowed to float down this orientation is lost, for the visual environment appears to the fish to be stationary.

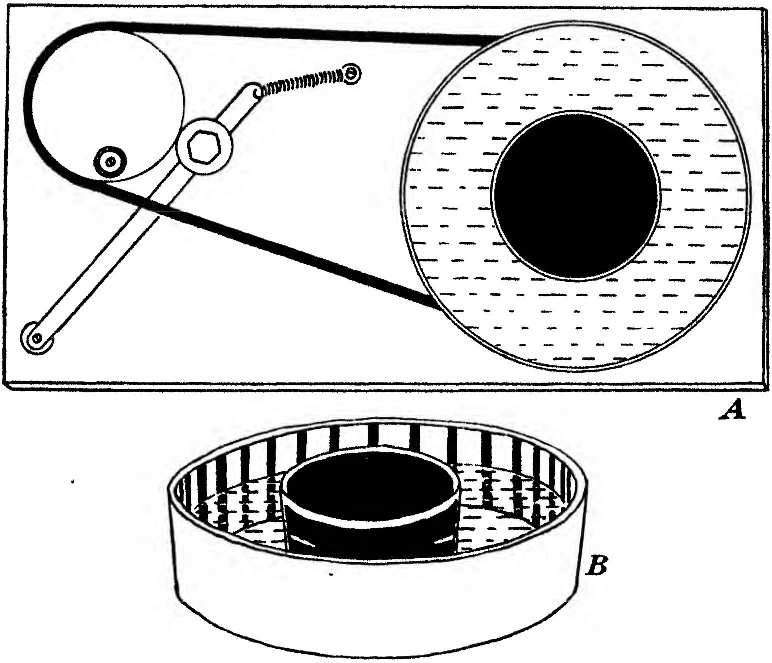

FIG. 10.—Apparatus used for Studying Rheotropism in Fish

A, plan ; *B*, elevation

It is clear from these experiments that the response is an optical one, and that the effect of the current is indirect.

> "I am convinced," writes Lyon, "that with the fishes experimented with (Fundulus, Scup, Stickleback, Butterfish) orientation in currents of fairly uniform velocity is usually an optical reflex. The current does not directly stimulate. Indirectly it does, by tending to move the fish away from the fixed points of its environment" (p. 155).

Tactile stimuli also come into the story, as can best be seen in experiments with blinded fish. Placed in a trough in a weak current they swim at random until they touch bottom, when they head upstream. Lyon placed some blind *Fundulus* in a strong tide-way ; they swam about irregularly and were carried downstream, but the instant they touched bottom they orientated themselves against the current. "This was very striking ; even slight and momentary contact with a spear of eel-grass or a tuft of sea-lettuce gave the necessary stimulation and reference point, and the animal instantly oriented itself" (p. 156).

The fish has still another possibility of orientation, in turbulent streams, by reacting to differences in velocity between one part of the stream and another. Thus "a blind fish placed in a trough where water is gushing rather violently, for example, through a small hole, or through a glass tube, may orient itself without contact with solids and strive hard to swim against the stream" (p. 157).

But in intact animals the so-called rheotactic response in the fishes studied is mainly a visual response, an example of visual compensatory movement.

Whether Lyon's explanation of "rheotropism" in fish is universally applicable is as yet uncertain, and some authors still hold that there is, in addition to the optical response, a real reaction to current or to pressure (Refs. in [16], p. 280). Gray [16A] finds no evidence of true rheotropism in fish.

2. FINDING AND MAINTAINING THE ECOLOGICAL NORM

We have dealt with this important aspect of behaviour to some extent already in Chapter II, giving special attention to the actions of animals removed from their normal surroundings to the artificial conditions of laboratory experiment. We have seen that many of the "tropisms" shown under experimental conditions can be interpreted as parts of a general effort to find or restore the ecological norm.

I propose in this section to give only a few selected instances illustrating how animals in natural conditions find, maintain or restore the environmental conditions that are necessary for their well-being.

The first problem to consider is how the proper ecological niche is found in the first instance by the young animal. Very often this comes about, or is greatly facilitated, by the action of the mother in depositing her eggs in a suitable spot. Thus butterflies and moths whose caterpillars feed on a particular plant generally give their young a good send off in life by laying their eggs on that plant. You will remember too the case of the plaice (p. 37, above) which spawns in a locality so chosen that most of the larvæ will be drifted to grounds on which they can live and thrive and grow up.

Colman [17] is of opinion that for the pelagic larvæ of shore animals generally the finding of the proper zone in which to settle must be largely a hit-or-miss affair, and there is no doubt that many larvæ do come to grief through chance settlement in unsuitable spots.

Davis [18], who has shown that many of the small bivalves and other animals living on the Dogger Bank are narrowly restricted in their habitat, each being limited to a particular grade of sand or mud in which alone they can flourish, is also of opinion that the pelagic larvæ of these forms find their appropriate soil merely by chance. They are distributed passively by the shifting currents, which sweep them indifferently to areas suitable and to areas unsuitable for their further development. It is known from Davis's work that many of these forms are subject to enormous fluctuations in numbers from year to year, and Davis suggests that the main cause of these fluctuations may be the action of the currents in distributing the larvæ to suitable or unsuitable grounds.

While chance no doubt plays a big part in the settlement of pelagic larvæ, it must be remembered that we know very little about the behaviour of larvæ on settlement, or about the conditions that lead them to settle.

It is probable that the settling down of pelagic larvæ is a much more precise and complex affair than we imagine, involving specific behaviour-acts or trains of behaviour.

Take for example the behaviour of the larvæ of the American oyster (*Ostrea virginica*), as studied by Julius Nelson and his son Professor T. C. Nelson. The former concluded from his studies of the movements of the larvæ that they tended to rise during flood tides and to sink during the ebb, with the result that they congregated well inshore, where the adult oysters are mainly found. These observations have been elaborated by T. C. Nelson and Perkins [19] and interpreted in terms of the response of the larvæ to currents and salinity. The work was carried out in Delaware Bay where fresh and salt-water layers are often very distinct. " The home of the adult oyster is very sharply limited to a narrow zone where fresh and salt water meet ; a zone subject to sudden and large fluctuations in salinity as well as of temperature and of other factors " (p. 19). Laboratory experiments show that the larvæ are stimulated to rise off the bottom and swim by a current of water and also by an increase in salinity ; calm water and decrease of salinity tend to make them sink to the bottom. When the larvæ are full grown they show " positive stereotropism " and seek contact with the bottom.

> " With most of the oyster larvæ at or on the bottom at the close of low slack water the early flood tide brings in along the bottom a layer of water of distinctly higher salinity, causing the larvæ to swim and thus to rise. As the tide gains in speed the effect of current is added to that of increased salinity, hence the larvæ receive the maximum stimulus to rise from the bottom. At high slack water the larvæ again sink toward or on to the bottom, but such as do reach the bottom receive during the ebb tide only the current stimulus, whereas the decrease in salinity tends towards a lessening of velar activity. In the main, therefore, more larvæ would be swimming during flood tide than during the ebb, whereas more larvæ would be on or near the bottom during ebb tide than on the flood " (pp. 17–18).

The net result would be to keep the bulk of the larvæ in the shallow water which is the ecological norm of the species, and to prevent them being carried out to sea.

> " Only as a result of the ability of the oyster larvæ to react to fluctuations in salinity and in speed of current has it been possible for successive generations of oyster larvæ to maintain themselves within the narrow coastal zone during the 13 to 18 days of their free swimming existence and finally to attach upon or close to their ancestral home " (p. 19).

Apropos of larvæ settling down on the appropriate soil there are some very interesting and significant observations by D. P. Wilson [20] on the marine worm *Owenia fusiformis*, which are worthy of attention. The larvæ is pelagic for some four weeks, after which it sinks to the bottom, where it metamorphoses into the tiny worm. But it will not metamorphose if kept in a clean glass dish, nor in a dish with a layer of fine mud ; it requires for this change a bottom of fine sand or grit similar to that in which the adult worm lives. " Metamorphosis is conditioned by the character of the bottom, particularly by the presence or absence of fine sand or grit " (p. 307). This case is particularly interesting, for not only settlement but a drastic structural change is induced by a suitable substratum.

> "Until the larvæ reach the bottom, and maybe until they encounter a substratum suited to their adult life, they retain their full pelagic structure and the protection of their long bristles. Having reached a suitable bottom, they can change with the least possible delay into typical members of the benthos " (p. 309).

Several other cases are known of the selection of a suitable substratum for settlement by pelagic larvæ (see Wilson, [20A]).

Here are two cases where settlement apparently takes place in response to a definite sign-stimulus. The larvæ of the compound ascidian *Botryllus* swim vigorously around by means of their tails. Grave and Woodbridge [21] observed that they responded instantly to a shadow by swimming upwards, and they surmised that this reaction would lead them to settle on the blades of the sea-grass *Zostera* instead of sinking to the bottom to be smothered in the mud. Experiment showed this interpretation to be correct ; they settled by preference on *Zostera*, which forms a suitable place of attachment for their sessile colonies. " The experiments indicate that the shadow response is an effective and important link in the chain of responses exhibited by the *Botryllus* larvæ, and that the entire series of its responses is nicely adjusted and co-ordinated to produce effects of survival value to the species " (p. 220).

The freshwater mussel *Anodonta* retains its eggs and larvæ inside its gill-plates until they reach the " glochidium " stage.

As Fig. 11 shows, the tiny mussel, now about 0·35 mm. long, is enclosed in a bivalve shell possessing two sharp triangular teeth, and it is provided with a long sticky thread, the byssus. It is now ready to enter upon the next phase of its life, when it attaches itself to a passing fish and lives a parasitic life imbedded in the skin of the fish. This curious mode of existence lasts about three months, when it drops off and settles down in the mud of the bottom to grow up to adult size.

It appears from the observations of Latter [22] that the presence of a fish near by, or any other gentle disturbance of the water, stimulates the parent to discharge the glochidia.

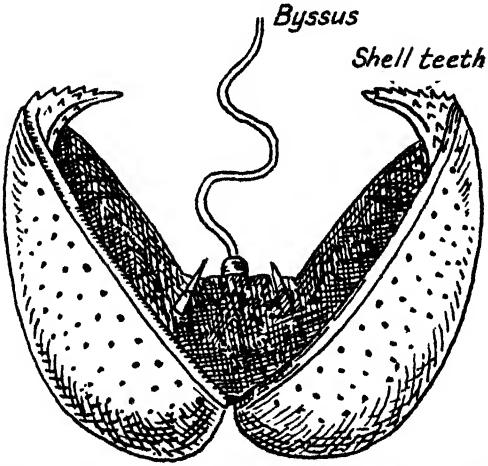

FIG. 11.—Glochidium Larva of Freshwater Mussel, *Anodonta* (after Latter, by courtesy of the Cambridge University Press)

> " On leaving the shell of the parent they slowly sink to the bottom or are carried along by the stream, their byssi floating loosely in the water. If there are water weeds in the near neighbourhood the threads become spread like a spider's web among the leaves and branches. If however a fish comes near them they are thrown into a state of extreme excitement and clap their valves together with extraordinary vigour and rapidity : this may easily be seen by putting the tail or fin of a fish into a watch-glass containing freshly discharged glochidia. The effect of this valve-clapping is to force the byssus straight out from the shell. If now a byssus comes in contact with a fish it sticks to it and the whole tangled mass of glochidia is thereupon trailed after the fish " (p. 191).

As soon as the glochidia come in contact with the skin of the fish the valves snap together, seizing a piece of skin between the sharp teeth.

This is an excellent example of response to a sign-stimulus, water disturbance being normally indicative in this case of the approach of a possible host.

When an animal has safely established itself in its ecological niche it is still exposed in the majority of cases to vicissitudes arising out of periodic or irregular changes in the environmental conditions. One thinks in this connection of the big changes brought about by the alternation of the seasons. In our latitudes and further north the advent of winter makes life very hard for many animals ; some migrate to warmer climates, some hibernate, others bury themselves and live through the cold weather in a state of suspended animation. So, too, in many hot countries animals have to cope with a long dry season, and we get the equivalent of hibernation in the similar state of " æstivation." Thus several mammals, such as the " fat sand mouse " (*Steatomys*) and the " fat-tailed gerbil " (*Pachyurus*) store up fat before the onset of the dry season and remain buried and dormant until the rains come again.

Animals living between tide marks have to face this same problem of responding adequately to environmental changes that occur in regular alternation. A few solve the problem by migrating up and down with the tide ; some, like the shore-crab, lie low in damp and sheltered spots when the water leaves them, or take refuge in pools ; others, like the limpet, sit tight conserving what water they can. Let us consider a few typical cases.

First some interesting observations by Mast [23] on the behaviour of *Fundulus* in relation to the ebb and flow of the tide. These little fish live in shallow water near the coastline. As the tide rises they follow it in over the flats, and retreat with it as it ebbs, grubbing for food in the sand. Often they penetrate into shallow pools on the beach which are filled on the flood and drain dry on the ebb.

> " If Fundulus gets into a tide-pool while the tide is rising it usually swims about in a deliberate sort of way, stopping here and there to root in the sand and to play with its companions. This behaviour continues until the tide turns or at any rate until it is very nearly high. After that the animals may still swim about as much as they did before, but they invariably, every few moments, return to the outlet of the pool and swim

> out and in again. Thus they continue to test the depth of the water in the outlet, and as soon as it gets too shallow they leave the pool and do not return. This accounts for the fact that they are not caught in these pools under ordinary circumstances" (p. 342).

Mast tried the experiment several times of closing up the outlet of a pool. If the tide was flowing at the time, nothing very much happened; the fish were flurried for a few moments but then resumed their feeding and playing. But with the tide at the full or beginning to ebb a very different picture is presented. The fish swim about excitedly and then make several circuits of the pool, keeping close to the edge as if looking for an outlet; after this they congregate near the dam and wriggle up to the very edge of the water.

> "Finally one flops entirely out of the water on to the sand. Others follow immediately much as sheep follow a leader. After they have left the water they continue flopping and proceed directly across the bar which separates the pool from the sea. Those that are left ordinarily swim about again for a few moments then collect as before, after which more escape. This is repeated, one group following another, until all or nearly all have escaped. In this way I have seen more than 200 of these fishes leave a tide-pool 50 meters long, 13 meters wide and 30 cm. deep, and travel across a sand-bar more than 3 meters wide and 10 cm. high, all in the course of half an hour. And I have seen them proceed in a fairly direct course toward the sea even against a moderately strong wind. I have also seen them persistently attempt, continuously for at least a minute, to go overland to the sea against a wind so strong that they could make no headway" (pp. 344–5).

It is not known how they manage to hop in the right direction, for the movement is predominantly towards the sea. Apparently they are not guided by vision, for if a screen is placed between them and the sea they still move in the right direction. The slope of the beach is not a determining factor for in crossing the sand bar between the pool and the sea they have first to climb up before they can slither down into the sea.

I can give a somewhat similar case of following up the receding tide from some observations made on a flat sandy shore near Plouha in Brittany. At a certain level on the beach (about the *Fucus serratus* zone) small hermit crabs of the species *Diogenes pugilator* (Roux)[1] were very abundant,

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[1] For this identification I am indebted to Dr. Isabella Gordon of the Natural History Museum.

and on an ebbing tide it was noticeable that they did their best to follow the water down the almost level beach. Specimens left behind in a shallow sandy pool almost all left it when a wave came into the pool and receded ; those that did not escape buried themselves in the sand. On the open beach at the margin of the ebbing tide there were hundreds of these little hermit crabs all moving towards the sea, and their method of reaching it was ingenious and characteristic. It should be mentioned that these observations were made on calm days when wave action was gentle. On the run down of each wave the hermit crabs either run with it, or let themselves be carried down, rolling over and over. On the reflux of the next wave they stand firm on the sand, generally with the apex of the shell pointing down shore and their big claws " stayed out " to prevent them being washed up. Then as the wave recedes they run or roll down with it as before, and thus they work their way gradually off-shore. Sometimes they bury on the reflux of the wave, and sometimes of course they are willy-nilly washed up the beach. If left behind on the sand some little distance from the edge they bury instead of moving down to the sea. So far as I could make out they mostly bury when they get a yard or two into the sea.

Burying is of course a very usual method of coping with the ebbing of the tide, with its consequent danger of desiccation, and it is practised by many animals, including the sand-eel, the shore crab (*Carcinus*) and very noticeably the little crab *Portumnus*. Many crustacea take refuge in pools, and *Carcinus* is often content to take cover under stones or weed which retain a certain amount of moisture.

Gastropods like the limpet and the dog-whelk mostly sit tight when left high and dry, retaining some water inside their shells ; on some rocky shores the dog-whelk (*Nucella* or *Purpura*) forms characteristic assemblages when the tide is out, clinging closely to the rocks [Plate II, (i), p. 70]. There is a very interesting case known of an animal that is active only when the tide is out, and goes to ground when the tide rises and covers it. This is the minute flat worm, *Convoluta roscoffensis*, which is not uncommon on the Brittany coast. It is peculiar in containing a great number of symbiotic algæ which give it a dark green colour. When adult it takes no food, but subsists upon the carbohydrates and fats manufactured by the green algæ it contains. To carry out photosynthesis the green cells require plenty of light, which they obtain when the animal lies exposed on the surface of the sand or mud while the tide is down.

Convoluta roscoffensis occurs in countless myriads, appearing as dark green patches of scum, distributed along a narrow zone on the shore. The upper limit of this zone lies at high-water neaps, and the lower limit is only a few yards seawards ; this restricted distribution ensures it against desiccation at neaps and gives a maximum exposure to the strong light required by the symbiotic algæ. It rises to the surface when the tide leaves this zone, and sinks rapidly under the sand when the returning tide laps it, but on dark nights at low water it is not to be found exposed, for it remains just beneath the surface of the sand. If you disturb an exposed patch by scratching the sand it rapidly disappears below ground, and the same effect may be produced if you walk near the patch. Vibration of the ground apparently acts as a sign stimulus of the return of the tide. The whole process is vividly described by Sir Frederick Keeble in his fascinating little book on these "plant-animals," as follows :

> " C. roscoffensis, having selected its station on the beach, maintains it in spite of time and tide. Small wonder therefore that [it] has learned to respond so swiftly to vibrations that it sinks below the sand at the approach of heavy feet. How sure and swift are the uprisings and down-lyings of C. roscoffensis may be learned by standing at the water's edge near by the situations known to be occupied by C. roscoffensis colonies. Scarcely has the tide run off them when a faint green discoloration of the sand marks the contours of each colony, and before the water has receded more than a few yards the dark greenness of the patch indicates that all the animals have risen to the surface. Or if, when the sea is smooth, we watch the incoming tide making its way with gentlest approach toward the patches, we see the animals inert and lying massed together, bound into scum-like lumps by the mucilaginous excretion of their bodies. They lie motionles, oblivious of the lapping waves a yard or so away. Then, as the latest wave washes over the patch, lethargy gives place to action and, in an instant, C. roscoffensis is gone. On stormy days, when the making tide announces its landward progress angrily—thundering like ramping clouds of warrior horse—the reverberations of the sand send signals to the colonies which make their dispositions underground long before the breaking waves can reach or damage them " ([24], pp. 22–3).

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CHAPTER IV

MAINTENANCE ACTIVITIES (*Continued*)

Inside its appropriate environment or ecological norm an animal often has a definite " home," and round this home a foraging area or territory [1]. This is very obvious in social insects like ants and bees, which construct a permanent abode for their own protection and the bringing up of their young, from which they issue in search of food and to which they return regularly. Here are some interesting details about territory in the wood ant (*Formica rufa* L.) which we owe to Elton [2]. In a small area near the New Forest he found seven nests of this species all close together, but each with its own system of paths or trackways leading to the trees on which lived the aphides which they " farm." These paths were generally straight, and from eight to eighty yards in length. " There was no connection between the trackways of neighbouring nests, i.e. the community of seven nests was divided into seven distinct units which worked with independent food territories, trees, and tracks " (p. 73). One of the nests was observed to split into two, which then divided up the original territory between them.

In all cases where there is a more or less permanent home, the problem of " homing " arises—how do animals find their way back after their excursions in the territory? Much attention has been given to this problem, particularly in social Hymenoptera, but the literature is so extensive that it would be foolish to attempt to summarize it here [3]. I shall consider instead a much simpler case, that of the common limpet, which has been carefully studied by Piéron [4].

If you examine a rough boulder, preferably peppered with barnacles, which carries lots of limpets you will find on close inspection that each limpet is tightly fixed down in such a way that the irregularities of its shell fit nicely into the rugosities of the rock, and if it has made its home among barnacles you will discover that its shell is adjusted to fit accurately against the adjoining barnacles. If you knock it off its perch you will see a mark or scar corresponding to its shell [see Plate II, Fig. (ii)]. On a smooth polished stone you will find the edge of the shell to be uniform, and the whole limpet to be smooth in surface. Generally speaking, limpets which have settled down on rough rock have a much-indented edge and strong ribs in the shell, whereas those that live on polished stones are " smooth " limpets [5]. You will discover also, if you spend enough time on the research, that the smallest limpet scars are about 10–15 mm. in length, indicating that it is about this size that the limpet settles down to inhabit a definite home.

These observations prove clearly that the limpet is a sedentary form, living in one definite spot for long periods of time. I have had one or two marked limpets under observation which inhabited exactly the same stance for six months at a time.

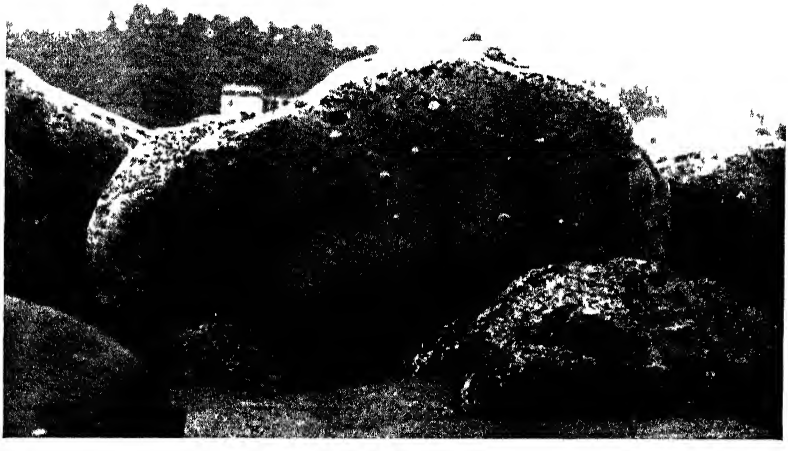
The limpets living near high-water mark do not move very much or very far from their home, and only when the sea covers them. Those living farther down the beach move about more freely—generally when they are submerged, but also when uncovered by the tide, if the air is moist. They make excursions for the purpose of browsing upon the algæ in the vicinity, and return to their home with great accuracy. Piéron made the interesting observation that some would hasten back to their home if he splashed water over them ; this apparently acted as a sign-stimulus of the rising tide and possible wave action, when the limpet has to sit very tight to avoid being washed away.

Limpets have been known to return to their home spot when removed 50, 60 and even 90 cm. away from it.

How do they find their way back ? Piéron observed that they retraced their outward track exactly on their return journey, and he carried out some experiments which showed that they had a muscular memory of the direction and distance they had travelled. Thus if he displaced a returning limpet it usually continued along the same direction until it should have reached its home, then, not finding it, wandered round the immediate vicinity until it struck it. If the sur-

Plate II

(i) Aggregation of Dog whelks on exposed rock



(ii) Limpet "homes" on barnacle covered rock

roundings are modified by chipping them with a hammer the limpet will still find its way back by muscular memory, though with hesitation. Further experiments showed that it has also a topographical memory of the immediate surroundings of its home. " Il existe, à la suite d'acquisitions répétées, une mèmoire permanente de la topographie des environs de la place habituelle, et une mémoire tres exacte du relief de cette place." This topographical knowledge is a tactile knowledge, acquired mainly by means of the feelers on the head ; the limpet is practically blind. It is clear that it does not regain its home purely by chance or by blind trial and error. That there is an active and determined effort to get back to and re-occupy the customary niche is amusingly illustrated by an experiment of Piéron's in which he placed a limpet in the home of another just as the latter was approaching it on its way back. The rightful owner, arriving at the site and finding it occupied, first turned to the right, then turned completely round, and jamming its shell against the interloper, firmly pushed him out, and settled in himself.

" Homing " of this nature is shown by various other marine molluscs—by *Calyptrea*, *Fissurella*, and *Siphonaria* for example, and it is probably quite a widespread phenomenon among littoral animals generally. Arey and Crozier [6] relate of *Chiton tuberculatus* which they studied in the Bermudas that it keeps to one limited area and does not wander very far, though it does not appear to " home " to a particular spot as does the limpet. The older chitons are more stationary than the younger. One old chiton was observed to live for over nine months within an area measuring 3 ft. by 2 ft.

A casual observation of my own gives a hint that sea-urchins may have homes to which they return. On the coast of Brittany I experimented with a specimen of *Psammechinus miliaris*, which lived in a crevice in a rock-pool near a buttress of *Corallina*. I moved it about 10 inches up the slope, whereupon it moved downwards, and 15 minutes later crept under the buttress from the other side, where it remained certainly for four hours.

Cuttlefish of the genera *Polypus* (*Octopus*) and *Moschites* are known to make at least temporary homes for themselves by erecting a barrier of stones in front of a crevice under a large rock, but I am not aware of any observations having been made on their homing capabilities.

Here is an interesting field of work for an enterprising field naturalist who has access to a rich littoral fauna—to determine what species have homes and territories, and how they find their homes after their feeding forays. (There is also much still to be found out about the seasonal migrations of shore animals up and down the beach.)

One is tempted to elaborate this fascinating subject of territory and homes and homing. There is the whole interesting story of territory in birds, which was alluded to briefly in the first chapter (p. 7), but for this I must refer you to the books of Elliott Howard [7] who worked the story out.

I will limit myself to giving two more cases of homing. The common toad is known to have regular lurking places in which it spends the daylight hours, issuing forth at night to feed. One which I had in a greenhouse lived for a fortnight in a corner behind a wooden box, then shifted its abode. Some months later it was found in another spot which it inhabited for at least three weeks. According to Miss Pitt [8]—" Not only has each toad its own home, but it sticks to that den and its own particular hunting ground for the greater part of the year. It knows its beat as well as we know the districts round our homes, and it makes its rounds regularly every night as long as the weather is mild " (p. 102). There is an obvious advantage to an animal in restricting its movements to a limited area with which it becomes thoroughly familiar, so that it knows where to expect food and what cover there is in which to take refuge from sudden enemies.

A case of homing in the common frog is perhaps worth putting on record. Several frogs, recognizable by their diverse coloration, inhabited for a whole summer a small pond in my garden. They came out of the pond only at dusk, and foraged in the neighbouring flower-beds, and they were always back again in the pond in the morning.

Topographical knowledge of limited areas is probably developed by many animals to a higher degree than we realize. I was surprised to find that a tortoise which had lived in my garden for some months knew his way about only too well. He had, like many of his kind, a passion for young peas, and had often to be removed from a bed of these situated near the bottom of the back garden. Placed in the front garden about 150 feet away, he found his way back to the bed on two occasions, taking, however, about two days to do it. On the third occasion, about four weeks later, when removed to the front garden, he immediately made for the door on the right-hand side of the house, but finding this closed moved rapidly across the front of the house to try the other gate leading to the back. Though the bottom of this was guarded by wire netting he managed to force his way through and made his way to the back lawn where he settled down to eat. Later in the day he was found making tracks down the garden, and when he was turned round to face the house he at once wheeled back and continued his march towards the bed. Knowledge of topography is known to be gradually learnt by experience in the case of bees and other homing insects. This is well illustrated by the observations of Phil Rau [9] on the homing of bees of the genera *Anthophora* and *Xylocopa*. He found that old bees could return to their nests with great speed and accuracy from distances of one to two miles. This power was not shown by young bees, which all get lost if transported far from home. Middle-aged bees show a better performance, about 50 per cent returning from great distances. The superiority of the old bees is due to their greater experience.

There can be little doubt that in most animals the details of the territory and the way home are learned by day-to-day experience.

3. Food-Finding Activities

To start with the simplest types first—the feeding reactions of *Amœba* and its larger congener *Pelomyxa* have been studied with interesting results by Kepner and his collaborators [10]. Both these forms show two distinct modes of response to food, according as their prey is motile or stationary. Kepner and Whitlock have found

> " Ameba proteus reacting to two types of food. The first type embraces the following forms : desmids, Mougeotia, quiet Oscillatoria, encysted Chlamydomonas, and bacterial gleas ; while the second group of food bodies comprises flagellates like Chilomonas, Peridinium, and Euglena, ciliates like Paramecium caudatum, Colpidium, Cyclidium, and rotifers.

The first of these groups of food objects is characterized by being non-motile, the second group by being motile. . . . Correlated with this conspicuous difference between the two types of food of Ameba there is a two-fold reaction on the part of these rhizopods. Ameba's conduct toward non-motile food is much less complex than its conduct toward motile food. The less complex type of reaction is concerned with ingesting forms that do not set up currents in the surrounding water and that do not present the contingency of escape. The more complex type of food reaction of Ameba is concerned with the capture of forms that set up currents in the surrounding water and that do present the contingency of escape" (pp. 397–8).

Pelomyxa also shows these two different types of response. Non-motile or stationary prey is simply approached and enwrapped by means of pseudopodia, which form a food-cup round it and finally close over it completely. The object is then passed into the interior of the body and digested in a food-vacuole or temporary stomach. Non-motile food is perceived by the chemical sense. Thus desmids in sunlight give off oxygen, a bacterial glœa gives off carbon dioxide ; to both these substances *Amœba* and *Pelomyxa* react positively. Motile prey, on the other hand, is perceived through the vibrations it sets up in the water. Thus if a ciliate is swimming near by, even though it does not actually touch the rhizopod, the latter will become aware of its presence and throw out pseudopodia around and above the ciliate, enclosing it in a watery prison, the walls of which close in upon it. This remarkable method of capturing a moving object is illustrated in Fig. 12.

We have here a pretty example of response to a sign-stimulus —water-vibration is reacted to as indicative of food. It is interesting to note that *Amœba* will react to a localized source of vibration as it does to a ciliate or flagellate, provided the vibrations are similar to those set up by its normal prey. As Schaeffer [11] has shown—" All sorts of particles, whether digestible or not, are eaten if properly agitated. Not only is it unnecessary for the agitated particle to lie in contact with the amœba, but vibrations produced by a needle are likewise reacted to positively, if the needle point is one-fiftieth of a millimetre or more from the amœba " (p. 60). So too, as we have seen, oxygen or carbon dioxide are treated as indicators of the presence of desmids and bacteria.

Gonionemus is a small medusa which employs the principle of the fishing net to capture its food [12]. It is described as swimming to the surface with contracted tentacles and there turning over, then extending its numerous tentacles in a horizontal fringe and letting itself sink slowly to the bottom (see Fig. 13).

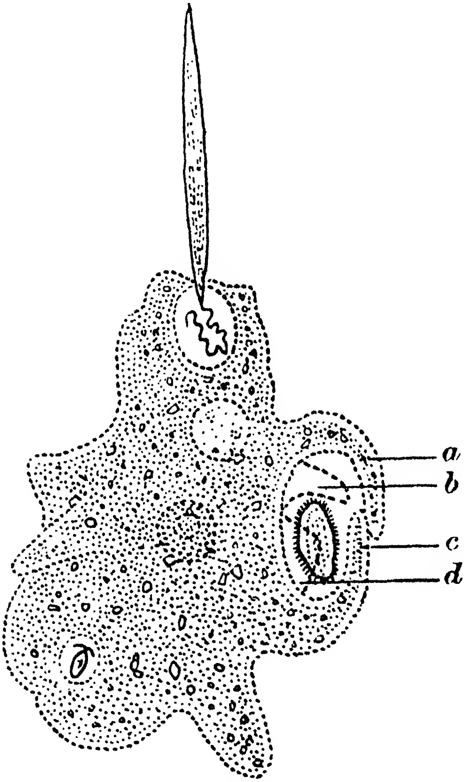


Fig. 12.—*Amœba* capturing Motile Prey (after Kepner and Whitlock, by courtesy of the Wistar Institute, Philadelphia)

Above a flagellate has been caught by the tip ; on the right a small ciliate is being enclosed by pseudopodia *a*, *b*, *c*, and *d*

Any small animals which it comes across in its descent are seized and stung by the widely extended tentacles. It may continue this process of fishing all day long. There is apparently no active and directed search for food, no pursuit of the prey, but the sinking with widespread tentacles is likely to bring it in contact with any available food, and may be regarded as in its simple way a food-seeking activity.

When a tentacle touches food it twists up in cork-screw fashion and carries the food towards the mouth, helped by the adjacent tentacles. If a tentacle is stimulated by a simple touch with a needle or fine rod it merely contracts, showing a simple negative reaction, but if the tentacles are stimulated by drawing a rod rapidly across them they show the characteristic screwing-up motion which is typical of response to food, and bend towards the mouth as if carrying food to it. This feeding response to " motile touch," as Yerkes [13] calls it, is clearly a response to a representative or sign-stimulus. As Jennings [14] says :

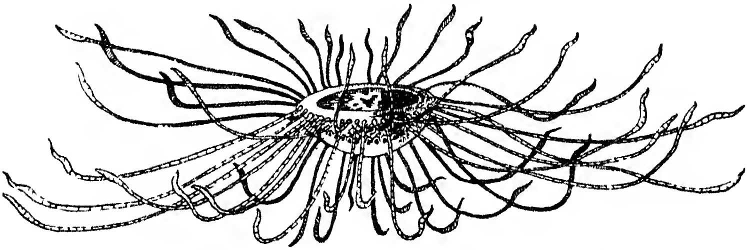


FIG. 13.—The Jellyfish *Gonionemus* " fishing " (after Perkins)

> " Usually, when something moves quickly along the tentacles of a medusa, this will be a fish or other small animal, well fitted to serve as food. So the medusa reacts to such a moving thing in such a way as to seize it and bear it to its mouth. If the object turns out not to be good for food, as is rarely the case, there is of course no harm done, and it may be rejected. If the medusa comes in contact with an object that is not moving, this will probably be a stone or a plant or other object not fit for food, hence the animal makes no attempt to take it. The behaviour is based, as it were, on the probability that any given case will correspond to the usual condition. Movement serves to the medusa as a sign of something living and fit for food, just as it does to hunters among higher animals and even among men. It is a most interesting fact that the positive reaction to a moving object is more rapid than to a quiet one, even though the latter is actually food, while the former is not " (p. 221).

A more familiar method of snaring prey is that shown by web-spinning spiders, who use a fixed net. Here also we find response to a representative stimulus—in this case to vibrations of the web, which normally indicate the presence of captured insects. The question has been studied with some care by Barrows [15]. He shows that *Epeira* finds an insect snared in the web purely by its tactile sense. If it is not in the hub of its web when an insect is caught, it runs to the centre to discover which radii are vibrating and runs along them to seize its prey. Barrows carried out experiments with a vibrating straw, whose rate and amplitude could be varied at will. He found that if the end of the straw, vibrating at a suitable rate, was applied to the web, the spider rushed up and bit it, sometimes spreading with its hind feet a few threads of silk over it. It responded to the vibration as to a living prey. These responses to the vibrating straw could be elicited equally well in darkness as in the light.

He found too that large spiders respond best to vibrations of large amplitude, little spiders to more rapid vibrations.

> " Roughly speaking," he writes, " a large spider responds most quickly to a vibration of considerable amplitude with a vibration rate of 24 to 300 per second. . . . The large spiders did not respond well to wires and forks with high vibration rate and small amplitude, but they did respond instantly to the vibrating wings of *Chrysops* (127 per sec.), *Microbembex* (208 per sec.), *Musca* (284 per sec.), where the amplitude ranged from 4 mm. to 10 mm. Small spiders responded quickly to vibrations ranging from 100 per sec. to 487 per sec. and even higher, though the amplitude was very small. This difference in responsiveness between the young and old spiders is probably correlated with differences in size and rate of wing vibration of the insects which are ensnared and used as food by young and old. In general, small insects have high wing vibration rates while the larger insects have lower rates of wing vibration " (pp. 320–1).

Certain burrowing spiders of the genus *Lycosa* which spend most of their life underground appear to be sensitive to the earth-vibrations set up by their prey. Wheeler [16] quotes the following from Emerton's paper on the subject. " When watching for prey, they sit with the front of the body out over the edge of the hole and the legs turned under. They are sensitive to the slightest movements on the ground, and when down in their burrows will notice the walking of an insect within an inch or two of the hole and come quickly to the top."

In Chapter II we referred to several cases where water-vibration acted as a sign-stimulus of food, and on page 63 we described the response of the glochidial larvæ of the fresh-water mussel to the same type of stimulus. A few more cases may here be given.

The octopus (*Polypus vulgaris*), according to Marie Goldsmith [17], is attracted as if to a prey by localized agitation of the water. Holmes [18] relates that young specimens of *Ranatra* (a long-legged water-bug) catch their prey by lying in wait with their forelegs stretched out.

> " They are like so many traps set ready to catch anything that comes in contact with them. Often, however, an object is grabbed at if it passes near a *Ranatra* without coming into actual contact with it. This action is probably a response to the impact of the water. If a *Ranatra* is hungry, touching the surface film with a needle near the insect will often cause it to grab about wildly in the effort to seize whatever may have caused the disturbance " (p. 160).

It has been shown by Matthes [19] that newts will follow a moving worm even when they have been blinded and deprived of their sense of smell. In this condition they react positively to the water-vibrations set up by any small object, e.g. a vibrated glass rod, provided this is within 1 cm. of them, and they will follow it about. This power of locating the source of water-vibrations is, however, not of much importance in their normal food-finding activities. Moving objects—and moving objects only—are perceived by the eye at some little distance and approached. Their sense of smell also helps them to find food, especially when it is motionless, and it enables them to distinguish whether a moving object is good to eat, for visual perception leads them to investigate any small moving object whether it be edible or not.

It is of course common knowledge that many animals are attracted by and seize their prey only when it is in motion. This is the case with frogs and toads for instance. They will snap at and pursue a moving insect or worm, or indeed any small object set in motion, but they will as a rule pay no attention to a motionless one. Cats, as everyone knows, are immediately attracted to anything in motion.

A less familiar case is that of the dragon-fly " larva " or nymph. According to Balfour Browne [20] in his delightful book on the habits of insects,

> " the nymph captures its prey by lying in wait for it or by slowly creeping about on the water-plants or on the bottom of the pond until its large eyes observe something moving within reach. It is curious that, although the eyes are very large, the sight appears to be very bad since the nymph only seems to see objects which are actually moving, and it cannot recognize food by the smell. For instance, if a piece of chopped worm is lying in front of the nymph it may so remain indefinitely without attracting attention, but, if the food is made to move by means of a fine wire, it will be at once seized and devoured " (pp. 97–8).

In the cases described, motion clearly acts as a sign-stimulus of food.

Here is an interesting observation by Miss Lebour [21], which illustrates the same point, and also indicates the value (to the prospective prey) of immobility or death-feigning. Referring to some very young lumpsuckers (fish of the genus *Cyclopterus*) which she had under observation in the Plymouth Laboratory, she writes :

> " The little Lumpsucker will go for quite large *Idotea*,[1] sometimes, however, attempting to eat one that is too large. It then gives it a bite and leaves it and the *Idotea* pretends to be dead. The fish will not go for the food unless it is actually moving, so the *Idotea* is safe until it has recovered and swims about again, when the fish will again chase it, and seems to enjoy the races after its food " (p. 15).

More usually, of course, food is found simply by smell or by sight, and it is unnecessary to illustrate this at any great length. I shall give a few cases from fish.

Many fish find their food by sight, familiar examples being the trout and the stickleback. It is easy to show that the latter is a visual feeder ; you have only to offer it in a glass tube a piece of worm or a crude imitation of a worm to have it eagerly biting at the visible but unattainable morsel. Many marine Teleosts are visual feeders, as for example the herring and the mackerel, many Gadoids and Pleuronectids, wrasse, gobies, blennies, weevers, dragonets and others [22]. Pipefish and dories actually stalk their prey, working stealthily up towards it.

A vivid description is given by Steven [23] of the feeding behaviour of the lemon dab or lemon sole (*Pleuronectes microcephalus*) which depends upon eyesight to spot its prey and forages principally by day. On the fishing ground near

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[1] A small Isopod crustacean.

Plymouth where Steven studied it, the lemon dab feeds exclusively on marine worms or annelids.

> " Tubicolous Polychætes, which form the bulk of the Annelid fauna, cannot be captured by lying in wait for them : they have to be hunted and that discreetly, otherwise they disappear to safety down their tubes. So the Lemon Dab, if observed in an aquarium tank, is found to be of a very restless disposition. It is constantly on the move, swimming for short distances with intervening halts for brief periods. It comes to rest in a characteristic attitude, with the head and forepart of the body raised well off the substratum. Remaining perfectly still in this position, the fish, by means of its very prominent and exceedingly movable eyes, scans the bottom in its immediate neighbourhood. Should it then observe a food organism—i.e. the anterior end of a worm cautiously emerging from its burrow—the Lemon Dab suddenly pounces upon it like a true hunter with a kind of forward leap, bringing its mouth down almost vertically upon its victim by a strong arching of the anterior part of the body " (p. 686).

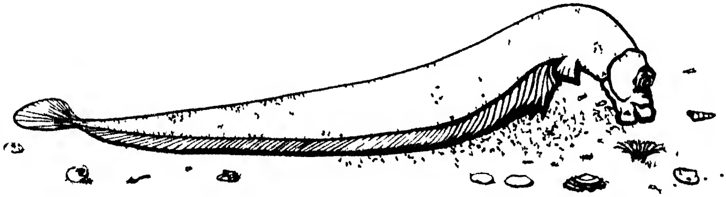

FIG 14—The Lemon Dab pouncing on a Tubicolous Worm (from Steven, 1930, by courtesy of the Marine Biological Association of the United Kingdom)

The common dab and the plaice behave in a similar manner when searching for food, but they do not raise the head quite so high before the pounce.

The sight of the wrasse is particularly keen, Bateson tells us [22], and he has often seen a large wrasse " search the sand for shrimps, turning sideways and looking with either eye independently like a chamæleon. Its vision is so good that it can see a shrimp with certainty when the whole body is buried in grey sand, excepting the antennæ and antenna-plates " (pp. 211–12).

In contrast to these visual feeders, there are many fish that find their food principally by smell. This is notably so in the majority of the cartilaginous fishes—skates and rays, dog-fish, sharks and so on—and in the eels. Let us take as an example the dogfish studied by Sheldon [24]. His observations were made in a large pool in natural conditions, and the food given consisted of crabs with a hole pierced in the shell to let out the juice. If a dogfish came within 3–4 feet of a crab it became excited and searched systematically over the bottom, investigating in particular spots that were grassy or uneven. It did not appear to make use of sight to any extent. " A crab hidden in eel-grass is found as quickly as one lying on the open bottom ; moreover, one is found equally quickly whether lying on the venter, exposing the dark carapace, or on its dorsum, with the light coloured venter showing conspicuously " (p. 56). Experiments with cloth packets containing either a crab or a stone showed that the fish were always attracted to the crab ; they would also violently attack pieces of cloth saturated with crab juices. The power of finding food is lost when both nasal capsules are blocked with cotton-wool.

Not a few fish find their food by touch, or possibly by a combination of taste and touch. Thus the lungfish *Protopterus* feels for food with its pectoral and pelvic fins, the rocklings with their barbels and pelvic fins, the loach with its barbels, and the sole with the villi on the lower side of its head ([22], p. 236). The red mullet has two long fleshy barbels on the under surface of the head, which it uses to feel out food in the mud ; I have often seen it fanning up the mud with its pectoral fins and pushing its barbels forward to explore the bottom. According to Bateson, " the rockling searches by setting its filamentous pelvic fins at right angles to the body, and then swimming about feeling with them. If the fins touch a piece of fish or other soft body, the rockling turns its head round and snaps it up " (p. 214). In the gurnards some of the rays of the pectoral fins are separate from the rest and act like legs on which the fish can crawl along the bottom. This is particularly the case with *Trigla lineata*, which according to Steven

> " spends most of its time crawling over the bottom of the tank by means of its long finger-like pectoral filaments. In addition to their locomotor function, the filaments are also very efficient tactile organs used in the finding and identification of food. As the fish creeps slowly over the bottom, the filaments are kept in continuous motion thoroughly ' fingering ' the

ground over which they pass. When anything which promises to be suitable as an article of diet is touched by one of the filaments, the fish suddenly wheels round upon it and either immediately swallows it, or subjects it to further tactile 'scrutiny.' *T. cuculus*, *T. gurnardus*, and *T. hirundo* also possess pectoral filaments and use them in the manner described, but to a progressively less extent. These species depend more and more upon the visual sense for the recognition of their prey, and dart upon it from a distance" ([23], p. 691).

These observations on the rockling and the gurnard remind me of a characteristic trait in the feeding behaviour of the aquatic South African toad *Xenopus lævis*. So far as my observations go, *Xenopus* does not appear to make much use of its eyes to find food ; they are perched on the top of its head and serve mainly to give warning of approaching danger. When a worm is thrown into the tank *Xenopus* gropes eagerly round for it with its hands, which have long thin fingers completely lacking in muscular power. The hands are brought together repeatedly as if sweeping things towards the mouth, and if they touch anything edible it is snapped up in a flash. The hind feet on the contrary do not possess this special tactile (?) sense and no response follows if they touch

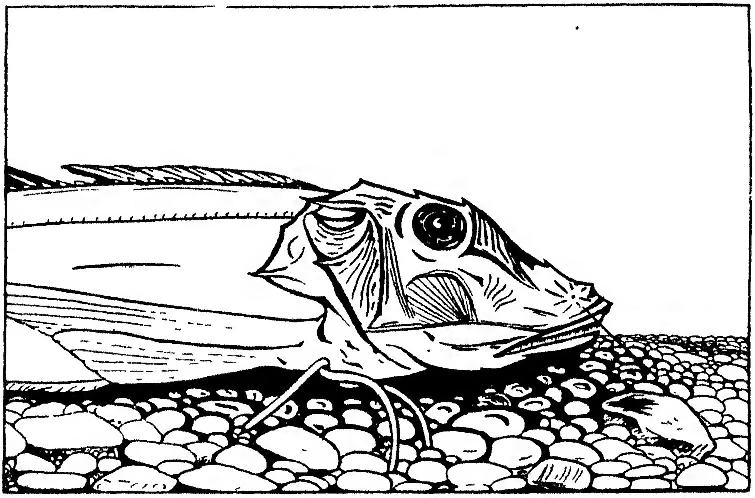

FIG. 15.—Gurnard (*Trigla hirundo*) "feeling" its way along the Bottom (from Steven, 1930, by courtesy of the Marine Biological Association of the United Kingdom)

the worm. *Xenopus* also investigates with its hands any object such as a finger introduced quietly below the surface of the water.

4. ESCAPE FROM ENEMIES

The ways of escaping danger from enemies are manifold, and I shall not attempt to catalogue them all. Many animals flee their enemies, trusting to speed and agility to elude them ; others bolt for cover. Many react to imminent danger by immobility, helped often by protective coloration ; some can even change their colour in adaptation to their surroundings. Others again actively defend themselves against an aggressor with tooth or claw, and some depend upon passive defence and the protection afforded by a shell, a carapace, or a covering of spines. Some may bluff and frighten their enemies by the sudden display of startling colours [25], but perhaps the most remarkable method of all is by autotomy, or the casting off by reflex action of a limb or tail that has been seized by the enemy.

We have already considered in Chapter II some aspects of the flight response in animals ; we have seen that many animals make for the open when alarmed, exhibiting so-called positive phototropism ; others plunge for the dark, showing negative phototropism. In the lowest animals, response to enemies and unfavourable conditions takes the form of a simple avoiding reaction. This may be illustrated in *Paramœcium* and *Planaria.* As Jennings has shown [14], *Paramœcium* reacts to any disturbing feature in the environment by a stereotyped avoiding movement ; it suddenly reverses the stroke of its cilia and swims backwards ; then it swings its head end to one side, and swims forward again. The change of direction may take it out of the sphere of the disturbing influence ; if not, the avoiding reaction is repeated again and again until the *Paramœcium* is headed away from the danger.

In *Planaria,* as studied by Pearl [26], there are two main reactions to stimuli, the positive and the negative. " The positive reaction is given only in response to weak unilateral stimulation of the anterior portion of the body. It is essentially a turning of the head towards the source of the stimulus. . . . The evident purpose of the positive reaction is to get the animal into regions of beneficial stimuli " (p. 700). Often it serves to bring the animal towards its food, but almost any weak chemical stimulus will induce it. To *strong* unilateral stimulation of any kind, mechanical or chemical, the planarian responds by a definite turning away of the head end and a retreat from the disturbing influence—a definite avoiding reaction.

In the higher animals not only are the methods of escape much more diverse but the perceptions involved are much more specific and differentiated. Let us take examples from right the other end of the scale. Here is what an expert says about game animals in Africa [27] :

> " Wild animals have three methods of detecting danger, scent, hearing and sight. Of these the first is immeasurably the most important ; the merest whiff of tainted air is sufficient to convey to their senses the exact nature and position of the danger, and to cause them to make off without further investigation. The hearing of the Bovidæ is also very keen, and at the mere crack of a twig the head of each individual in a herd will go up at once ; although if the sound is not repeated, and no further suspicion engendered by the testimony of other senses, the air of confidence is soon resumed, bush noises of an innocent nature being so common as to call for no more than passing notice " (p. 350).

Sight is also most important, with this peculiarity that it is mainly moving objects that are noticed, motionless enemies being often completely overlooked. To quote Stephenson-Hamilton again :

> " The nature of the eyesight of wild animals, and especially of antelopes, is remarkable. It is obvious, from the experience gleaned in perfectly open countries, that the latter, as well as zebras, are very far-sighted animals, and can clearly distinguish moving objects at great distances, but, quick as they are in this respect, they appear to be quite unable by sight alone to comprehend the nature of a stationary one, even when close at hand . . . if the wind is favourable and the sportsman stands or sits in a perfectly immovable position, all wild animals, of whatever description, are prone to walk almost on to him, without apparently having the smallest idea of his presence, notwithstanding that they may be gazing straight in his direction " (p. 351).

Everyday experience provides us with many examples of this truth, that moving objects particularly are taken to be indicative of danger. If you keep still you may watch a butterfly or a bird for many minutes, but make a movement and it takes to flight. When you are hunting for specimens on the shore you must approach each pool cautiously and look well ahead, if you want to see what it contains in the way of fish or crabs or shrimps. As you come near they dart or scuttle into cover ; the hermit crabs lie motionless on the bottom ; and only after some time, if you remain quiet, do they all venture out again.

This response to moving objects is particularly characteristic of those insects and crustacea that have well-developed compound or facetted eyes, and it is probable that this type of eye is specially well adapted for the perception of motion [28].

Closely related and similar to the response to movement is the response to sudden shadow shown by many animals, even by those with poorly developed eyes [29]. Tube-dwelling worms such as *Sabella* and *Serpula* respond to a shadow cast upon them by a rapid retraction of their crown of tentacles. Piéron relates that the limpet when walking abroad huddles down and adheres more firmly if a shadow is cast over it [4]. I have observed a similar reaction in *Littorina rudis*, which was brought to my notice in a curious way. Walking over a beach in Brittany one morning in bright sunlight my attention was attracted by a rattling noise, which turned out to be caused by these little winkles falling off the rocks to which they had been attached. I soon found out that this occurred when my shadow crossed them, but that only a small percentage of the winkles actually fell off. Closer examination and a few simple experiments soon disclosed what was happening. When at rest on an uncovered but moist rock these little molluscs are generally attached to a greater or less extent by their foot, the operculum being pushed to one side ; no part of the head, foot or mantle is commonly exposed. The effect of casting a shadow was to elicit a slight jerk of the shell towards the rock, evidently due to a contraction of the shell-muscle. Generally this led to a closer adhesion of the winkle to the rock, but on vertical surfaces it often resulted in the winkle becoming detached and rolling off. The " crouching " response could be elicited also in winkles living in shallow pools.

Mosquito larvæ come up to the surface to breathe ; when in this position a sudden shadow sends them wriggling down to the bottom. According to Hess [30], who has studied this reaction in *Culex*, a very slight diminution of the light will bring about descent, provided it happens abruptly ; increase of illumination has no effect in producing this reaction, but when they reach the bottom they seek obscurity and avoid the light.

Here is another simple case among insects. The caterpillars of the Small Tortoiseshell (*Vanessa urticæ*) and Peacock (*V. io*) butterflies, which live on nettles, wriggle when touched and drop to the ground ; this response is often given if a shadow passes over them [20].

Even among mammals one comes across this avoiding response to shadows. Thus Miss Pitt relates of the short-tailed field vole (*Microtus agrestis*) that tame specimens pay no attention to sounds or movements on their own level, but respond at once to a shadow passing overhead, by darting out of sight [8].

Sometimes the response to sudden shadow takes the form of active defence instead of a simple avoiding reaction. Many of the "sea-slugs" (Nudibranchiata) have brilliantly coloured and curiously shaped processes (cerata) on their backs, which are provided with stinging cells, and are presumably weapons of defence. Garstang [31] tells us that some of these, especially such as are equipped with well-developed eyes, respond to a shadow by retracting the head and briskly erecting the cerata. The reaction is well shown in *Hermæa bifida* and *Coryphella gracilis.*

The long-spined sea-urchin *Centrostephanus longispinus*, which occurs in the Mediterranean, reacts to a shadow cast by a cloud or a passing fish by erecting its spines as if to ward off an intruder [32].

A defensive response to moving objects is shown by the pedicellariæ (small pincer-like organs) of starfish, but here the movement is perceived not visually but by tactile and kinæsthetic sense. As Jennings has shown in *Asterias forreri* [33], the pedicellariæ do not respond to immobile objects, such as grains of sand, which come in contact with them ; they react only to moving things, especially those which when seized exert a pull, e.g. small crustacea. "Thus the pedicellariæ are so constituted as to attack, under natural conditions, only *living* creatures ; inanimate objects, keeping quiet, are left alone" (p. 68). Contact with another starfish or other animal is the surest way to arouse the pedicellariæ to attack, but here in addition to the tactile stimulation chemical reception may be involved.

One or two cases are known in aquatic animals where a flight response follows a specific chemical stimulus, just as many land animals scent their enemy and flee from him.

Thus the scallop, *Pecten jacobæus*, studied by Bauer [34] swims away when its enemy the starfish approaches close enough to come in contact with the tentacles of its mantle. As this escape reaction can be induced by dropping pulped starfish skin on the mantle edge, it may be presumed that the stimulus is chemical. The same author described a characteristic flight response in the small marine snail *Nassa*, which was later studied in more detail by Weber [35] and Hoffmann [36] and shown to be brought about by a specific chemical stimulus. In this case also the starfish is the enemy. When a starfish pursuing a *Nassa* touches the hind end of its creeping foot, the snail twists its shell forward and to the side ; then stretching out its foot and letting go of the bottom it brings the shell over with a violent jerk. In this way it manages to leap to one side, then reattaches itself and repeats the jump first to one side, then to the other, up to ten times, thus moving rapidly away from its enemy in a zigzag line. Hoffmann showed that the response could not be elicited by mechanical stimulation, but that the secretion from the skin of starfish and sea-urchins brought it about readily. It could be elicited also by a few chemical substances. The freshwater snail *Physa* is known to carry out similar flight reactions when touched by the little leech *Glossosiphonia* which feeds upon it ; here also it is probable that the stimulus is a specific chemical one.

These few casual examples may perhaps be sufficient to illustrate the variety of ways in which animals become aware of approaching danger, and I shall give only one more. The deafness of the adder is proverbial, but Hudson [37] tells us it is highly responsive to the vibrations set up in the earth by advancing footsteps. In his delightful essay *Hints to Adder-Seekers*, he writes :

> " In spring you must go alone and softly, but you need not fear to whistle and sing, or even to shout, for the adder is deaf and cannot hear you ; on the other hand, his body is sensitive in an extraordinary degree to earth vibrations, and the ordinary tread of even a very light man will disturb him at a distance of fifteen or twenty yards. That sense of the adder, which has no special organ yet may serve better than vision, hearing, smell and touch together, is of the greatest importance to it, since to a creature that lies and progresses prone on the ground and has a long brittle backbone, the heavy mammalian foot is one of the greatest dangers to its life."

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CHAPTER V

CHARACTERISTICS OF INSTINCTIVE BEHAVIOUR

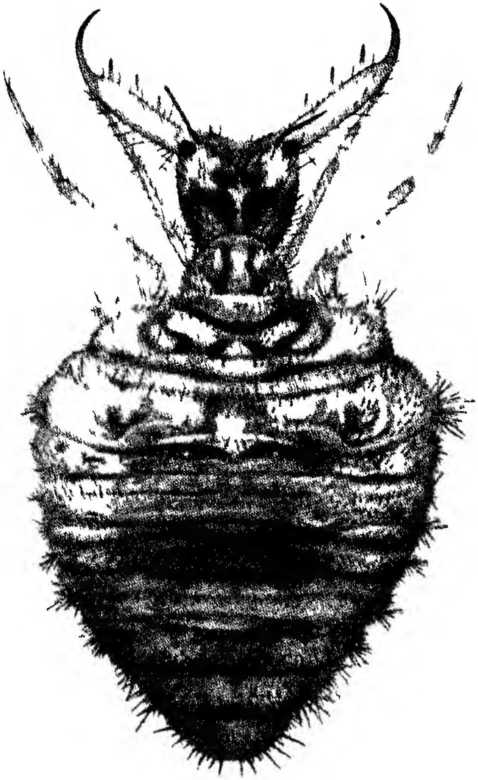
By far the greater part of the behaviour of animals falls into the category of instinctive action ; only in the higher vertebrates does adaptive or intelligent behaviour play any great role.

I propose to introduce the subject of instinctive behaviour and its characteristics by considering in some detail one typical case, and for this I have chosen the behaviour of the ant-lion.

The ant-lion (Pl. III), which is the larva of the Neuropteran genus *Myrmeleon*, presents a good example of specialization both in its behaviour and in its ecology. Though of wide distribution, occurring upon the European continent as far north as Sweden, it is limited in its habitat to areas or patches of dry sand and dust. It captures its prey, small arthropods of all kinds including ants, by the stereotyped method of the funnel-trap. A monographic treatment of the group has recently been published by W. M. Wheeler [1], who discusses also the remarkable behavioural convergence shown by the larva of *Vermileo*, the worm-lion, which belongs to the Diptera.

The following description of the formation of the funnel is based upon personal observations made one June morning on the Ile de la Barthelasse, near Avignon. The ant-lion begins by tracing a rough circle on the sand, moving backwards with its body completely covered, and flicking the sand out by rapid backward jerks of its head. If it encounters largish objects in the course of this circling, such as masses of adherent sand much bigger than its own body, it removes these by getting under them and moving backwards, half carrying and half pushing the mass to deposit it outside the circle. This done it returns to its task and works round the circle progressively further in, either clockwise or counter-clockwise, with occasional rests. Smaller objects, such as

PLATE III



THE ANT LION

(After Doflein by courtesy of Gustav Fischer)

little bits of wood or tiny pebbles, are carefully balanced on the mandibles and flicked out with a specially strong effort. When the funnel is half-made there is left a flattish crater with a conical mound in the centre. The ant-lion works round in the furrow, keeping the body always covered and flicking sand all the time ; this soon reduces the cone to small dimensions, and finally the ant-lion finds itself at the centre of a neat funnel, and ceases its labours. The whole process takes about fifteen minutes.

The funnel is somewhat labile, and requires cleaning up and deepening from time to time ; this the ant-lion does by circling round at the bottom and flicking out sand and other small material with its head. It can direct the jets of sand to one side or the other. When it is lying at the bottom of the funnel any fall of material elicits a head flick ; if this fall is caused by a wandering insect the response is likely to bring the insect tumbling down within reach of the formidable jaws. I could not determine whether the ant-lion aimed its jets at the intruding insect or not.

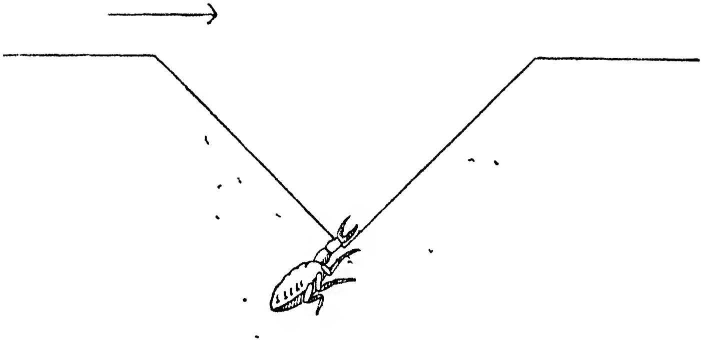
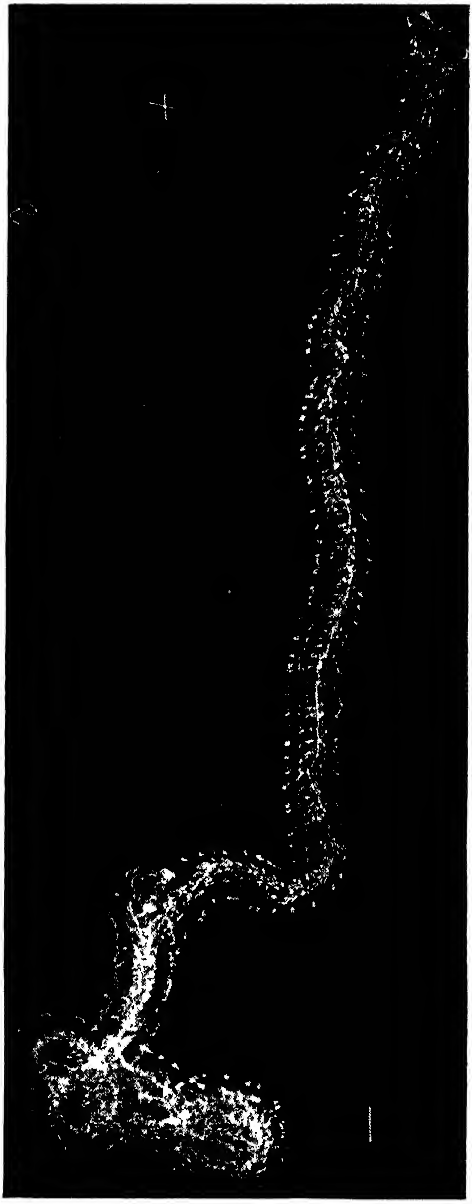


FIG 16.—Section of Funnel, showing Ant-lion in position (after Doflein, by courtesy of Gustav Fischer)
Arrow indicates direction of Incident Light

This impressionist sketch of the ant-lion's activities covers, as it happens, the main features of its ordinary behaviour, as it is described by the numerous authors cited by Wheeler. It appears, however, that the circling method of making the pit is not invariable, and that, especially when the medium of excavation is unsuitable or the temperature is low, the pit may be formed by direct digging. Wheeler also says that the excavation is generally carried out at dusk or during the night.

We owe to Doflein [2] a very full and interesting study of the behaviour of the species (*M. formicarius*) found in southern Germany. His work is of general importance from two points of view, first because he draws attention to the close connection between instinctive behaviour and ecological habit—he rightly describes his ant-lion as a "Lebensspezialist"—and second, because of his attempt to reduce its behaviour to a number of simple reflexes. We shall consider first the sounder of these views, that which regards the ant-lion as an ecological specialist. The ant-lion has a very definite habitat or station. It lives in dry sand or dust, sometimes in humus, and the material must not be too powdery. The funnel must be in a sunny and dry spot, preferably one sheltered from the rain by an overhanging bank or by a tree-root or other vegetation. For this reason it is mostly found on the edge of woods, in clearings or on sandy slopes or banks, but not in the deep shade of woods. In such places ants and other insects are abundant, and a certain protection from wind is ensured. So definite are the environmental conditions required that anyone with sufficient knowledge and experience can prophesy with certainty where the funnels will be found. They lie generally on a southerly aspect.

How does the young ant-lion manage to find a suitable spot in which to settle down? This is partly due to the fact that the mother lays her eggs as a rule in places suitable for the development of her offspring. Should the eggs be laid in an unsuitable spot, the young larvæ will wander round until they come across conditions adapted to their welfare, and their normal responses are such as to guide them to the right place. Thus one of their typical reactions in experimental conditions is to carry out "Suchbewegungen" or exploratory movements, moving (invariably backwards) in irregular, often spiral, courses. If there is a definite source of light they will move, always backwards, towards it (Plate IV). Further, they show a definite thermotaxis, collecting in the region 28°-35° C. when exposed to a temperature gradient;



TRACK OF ANT-LION MOVING TOWARDS LIGHT AT ×.

in natural conditions they are most active at 25°–30° C. If then the newly hatched larvæ find themselves in a shady or damp or stony place they begin, so soon as the sun's rays strike them, to carry out exploratory movements, creeping in the direction of the light, and seeking warm spots in which to settle down. When a suitable dry, warm, and sandy place is found in the course of these exploratory wanderings, the young ant-lion starts to excavate its first funnel. If insect prey is abundant the ant-lion may remain there for months ; if catches are poor it will shift its ground in search of a better pitch. In its normal position lying in wait at the bottom of the funnel it maintains an orientation to light such that its head and jaws are turned away from the source of illumination and face the sunny side of the funnel (see Fig. 16).

The ant-lion is closely adapted both in structure and in behaviour to life in the sand. It is uneasy when removed from the sand, and its exploratory movements both in experimental and in natural conditions must be regarded as attempts to restore the ecological norm. It shows pronounced thigmotaxis or stereotropism, and settles down comfortably and at peace only when it feels sand all round it (p. 109). It anchors itself firmly in the sand at the bottom of its funnel, and this firm hold is important when it is a question of mastering its prey.

> " In the ant-lion," writes Doflein, " we have an example of the most thoroughgoing adaptation of structure to the conditions of life. This structure and the method of functioning of the organs, which is inherited with it and is nearly invariable, put the animal in a position to carry out its remarkable and apparently so difficult mode of existence. With this goes an inability to adapt itself to unaccustomed conditions, and it very quickly succumbs to an altered environment " (p. 134).

The behaviour of the ant-lion is characteristic of that type of animal behaviour—the closely adapted or specialized or instinctive type, which we may contrast with the regulatory or adaptable type, most common among the higher animals.

The ant-lion, like other instinctive animals, is a creature of routine. Successful within one narrow and specialized line of activity, it is apt to be helpless and inhibited when confronted with the unusual. Thus the ant-lion will not eat unless it can pull its prey down beneath the sand. Bierens de

Haan [3] has shown that if it is kept in a pill box without sand it will not feed, though there may be plenty of ants available ; it may ward them off or even attack them, but it will not kill and eat, even after it has been without food for a week. The conditions are unusual ; normally it knows and recognizes food only in association with the cone-trap in the sand ; unless it can carry out the whole normal routine of pulling its prey beneath the sand it appears powerless to act. Its behaviour is specialized on the perceptive as well as the executive side.

We shall further illustrate a little later on this stereotypy which is so characteristic of instinct, but before doing so it will be convenient to consider Doflein's other main thesis—that the ant-lion is nothing more than a reflex mechanism. " So long as the animal is a larva," he writes, " it is a pure reflex automaton, it functions like a small machine " (p. 127). So far from being an ingenious and cunning trapper of its prey, as the older observers thought, it is, according to Doflein, merely a highly specialized mechanism, constrained by its structure to act in this specific way and no other.

In Doflein's view, its life is ruled by three main reflexes—the burying reflex, the flinging or flicking reflex, and the snapping reflex, which are all automatically elicited by the stimulus appropriate to each (p. 112). There are other reflexes of minor importance, and its whole behaviour is made up of chains of reflexes.

This conclusion has been challenged by Bierens de Haan and other writers, who point out that the behaviour of the ant-lion shows the main characteristics of conative or directive action, and is by no means forced upon it by external stimuli. Thus the burying " reflex," by means of which the ant-lion station at the bottom of its funnel sinks itself more deeply into the sand, has two distinct aims. It may be a defensive reaction, as when the animal is disturbed mechanically or by the approach of a large visual object, or it may be part of the feeding behaviour, for as we have seen the ant-lion always pulls its prey beneath the sand, and will not eat until it has buried it. Thus the burying " reflex " may be elicited by two completely different perceptions, in relation to two different needs. The burying action itself by no means resembles a simple reflex, since it involves variable and complex movements of the limbs and hind body.

The flicking reflex also has two different objects—(1) the construction of the funnel, and (2) the bringing down of the prey. In the first case, funnel-making is not initiated only by the external stimulus of falling sand, for an ant-lion sitting quietly in the sand may suddenly start to trace out its funnel, of its own initiative. In the second case, flicking is generally a response to falling sand, but it may take place without this stimulus. If the ant which it has seized is removed from the funnel, the ant-lion will start to flick vigorously even though no sand is being dislodged ; in such circumstances, when it is trying to bring down an ant that is not there, it digs its head under the sand to get material to flick, and it may go on doing this for ten minutes. This is clearly a directive action, with a definite objective, and not a mere mechanical response to stimulation.

In general, it is the aim of the action in relation to the animal's need that decides what the action will be, and determines the order of the so-called reflexes involved in it. As Wheeler [1] maintains : " Instead of analysing the ant-lion's activity into elements which, after they have been recognized and named, cannot be put together again to yield any intelligible meaning, it would seem preferable to start . . . from a consideration of the insect's behaviour as a whole " (p. 129). Thus the whole cycle of food-getting activities, which starts with the construction of the funnel-trap, and culminates in the capture and sucking dry of the prey, has all the characters of a goal-seeking or directive activity. Furthermore, the details of the process are to some extent variable and adapted to the special circumstances arising. We have seen that if a mass too heavy to flick out is encountered when it is making the funnel, the ant-lion will balance it on its back and carry it outside the circle. If the object is too large to move at all, it will stop work and construct the funnel elsewhere. The making of the funnel is therefore not a pure reflex chain of actions of an absolutely routine and invariable nature, but adjustable to the particular circumstances of the case. Take now the snap reflex—the seizing of the prey is not generally effected by a simple reflex snap, for if the ant-lion does not get a good grip first time, it tosses the insect up in the air or against the walls of the funnel until it can seize it the proper way ; if during this process the insect attempts to escape, the ant-lion showers sand after it to bring it down. A case has been observed by Stäger [4] in which a very hungry ant-lion actually left its funnel in pursuit of an escaping woodlouse and penetrated into a neighbour's funnel to seize it.

We see then that the chain-reflex theory of the ant-lion's behaviour put forward by Doflein does not adequately cover the facts, and must be replaced by a description in terms of needs and efforts to satisfy needs.

From this study of instinctive behaviour in the ant-lion we may draw the following provisional conclusions : (1) that instinctive behaviour is a form of directive activity, (2) that instinctive behaviour is closely related to the conditions of life to which the animal is adapted, (3) that it is limited and stereotyped, but that (4) it is not entirely a routine and invariable activity, being to a certain extent adaptable to varying circumstances.

We may go on now to fill out this preliminary characterization of instinctive behaviour by considering some other cases, expecially among insects and spiders, where this kind of behaviour is seen in its most typical form.

First of all, let me illustrate an important point on which I have not yet touched, namely that instinctive behaviour does not need to be learned in any ordinary sense of the word. The hunting wasp goes through the whole elaborate routine of making a nest, provisioning it with paralysed caterpillars or spiders, laying eggs thereon, and sealing up the nest, without any individual experience to guide it, and, so far as we know, without any knowledge of the ultimate aim or end of its activities. A young spider just out of the egg can make the typical web of its species, though on a small scale, straight away, without tuition and without fumbling.

Professor W. E. Ritter [5] gives a delightful account of how young trap-door spiders build their first tubes and close them with a hinged lid. The spiders in question belonged to a species common in California and were taken from the nest immediately on hatching ; they had no opportunity of learning by imitation or otherwise the method of tube construction. Placed in a pan of moist earth in the laboratory, they began at once to make tubes. Being very small, not more than two to three millimetres in length, the tubes they made were tiny, but in all respects a miniature copy of the full-sized nest, which is about an inch in diameter and four to seven inches deep. The baby spider begins by making a hole in the earth, just large enough for it to get in and out ; the mouth of the hole is sharp edged and almost a perfect circle. The lid is constructed in the following way : a minute projection is fashioned on the edge of the hole and to this are added pellets of earth brought up from the bottom of the hole, which is thereby deepened. After each pellet is affixed, the spider turns round and sweeps its spinnerets over the under surface of the growing lid, depositing a covering of silk. This process is continued until the lid is big enough to close the orifice of the tunnel.

> " But," as Ritter says, " a mere cumulation of materials, clay and web-substance, would not make the lid. Obviously there must be some fashioning of materials. This modelling of raw materials into the nicely fitting, freely working trap-door is the really astonishing part of the whole operation. Each deposition of clay is immediately followed by a shaping operation, this being done chiefly by the same body members by which the earth was brought to the lid and put in place. By this means the lid is given its proper circular outline and thickness. After the lid has become broad enough to reach nearly across the orifice it is pulled down from time to time with sufficient force to do considerable toward bevelling its own and the mouth's edges for producing that nice fit which is so conspicuous a feature of the completed product. Following each trial closure the lid is pushed open again for further construction work" (p. 82).

When the nearly finished lid is pulled down for fitting, and a gap is shown at one side, it is here that the spider adds more material and shapes it to fit. As Ritter says, it seems almost incredible that this action can be purely instinctive and unlearned, but the facts leave no room for doubt.

I pointed out, apropos of the ant-lion, that instinctive behaviour is curiously specialized or stereotyped. Inside the narrow circle of its normal activities the instinctive animal appears extraordinarily clever ; confronted with the unusual it is generally, though not always, completely at a loss, and may act in an amazingly stupid way. I shall give some further examples of this stereotypy or rigidity of instinctive behaviour, taking them mostly from Major Hingston's book [6].

One may refer first of all to the classical case of the processionary caterpillars described by Fabre [7]. These caterpillars live in company on pine trees, and make excursions for food, proceeding always in single file, head to tail, following the silken trail laid down by the leader and his successors. Fabre succeeded in establishing a procession round the edge of a large vase in such a way that a continuous circle of caterpillars was formed. For a whole week the procession moved endlessly round and round the edge ; no caterpillar had the initiative to break away from the trodden path to seek food or shelter. At last, on the eighth day, some moved off, apparently more by accident than design, and the fatal circle was broken. Such a contingency as the formation of a closed circle could hardly arise in Nature ; when it did happen in experimental conditions the caterpillars could not cope with it, but continued the routine follow-my-leader movement which got them nowhere. Wheeler [8] records a similar observation on the ant *Eciton schmitii* which for two days walked in endless procession round the edge of a jar.

I particularly like too the story of the mason-wasp *Sceliphron* who built her nest on a mantelpiece in the study of the Archdeacon of Rangoon. He described the case in the *Journal of the Bombay Natural History Society*, and the story is retold by Hingston as follows.

> " Having finished her nest, the wasp began to decorate it. She coloured and shaded it with the utmost care, making it exactly like the bark of a tree. For a fortnight she worked at the ornamentation. She made little grooves on it like those on the bark ; she mottled it with a mixture of green and yellow clay ; she brought green chalk and white chalk to make patches of lichen on it ; she fetched bits of grass to act as tiny twigs. In the end the resemblance to bark was marvellous, and the whole was quite an artistic piece of work " (p. 75).

She normally builds on the bark of a tree, where this decoration would be very effective in concealing the nest, but the result of her devoted labours on the mantelpiece was of course to render the nest highly conspicuous. She had no power of altering her normal procedure to suit the unusual situation.

The Indian ant *Messor barbarus* has the useful habit of establishing a rubbish dump about eight inches away from the nest, which is made in the ground ; to this heap the ants carry the discarded husks from which they have removed the seeds they use for food. Hingston discovered a nest of this species situated in a very unusual place, namely in a vertical wall. He expected to find that the ants would simply drop their refuse from the mouth of the nest. Not a bit of it ! The ants solemnly carried their burdens eight inches down the wall, laid them carefully against the wall as if on a heap, and dropped them. This went on for months. They could not break away from their normal instinctive routine, which was here meaningless and time-wasting.

Dung-beetles of the genus *Onthophagus* live a simple and stereotyped life. Finding a pad of dung they make vertical burrows beneath it and live in the bottom of the burrow. When they want food they climb up into the dung and collect an armful which they take down into the burrow to eat. Hingston carried out the following simple experiment : while the beetles were in the dung he laid a sheet of paper under it, projecting all round about three-quarters of an inch. When the beetles try to return to their burrows they are stopped by the paper. They scratch at it for a whole day, but do not attempt to get round the edge ; even after three more days some are still trying vainly to get through the paper, others have deserted the patch of dung, and none has made the simple detour round the paper which would quickly bring it to its burrow. The up-and-down movement is so ingrained in the insects that they cannot deviate from it.

If they are placed in a vertical tube half-filled with sand they climb up and escape ; but if the tube is laid horizontally they try to climb up and they try to climb down, but they never attempt to move sideways, though escape that way would be easy. They are hypnotized by the routine of instinct.

The spider *Sparassus* makes a very ingenious nest for her eggs by coiling a blade of grass in a spiral and securing it with silk, depositing her egg-mass inside the hanging cradle so formed. Hingston removed the egg-bag from the nest and laid it alongside, expecting that the spider would have the sense to put it back again. Instead of doing this, the spider examined the bag, crawled all over it, and then proceeded to anchor it down to the grass blade, in the full glare of the sun, which would soon destroy the eggs. Her routine is to make the nest, lay the egg-bag within it and anchor it down ; she cannot break this routine when anything goes wrong ; an egg-bag is something to be anchored down, and anchored down it is, even when it lies outside the nest.

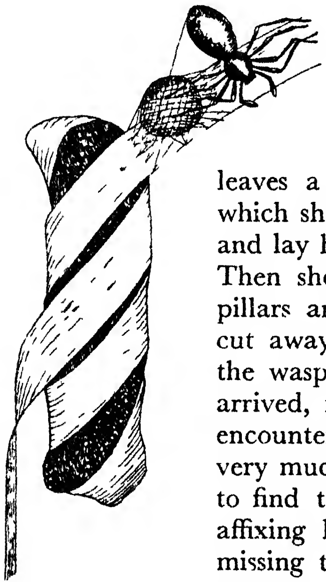


FIG. 17.—Sparassus anchoring Egg-bag outside Chamber (from Hingston)

The wasp *Eumenes* builds a dome-shaped cell of mud, and leaves a hole near the summit, through which she can reach the top of the dome and lay her egg there, out of harm's way. Then she provisions the cell with caterpillars and closes up the hole. Hingston cut away the top of the cell just before the wasp had fixed her egg ; the wasp arrived, felt round for the correct spot but encountered empty space. She became very much agitated and tried several times to find the right spot ; finally, instead of affixing her egg a little to the side of the missing top, she extruded it in the air at the exact spot where the top should have been, so that the egg fell to the bottom of the cell. Her instinct for the right spot was exact—and futile. She showed, in this case, absolutely no power of deviating from the instinctive routine to deal with an unusual situation.

Further, her instinctive actions must follow one another in an invariable order. First she builds, then she lays the egg, then provisions the cell, and finally closes it up. While she was away collecting caterpillars, Hingston broke away the upper margin of the cell. On her return she noticed that something was wrong, and felt the broken margin with her antennæ. Then she flew away, but brought back, not a pellet of mud to repair the damage, but a caterpillar which she stuffed into the cell. She completed the provisioning of the cell and closed it down, leaving the upper margin still cut off. She could not in this case break off provisioning in order to patch up the cell, for the time for building was past ; she could not go back from stage three to stage one of her chain of activities.

Dung-beetles of the genus *Gymnopleurus* are held fast in an orderly and inflexible routine of activity. Working in pairs, they find a piece of dung, shape a ball from it, roll this ball along and bury it and themselves in some convenient spot. Hingston relates how he found a pair that were just about to dig into the dung and offered them a ready-made ball. They would have none of it ; they were geared up to *make* a ball. While they are rolling their ball away they will always accept one in exchange ; but if, when so engaged, the ball is taken from them and they are put back upon the dung, they will not start to make another ball, but look round everywhere for the missing one. They are past the ball-shaping stage of their routine and cannot go back to it.

Perhaps the best example of the inflexibility of instinctive routine is that given by Hingston apropos of the spider *Araneus nauticus*. This species first makes a triangular frame for its web ; then it runs radii across the space converging at the centre, round which it makes a small hub. The fourth stage in the process is to run a spiral thread three or four times round, crossing all the radii. This spiral forms the bridges on which the spider stands while making the last and most important part of the web, the viscid spiral by means of which it snares its prey. If, while it is laying down the viscid spiral, one or two of the bridges are cut, the spider does not replace them, but goes round as best it may (see Fig. 18). It cannot go back on its orderly routine and spin a plain thread. If all the bridges between two radii are cut the spider goes right up to the hub and down again, dragging the viscid thread after it.

Hingston pushed this experiment to its extreme, by cutting all the bridges just before the spider started to lay down the viscid spiral. To get round, it had usually to climb right up to the hub and down again along adjacent radii. Notwithstanding the hopelessness of the task, it carried on in this way until the full length of viscid thread was extruded. The result was of course a mess, a disorderly tangle of viscid thread and radii. Yet the spider blindly finished its work and settled down in the centre of the shapeless web. The normal rhythm of web-making was inflexible, and it was persisted in, although the result was deplorable. The spider could not reverse the rhythm to make the simple and necessary adjustments. Spiders in general seem to have very little power to repair even small injuries to the completed web, but prefer to destroy and remake it.

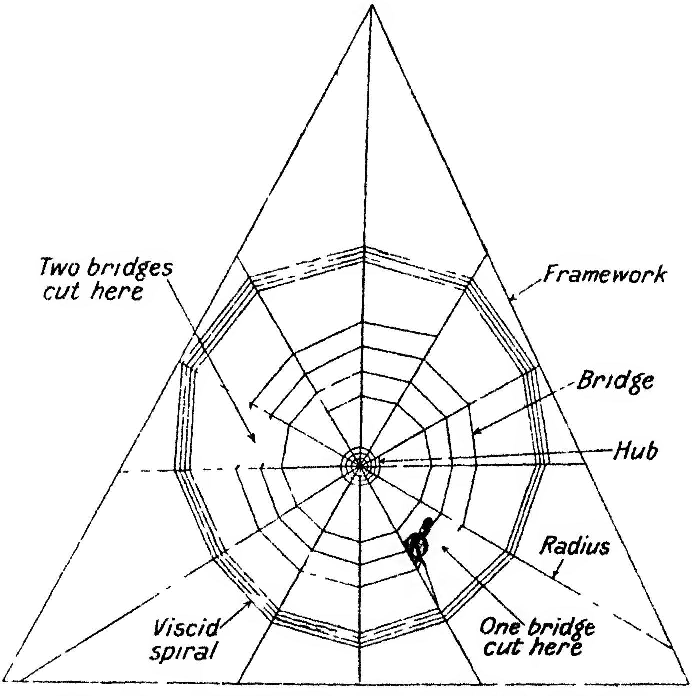


Fig. 18.—Web of *Araneus*, showing how, after a Bridge is cut, the Spider cannot remake it, but crosses over by another Bridge (from Hingston)

While instinctive behaviour is then characteristically stereotyped and invariable, and usually irreversible, it would be a mistake to suppose that it is incapable of some flexibility and adaptiveness. Even Fabre, who stressed the distinction between instinct and intelligence to an excessive degree, had to admit that instinctive animals sometimes showed a glimmering of " discernment." Purely instinctive, absolutely unintelligent, behaviour is probably a myth, just as much as purely intelligent behaviour unmixed with instinct. One should remember also that there is no such thing as Instinct with a capital I, meaning by that some special power or faculty.

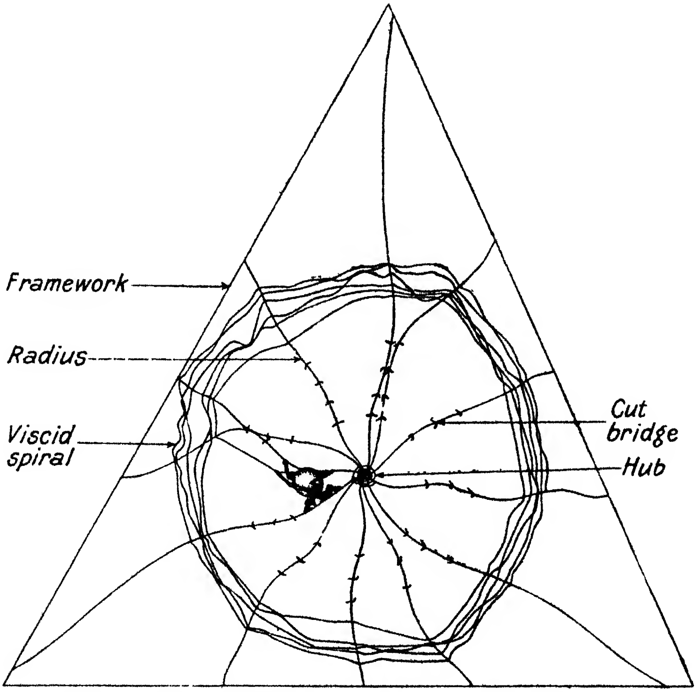


FIG. 19.—Web of *Araneus*, showing how after all Bridges are cut, the Spider cannot remake any of them, but persists in building its snare (from Hingston)

There is a kind of behaviour which we may properly call instinctive, and a kind which we may describe as intelligent or adaptive, but there is no absolute dividing line between them.

So we find that animals whose behaviour is predominantly instinctive, or specialized and stereotyped, sometimes show some limited power of adapting their behaviour to unusual contingencies. I shall give one or two examples, again taken from Hingston.

We have seen that the wasp *Eumenes* is apparently the slave of its instinctive routine. Hingston discovered, however, that she could on occasion deal intelligently with an unusual or abnormal situation. It is her custom, after she has made and provisioned a number of cells adjacent to one another, to cover the lot with a layer of mud. When she had started to do this, Hingston made a hole in one of the completed and closed cells. She found the hole and repaired it. This is not so remarkable, because she was engaged in plastering at the time, and it needed only a little deviation from her normal routine to plaster up the hole. But Hingston broke into the cell again, making a large hole, through which he pulled out the caterpillars that were stored in it. After a time she noticed the hole, and began to repair it, but instead of stopping it up completely she shaped it in a circular form and kneaded a rim round it, like the rim she normally makes on the hole which, you will remember, she leaves for provisioning. Then she went away and brought back, not more mud to plug the hole, but a caterpillar. She provisioned the cell with its normal complement, then plugged it up, and proceeded with her work of coating the whole group of cells. Here there was a definite deviation from routine, a repetition of part of it, to meet the accident of a broken and depleted cell.

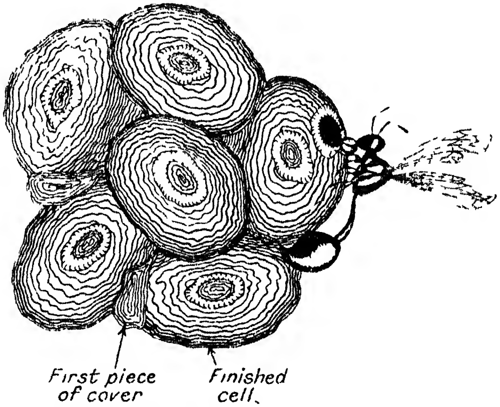


FIG. 20.—*Eumenes* making Rim round Hole in side of Cell

Fabre observed that the dung-beetle *Scarabaeus sacer*, if its ball were pinned to the ground, would get under it and push the ball up and off the pin. This is not much of a feat, for the beetles in rolling their ball along often have to hoist it up a slope or over an obstacle. Hingston went one better with the Indian species *Gymnopleurus miliaris*. He transfixed their ball with a long slender stake, projecting an inch above the ball. The beetles, finding that their ball is stuck, climb to the top of the ball, dig down beside the stake and separate the ball into two halves, which they then stick together and mould into its original shape. There is here real adaptation of behaviour to a situation which must be entirely new to them. This is even clearer when we consider a further experiment of Hingston's. He suspended the transfixed ball above their heads, so that it swung like a pendulum just clear of the ground. When the beetles touch it it swings; they are therefore not up against the normal problem of a ball that has got stuck and refuses to move. But they realize that something is wrong, climb on the ball, and encounter the

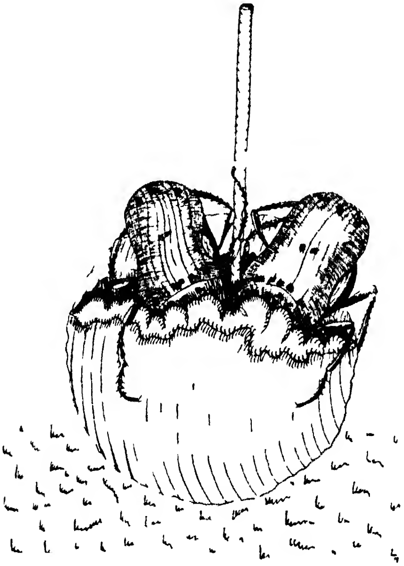


FIG. 21. Dung-beetles cutting down into Staked Ball (from Hingston)

stake, when they act as before and cut the ball in two, freeing it from the stake.

It would be easy to multiply examples of adaptive modification of instinctive behaviour, especially among vertebrates, and the subject will be considered again in a later chapter (Chapter VIII). The two cases given will suffice for the moment to illustrate the point that instinctive behaviour is not always completely stereotyped and invariable, but may be mixed with a glimmering of " intelligence."

Nevertheless, it remains broadly true that instinctive behaviour is characteristically specialized, stereotyped, and little susceptible of adaptive modification.

As our examples so far have been taken exclusively from insects and spiders, I should like to illustrate this point further by reference to some other groups of animals.

The young of many birds, for instance plovers, game-birds and gulls, are able to move about actively soon after they are born ; they are often protectively coloured, and have the useful instinct of squatting quite still on the approach of danger, which is signalled to them by the warning note of the parent birds. I well remember spending a long time hunting for a young oyster-catcher on a rocky shore in Cornwall. I knew he was there, for I had watched the nest for some days and noted that the eggs had hatched. Furthermore, the parents were flying round uttering the distinctive warning pipe. Finally I found the young one pressed up against a narrow ledge on a bare rock ; he was most difficult to distinguish against the rock, being coloured exactly like it, and he remained absolutely quiet even when I picked him up. This is an example of an extraordinarily effective instinctive activity ; protective coloration and absolute immobility combine to render the young bird peculiarly inconspicuous—in its normal surroundings.

But young birds of this " precocious " type will squat on a carpet indoors where they are not in the least hidden by their normally protective coloration. What is still more odd, if while they are squatting in their normal environment they are turned over on their back, so that the very conspicuous white underside is exposed, they still " stay put " in this uncomfortable and dangerous attitude. This simple but illuminating experiment we owe to H. J. Tomlinson [9], who carried it out with very young lapwings and lesser terns. The young terns squat among the pebbles of the beach ; when inverted they remain motionless for quite a long time. In one case the experiment lasted about fifteen minutes, during which the young bird made no attempt to right itself, showed indeed no sign of motion at all. Experiments with young lapwings in pasture land gave similar results. Another observation by Tomlinson shows the extraordinary strength of the squatting instinct.

> " On one occasion," he writes, " I found a young lesser tern crouching on the sea-coast close to the water's edge, the tide being on the flow. As I watched the bird it remained, as I expected, so motionless that it might have been thought dead. Nearer and nearer came the wavelets lapping on the beach, and great was my astonishment to find that the bird allowed the water to pass over it rather than move and thereby betray its presence ! " (p. 362).

That is a good example of the rigidity of instinctive behaviour. The next case also illustrates the limitations of instinct. The Californian woodpecker (*Balanosphyra formicivora*) has the useful habit of storing acorns for food, pecking holes in trees and ramming the acorns in [10]. It stores in the autumn when acorns are plentiful, and utilizes them in the winter when food is scarce. In some areas where telegraph poles are plentiful it stores its acorns in the long cracks which develop in these poles, which are stripped trunks of the Douglas fir. At the time when it makes its provision, the cracks are wide open, and they are often crammed tight with the acorns. " Then comes the rainy season. Poles, cracks, acorns and all become thoroughly soaked. As a consequence the swelling wood tends to shut up the cracks—with the inevitable result to the stored acorns." These are crushed out of recognition and by next dry season when the cracks open they have reached the consistency of old leather. The great majority of the acorns thus stored in the telegraph poles are rendered useless for food and the object of the activity is defeated. This particular instinctive action is here maladaptive. A more striking example of the ease with which this normally useful activity becomes foolish and wasteful is afforded by the following observation by Ritter (1930).

> "A long-abandoned miner's house . . . was in full possession of the woodpeckers and was riddled with holes of the acorn-storing kind. The box-like window and door casing were particularly utilized in this way. The nuts put through the holes here drop into the inclosed spaces and are lost to the birds. Removal of the casing boards discovered great quantities—surely thousands—of acorns in these spaces. These nuts are a total loss to the birds. As for the poles, it is almost certain that the birds go right on putting acorns into cracks autumn after autumn only to be wetted, squeezed and rotted to uselessness the following winter."

Many other examples of the futility and wastefulness of instinctive behaviour once it moves out of its normal groove are given by Ritter in his book [5]. It is characteristic of instinctive behaviour that it is adaptive and useful within the narrow limits of the species' normal and specialized life, but stupid and inelastic when faced with the unusual [8A]. Instinct is a specialized capability, with little power of adaptability, while intelligence is essentially a general capacity, applicable to a considerable range of varying circumstances.

Let me illustrate the limitations of instinctive behaviour by a few more examples.

Here is another bird one.

> "The ringed plover usually lays its eggs in the shingle, where they are most effectively lost to ordinary vision, and Professor Newton calls attention to the interesting point that when the bird breeds on grass uplands it still paves its nest with small stones—the ways of the past living on in instinctive promptings even when they have ceased to be relevant" ([11], p. 296).

Many fish are curiously stereotyped in their manner of feeding. The common sole feeds exclusively on the animals it finds on the bottom ; it commonly feeds by night, moving over the ground and feeling for its prey by means of the short cirri on the underside of its head. Although it can see perfectly well, it will pay no attention to a worm hanging over its head ; even if the worm touches it, it will not seize it, but goes hunting for it in the sand ; it will not snap up the worm unless it can feel it under its head [12]. The dragonet (*Callionymus lyra*), according to Steven [13], is likewise limited by its peculiar habits to ground food. It skims along within a centimetre of the bottom and completely ignores any food that may be swimming above it. On the other hand, species like bass, bream, dory and pollack, eat food readily while it is in suspension in the water, but ignore it when it has reached the bottom (Bateson). The three-bearded rockling (*Motella tricirrata*), which finds its food by smell and touch, will not pay any attention to a swimming worm ; it sees but does not recognize it. Perhaps the most interesting case of specialized perception that Bateson observed was that of the pollack. This fish, like the wrasse and the grey mullet—all visual feeders—would snap at a worm suspended outside the glass wall of the aquarium or even stuck to the wall. It would take no notice of a straight wire waved about outside the tank, but if the wire were bent in a sinuous curve like the body of a swimming worm the pollack would often make a dash at it and attempt to seize it.

These few observations on fish lead us on to consider another characteristic of instinctive behaviour, namely its specificity. Not only is instinctive behaviour, generally speaking, stereotyped, but each species has its own particular and specific mode of behaviour. A familiar example of this truth is afforded by the nests of birds, the construction of which is of course an instinctive activity. Just as each species of bird has a distinctive egg, a specific note or song, so also the nests they build are specifically distinct one from another. Thus, as every schoolboy knows, the nest of a song-thrush can easily be distinguished from the nest of a blackbird, though both are built on a similar plan. The interior of the thrush's nest is neatly plastered with mud ; there is a layer of mud also in the blackbird's nest, but it is covered over and hidden by a lining of soft dried grass. There is of course slight variation in detail between one thrush's nest and another, between one blackbird's nest and another, according to its location and what materials were used, but the specific type is remarkably constant ; each species has its own particular way of making a nest, from which it hardly deviates.

The specificity of instinctive behaviour is shown also in the food habits of many animals. To take a familiar case—every collector knows that if he wants to find a particular caterpillar he has to try in most cases one particular food plant, or one of a small range of likely plants. Thus if he is looking for caterpillars of the Small Tortoiseshell (*Vanessa urticæ*) he seeks out a bed of nettles and does not waste time searching elsewhere. So too if he is after the Small Ermine Moths (*Hyponomeuta*), he looks for *H. padella* on apple or hawthorn or blackthorn, and for *H. cognatella* on *Euonymus*.

Another well-known example of specificity in food habits is afforded by the hunting wasps, which provision their cells or burrows with paralysed insects on which their larvæ feed. Each species has its own favourite prey, sometimes one particular species, sometimes a general type, like small caterpillars or spiders, and it will collect nothing else.

Here are one or two less familiar cases of specialization in feeding habits. The sea-anemome *Eloactis producta* inhabits sand flats on the American Coast where *Balanoglossus* is abundant. Hargitt [14] who studied their habits in captivity offered them crab meat, bits of fish and clam and other edibles, but they refused them, and fed only on living *Balanoglossus*, though later on they were persuaded to accept the worm *Hydroides*.

The marine snail *Busycon canaliculatum* feeds principally on oysters. Copeland [15] found that while it did respond to olfactory stimulation by fish juices the response to oyster juice was much more rapid and pronounced.

Gillespie, who has carried out some very interesting observations in the Edinburgh Zoo, found great difficulty in feeding the King Penguins (*Aptenodytes pennanti*) which he has been so successful in keeping and rearing [16]. In a state of nature these birds feed on small crustacea and cuttlefish, and they are apparently most unwilling to accept any substitute. They will not pick up and eat dead fish whether on land or in the water. They will not even eat living fish, like eels and lampreys, swimming in their pond. Before they will eat a fish, it has to be placed in their mouth, and some of the penguins have to have the fish pushed down their throat. They do not seem to know, or to learn, how to deal with a fish properly, for if it is placed crosswise in their mouth, they do not shift it into the proper position for swallowing, but throw it out. It is not that they do not like fish, or that they do not thrive upon them, for they eat quantities of herring and haddock—but they must be " spoon fed."

To take one more case—according to Mr. Noel Burnet [17], the Koala or little marsupial " bear " feeds only on eucalyptus leaves, and is so fastidious that of the 400 kinds indigenous to Australia it finds only about a dozen suitable for staple food.

This specificity of instinctive behaviour is often noticeable on the perceptive side—many animals respond only or chiefly to a quite specific stimulus. By successfully imitating a mew you can throw a young and unsophisticated cat into a state of bewilderment ; it searches everywhere for the phantom cat and is thoroughly puzzled when it cannot find it.

Here are two cases of response to a specific sound reported by Beebe [18]. The first relates to the sloth.

> " I have taken away," he writes, " a young sloth and hooked it to a branch five feet away. Being hungry it began at once to utter its high, penetrating penny whistle. To no other sound, high or low, with even a half tone's difference does the sloth pay any heed, but its dim hearing is attuned to just this vibration. Slowly the mother starts off in what she thinks is the direction of the sound " (p. 98).

The second case is even more striking. The variegated tinamou (*Crypturus variegatus*), a large and primitive game bird which he studied in British Guiana, produces a solitary egg and the chick is looked after for a short time by the male. Beebe hatched out an egg of this species in an incubator and found the chick ready to run about and feed an hour or two after it was born. He attempted to attract it to him—

> " I tried calls and whistles with no apparent effect, until I imitated the note of *Crypturus* itself. Like a flash the chick turned in my direction, ran six feet toward me, and crouched beside my foot. I tried it again and again, then summoned the members of my staff to watch. The shrillest whistle brought no response, but the very first note on F natural above middle C attracted and held the little bird's attention, and the following notes brought it headlong. After such a reaction it was much more alert and willing to attempt another bit of food, and not only this, but its sense of direction was almost perfect. When I held my face close to the ground and called, the chick ran, not only toward me, but stopped at my mouth, although I had finished calling before it reached me " (p. 199).

Seton Gordon [19] relates how he was able to attract the nesting female ptarmigan to him by imitating the distress signal of the chick, and how the same experiment succeeds with the dunlin. Ogilvie [20] points out how the squatting or " freezing " response, which is so widespread among the precocious chicks of game-birds and plovers for instance, is elicited and maintained by the specific warning note of the parent birds. I cannot forbear to quote his vivid description of the behaviour of young partridge chicks. When the parent utters the warning cry, the chicks

> " squat flat on the ground, as if they were trying to squeeze themselves into the very earth itself, with nothing to show the presence of life but their little black, beady eyes. As long as the danger remains imminent, the parents keep up an incessant chuck-chucking, and the chicks remain absolutely still and motionless. . . . A chick that is only two or three hours old will squat at the warning cry, with the same celerity and certainty as a chick of three or four weeks. It can be no question of learning by experience and parental training. It will squat at that cry, and at that cry only, though not from any knowledge of the safety so acquired. Partridges reared under a hen never squat, although danger is threatening, and the foster-mother is clucking in a dreadful fluster. . . . The necessary stimulus is absent, and that stimulus is supplied by one particular cry of the parents and nothing else " (p. 49).

Here are two examples of a specific stimulus affecting other senses than the auditory. It is well known that the males of certain moths are attracted in an extraordinary way by the scent of the female, and Fabre's observations on the Great Peacock Moth (*Saturnia pyri*) are probably familiar to most readers. It is highly probable, Eltringham tells us [21], that the male's sense of smell is extremely specialized, so that it perceives only the smell of the female and is indifferent to other odours.

> " The presence of other scents, appreciable by our own faculties, has no disturbing or inhibiting effect. Many years ago, I experimented, in company with another entomologist, by placing a female *Pachys betularia* (Peppered Moth) in a muslin-covered box on a table in an ordinary living-room. The window was opened about a foot at the top, and the room was considerably clouded by tobacco smoke. In about an hour no less than seven males of the same species had entered the room " (p. 79).

Miss Frances Pitt [22] describes an interesting case where the specific stimulus appeared to be tactile. A young fox cub which she had reared by hand had reached the stage when it could shift over from a milk to a meat diet. She offered it little strips of rabbit flesh, without the skin, but it refused them steadily.

> " Feeling sure the fox-cub had reached the age when it was desirable she should eat solid food, I continued to put the meat before her, while

she as resolutely turned her snub nose away, until I accidentally placed near her a piece of rabbit leg that had *some fur attached.* She smelt the meaty part with as little interest as before, until her nose touched the fur, when an amazing transformation occurred. The soft rabbit fur had acted as the trigger which, when pulled, released the instinctive knowledge that here was something to eat. She growled like a little fury, at the same time seizing and shaking the rabbit leg" (p. 111).

After worrying the leg she began to eat it.

While it is generally true that the effective stimuli in instinctive behaviour are specialized, particularly in the most purely instinctive types, there do exist instincts in which the action is directed towards a class of objects, rather than to one particular or specific object. This is the case in many mammalian instincts. Thus the dog and some other carnivores have the instinctive habit of burying food, and any kind of food and even some other objects [8A] may elicit the response. Another interesting example is the retrieving response in rats, which has been the subject of very thorough study by Dr. Wiesner and Miss Sheard [23]. A female rat with young will always bring back to the nest any of her offspring that stray or are removed from the nest. The instinct gradually dies away as the young grow larger, but it is generally very strong while the offspring are small and tender. The curious thing is that the mother rat will also retrieve young mice, young rabbits, young kittens, and even young chicks, provided always that they are quite small. As Wiesner and Sheard put it "the rat is not 'interested in' her own young because they are hers (and recognizable as such by some odour or other property) nor because they are rats, but because they are small young creatures; and any object to which these terms apply is 'her young' to the rat" (p. 135). It is, however, possible that there is some specific quality common to the whole class of "small young creatures," so that the retrieving response may be more specific than it appears.

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CHAPTER VI

INSTINCTIVE BEHAVIOUR IN RELATION TO DEVELOPMENT AND REPRODUCTION

It is characteristic of instinctive behaviour that it is closely connected with bodily changes, such as take place in the development of the individual and in its reproductive activities. Changes and developments of instinct go hand in hand with the structural and physiological changes that occur in development and reproduction.

I can best illustrate the close relation which exists between instinctive behaviour and stage of development by considering in some detail the behaviour of very young birds.

As is well known, baby birds fall roughly into two classes—the nidicolous or altricial type, and the nidifugous or precocious. The first are helpless at birth, the second active. Typically nidicolous are the penguins, petrels, gannets, cormorants, herons, bitterns, pigeons, cuckoos, parrots, kingfishers, swifts, woodpeckers, and the great assembly of perching birds. Predominantly nidifugous groups are the divers and grebes, geese and ducks, game birds, plovers and waders.

The distinction is essentially one of the degree of development, nidicolous types being hatched at a relatively early, nidifugous at a relatively late, stage of development ; contrast for example the naked and blind blackbird nestling with the active bantam chick.

The terms nidicolous and nidifugous relate to the fact that the precocious, well-developed types are able to leave the nest very shortly after they are hatched, while those born early and helpless have to be fed in the nest for some days or weeks until they develop sufficiently to fend for themselves.

Generally speaking, nidifugous young are born in nests made on the ground or in close proximity to water, and their earliest method of locomotion, for escape or food-finding, is by running or diving from the nest—take for example the pheasant chick and the young grebe. The nests of nidicolous birds on the contrary are built mostly in bushes or trees, in holes or on ledges, from which escape can be made most effectively by flying, and it is not until the power of flight is developed that these birds normally leave the nest. This rule is not without exceptions, but it remains roughly true.

Correlated with the difference in stage of development on hatching is a difference in the size and weight of the egg. Generally speaking, nidifugous types have relatively larger eggs than the nidicolous forms, more yolk being required to provide for the extended development within the egg. The relation is of course complicated to some extent by the number of eggs laid and the rate of laying. Thus " Laridæ and Limicolæ throughout their whole size-range lay eggs about 2½ times as heavy as those of Oscines [Passeres], about twice as heavy as those of game-birds (Galli), and about 1½ times as heavy as those of owls " ([1], p. 458). The Laridæ (gulls) lay rather heavier eggs even than the Limicolæ (plovers). " The parrots (Psittaci) and doves and pigeons (Columbæ) have relatively very small eggs, as also the other great group with nidicolous young, the Oscines. The Galli have relatively smaller eggs than most birds with nidifugous young. Apparently size is here in inverse relation to number " (p. 459).

We shall consider first the behaviour of nidicolous nestlings.

F. H. Herrick, in his interesting book on the *Home Life of Wild Birds* [2], describes a characteristic response of nidicolous nestlings, which consists in sitting up with head extended and widely opened mouth, in readiness for food. Take, for instance, his vivid account of this behaviour in the nestlings of the American robin (*Merula migratoria*) :

> " Suddenly down comes one of the old birds with all its weight on the limb. The young have felt such vibrations before and know what to expect. Up go the three heads at once, each mounted on a slender stalk, and each bearing at its apex what might suggest a full-blown, brilliant flower, for as is well known, the extent of their gape is extraordinary and the inside of the mouth has a bright orange hue. The young tremble with violent emotions as they jostle, struggle, and call with undiminished zeal even after being fed " (p. 39).

Is this behaviour inborn, or, as Herrick's second sentence would seem to imply, learned by experience? The evidence he presents in other cases seems to indicate that it is inborn or instinctive. Thus of newly hatched cedar birds or waxwings (*Ampelis cedrorum*) he relates that they responded to a touch on the nest by raising the head and opening the mouth. Plate V (i) here reproduced from his book shows a cedar bird about thirty-six hours old, blind, naked, and helpless, giving the " characteristic instinctive response to any sound or vibration, as when the parent brings food, or the nest or branch is tapped " (p. 62). Miss Frances Pitt [3] describes the same sort of behaviour in nestling thrushes and blackbirds. " How sensitive nestlings are to the slightest shake of the surrounding branches may be tested by gently moving one of the boughs, when the four or five heads will shoot up into the air, and beg with open beaks for food " (p. 50).

One interesting and significant thing about this response is that the stimulus is generalized and not specific—any sound or vibration resembling that made by the approaching parent is treated as a sign of coming food. Herrick writes of the five-day-old young of the Red eyed Vireo (*Vireo olivaceus*) that:

> " Any vibration of the nest, as when the feet of the old bird touched the main stem to which it was fixed, or any sound above or below electrified the young, and up popped their heads like two jacks in a box. With mouths wide agape, they would clamour and quaver, expressing their emotions not only by the vibration of the wings but by the shaking of the whole body. But the young at this tender age are unable to discriminate with any exactness. The quivering of a leaf, or the stirring of a twig close at hand, the flutter of a wing or the voice of any passing bird would throw them into the same state of excitement " (p. 65).

In general, many immature birds, according to Herrick, show the positive response to indiscriminate stimuli ; they will respond as promptly " to the flutter of a leaf or the call note of any passing bird as to their own mother's voice." This last point is important ; though the call-note of the parent is specific, the response is given equally well to the notes of other birds ; thus Herrick observed that nestling bluebirds responded to the cry of goldfinches flying over the nest. The response has much of the automaticity of a reflex, and there is no reason to believe that it is a deliberate or conscious action. It is, however, not entirely an automatic or "forced" movement, but at least dependent upon the state of nutrition of the nestling, as the following observation by Bickerton [4] amusingly shows. He was watching the nest of a missel thrush containing one nestling and three infertile eggs; the parents came repeatedly with food—enough for the normal brood of four or five—but the little bird, in contrast to the normal behaviour of nestlings, remained completely inert. "He never once thrust up his head from the recesses of the nest to open his gape wide, and engulf the dangling prey. . . . He simply lay unresponsive at the bottom of the cup, and took not the slightest interest in the proceedings; indifferent to his parents' obvious intimation that the next supply was at hand and ready for absorption" (p. 101). The obvious explanation is that he was stuffed with food and no longer hungry.

This episode clearly shows that the positive response is essentially a food response, and that there are at least two elements in it, the perception, and the physiological state of hunger.

Apart from this generalized feeding response, the nidicolous nestling shows very little activity; it lies inert in the nest, awakened to life only at the signs of approaching food. Until it is fledged it shows no sign of fear, nor any attempt at escape. Of course, when it is young and helpless, it could not escape if it tried, and the instinct to flee must await a certain degree of maturation of the bodily structure before it can manifest itself. The instinct appears rather suddenly, towards the end of life in the nest, and about the same time as the power of flying develops.

Let us take an illustration from Herrick. Young catbirds (*Galeoscoptes carolinensis*), a typically nidicolous species, when about a week old, show no sign of fear, but give the positive or feeding response to all sounds or vibrations.

> "You could handle them at will; they were absolutely fearless. If such a nest is overturned they will cling to it but will never cower or crouch. As we have seen, the clipping of a leaf at this nest two days later sent them off in a panic, and all hurried to the nearest cover. Should you succeed in catching them under such circumstances, which is doubtful, and try to replace them in the nest, they will pop out repeatedly as if mounted on springs, and if you try to hold them in the hand they will struggle, squeal and fairly shriek in their endeavours to escape.

PLATE V.

(i) LATELY HATCHED CEDAR BIRD

(After Herrick by courtesy of G. P. Putnam's Sons Ltd.)

(ii) HERRING GULL SQUAB "HIDING"

They are now covered with a coat of slate-coloured feathers, but fly with difficulty. When placed on open ground they hop off at once toward the nearest bush. No greater change in the behaviour of a wild bird is ever witnessed than that which the sense of fear brings to pass " (p. 118).

We see then that the instinct to escape appears only when bodily development has reached a certain stage, and it is usually timed to correspond with the development of the wing-quills and the power of flight. Sometimes it becomes active rather too soon, before the little bird can fly properly, with the result that if it is frightened from the nest it comes to grief.

It is interesting to note, in connection with the " freezing " instinct so highly developed at birth in many nidifugous chicks, that some nidicolous birds soon after they have left the nest show a similar behaviour. Young blackbirds and thrushes, according to Miss Pitt [3], remain stiff and motionless when frightened. " As long as they think they are invisible the young birds remain quite still, in the case of young thrushes with their feathers drawn tight and their beaks pointing skywards, for in this attitude the spots on their breasts and throats appear like lines, and these lines make them very hard to see among twigs, grass and leaves " (p. 53). Herrick relates of the young American Robin (*Merula migratoria*) that after leaving the nest it goes to cover instinctively and lies motionless in the grass as if hiding.

We now turn to the behaviour of the new-born nidifugous chick. Far from being sluggish and inert, it is active almost from birth. Born more fully developed, able to run about or swim almost at once, it shows a much fuller and more differentiated instinctive life than the nidicolous nestling. Its instinct to escape or to take cover is fully matured and active from birth, or very shortly after. Thus snipe chicks will squat and freeze when only a few hours old ([4], p. 53). We may recall also the description given by Ogilvie of the behaviour of quite young partridge chicks, who squat and lie motionless at the specific warning cry of the parent bird (see p. 112, above). Here is another example, also from Ogilvie, relating to the newly hatched young of the Golden Plover. " As long as the parents are uttering their alarm note, so long will these little fluffy balls, only hatched perhaps a few hours ago, remain squatted and motionless, with their necks stretched out, their bodies buried in the golden moss, so that all the lighter underparts, including the light eye streak, are hidden from view " ([5], p. 5). So inconspicuous are these little birds when they squat that Ogilvie found them more readily by feel than by sight.

It would be easy to multiply examples of this precocious and instinctive escape or " take cover " response of nidifugous birds, but two more must suffice. In the River Deben in Suffolk, where the Shelduck thrives and brings up large families, I have often observed the striking response of the young ducklings to approaching danger. When undisturbed, they swim along behind their parents, in little flotillas of twelve or more. If you approach them in a boat the adults rise from the water and fly round, uttering piping and guttural warning cries ; the young birds dive like a flash and scatter under water, collecting later near the parents when the danger is past. This action must be purely instinctive, and not learned by imitation, for the parent birds do not dive to escape danger, but take to their wings.

The young Herring Gull shows at a very early age a peculiar and characteristic escape response, which is illustrated in Plate V (ii). As early as two days old, the squab, which can run but not fly, tries to hide in the crevices of the rock round its nest, on the approach of the observer. This behaviour persists all the time—two weeks or more—that the young live in the nest, with this peculiarity, that very often only the head is hidden from sight, the rest of the body being exposed. The squab lies quite motionless in this attitude, but if picked up will show fight. In North America, according to Strong [6], the young herring gull shows exactly the same ostrich-like behaviour, and Watson [7] describes similar behaviour in the Sooty Tern. In this species, the young bird for the first one to four days " feigns death " if disturbed, but after that runs to cover. " Hiding is never in any sense complete ; indeed, the reaction seems to be almost thigmotactic. The moment the young bird can put its head in the crotch of a limb or get its body in contact with some solid body locomotion ceases " (p. 133). The hiding response is thus curiously incomplete, and one would think ineffective, but probably the immobility of the body is itself quite protective.

In contrast with the nidicolous nestling, which responds to a generalized sign-stimulus (for food), the escape reaction of the nidifugous chick takes place, as we have seen, in answer to a specific stimulus, the warning note of the parent—at least in many cases. So, too, the nidifugous chick comes running to its mother in response to a specific call-note, as we see every day with chickens, and as was illustrated above (p. 111) in the case of the young tinamou *Crypturus*.

We may note too the significant fact that the instinctive responses which we have noted in young birds are responses to stimuli which are indicative or prophetic of coming situations. The responses are anticipatory or proleptic, that is, have reference to something which is about to happen or is likely to happen. Thus the helpless Passerine nestling opens its mouth in anticipation of food, when it feels the bough shake ; the partridge chick runs and hides in anticipation of threatened danger, when it hears the warning note. I do not mean that there is conscious anticipation of the results of these actions—it is difficult to see how there can be—but the fact still remains that the actions are pre-adapted to the situation which is likely to arise. Why this should be so is one of the many unsolved problems of instinct.

In contrasting these two types of juvenile behaviour in birds we see to what an extent instinctive behaviour is related to and dependent upon bodily development. Instincts appear *pari passu* with the maturation of bodily structure, without practice, without exercise. One should think of instinctive behaviour as being an integral part of the life-cycle, a link in the long chain of processes that lead to the attainment of the adult form and adult activities [7A].

The activities of young birds which we have described are directed primarily towards self-maintenance and self-preservation and only indirectly towards development, but it is not difficult to adduce cases where behaviour plays a direct and indispensable part in the general process of development. To help them break the egg-shell many birds develop at hatching-time a hardened knob on the end of the beak—the so-called egg-tooth. This is used by the young bird in its efforts to escape from the shell, but without active struggles hatching would not take place ; specialized structure and behaviour are equally involved in the process.

When the dragon-fly nymph is ready to burst its bonds and become the perfect insect it climbs up from the water to a convenient perch, splits across the back and slowly draws out its head and legs and wings, which gradually expand and dry as the insect pumps air and blood into them. Here instinctive acts form part of the developmental chain, and without them the hatching out of the dragon-fly could not successfully take place.

The scurrying caterpillars which we see on the road in summer and autumn are mostly hastening to find a suitable spot in which to pupate. The selection of the right place is an instinctive act of great importance for successful metamorphosis. When the place is found, the spinning activity of the caterpillar is in many cases necessary to support or to form a covering for the chrysalis. Thus the Large Cabbage White butterfly (*Pieris brassicae*) seeks out walls or other vertical surfaces, to pupate by preference under a sheltering ledge or projection. First spinning a little pad of silk which it grips with its last pair of claspers, it later weaves a strand of silk round the middle of its body, thus attaching itself by a sling to the wall. When the larval skin splits open, it is worked off the chrysalis by energetic wrigglings, being pushed through the silken sling. Just before the larval skin is finally got rid of, the chrysalis fixes itself to the pad by means of two minute hooks on its tail, and is now safe and sound until it hatches out (see Fig. 22). Here morphogenetic changes and instinctive activities are closely linked, to bring about the end-result—successful hatching of the butterfly. Elaborate cocoons are of course spun by many moth caterpillars to ensure the safety of the pupa.

In all these cases instinctive acts form an essential part of the developmental process. The process of successful development is one continuous unity, involving not only differentiation of form and function but, as essential elements, behaviour activities also.

It is perhaps in the master-function of reproduction that we see most clearly this fusion in one unitary process of behaviour acts and physiological and structural changes. I referred in the first chapter to the reproductive cycle in birds. Here behaviour plays a very great part—in migration, selection of territory, nest-building, the care and feeding of the young. These behaviour acts are very closely correlated and linked with changes in the reproductive and other organs, so that for example the first egg is ready to be laid when the nest is fully completed. As Herrick well puts it :

> " The parental instincts begin to control the life of the adult with the periodic revival of the reproductive functions, and vary greatly in their scope and intensity at the different stages of their reign as well as in different species of birds. They are periodic, recurring at definite intervals during sexual life and in serial form, one kind of act usually leading to the next in sequence, and so on until the series is complete. . . . Birds seem to follow one line of conduct, whether it be sitting over the eggs, brooding, or tending the young, until their instinct in that particular direction has been satisfied, thus normally completing one term of the series before passing to the next in sequence " ([2,] pp. 3-4).

There is a definite physiological cycle running its course beneath the overt cycle of behaviour. Perhaps it would be more accurate to say that there is one reproductive cycle which manifests itself, on the one hand, in physiological changes, and on the other in overt behaviour. This cycle is a unitary and continuous process, moving through a definite trajectory to a definite end ; during this time all the activities of the organism, behavioural and physiological alike, are integrated in one movement towards the goal of the reproducton of the species.

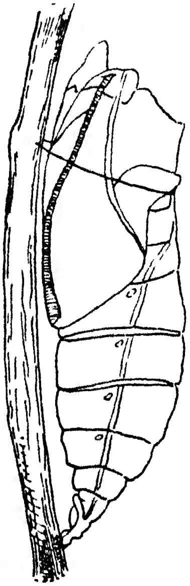

FIG. 22. — Slung Chrysalis of *Pieris* (after Carpenter, by courtesy of Methuen & Co. Ltd.)

To illustrate this combination of physiological changes with behaviour acts in the process of reproduction is almost a work of supererogation, and the abundance of examples renders choice difficult. I shall take only a few familiar cases.

In the spring the frogs awake from their winter slumber and collect in particular pools for the purpose of spawning, often travelling considerable distances to reach these pools of predilection. At this time the testes are fully developed and the ovaries swollen with ripe eggs. It is not known what external stimulus, if any, sets this spawning migration going ; temperature at the time does not seem to be responsible, for frogs may spawn under the ice ; possibly sunlight has something to do with it. A pond frequented by frogs for the purpose of spawning is an amazing sight. It is crowded with frogs, most of them paired, the male tightly clasping the female round the breast ; unmated males swim feverishly around seeking a mate. All is excitement, and the normal timidity of demeanour is completely lost. From the pond arises a deep continuous murmur of croaking, like the sound of distant motor-bicycles. Down the banks of the pond come late arrivals, sometimes already paired, the female carrying the male on her back. Two or three weeks later, when all the spawning is finished, and the eggs have been laid in crowded masses in the shallow parts of the pond, you will hardly find a frog in the pond ; they have scattered over the adjoining country and those left behind have resumed their normal timid demeanour, diving to cover on the approach of an observer.

There appears at the season of reproduction a well-marked sexual difference in coloration ; the males are mostly dark in colour and have bluish-white shining throats, while the females tend to a reddish brown, with a mottled throat. The most striking reproductive change is, however, shown by the " thumb " of the male. The innermost digit of the hand becomes greatly swollen and thickened, forming a dark-coloured pad, on the palmar surface ; this is developed in connection with the intense clasping action of the fore limbs round the breast of the female. The fore limbs of the male are very thick and strong.

Spawning migrations and reproductive modifications of structure are shown also by the newts. Normally land dwellers, they collect in ponds for spawning, and the male especially modifies his structure at this time, developing a crest along the back and a beautiful frilly tail. This is specially conspicuous in the Crested Newt (*Molge cristata*), and in all species it seems to be used in sex play for the courting of the female (see [8]). After spawning is over most newts leave the water and the fine crests and frills disappear. Other changes occur, for instance in the eye and the skin, at the time of reproduction, which are reversed when terrestrial life is resumed. A newt which has once climbed out of the water at the end of the spawning season shows a silvery film all over its body if it is put back in the water, indicating a certain drying up of the skin. It should be mentioned that a special instinctive activity on the part of the female is involved in the laying of the eggs. These are fixed singly to the leaves of water-plants, and the method of procedure is as follows. The female grasps between her hind feet a tuft of water-weed, strongly arching her body; an egg is then released which is guided on to the weed by the hind feet and adheres by means of its thin mucus coating.

Reproductive or spawning migrations are carried out by many, perhaps by most, animals, from planarians to mammals. Thus the little flat-worm *Planaria alpina*, when its sexual organs are developing, becomes positively rheotactic, and moves upstream where it deposits its cocoon. After this it moves downstream again [9]. The general analogy with the spawning migrations of fish is striking; they also for the most part move up current to their spawning grounds, and with the current when they disperse after spawning (see above, p. 37). These spawning migrations are in general associated with the ripening of the sexual products, though they may be carried out well before the process of ripening is complete. They are part of the general reproductive cycle, and essential for its success.

The close relation between behaviour and the physiological processes preparing for and accompanying reproduction may be very clearly demonstrated also in the sexual cycle in mammals, which has been very fully studied of recent years [10].

In the female of practically all mammals there is a periodic preparation for mating and the bearing of young. In between these periods of " heat " the female is non-receptive of the sexual advances of the male and indeed actively rejects them. The onset of a sexual period is marked by certain changes in the lining of the uterus—growth and congestion, and a breaking down of the epithelium. These physiological changes are dependent upon a secretion from the ovarian follicles, and this in its turn upon a secretion from the anterior lobe of the pituitary gland. Correlated with these changes in the uterus there appears a marked change in the behaviour of the female, leading her to be receptive of the male at a particular stage in the cycle. Anyone who has kept dogs is familiar with the process of events in the bitch. When she is coming on heat she is attractive to the male but discourages their advances; about the ninth day she becomes actively desirous of copulation and facilitates it; after this phase has passed, especially if mating has taken place, her behaviour undergoes another change and she snaps angrily at any suitor.

The change of behaviour in the rat at the period of heat is thus vividly described by Dr. Wiesner and Miss Sheard [11].

> " During interval the female permits its ano-genital region to be licked by the male; but when the latter attempts to mate, she resists by kicking with a hind foot, or by assuming one or other of a number of typical postures all tending to reject or restrict the approaches of the male. During heat the behaviour of the female towards the male is markedly different. Thus a female in heat responds, in most instances, to the licking and smelling of the male by running away for a short distance, displaying the galloping movement already mentioned; this heat gallop seems to act as an incentive upon the male which then pursues the female eagerly. When he reaches the female, he attempts to clasp her and she, instead of turning or kicking or making any other rejective response, halts (halting response). The male can then mount the female; the latter responds to the act of mounting by arching its back (mating reflex) so that the coccygeal region is elevated " (p. 2).

When fertilization of the eggs discharged from the follicles has taken place, the physiological and behavioural changes associated with pregnancy set in. The uterus receives the ovum which roots itself into the epithelium. There is a great development of glands and blood-vessels in the walls of the uterus, which grows *pari passu* with the development of the embryos; there develop also the elaborate placental arrangements for the nutrition of the fœtus. At the same time the mammary glands begin to swell and differentiate, so that they are ready to secrete milk by the time of parturition. These changes appear to be dependent upon a secretion from the corpus luteum, a structure which develops in the ovarian follicles that have discharged their egg, but a hormone produced by the anterior lobe of the pituitary appears to be of even greater importance.

The behavioural changes accompanying pregnancy are not at first very well marked; the animal generally becomes more sluggish and inclined to lie up. But when parturition is imminent the prospective mother begins to make preparations for it, often constructing a nest for the reception of her young in some dark and sheltered spot. The nest may be made of straw and similar things, as in the rat, or the mother's own fur may be pressed into service, as in the rabbit. In the act of giving birth the instinctive activity of the mother is important. Often she facilitates the delivery of the fœtus, and when it is born she severs the umbilical cord and removes the fœtal membranes. When the young have been produced the process of nursing and care begins and continues without remission until the need for it is gone. If the young are moved or leave the nest the mother generally looks for them and brings them back. This is a characteristic activity of the maternal rat, and is sympathetically described by Wiesner and Sheard as follows :

> " Retrieving occurs both in primiparous and multiparous rats and can sometimes be observed even during parturition, when the female carries the first-born young to the lair before the series of deliveries has come to an end. The mother grasps the young with the incisors. This does not seem to hurt the young since they rarely squeal when being carried, but often do so when handled by an observer. Usually the female takes hold of the skin of the mid-dorsal region and displays considerable skill, even though she be primiparous. On the other hand, not a few primiparous rats are rather clumsy—attempting to grasp the young by the head, or one of the paws—during the first two days following parturition, whereas later on they show considerable improvement in the performance of the retrieving response. . . . Once the rat has caught hold of the young she runs towards the nest and deposits it. . . . The rat either drops the young when she has arrived in the nest or else lays it down rather gently. Generally speaking, the female displays a certain gentleness in dealing with young, both in approaching them and in depositing them " (pp. 27–8).

It is noteworthy that the maternal impulses die away as the young grow up, so that the mother finally becomes indifferent to them. Wiesner was able to extend the period of maternal care very considerably by substituting newly born young for the older brood. He found also that retrieving behaviour can be induced in virgin females by injection of extracts containing pituitary hormones.

In all this complex cycle of behavioural and physiological changes which subserves reproduction and the care of the young it is important to note the anticipatory or proleptic character of animal's activities. Its body acts as if it knew what was going to happen, and its overt behaviour likewise seems to imply foreknowledge of coming events. But of course we have no reason to assume such forethought, and many reasons for denying it to the animal.

While in normal circumstances all these processes and instinctive acts are welded in one continuous cycle, and are ultimately dependent upon the action of certain hormones, it is a fact of much significance that some of them can take place in the absence of the full conditions that are normally necessary—the response or train of activity appears when only a part of the normal stimulus-situation is present. This is the case for example in the curious phenomenon of pseudo-pregnancy. First brought to scientific fame by the researches of Hill and O'Donoghue (1913) on the marsupial "Cat" (*Dasyurus viverrinus*), it is an occurrence well known to all who have to do with dogs. Virgin bitches, especially when old, may exhibit maternal behaviour, at a time after the period of heat roughly corresponding to the probable date of parturition had the bitch conceived. Here is the description of a mild case of it which came under my observation. A virgin fox-terrier bitch, about eighteen months old, came on heat about May 8 ; the period was somewhat lengthy and ill defined but was certainly over by the 30th. A few days before July 20 it was noticed that she appeared melancholy and worried and lay about the house, refusing to go out. No attempt to make a bed was, however, observed. Her belly was somewhat swollen, due to the growth of the hindmost pair of mammary glands. On July 20 she went to the bottom of the garden, and dug up a bone, lying beside it and growling when approached, but not grabbing it as she normally does when anyone comes near a bone she is eating. This behaviour persisted for about three hours. Then she brought the bone into the house and curled herself round it, as if nursing. She flew at the cat with whom she was normally on the best of terms. This behaviour lasted for some hours, after which she dug a hole and buried the bone.

A more fully developed case is that reported by Loisel of a mongrel bitch which had never been served, but regularly showed the onset of lactation and the appearance of maternal behaviour.

> "As soon as the milk rises the bitch is fretful and restless like an animal at the onset of parturition; she whines at intervals, often throughout the day and for the greater part of the night. If she can, she will then go to the attic at the top of our flat and make herself a bed in which she will remain. Whenever she finds a rag she starts pawing and trying to cover up with her muzzle some imaginary object. Last year (1905), 26th July, three or four days after the onset of the rise of milk, the bitch made herself a bed in a bundle of hay in the laboratory, whining all the time. I then put beside her three baby rabbits nine days old; she immediately stopped whining and started licking them with obvious satisfaction; as the rabbits attempted to suckle, she spread her legs out to let them reach the teats" (Quoted from Wiesner and Sheard, p. 7).

When the bitch was with difficulty called away from the young rabbits she covered them up with the hay, piling it over them with her muzzle.

Pseudo-pregnancy occurs also in the rabbit, changes taking place in the uterus and the mammary glands similar to those of true pregnancy but culminating earlier. The pseudo-pregnant rabbit may pluck her breast and prepare a nest, about the eighteenth day, normal pregnancy lasting about thirty days ([10], Marshall). In the marsupial "cat" normal pregnancy lasts eight to fourteen days.

> "In its absence pseudo-pregnancy occurs, and is accompanied by a series of changes in the reproductive organs and mammary glands essentially similar to those taking place in gestation. The pouch enlarges and the sebaceous, sweat, and mammary glands also hypertrophy as well as the internal organs. At the end of the period the animal has been seen to clean out its pouch for the reception of young, showing that the developmental and cyclical changes of the sexual organs may extend even to the instincts associated with parturition and the nursing of the young, although true pregnancy had not taken place" ([10], Marshall, p. 36).

In concluding the somewhat slight sketch of the characteristics of instinctive behaviour contained in this and the preceding chapter, I should like to quote one well-known and excellent definition of instinct, that given by Lloyd Morgan in 1896.

> "From the biological point of view," he writes, "instincts are congenital, adaptive, and co-ordinated activities of relative complexity, and involving the behaviour of the organism as a whole. They are not characteristic of individuals as such, but are similarly performed by all like members of the same more or less restricted group, under circumstances which are either of frequent recurrence or are vitally essential to the continuance of the race. While they are, broadly-speaking, con-

stant in character, they are subject to variation analogous to that found in organic structures. They are often periodic in development and serial in character. They are to be distinguished from habits which owe their definiteness to individual acquisition and the repetition of individual performance " ([12], pp. 27–8).

The reader who has followed our discussion of the subject will appreciate the value and adequacy of this definition. He may be referred to the works of William McDougall [13] for a very full and stimulating treatment of the problems of instinct, with special reference to instinctive behaviour in man ; also to two valuable papers by Bierens de Haan [14].

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CHAPTER VII

DEVELOPMENT OF BEHAVIOUR AND LEARNING

I propose in this chapter to consider, with special reference to Vertebrates, the main features of the development of behaviour. I shall deal first with the earliest appearance of co-ordinated movements in the embryo or larva. Then I shall consider very briefly the phenomena of the pre-functional growth or maturation of behaviour, and finally at greater length the processes of learning, which continue and complete the work of development or differentiation.

We owe to Coghill [1] a very complete and careful study of the development of the nervous system in *Amblystoma* in relation to the development of its first co-ordinated movements, such as swimming, walking and feeding. As was to be expected, he found a close correlation between the two things ; as the nervous system grew and developed, more and more complex behaviour appeared. But the really interesting thing that emerged from his work was the demonstration that behaviour is from the beginning a unified or integrated activity.

The first sign of activity which the young larva shows is a bending of the head to one side ; soon this flexure extends to the body and the tail, so that the larva curves itself into a complete coil, first on one side, then on the other (see Fig. 23). At the next stage this coiling movement, starting from the head, is reversed before it reaches the tail, and we get the alternating to-and-fro movement of the body and tail which leads to swimming, and forward progression (Fig. 24).

Soon after the establishment of swimming, the limbs begin to develop, first the fore-limbs, then the hind limbs. While the fore-limbs are still small they move only when the body moves, being drawn close to the body when the animal is swimming forward ; separate and independent reflex movements cannot be elicited until a day or two later. The first limb movements, then, are an integral part of the total reaction of the animal, and only later acquire any independence. As Coghill expresses it—" The local reflex of the arm is not a primary or elementary behaviour pattern of the limb. It is secondary, and derived from the total pattern by a process of individuation " (p. 19). The same thing holds good of the movements of the hind limb.

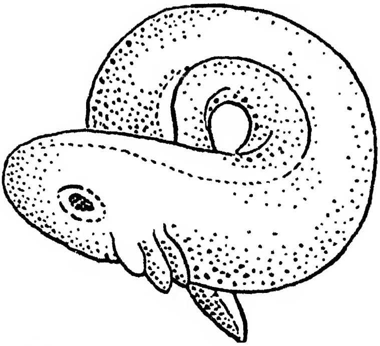

FIG. 23.—Coiling Movement of Young Larva of *Amblystoma* (after Coghill, by courtesy of the Cambridge University Press)

As the limbs develop, walking becomes possible, and it comes about in the following way. The fore-limbs are stretched forward together, the head is raised slightly, and propelled forward by a backward movement of the arms.

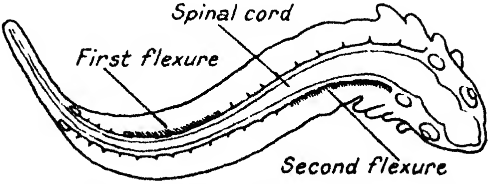

FIG. 24.—First Swimming Movement of *Amblystoma* Larva (after Coghill, by courtesy of the Cambridge University Press)

> " From such an attitude as this the animal has been seen to strike into its first walking gait. This is done by flexure of the anterior part of the trunk laterally and abduction of the arm on the convex side with adduction of the arm on the concave side. The first alternate movements of the fore limbs in walking are therefore integral parts of trunk movement. The primary co-ordination in the performance is not directly between

the two limbs. Each limb, on the contrary, is directly integrated with its own side of the trunk. Furthermore, movement of the trunk in walking is nothing more nor less than the swimming movement with greatly reduced speed. It is a slow sinuous flexure progressing from the head tailward" (p. 25).

Walking thus develops from swimming, and it does not arise by the combination of separate limb reflexes ; the movements of the limbs are at first integrated with the movements of the trunk and only later acquire some measure of independence.

It is to be noted that both swimming and walking develop from the beginning as unified and co-ordinated movements, crude and imperfect at first, but quickly acquiring precision and refinement ; they do not come about by the combination of separately developed local movements or reflexes.

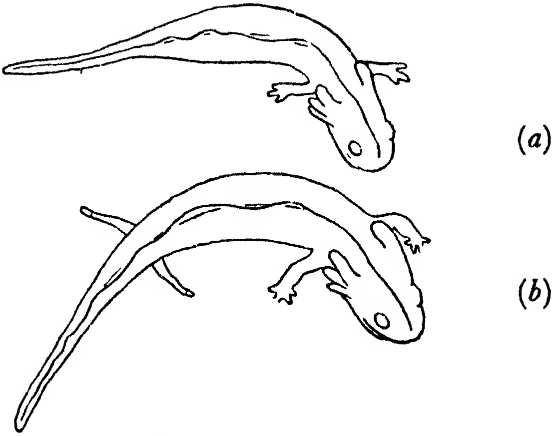

FIG. 25.—Initial Act of Walking by *Amblystoma* Larva with (*a*) two limbs, (*b*) four limbs (after Coghill, by courtesy of the Cambridge University Press)

Wholeness or unity of behaviour is there from the beginning ; the special movements of the limbs develop by differentiation within the total pattern ; only at a relatively late stage do apparently discrete and separate reflexes appear. As in development generally, so in the development of behaviour, the process is essentially one of differentiation *within a whole.* As we shall see later, this law holds good also in the process of learning, which is a continuation of development.

Coghill's general conclusions have been verified in a number of Vertebrate embryos and larvæ, notably in the toad-fish (*Opsanus tau*) by Tracy [2], in the chick by Kuo [3], and also in rats, kittens, oppossums, and in human embryos [4]. In all these cases behaviour develops from a generalized or mass activity, which gradually becomes specialized or differentiated. Distinct reflexes arise rather late in this process of differentiation. The same principle has been demonstrated in the earthworm *Eisenia* by Prosser [4A].

The theory that the reflex arc is the basal unit of behaviour, and that all behaviour can be satisfactorily accounted for as a concatenation of reflexes, conditioned or unconditioned, has always been a favourite assumption of the physiologist when he has tried to study behaviour.

It will be seen that it receives little support from the facts of development. Early behaviour does *not* arise through the addition and combination of originally separate reflexes.

We turn now to the question of the maturation of behaviour. This also is a phenomenon of growth and differentiation. As we have seen in the preceding chapter, instinctive behaviour arises *pari passu* with development of structure, being an integral part of the general processes of development and reproduction. We may express this by saying that instinctive behaviour arises by *maturation*. It is, as we have seen, characteristic of instinctive behaviour that it is "unlearned" or innate, that it does not require preliminary practice or learning, though it may be improved by subsequent practice. We find also that an instinctive action may improve and become perfected, without practice, by this same process of maturation. Normally, of course, particularly in Vertebrates, both practice and maturation play a part in the perfecting of juvenile behaviour, and it is difficult to separate the two, except by carefully devised experiment. Carmichael [5] has, however, been successful in showing that the development of co-ordinated swimming movements in the tadpoles of frog and *Amblystoma* is independent of functional exercise and comes about by a process of maturation. He kept young larvæ anæsthetized by chloretone until the controls reared in pure water could swim well. He then transferred the anæsthetized larvæ to clean water, and found that as soon as the effect of the anæsthetic had worn off the larvæ were able to swim quite as well as the controls, which had had the advantage of practice. The faculty of swimming therefore ripens with the advance of general development.

It was shown by Breed [6] many years ago that the accuracy of the pecking response in chicks improves from the second to the twenty-fifth day after hatching. The improvement is rapid at first, then much more gradual. If the data are plotted, a curve resembling a learning curve is obtained. Breed suspected that the improvement shown was not due altogether to practice, and a little later, in collaboration with Shepard [7], he was able to demonstrate that maturation played an important part in the development of this instinctive response.

It is known that chicks reared in complete darkness never peck. Accordingly batches of chicks were kept in the dark for three, four and five days, before their accuracy of pecking was tested. It was found that on their first trial the accuracy was very poor, and somewhat below that of two-day-old chicks reared in the light. But in the first two days of practice their progress was very great and lifted them at once up to, and even above, the level reached by the normal (control) chicks of the same age which had practised from birth. The authors concluded that " a given amount of practice, quite constant for the different groups, is necessary to smooth the way for the operation of a native capacity *whose efficiency is largely a function of the age of the animal* "[1] (p. 281).

In later and more elaborate studies by Bird [8] further evidence is adduced that the capacity for accurate pecking improves with age, independently of practice. (See also Cruze, [8A]).

One meets the same phenomenon of maturation or growth of capacity in learning to play a game like tennis or golf. Constant practice will bring one up to a certain level of proficiency ; it is then wise to knock off playing for a few days ; when one resumes, one often finds that one's play has improved in the interval, that the capacity has ripened or matured. It is an established fact that intermittent practice is more effective than continuous training. You may see clearly in the development of a young dog the mingling of maturation and learning which is typical of the development

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[1] Our italics.

of behaviour, in Vertebrates at least. A young puppy is very difficult to train, except to the simplest inhibitions ; it is only after six months or more, as its mind matures, that it begins to learn effectively.

The interplay of maturation and learning in young animals is nicely illustrated in Miss Frances Pitt's vivid account [9] of how a young song-thrush developed the snail-cracking habit which is characteristic of this bird, and the case will serve to carry us over to the problems of learning.

Jack the thrush was brought up by hand, and when full grown he was offered a number of snails (*Helix nemoralis*) one day ; he took no interest in them until they protruded their heads and tentacles when he pecked at them. The experiment was repeated daily with the same result, except that once he picked up a snail by the lip of its shell and shook it, as he would a large earthworm, but it slipped from his beak and nothing further happened.

> " On the sixth day," writes Miss Pitt, " the thrush seemed to lose all patience—a couple of snails began to crawl about the cage, and when he flew down to investigate the nearest, it, as usual, vanished into its house. He picked the snail up by the lip of its shell, swung it backwards and forwards, and brought it down with such a thump on the ground that it flew from his beak and half across the cage. He hopped after it, picked it up, and, jumping on one of the anvils—the experienced thrush stands *before* the anvil, not *on* it—for I had put an assortment of stones ready for him, beat the snail several times upon it, hitting it first on one side, and then on the other, with a swinging, to-and-fro motion. He was not expert enough, however, to crack the snail's shell, and it slipped from him and rolled away. But he seemed pleased with his discovery that the snails could be hit on a stone, and went on trying first one shell and then another, until, after fifteen minutes' hard work, one, weaker in the shell than the rest, gave way. He had cracked his first snail ! Once the shell was broken, it did not take him long to pound it to bits, extract the snail, and swallow the succulent morsel " (pp. 41–2).

After this first success, which took a long time to achieve, the thrush rapidly became an expert, and was soon able to break open a snail with a few skilful blows.

Miss Pitt concludes that the thrush had no specialized instinct leading him to crack snails the first time he saw them ; the technique had to be learned laboriously. But it has a generalized instinct (which gradually matures) to beat on the ground any large or unmanageable piece of food or other object of interest. It deals thus with large worms or grubs, and in captivity with objects like pill-boxes or paper balls. Out of this generalized instinct there differentiates, by dint of trying, the capacity to break open snail shells. Instinctive behaviour and learning are here closely interwoven.

In the life of young animals, as we see particularly in mammals and birds, learning by experience plays a very great part, and leads to a rapid enrichment and differentiation of their perceptual world. To take a simple illustration—a very young pup when taken out for a walk is very apt to follow anyone he meets, but it is not long before he discriminates between strangers and the people he knows ; familiar individuals become differentiated from others in his perceptual world. A newly hatched chick pecks indiscriminately at any small object, but soon learns by experience to distinguish between what is edible and what is not.

Modification of behaviour through experience is of course a very widespread phenomenon. It is a familiar fact that most animals kept in captivity become to some degree tame. They gradually learn by experience that the approach of human beings bodes them no ill, and instead of showing fright and attempting to escape or to hide they remain unperturbed or even draw near to see if the observer has brought them food. Even insects may become tame, as Forel [10] among others has shown.

> " Thus a *Dytiscus marginalis* that I had in a bowl, and which I was in the habit of feeding when I returned, finally became somewhat tame. Instead of flying to the bottom of the bowl when I entered, as he did at the beginning, he started to jump almost out of the water and immediately seized what I gave him, even the end of my fingers " (p. 118).

This process of habituation to captivity has been studied with some care by Doflein [11] in the prawn *Leander*. He found that they soon got accustomed to the ordinary events in the aquarium, such as the changing of the water ; while freshly caught prawns would react defensively, old stagers took no notice. The reaction to shadows soon ceased, and little notice came to be taken of moving objects outside the aquarium. Prawns which at first leaped away from a finger learned to gather round it expecting food, and they would take food readily from the fingers or a pair of forceps. Having been fed every second day for two to three weeks at one corner of the aquarium, they collected there when the observer approached and held his hand near the surface of the water. It is noteworthy that when they were placed in a new aquarium this habit was abolished and had to be re-learnt.

Everyone who has kept fish in an aquarium knows how readily they learn to inhibit their normal flight response and to associate the appearance of human beings with a possibility of food.

Here is a case of " natural " learning in a young Axolotl which I have observed myself. It was about 10 cm. long when I got it, and was kept in a shallow earthenware dish and fed from time to time on worms, which it seized with a rapid but somewhat ill-directed snap. Some three months later I noticed that when I came near the dish the axolotl would approach the surface and put its head up as if expecting food, and would sometimes snap vaguely. This behaviour always recurred whenever anyone bent down over the dish. Evidently the axolotl had established an association between the vaguely perceived face of the observer and the possibility of food. My attempts, continued over about three weeks, to teach it to associate a particular stone in the dish with food were unsuccessful, apparently because the general response to the approach of the observer was dominant.

These few cases of " natural " learning (which everyone can multiply from their own experience) may serve to introduce us to a consideration of animal learning as studied by laboratory experiments.

The subject of animal learning is a difficult one to treat in an elementary way, for several reasons. In the first place, it is probable that the term covers two different processes, which we may call provisionally habit-learning and problem-solving. In the second place, the theory of learning is at present in confusion ; the older views, especially that associated with the name of Thorndike, appear to be breaking down, and the new views are still in course of active development. In the circumstances, all I can do here is to describe a few simple cases of learning by which to test the claims of the conflicting theories. The higher forms of learning I shall consider in the next chapter, when we come to study "insight" learning.

It is uncertain at present whether the Protozoa can learn. Some of them, notably *Stentor*, have a certain flexibility of behaviour, and try one method after another of avoiding unpleasant conditions [12]. But these methods are themselves stereotyped and tend to follow one another in a stereotyped manner, and it is doubtful whether experience really counts. Experiments which seemed to demonstrate that *Paramœcium* could learn to deal with an awkward situation have been shown to be inconclusive [13].

Clear evidence of ability to learn has been obtained experimentally in the Annelida, notably in the earthworm and in *Nereis*. Yerkes [14] succeeded in training an earthworm to take the right way out of a very simple labyrinth consisting of a T-shaped arrangement of channels, the entrance lying along the shaft of the T. The left branch of the T was protected by a strip of sand-paper and a couple of electrodes giving a weak shock. Five tests were made every day, and on the fourth day a tendency was shown to turn to the right. At about the thirtieth trial the habit of turning to the right and the safe way out was well established ; the worm had learned to avoid the shock waiting for it in the left arm of the apparatus. It is somewhat doubtful whether the worm really distinguished one side from the other, but it certainly developed a motor habit of turning to the right. Heck [15],

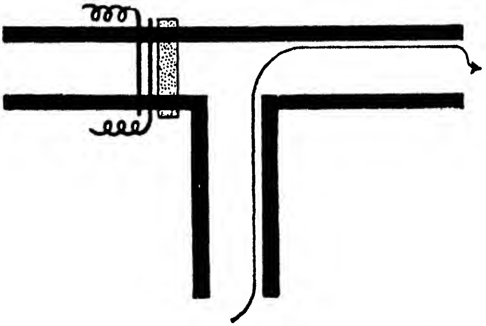

FIG. 26.—Earthworm " Labyrinth " (after Yerkes)

Arrow shows path of worm on thirtieth trial who repeated and confirmed Yerkes' results, found that if after training the conditions were reversed and the right arm protected by electrodes, the trained worm still kept turning to the right, and took a long time to break this habit ; sixty-five trials were required before it learned to turn to the left, now the proper way out.

Learning of a different sort has recently been demonstrated by Copeland [16] in the marine Polychaet, *Nereis virens*. This worm will live comfortably in a glass tube open at both ends, moving forward to the mouth of the tube if food or food juice is placed near it. Copeland kept one under conditions of dim illumination, and switched on a light a minute or so before feeding it. Two trials were made each day. For the first four trials the light had no effect, and the worm did not start moving forward till the food was presented. At the fifth trial, however, it began to move forward before the food was there, and afterwards, with a few exceptions, it moved forward quickly as soon as the light appeared. Light had become a sign of the imminence of food.

The converse experiment was also tried, the worm being kept in the light, which was switched off before feeding. Although the effect of sudden shading is normally to cause the worm to retract slightly, it rapidly associated the occurrence of darkness with feeding, and after about five trials it began to move to the mouth of the tube, in advance, and expectation, of feeding, as soon as the light was extinguished. With further training, the worm was even able to respond to both sudden illumination and sudden darkening, in two successive trials carried out on the same day. Both light and darkness here acted as sign-stimuli.

It is noteworthy that, as the training proceeded, the worm developed a tendency to remain near the mouth of the tube, ready for action, extending its head and the fore part of its body out of the tube as soon as the sign-stimulus appeared.

Nereis is, so far as I know, the lowest animal in which a " conditioned " response—to use the Pavlovian term—has been clearly demonstrated. The speed with which it was established is surprising.

A good many training experiments, mostly with simple labyrinths, have been carried out on Invertebrates, with positive results [17]. Gastropods, so far as tested, appear to show about the same degree of educability as Annelids. Insects and Crustacea show greater powers of learning, and a very high level is reached by social insects like the honey bee.

It is, however, in Vertebrates that the learning process has been most thoroughly studied, and it is here that it reaches its fullest development. Before going on to consider the theories of learning I shall give a few simple cases which have come under my own observation.

A year or two ago I spent some time training sticklebacks (*Gasterosteus aculeatus*) to take their food out of a small glass jar placed on the bottom of their aquarium [18]. This sounds an easy problem, but it proved very difficult at first, for the reason that the sticklebacks, being visual feeders, were strongly attracted by the sight of the food, and spent a long time during the first few trials in fruitless efforts to seize the food through the glass. This prevented them at first from making the simple detour over the rim of the jar which would lead them to the food. With one exception they all solved the problem by chance after one or two tests. Having desisted from their fruitless direct attacks, they swam about through the tank, and happening to pass over the mouth saw the food from above and darted straight down into the jar and ate it. After a very few chance successes of this kind their behaviour changed ; they alternated with the direct attack through the glass definite rises towards the rim of the jar, going in over the edge after a few of these tentative rises ; as time went on entry was effected more rapidly, until in the end the fish sometimes went directly to the mouth of the jar and straight in. They had learned to resist the direct attraction of the food and to take the roundabout way. Before the experiment was started, the empty jar was placed in the tank but excited no interest ; after the experiment had progressed some way the empty jar placed in the tank was immediately entered ; it had become an object of interest or significance.

I want you to note in this simple experiment the following points : (1) that the behaviour was throughout conative or directive, the stickleback was trying all the time to seize the food ; (2) that after the first two or three chance successes, the trick was learned rapidly, there was a marked fall in the time required to solve the problem ; and (3) that there was a change or a differentiation in the perceptual field, by which the jar began to stand out as a significant object.

Take now another simple case. A young dog, as you know, is very fond of playing with a ball, especially if you will take the trouble to throw the ball for it. I had little difficulty in training my terrier bitch Gina, when she was about a year old, to fetch her ball when I threw it. The method was to ignore the ball if it was dropped too far away, and to pick it up and throw it if Gina brought it within reach. The word " fetch " was used also as a cue to encourage her to retrieve the ball. What is interesting is the extension or elaboration of the trick which Gina invented for herself. She soon formed the habit of looking for and picking up her ball and dumping it at my feet—generally at a most inconvenient moment—so that I might play ball with her. If I paid no attention she would sometimes push up against my foot with it, or drop it on my foot. You will note that we have to do here, not with a simple automatic response, but with a somewhat elaborate train of actions all directed to the end of making me play with her ; it was the aim or objective that determined the further development of the first simple training.

Initiative in behaviour and the dominance of the end or goal are shown even more clearly in a second trick learned by the same bitch shortly afterwards. She was taught, with some ease, to run after and seize a penny or other coin and to bring it to one of us, receiving as a reward a small fragment of cheese. This trick was learned in the course of a few days, and then underwent development and elaboration in furtherance of her passion for cheese. She soon began to search for any coin that might be lying about, even stealing coins off the table, in order to hold us up for cheese. And she would generally refuse to drop the coin she brought unless she saw a prospect of reward ; if one of us made it clear that he or she had no cheese to offer, Gina would carry the coin to the other, and drop it with a satisfying thud if cheese were forthcoming. Often the coin would be dropped, as a hint, if cheese was not offered.

Thus the reward, which was intended to be incidental to the learning process, an incentive to rapid learning, became very quickly, from the dog's point of view, the aim or goal of the action, and the coin acquired functional significance as a means to the end so eagerly desired. Much ingenuity was shown in discovering stray coins, and other small objects were on occasion pressed into service. I have known her bring a bottle cork and a small brass hook in the hope of receiving the coveted reward. Coins and small objects generally had acquired a special significance in her perceptual world, and were actively sought for. I want you to note in this case, as in the other one, that there is much more involved in this process of learning, especially as elaborated by the animal herself, than a simple motor habit ; there is a definite train of conative activity initiated by the animal and leading to a definite objective.

With another dog, a toy Yorkshire terrier of high intelligence, I established more or less accidentally what looked like a simple conditioned response. He had a habit, quite a normal one, of chasing any stray dog out of his garden. I used to call his attention to an intruder by clapping my hands and saying " Chase him out." After I had done this on one or two occasions, I started clapping my hands when no strange dog was there ; Punch used then to rush into the garden, barking vigorously, in the full and obvious expectation of finding an intruder, and be much puzzled when he could not find one. I relate this almost trivial observation to make clear again the dominance of the end or aim of the action ; it was perfectly clear from his actions and demeanour that he expected to find another dog ; it was this expectation which led him to rush out, not a simple mechanical association of clapping with running into the garden.

I will give one further instance of learning in dogs, which like the previous ones is of some importance in connection with the theory of learning which we are about to consider. Gina, the same terrier bitch I have been talking about, when she was about a year old, was sent flying by a motor-van which came upon her suddenly as she leapt out of a hedge. She was more frightened than hurt, and bolted yelling for the garden, taking cover in the midst of a dense asparagus bed. This one painful and vivid experience sufficed to stamp into her a wholesome dread of motor-cars in general and of this motor-van, and its driver, in particular, which lasted for months. Motor vehicles for some time stood out in her perceptual world as terrifying objects to be carefully avoided.

I have described these few simple instances of learning, not as anything out of the way or remarkable, but as illustrating some of the salient characteristics of learning in Vertebrates—notably its conative basis, and the alteration in the perceptual field which accompanies learning.

The classical theory of animal learning, which held the field for many years, was that propounded by the American psychologist Thorndike [19], on the basis of his pioneer experiments with cats, dogs and chicks. He was the inventor of the " puzzle box " method of studying animal learning, and his work gave a great impetus to the laboratory study of animal behaviour, by means of such boxes and mazes of all kinds [20].

His main series of experiments were carried out with kittens which had been without food for fourteen hours and were thus very hungry. He placed them in various types of puzzle box, which could be opened from within by various simple means, as for instance by pulling a ring attached to a pulley or turning a button latch. He noted the time they took to get out, and on repeating the tests he found that the times decreased on the whole rather steadily. Cats, of course, hate being shut up in confined quarters, and Thorndike's kittens were no exception. They struggled vigorously, tried to squeeze through the slats of which the boxes were made, thrust their paws through any opening, and clawed at any loose or shaky object in the box. Thorndike's explanation of the process of learning was as follows :

> " The cat that is clawing all over the box in her impulsive struggle will probably claw the string or loop or button so as to open the door. And gradually all the other non-successful impulses will be stamped out and the particular impulse leading to the successful act will be stamped in by the resulting pleasure, until, after many trials, the cat will, when put in the box, immediately claw the button or loop in a definite way " ([19], p. 36).

Out of purely random or undirected activity the actions that chance to be successful are selected and emphasized by the resulting pleasure. The animal is, as it were, passively affected by fortuitous successes or failures, which impress *this* act upon it and wash out that other ; learning or the formation of associations is a more or less mechanical process imposed upon the animal ; there is no reasoning, no inference, no judgment by results, necessarily implied. To quote Thorndike again :

> " The one impulse, out of many accidental ones, which leads to pleasure, becomes strengthened and stamped in thereby, and becomes more and more firmly associated with the sense impression of that box's interior. Accordingly it is sooner and sooner fulfilled. Futile impulses are gradually stamped out. The gradual slope of the time curve, then, shows the absence of reasoning. They represent the wearing smooth of a path in the brain, not the decisions of a rational consciousness " ([19], p. 74).

Thorndike considered the connections between situation and response to be neural in nature, and learning to be due to the facilitation of these connections ; he attempted thus to give a physiological explanation of learning.

Thorndike's conclusions, though widely accepted, did not go without challenge. His critics from Hobhouse [21] onwards fastened upon various weak points both of method and of interpretation. It was early pointed out that his kittens were probably in a scared and panicky state, in no condition to exert their normal powers of learning. The random movements on which Thorndike laid so much stress were simply the expression of panic. It was shown, too, that many of Thorndike's time curves did show a sudden drop instead of an even decline, indicating that the animal at that stage had made a big step towards the solution. The fact that the cat did not always use the same stereotyped method of obtaining release—it might for instance pull the loop with its paws or with its teeth—was adduced as evidence that the process of learning was not a brainless and mechanical one. The phenomenon of " transfer of training," as when a cat which had learned to pull at a loop at the front of the cage quickly learnt to pull the loop when it hung at the back, also tells against the mechanical theory of learning ; the loop has become a significant object in the perceptual field ; it is attended to ; it has become for the cat something to be moved as a means towards escape. Psychologists pointed out that Thorndike had ignored the essentially conative nature of the whole process, and had underestimated the importance of attention. According to Stout [22], Thorndike's theory could hold good only in cases where action had become fixed and automatic through much repetition, and attention had ceased to be necessary. McDougall [23], among others, drew attention to the improbability of Thorndike's explanation of stamping-in ; it is not really conceivable, from the mechanistic point of view which Thorndike here adopts, that the effect (pleasure) should influence or " stamp in " the neural process which has preceded and led to it. According to McDougall, the results should be interpreted in terms of mental activity, the function of which is

> " to govern present action by anticipation of the future in terms of past experience ; to make, in short, effects precede and determine their causes. The cat's movements are in the main not merely reflex responses to stimuli. Rather they are throughout governed by the purpose of reaching the food.[1] This involves some anticipation, however vague, of the goal. We may fairly suppose that, as the process is repeated, this anticipation becomes more definite, as also anticipation of the various steps of action by which the goal is reached " (p. 195).

A few years ago the Thorndike experiments were repeated, as nearly as possible in their original form, by Adams [24], who came to the conclusion that the methods and apparatus adopted were ill-adapted to their purpose and led to erroneous deductions being made. His own cats did not exhibit the frenzy of movement which invalidated many of Thorndike's experiments ; they were much quieter and more self-possessed in their behaviour. Thorndike had stated that in his experience his cats never surveyed the situation and made up their minds what to do. Adams found that his cats did just this in the majority of cases. They spent, as a rule, little time in trying to get out, and much in looking over the situation. The first solution came as a rule by accident, but one large cat did the right thing from the start. Attention to the successful act seemed to facilitate its repetition ; the more deliberate and attentive the animal, the sooner it acquired a high degree of efficiency. In general, Adams concluded, the learn-

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[1] Thorndike's cats were fed as soon as they escaped from the box.

ing process could not be accurately described as the gradual elimination of useless or unsuccessful movements. The process had this appearance only in the few cases where it was associated with excitement and consequent inattention on the part of the cat. The total time taken was often irrelevant ; it depended very much on whether the cat was trying to get out, or was occupied in some other way, as for instance in grooming itself.

There is plenty of other evidence against the general validity of the Thorndike theory, but we cannot go into that now. We may safely say that two of the main ideas on which it was based have gone by the board—first, the more or less automatic selection of successful from purely random movements, and second, the importance of mere repetition.

To take the first point—it is probable that purely random activity does not occur, save in exceptional cases, where, through panic or intense excitement, the animal loses control of its behaviour. It is much more likely that when confronted with a problem the animal from the beginning *tries to solve it.* Its efforts may be at first ill-directed, and from our point of view apparently stupid, but it persists and varies its methods until one solution fits. The solution thus comes by real trial and error—if one method does not work another is tried until the solution is found. Sometimes of course, as we saw in the stickleback, the solution may occur by chance while the animal is doing something else and just happens to get into a favourable position for solving its problem.

This view, that learning is from the beginning a series of organized attempts at solution, has been clearly formulated by Krechevsky [25]. He points out that " very few serious experimenters would now wish to defend the concept that a learned response consists of a number of independent stimulus-response connections. Gradually, the concept that a learned response is an integrated *unity*, a systematic whole, has gained the acceptance of most animal psychologists " (p. 516).

This applies not only to the successful or final response but to the various unsuccessful attempts which have led up to it. The opinion, that in learning the animal is always trying by one means or other to solve the problem, has also been stated explicitly by McDougall [26], who writes apropos of the rats used in his Lamarckian experiment :

> " A rat, placed in a water-maze furnished with a single route of escape from the water, swims perpetually to and fro until he finds the place of exit. This swimming to and fro might plausibly be described as random locomotion. Yet repeated observation of this behaviour in hundreds of instances convinces me that, even when a rat is taken from the nest box in which it has been born and bred and is immersed in the water for the first time in its life, its swimming is not utterly random, not entirely blind ; even on this occasion the rat is seeking a way out, is looking for a way of escape. This seems to me a typical form of primitive goal-seeking behaviour prior to all experience of the goal " (p. 263).

A similar view is expressed by Lashley [27] in connection with experiments in light discrimination with rats.

> " In the discrimination box," he writes, " responses to position, to alternation, or to cues from the experimenter's movements usually precede the reaction to light and represent attempted solutions which are within the rat's customary range of activity. . . . The form of the learning curve is the more significant when considered in relation to such behaviour. In many cases it strongly suggests that the actual association is formed very quickly and that both the practice preceding and the errors following are irrelevant to the actual formation of the association " (p. 135).

Krechevsky supports this view with experimental evidence showing that rats confronted with problems of various kinds adopt first one and then another type of attempted solution until they hit upon the right one. These attempted solutions Krechevsky calls, rather quaintly, " hypotheses." In this new theory there is no room for chance or for random behaviour ; the very first responses are meaningful and unified, representing real, if inadequate, attempts at solution. According to Krechevsky, " Learning consists of changing from one systematic, generalized, purposive way of behaving to another and another until the problem is solved. The learning process *at every point* consists of a series of integrated, purposive behaviour patterns " (p. 532).

Once the correct solution is reached, the situation acquires a new meaning for the animal ; the significant elements of it begin to stand out—the mouth of the jar in the case of the stickleback—and the solution once found is retained. Subsequent trials facilitate and accelerate the solution, but essentially the solving of the problem comes suddenly and in one piece ; the solution is not gradually acquired by the establishment of a motor habit, as Thorndike maintained.

The importance of mere repetition is much exaggerated in the Thorndike theory, as he himself has lately recognized [28]. Practice is of course important when it is a question of acquiring manipulative skill, as in learning a skilled craft or in becoming expert at an athletic game ; and here no doubt maturation also comes into play. But there is a difference between this kind of habit-learning and the types of learning which we have been considering—problem-solving and the establishment of conditioned responses. In these the evidence goes to show that practice or repetition is accessory and contingent to the real act of learning. No doubt learning is facilitated and improved by practice even here, but it is not essential. We know that learning may take place in one experience, if the impression is sufficiently vivid—as in the case of Gina learning to dread motor-cars after being once knocked over. Here repetition is unnecessary.

Adams, in an important paper [29] published in 1931, has endeavoured to show that the essential thing in learning is adaptive response leading to economy of effort. This economy of effort, or reaching the goal by the easiest way, usually becomes more marked and more obvious by reason of repetition, and shows itself often in a reduction of the time required to solve the problem, but the learning is not caused—only improved—by the repetition. In a form of learning which we shall consider in the next chapter, insight learning, the solution comes in a flash and once discovered is retained—there is no need for practice. As Adams points out :

> " The familiar fact of insight *alone* is sufficient to demonstrate once and for all that there is no real or necessary or causal relation between learning and repetition or frequency of repetition. Whatever else insight may or may not be, it is a kind of learning which does not require repetition in order that its expression should attain maximal economy. . . . One thing at least is finally established by the mere occurrence of insight and that is that learning is *not* caused by repetition " (p. 157).

It is very important to note that in all learning there is a goal or expectation, and without incentive learning will not take place. We saw clearly this dominance of the aim or objective in the illustrations we gave of learning in dogs. It is clear also in the stickleback case. In the conditioned response of *Nereis* desire for food is the driving force. The dog that rushed out on the clapping of hands did so in the expectation of finding an enemy. It is well known that a conditioned response rapidly disappears if expectation is consistently baulked.

Learning is then essentially part of a conative or goal-seeking activity, which aims at the satisfaction of a need. When the animal is confronted with a problem, when it cannot reach its goal directly and its need is therefore obstructed, it tries by various methods, often ill-adapted, to reach its goal. Success may come in the course of this varied and persistent striving, or it may come by chance when the animal has desisted from its direct effort and is doing something else—as in the case of the stickleback. Success, however achieved, directs the animal's attention to the significant features of the perceptual field, those which are significant as means to the end pursued.

These features thus come to stand out in the field. To put the matter in technical language, the perceptual field is organized with respect to these significant features, and when the same situation is presented again the field retains its special organization—the animal sees it again in this special way. It is therefore able to repeat the solution, for it now perceives the situation in the light of its first success. In the case of the stickleback, for example, the rim or mouth of the jar acquired significance on the first entry (or the first few entries) and retained that significance in the succeeding trials, so that the solution once found could be easily repeated.

This slight sketch of a theory of learning applies more particularly to problem-solving. The process is somewhat different in the establishment of a conditioned response, which is a simpler matter, but here also goal-seeking is the fundamental thing. The change or reorganization in the perceptual field is a very striking feature of the process, for the conditioning stimulus rapidly acquires significance as an indicator of what is likely to happen, as a pointer towards the goal. Light or darkness for example quickly become for *Nereis* signs of approaching food. The coin becomes for the dog Gina first a sign of the coming reward and then very quickly a means for demanding it.

As I said at the beginning, the problems of learning are very difficult, and theories on the subject are in a state of flux. I have endeavoured to give some idea in a tentative way of the theory which I think is likely to turn out the most adequate and satisfactory [30].

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CHAPTER VIII

“INSIGHT” LEARNING

In discussing instinctive behaviour (Chapter V) I laid great stress upon the unvarying and stereotyped nature of it, its specialized and limited range. What we may call, for lack of a better name, “intelligent” behaviour is characterized by its adaptability, its power to deal with the unusual, to solve practical problems. One must not, of course, think of Instinct and Intelligence as two distinct powers or faculties, and one must not lay too much emphasis on the contrast between instinctive and intelligent behaviour. There are no hard and fast distinctions in Nature, and instinctive behaviour is rarely unillumined by some small glimmering of intelligence. In the same way, intelligent behaviour is based upon a solid foundation of instinct.

Speaking very generally, one may say that instinctive behaviour is typical of the great group of Arthropods, and particularly of Insects, while adaptive behaviour is best shown by Vertebrates, particularly by the higher forms. This difference is clearly connected with the fact that the higher Vertebrates pass through a period of infancy, during which their psychical development is dependent upon exercise and experience, whereas the insect is, so to speak, born already grown up, with its faculties mature and ready for use. (When I say “born” I include such effective rebirths as the hatching of the imago from the chrysalis or pupa or nymph.) Instinctive behaviour is, as we have seen in Chapter VI, closely related with bodily development, and, as Demoll [1] points out, the rigidity of instinctive behaviour in insects finds a close parallel in the rigidity and inadaptability of insect development. Both activities are fixed, automatic, and dominated by invariable routine.

In striking contrast with the rigidity of insect development is the plasticity of development in the higher Vertebrates, particularly the development of behaviour. The instincts of young mammals, for instance, are easily modified by differences in upbringing, so much so that some authors have denied the existence of definite instincts altogether, ascribing the psychical development of the young mammal mainly to " conditioning " or learning. Thus, to take a simple example, we know that most kittens " instinctively " hunt and kill mice and young rats ; experience, training, example, appear to be unnecessary for the development of this mode of behaviour, though they undoubtedly favour its early appearance. But, as Kuo [2] has shown, kittens brought up with rats from an early age become friendly with them, refuse to kill their rat companions, and usually refuse to kill other rats. In fact, according to their early upbringing and training, " Kittens can be made to kill a rat, to love it, to hate it, to fear it or to play with it : it depends on the life history of the kitten " (p. 34). We all know that nursing animals will adopt and bring up with their own young the most diverse and strange sucklings, and that the mixed broods brought up together become friendly and play with one another. Here is a simple case, related by Miss Pitt [3]. A very young rat was given to a cat with one kitten and was brought up by it ; it was treated just like a kitten, being fed, washed and carried. The kitten and the rat grew up on good terms with one another and used to play together. After this, neither the cat nor the kitten would attempt to catch and kill rats.

Modifiability or adaptability of behaviour is then characteristic of the young of the higher Vertebrates, and is shown in their relatively great power of learning, of adapting their instinctive behaviour to unusual circumstances.

In the last chapter we considered the essential features of the learning process as shown in animals generally, and we shall now continue the discussion, with particular reference to the higher form of learning known as " Insight " learning.

This type of learning, which so far as we know at present, is limited to the higher Vertebrates, was first studied by Hobhouse [4], but little attention was paid to it until it was brought to the fore again by Yerkes [5], and particularly by Köhler [6], who introduced the term " Insight " to characterize a particular type of behaviour shown by his chimpanzees.

In complete contrast to Thorndike and the laboratory experimentalists, who set problems that were often too complicated and difficult for the animal to grasp, Köhler devised very simple problems for his chimpanzees, and all of one general type, which he thus describes :

> " The experimenter sets up a situation in which the direct path to the objective is blocked, but a roundabout way left open. The animal is introduced into this situation, which can, potentially, be wholly surveyed. So we can see of what levels of behaviour it is capable, and, particularly, whether it can solve the problem in the possible ' roundabout ' way " ([6], p. 4).

The objection to using complicated apparatus, like puzzle boxes and cases with elaborate bolts and fastenings, is that one can never be sure whether the animal understands what it is doing ; it may merely be building up a complex habit without any real grasp of the situation. Tests should be planned with reference to the animal's capacity, and apparatus should not be unduly complicated.

The simplest form of the " roundabout " or detour experiment is to set up a blind alley of wire netting, introduce the animal into it, and place some food just outside the blind end. A chimpanzee, or a dog, or a very young child, will grasp the situation at once, and run out round the corner to reach the attractive object ; this is a simple case of an insight solution. But fowls subjected to the same experiment do not sum up the situation and find the solution straightaway ; they rush up and down inside the alley trying to get directly at the food ; only gradually does one after another hit upon the plan of running round the corner ; there is a period of trial and error, and the solution is found more or less by chance. You will remember the similar case of the stickleback learning to find its way into the jar for food. A real insight solution is independent of trial and error, its criterion is " the appearance of a complete solution with reference to the whole layout of the field," the grasping of the essential relations, temporal, spatial and causal, between the situation and the goal. It appears suddenly, and is carried out as one continuous, unhesitating action.

With this preliminary explanation, we may go on to consider in more detail some of Kohler's experiments. They are all of the same general type—the direct attainment of the objective is barred in some way, but it can be reached by indirect means. They fall into three main groups. In the first, simple roundabout ways must be taken ; in the second, tools must be used if the objective is to be reached ; in the third, tools or implements must be shaped or constructed or their use elaborated. Köhler was careful to test his animals first on simple problems, and gradually work up to more complicated experiments.

One of the simplest tests employed was to place a bunch of bananas outside the bars of the cage, beyond the reach of the animal, leaving one or two sticks inside the cage. This was tried first with Tschego, an adult female chimpanzee, who to begin with paid no attention to the sticks, but tried vainly to reach the objective with her hand, and then gave it up. After half an hour or so, some younger chimpanzees, outside the cage, came near the bananas. Suddenly Tschego got up, seized a stick and pulled in the bananas, cleverly placing the stick on the far side of the bananas, so as to hook them in. She used either arm indifferently.

Nueva, another female, also learnt this trick on her own initiative and suddenly.

An interesting thing then happened. If there was no stick available, or if it lay some distance away and was not noticed, all sorts of objects were used as substitute sticks in an attempt to draw the food nearer—lengths of straw, rags, pieces of wire, and so on. On one occasion Tschego went and fetched her sleeping-blanket, pushed it through the bars and flapped it at the bananas, trying to pull them towards her. One rolled on to the edge of the blanket, whereupon she altered her procedure and drew the blanket gently towards the cage.

Any movable object, especially of a long or oval shape, appeared to acquire the functional value of a stick, or means of attaining the objective.

In another simple test the apes are enclosed in a room with perfectly smooth walls which they cannot climb ; the fruit is fixed to the roof, at such a height that they cannot reach it by jumping, but a box is placed in the middle of the room. After a few minutes one of the apes, Sultan, stopped leaping at the fruit, noticed the box, tipped it towards the objective, and when still a foot or two away climbed on it and reached the food with a leap. The action was somewhat clumsy and unfinished on this first occasion, for the box was not pushed right under the fruit, and it was placed open side uppermost, so that Sultan had to take off from the edge. But it was a direct and continuous action from beginning to end.

Next day Sultan did better, dragging the box from a distance of five metres and placing it almost directly beneath the fruit.

All the apes discovered this method of using boxes as a means of getting at objects too high for them to reach, and they gradually learned to utilize other things as well—tables, ladders, stones, blocks of wood, coils of wire and so on ; all these objects acquired the functional value of footstools. The most amusing development of the footstool plan was Sultan's attempt to use human beings in this way. He tried this first with Köhler himself, who did not grasp what he was after and pushed him away, but the keeper passing through the cage shortly after, Sultan ran up to him, took his hand, pulled him towards the fruit, and made unmistakable efforts to climb on his shoulder. The keeper freed himself and moved away, but Sultan's intention now being clear, Köhler told the man to let Sultan have his way, when he pulled him near the fruit, leapt on his shoulder and secured it. All the apes developed the habit of using one another as footstools or jumping-off places.

Another method which the apes discovered of reaching high objects developed out of a form of play which they invented for themselves. They stood a stick, or other long object upright on the ground, or nearly so, clambered rapidly up it with feet and hands, and then fell with it to the ground or leaped off as it fell, in this way reaching the branches of a tree or the roof of their cage or some other high perch. This use of a jumping-pole started first as a game, but it was very soon converted into a means of reaching suspended fruit, and the apes became extraordinarily expert at it. One of them, Chica, was able to climb up a bamboo pole to a height of four metres before the pole fell over.

From these simple achievements—the use of a stick as a rake, the use of a box as a footstool, and the use of a jumping-pole—the chimpanzees went on to more difficult and impressive feats.

Sultan was given a couple of bamboo rods of such a thickness that one could be inserted into the other to form a double rod. Outside the cage, at a distance which he could not reach with either stick, lay some bananas. Sultan tried vainly to reach his objective with one stick, then pushed the stick out as far as it would go, and shoved it along with the second stick until it actually touched the food. This was of course ineffective, but he seemed to find satisfaction in establishing contact. After an hour Köhler gave up the experiment as apparently hopeless and left the keeper to watch Sultan. Within five minutes Sultan succeeded in fitting one rod into the other and drawing in the fruit. The keeper described Sultan as first of all squatting indifferently on his box, then picking up the two sticks and playing with them. While doing so, he happens to hold the two sticks in line, one in each hand, whereupon he inserts the thinner one a little way into the thicker, runs to the bars and starts to pull in a banana with his double stick. When one of the sticks falls, he fixes them together again.

Having once discovered this method of fitting two sticks together, he never forgets it, but seems to take a delight in employing it. He is given three bamboo rods, the two thicker fitting over the ends of the thinner. After a while he learns to make a triple length of rod with these, when the fruit is lying too far away to be reached with the double rod. On another occasion he was given a narrow strip of wood just too broad to fit into the bamboo. He set to work to gnaw the end down so that it would fit into the tube, and succeeded in pushing it in a little way.

Double sticks were put together also for the purpose of knocking down suspended food, and Chica on occasion applied this method to make a longer jumping-pole.

In the same way, the box method of reaching an objective is susceptible of development; first two boxes are used, one placed on top of the other, then three, and sometimes as many as four. These building operations are somewhat clumsy, and the structures are often rickety and unstable, but the attempts are spontaneous and deliberate, and represent real insight solutions of the problem. Köhler points out that his chimpanzees had no understanding at all for static equilibrium, and this is amusingly illustrated by the way in which they attempt to utilize an ordinary ladder.

Sultan, when first given a ladder, made no attempt to lean it up against the wall, but stood it vertically under the objective and attempted to climb up it, using it in fact as a jumping-stick. When this failed, he stood it up against the wall, but *edge on*, and tried to ascend it. After some time he did manage to place it against the wall in the proper way, but almost vertically, trying, it would seem, to fit it to the wall while remaining more or less under the objective.

These are some of the main experiments which Köhler tried with his chimpanzees. They illustrate the principal features of " insight " solution—its comparative independence of trial and error, its sudden appearance in a more or less complete form, indicating that the animal has in some way grasped the essentials of the problem and seen the way to its solution.

But these outline descriptions hardly do justice to the vividness and subtlety of Köhler's observations, and I strongly recommend everyone who is at all interested to read and study with care Köhler's classical volume

Köhler's work gave a great impetus to the psychological study of animal behaviour, and during the past decade many interesting papers have appeared which derive their inspiration and method largely from him [7]. It has been shown that " insight " is not a prerogative of the anthropoid apes, but is manifested also by monkeys, cats, raccoons, rats, and other mammals, and probably also by some birds.

I shall give one or two examples. Very successful work with monkeys was that by Bierens de Haan [8], with a female capuchin monkey (*Cebus hypoleucus*), which gave exceptionally good results compared with other monkeys that have been tested.

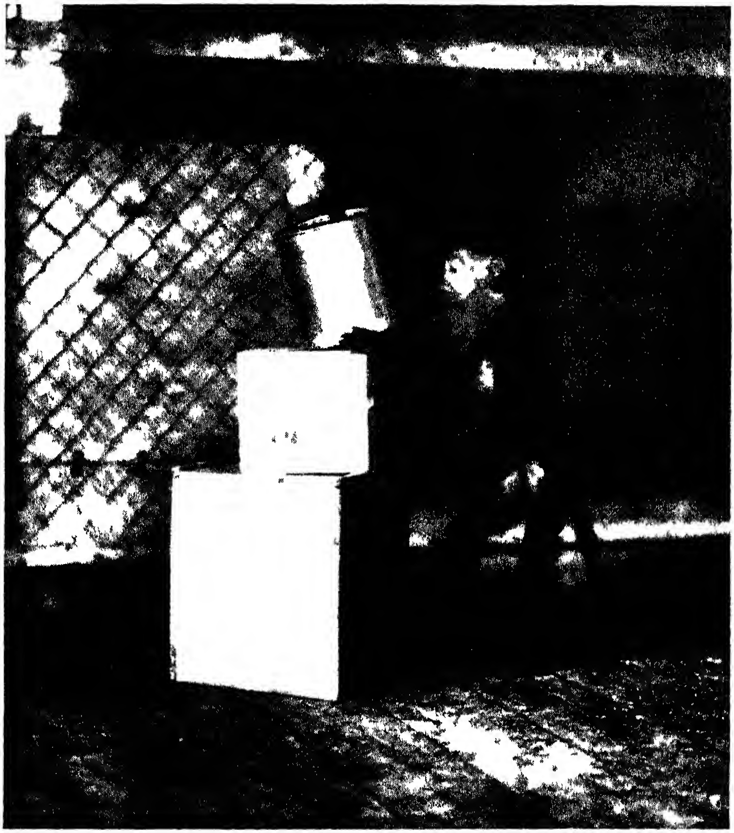
She was able to use a stick as a rake or a jumping-pole, just like Köhler's chimpanzees, and she learned of her own initiative to use boxes as footstools. Given a single box on which to mount, she trundled it, after a few abortive attempts, right under the suspended dainty and secured her desire. The single box was then placed under the objective and a smaller one left handy. First of all she tried to throw the smaller box at the fruit, but later on, during the first day of this test, she succeeded in placing the second box on the first and reaching her goal. Next she was tested with two boxes, neither of which was in position under the objective. She solved this problem in two minutes, first placing one box under the fruit and then the other on top.

The experiment was not very successful with three boxes, which she had difficulty in handling, but when one was replaced by a large tin, she quickly built them up into a three-storied tower, and attained her end (Pl. VI). Even when one of the boxes was hidden in her sleeping-den this did not cramp her style ; she went to look for it and dragged it out to use in her building. She would combine with her building operations the use of a stick to knock down the fruit, as did also Köhler's chimpanzees.

Bierens de Haan concluded that in general capacity she was little, if at all, inferior to the best of Köhler's chimpanzees. Unfortunately she died before her powers could be fully tested out. Extensive data on the use of " tools " or implements by a *Cebus* monkey will be found in Klüver [8A].

McDougall [9] got good results with a Bornean monkey (*Macacus nemestrinus*) and with two raccoons. The monkey was kept on a light chain which was fastened to a belt round her waist and attached to a tree. The chain was looped once round a stake in such a position that she could not reach a banana placed on the ground. After vainly attempting to unwind the loop she seized it in both hands and tried to lift it off the stake, and she succeeded in this after several attempts. In later tests she succeeded more rapidly, reducing her time from several minutes to twenty seconds. A somewhat similar experiment succeeded also with one of the raccoons. In this case the stake was a light one and fitted loosely into a hole in the ground ; the raccoon quickly learned to pull up the stake. In a simpler experiment where the chain was merely hitched round a post, the raccoon easily disengaged it. Sometimes she would back towards the post, keeping her eyes upon the bait, and reach out with her fore paw for the post, before passing round it. " Dum's action," writes McDougall, " in reaching out backwards towards the

PLATE VI



CEBUS MONKEY BUILDING

By courtesy of Dr. Bierens de Haan

post as she backed towards it seems to me an interesting bit of evidence of action directed towards an object not in the perceptual field, and, therefore, forming no part of the visual or perceptual configuration " (p. 260).

Examples of insight solutions are shown also in Adams's experiments with cats [10]. One of his cats solved the difficult problem of pulling up from the outside a string (attached to a piece of liver) dangling inside a cage. Adams's description of its behaviour is as follows :

> " Tom walked all round the cage and looked over the whole situation from all sides, but did not once paw through the sides toward the liver. He frequently looked up the string to the place where it was tied, sometimes staring intently at it for some seconds. Finally, after one of these pauses, when he had been in the situation a total of two minutes and thirty seconds, he turned away suddenly from his intent stare, went to the right back corner and climbed to the top of the cage. He went directly to the centre, reached through the top and pawed up a loop of the string, but was unable to bring this through the wire " (pp. 110–11).

Adams then simplified the problem by untying the string and fastening it to a small stick which was placed on top of the cage. When Tom was readmitted, he climbed up to the top of the cage as before, and clawed at the string where it was knotted to the stick.

> " He then took the string in his teeth, moved backward about 15 cm., and sat down. Then with a sweeping motion of his right foreleg, using it as an arm, he took hold of the string with his paw as far in front of his mouth as he could reach, raising the liver perhaps 30 cm., stood on the portion of string gained thereby, and took a new and nearer hold with his teeth. Immediately, then, he turned his back on the reward, and jumped down from the cage, keeping the string in his teeth, and with the—to me—quite evident and confident anticipation that the liver would follow " (p. 111).

Unfortunately he was baulked of his well-earned piece of liver, which was knocked off as the skewer holding it caught in the wire mesh of the cage. Next day, however, he tried again in the same way and had better luck, taking the stick in his teeth and jumping down with string and liver complete.

This success encouraged Adams to think that his cats might not be so very inferior in intelligence to apes and monkeys, and induced him to try the box experiment with them. This is much more difficult for cats than for apes, for their fore paws have not the grasping power of hands, and they are of course not accustomed to moving large objects about; it is doubtful whether they regard things like boxes as being movable at all. Adams therefore carried out some preliminary experiments in training his cats to move a light box by means of pulling on a string attached to it. They had already had experience of pulling in strings to get food. This training proved a difficult matter, but finally three cats learned to move boxes in this way. Of these, one was successful in the main experiment, and pulled a light box under the suspended meat, on her fourth trial. She apparently succeeded in her first trial also, but almost certainly by chance; she pulled the box directly under the meat, but without appearing to direct her movement thither. Her behaviour in the successful fourth experiment is described by Adams as follows:

> "The liver was suspended at a height of 85 cm., and the box was 50 cm. east of the point directly under the liver, with its long dimension at right angles to the direct line to that point. As soon as she was put in, Tabs climbed on the box and stretched repeatedly toward the liver. She shortly gave over this reaching, and walked round the room. After more than a minute of this, she stood up under the liver and reached toward it. Then she sat under it, and looked from it to the box and back again several times. Then she suddenly got up, ran to the box and started to pull it straight toward the liver. It was about 12 cm. away when she dropped the string, wandered off into a corner and sat down to wash without another glance at the liver. After more than a minute of this she suddenly paused and became rigid for a period of four or five seconds, in the posture of washing, with one hind leg sticking up at an angle of about 80 degrees from the horizontal, and with the liver throughout this period in her line of regard. Her ears were pricked forward and there was no relaxation from the awkward posture. At the end of this period of immobility, she abruptly got up and ran to the box, climbed on it and reached toward the liver. After several such futile efforts, she sat down and looked from the liver to the box, on which she was sitting, several times; then, again abruptly, she got down off the box, took hold of the nearer string, and pulled the box squarely under the liver, a distance of more than 30 cm., inasmuch as she had previously left the box with its nearest part about 12 cm. away from the point directly under the liver. She climbed on the box at once and got the liver" (pp. 153–4).

The time taken was just under five minutes.

Those who know cats will appreciate the vividness and accuracy of this description of cat behaviour. The story told is indeed a remarkable one. It illustrates most clearly the parts played in insight learning by conation and perception.

Even in rats evidence has been obtained of insight behaviour —notably by Helson, Higginson and Maier [13].

In Helson's experiments [11] the rats had to pass down one of two passages, which were separated by a partition. At the end of each passage there was a grid let into the floor which could be electrified so as to give the rat a mild shock. One or other of the grids was active in chance rotation, so that the rats could not learn which to avoid. Two rats solved the problem by the novel and sensible method of climbing on the partition and walking along the top of it to reach the goal, thus avoiding both grids. This solution was so unexpected that the experimenter was taken by complete surprise.

Higginson's experiments [12] were carried out with a complicated circular maze, in which the entrance to " alley 3 "— the way to the goal—could be closed by a tightly fitting door. The rat running down alley 2 had this closed door on its right and passed into a cul-de-sac. If it ran to the end of the cul-de-sac and came back (a distance of 6 feet) the door was opened and it found it open on its left ; if it failed to run the full distance to the end of the blind alley it found the door closed when it returned. In the course of this training it never found the door open on its right. A high degree of efficiency was attained, and the habit was firmly established of running the whole length of the blind alley before returning to find the door open on the left.

Then one day the door was opened before the rats reached alley 2, and they found the way to alley 3 lying open to them on their right.

> " We expected," writes Higginson, " that with this amount of repetition, the animal would run, in spite of the open door, to the end of the alley and back again and so into alley 3 to the left. Curiously enough but four of the nine rats did this and these four immediately shifted. The remainder exhibited the type of performance which most interested us. They stopped suddenly and without interference ran the remainder of the maze correctly, thus dropping at once six feet from the previous pathway and turning in a different manner. . . . Now the sudden elimination of six feet from the total pathway set up under continued

> repetition is wholly inexplicable in the usual categories of 'kinæsthetic patterns' and 'frequency and recency' of performance. Since the animals had never entered the door turning to the right, they could not have done so when the door was open, if we take frequency as the basis of the performance; and if kinæsthesis ruled the animal the lifting of the door should not have made any significant difference in performance; but since it did that fact must find explanation in visual terms" (pp. 340–1).

In other words, the rats noticed and grasped the significance of the open door, its relation to the goal, even when it meant breaking the established routine of running past it when closed and finding it open on the left when they returned. These rats then were not mere kinæsthetic machines, passively trained to run a certain course; they took advantage at once of a short-cut to the goal, showed insight into the new lay-out of the field.

We have now considered a number of typical cases of insight learning, which is characterized by the fact that the animal sizes up the situation before it acts, and when it acts solves the problem more or less completely, though it may of course improve upon its performance when it does it again. In trial and error learning, which we considered in the last chapter, insight arises in the course of learning, if it arises at all. There is no hard and fast distinction between the two forms of learning, and there are two essential features which are common to both. One is that learning is essentially determined by conative activity, an effort to reach some goal; without incentive there is no learning. The second is that learning implies a modification or reorganization or differentiation of the perceptual field, whereby the animal becomes aware of objects *in their relation to the goal.* Thus the jar acquires significance to the stickleback as potentially containing food, and its rim comes to stand out as indicating the way to the food. In the same way a stick, or any object which can be used as a stick, acquires significance to the chimpanzee as a means of attaining the longed-for fruit. Learning is therefore not confined to the executive side of action but takes place as well on the perceptive side. In insight learning the animal perceives the significant relations before utilizing them; in trial and error learning the animal has to test out various possibilities, often quite inadequate ones, before hitting upon a good solution. But in both cases, when learning occurs, the perceptual situation undergoes a change or differentiation, in such a way that objects which are significant in relation to the goal come to stand out and are attended to.

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CHAPTER IX

PERCEPTION AND GESTALT THEORY

As we have seen, especially in Chapter II, animals in their natural surroundings are rarely subjected to pure or isolated physico-chemical stimuli ; they respond to, or seek out, definite " situations " or complexes of stimuli. Many of them can live and thrive only in a particular set of conditions, in a special ecological niche, which they must find and maintain on pain of death. Much of their behaviour in the laboratory can be interpreted as an attempt to escape from unusual conditions and to restore the ecological norm. We have seen that the primary thing to study in animal behaviour is the normal response of the animal to its normal ecological perception-complex, and that only through complete knowledge of the " natural history " and natural behaviour of the animal can we hope to understand its behaviour in experimental conditions. It is true that we can analyse the stimulus-complex into its elements, and we can study the reaction of the animal to these isolated stimuli. We can, for example, study its behaviour in relation to rays of light of any given wave-length, but it is doubtful whether the results to be obtained have any great value in helping us to understand normal behaviour. It may happen that the animal responds to an isolated element which is representative or indicative of the whole normal complex ; thus light may be indicative of a way of escape, if the animal in its normal life naturally flees to the open.

One has to bear in mind constantly that instinctive behaviour is closely adapted to a rather narrow range of specialized conditions (see Chapter V) and that the animal is apt to be completely at a loss when removed from its ecological norm, or confronted with some unusual happening.

These considerations help us to understand some very curious and at first sight puzzling observations on the perceptions of animals which have been made in recent years.

In 1914 the psychologist Volkelt drew attention to some quite simple observations on the behaviour of spiders and insects, from which he drew far-reaching conclusions as to the nature of animal perception [1]. The spider studied was one of those that lurk in a silken tube attached to their web, lying in wait till an insect becomes entangled, when they rush out and kill it and bring it back to the tube to devour. Volkelt found that a fly which is caught in the irregular network near the mouth of the tube is not attacked. Further, a fly entangled in the entrance to the tube is treated as an enemy and not as prey. When he introduced a fly (of the kind normally eaten) into the rear end of the tube and caused it to move forward, the spider retreated before it right out of the tube, defending itself against this strange object. Volkelt drew the conclusion that the spider does not perceive or recognize the fly as a separate always identifiable object ; it reacts to the fly as prey only in the normal complex " fly-in-web " ; the fly in any other context is not recognized as a fly but treated as something unusual and menacing. He took these facts to mean that animals in general do not perceive their surroundings in such an " articulated " way as we do ; their perceptual world is not " dinghaft gegliederte," or articulated into clearly separate and distinct things or objects ; they perceive things only as ill-distinguished parts of a general complex, and always in their relations to that complex, so that when a thing is isolated from its normal context it may not be recognized for what it is.

It is a well-known fact that if a bee-hive is shifted a few feet to the side, the returning bees tend to collect at the old spot and take some time to find the displaced hive. Volkelt interpreted this as further evidence in favour of his view that animals perceive only complexes ; the bees, according to him, know the hive only as a slightly differentiated part of a perception-complex which includes the surroundings of the hive, and they look for it in its normal position in this complex. Similar observations have been made on birds ; if their nest is moved while they are away they look for it in its original position, and may completely ignore it in its new surroundings.

Here is a case reported by Hartley [2]. It refers to the Grey-breasted Martin of British Guiana. The nest and eggs of a pair of these birds were removed a few feet away from the original nesting site and placed in a conspicuous position. The birds looked for the nest in the old place and paid no attention to it in its new position. On the following day they commenced to build a new nest on the old site. When this nest was destroyed they gave up building, but continued to roost at that spot.

Although there is a solid core of truth in Volkelt's general conclusion, his original instances do not prove all that he maintained [3, 4]. Thus in the case of the spider one might well ask whether with its poorly developed eyes it can form any clear image of the fly at all. In the second place, bearing in mind the routine, stereotyped nature of instinctive behaviour, one might attribute its confusion to the fact that the normal sequence of events—fly caught in web, perceived through the vibrations of the threads, seized, and borne back to the tube—was completely upset, and the spider had to deal with a quite unusual situation. Further, it has been shown by another observer (Baltzer) that this spider will seize flies offered to it outside the web, provided that they actually touch one of its legs [4].

The case of the bees and the displaced hive is susceptible of a quite different explanation from that advanced by Volkelt. The careful studies of Wolf [5] have shown that it is only the older, experienced bees that are confused by the shifting of the hive ; young bees that do not know the surrounding country well fly direct to the new position of the hive. It appears from his work that on its first outings the bee finds its way back by sight, but as it becomes more experienced it comes to rely on a kinæsthetic habit, so that it flies back more or less automatically to the spot from which it set out. Experiment has shown that the seat of this kinæsthetic sense is in the antennæ, and when these are cut off the bee has to depend upon its visual sense again ; in this state even old bees are not misled by the shift of the hive but find it by sight without difficulty. The facts adduced by Volkelt accordingly do *not* demonstrate that bees are unable to recognize the hive as a separate object.

Nevertheless, there is a good deal of truth in Volkelt's general contention that the objects in an animal's perceptual field are not so clearly articulated as in our own perception, but are perceived usually in their natural connections with one another. This view is accepted by Bierens de Haan [4] who has brought forward some rather striking evidence in its favour. He holds with Volkelt " that animals in general react to a whole situation, and often show a curious incapacity out of such a complex to isolate fragments that must be of great importance to them and are unable to recognize these fragments in other complexes " (p. 38).

A very clear illustration of this curious fact is afforded by his observations [6] on the cuttlefish *Octopus vulgaris.* This cuttlefish will instantly seize and eat a crab which is moving over the bottom, but Bierens de Haan found to his astonishment that it does not recognize a crab dangled on a string in front of its eyes ; it may even attempt to remove the crab by directing a jet of water upon it with its siphon. But as soon as the suspended crab is released, and allowed to crawl on the bottom, the octopus shows excitement and seizes it at once. The octopus does not recognize the crab as such in an unusual situation, but regards it as an indifferent or annoying object. This experiment shows that the perception which

> " gives rise to the instinctive actions of jumping and seizing the prey is of a complex character, namely, that of the crab making the special movements of swimming or creeping. Another complex, that of the crab sprawling on a string, does not give rise to the usual reaction. This shows, too, that the octopus is unable to detach the principal object from the new situation and to recognize in it the same object that was the centre of the other more usual situation " ([4], p. 40).

Like all other creatures of instinct, the octopus is rigidly specialized in one way of life. It has never in its experience, nor have its ancestors, come across a crab except in the crab's normal surroundings, crawling along the bottom as a crab always does. It is, as it were, geared up to respond to the normal complex of perceptions which includes a normally moving crab, and apparently it cannot see the crab *as a crab* except inside this habitual complex. This observation of Bierens de Haan throws a great deal of light upon the probable nature of the perceptual field in instinctive behaviour.

An incidental observation by Bateson [7] on the behaviour of the Three Bearded Rockling (*Motella tricirrata*) seems to fit in here. This fish finds its food by smell and taste, normally hunting by night along the bottom. It pays no attention to a worm thrown into the water. One fish learned after a few months in a shallow aquarium tank to come to the surface and take food from the hand. But even then it seemed not to recognize a worm swimming in the water, though it would eat it if it found it in the sand.

Bierens de Haan gives two more instances where the response was to complexes rather than to single features of the perceptual field ; his observations relate to a young Pig-tailed Macacque, and I shall quote his account of the more striking of the two cases.

> " In a choice-apparatus with two doors I had trained it to find its food behind the door that was marked by a card with a red circle, while over the other door a card with a blue triangle was placed. When the animal was well trained, I changed the blue triangle for a blue circle or a red triangle, leaving the red circle as it was. Had it been trained to go simply to the red circle, as I supposed it was, then there would have been no reason for the monkey to make errors now, as the red circle remained visible as before. Instead of this, the animal now made about 50 per cent errors—that is, it was quite confused. The only possible explanation of this sudden confusion, as all other circumstances remained the same, is that the animal was not trained simply to go to the red circle, but to go to the red circle in opposition to the blue triangle, so that, when this latter figure was changed, the red circle lost its meaning as a guide to the food. As soon as I showed the former combination of figures, the animal was again at home, and made no more errors " ([4], pp. 41–2).

This example, we may note in passing, is a very good illustration of the truth that an animal does not necessarily attend to and respond to those features in its environment that seem significant to us. A red circle would be to us a very conspicuous and striking visual object, but it seems to have no significance at all to the monkey as a separate object. " It would be wrong," as Bierens de Haan points out, " to assume that an animal in training is explicitly aware of a problem that is put before it," in the way that we are aware of it. " It seems more in accordance with the facts to believe that during the training some more or less complex image gradually acquires the meaning of an indicator to the reward" (p. 43).

Another set of cases is known in which the animal responds not to one particular stimulus, one particular feature of the perceptual field, but to this feature *in relation to* another. I refer to the numerous experiments that have been carried out of recent years on "relative choice." This has been demonstrated, for example, by Köhler in chicks [8]. He trained them to respond to the darker of a pair of grey colours, and when this training was complete he tested them with a new pair, consisting of the darker of the original pair and one still darker; he found that they responded not to the original shade but *to the darker of the new pair.* The original training therefore had not been to a particular shade but to "the darker of a pair"; the response was to a relation. Many examples of relative choice are now known [9], and the phenomenon has been demonstrated even in fish [10].

These observations show clearly that animals may respond, not to simple physico-chemical stimuli, nor to isolated perceptual objects, but to perceptual complexes, to things perceived *in their relations to one another.*

This brings us to a consideration of the principle of "Gestalt," according to which response is primarily to the perceptual field as an organized whole, and if to a part of the whole, then to that part in its relations to the whole.

The theory of "Gestalt," which originated in the field of human psychology [11], is not altogether easy to grasp, and it has not yet been fully applied to the study of animal behaviour, though a good beginning has been made by Miss Hertz [12]. Nevertheless, I shall try to make the main idea of it clear. According to the Gestalt theory, the perceptual field is essentially an organized whole, of which the parts or presumed elements are not really distinct or separate, but are characterized or defined largely by their relations to the whole. Thus, to take the simplest possible case, a luminous point can be perceived only in its relation to, its contrast with, a darker ground. In the same way, the dimmer of a pair of lights can be perceived as such only in its relation to the brighter.

The theory is most fully developed and easiest to understand in connection with visual perception. We must realize first of all that visual perception is something other than the physiological action of light-stimuli upon the retinal elements. If an " image " is cast upon the retina, this means, physiologically speaking, that a large number of adjacent visual elements are stimulated, and in different ways, according to the wave-length and intensity of the light-rays falling on each. But these elements are in the main independent of one another,[1] and the so-called image is merely a mosaic of differently stimulated rods and cones. If we perceive an image or pattern—as we do—this means that the indifferent retinal mosaic is in some way organized centrally, so that wholes or patterns or Gestalten are seen, and not a mere mosaic of unrelated light-stimuli.

Stimulation, as such, is completely unorganized ; sensory organization is necessary before perception becomes possible ; and the organism responds, not to the raw physiological stimuli, which form an indifferent mosaic, but to its own perceptions, to the forms or patterns which it carves out of the sensory material. As Köhler [13] says, in visual perception " the organism will respond to an objective constellation of millions of stimuli by developing, first of all, an organized field, many and perhaps the most essential properties of which have no physical partner among the single stimuli " (p. 137). Response will be to the visual pattern or image perceived as a whole.

The perception of an image or pattern is of course very familiar to us, so much so that we do not realize how extraordinary a thing it is. A dog very quickly learns to recognize his master by sight, even at some little distance ; we must assume that he sees an image of his master. Now this image is not a fixed and invariable one ; it is different in size according as the master is distant or near at hand ; it is different in shape according as the master is seen full face or in profile, standing up or lying down ; it varies according to the way the master is dressed. Yet notwithstanding these large variations the image is recognized as that of the master.

[1] There is some evidence that the retina may act physiologically as a whole.

What really matters is the whole-perception, the general pattern; the details are quite unimportant save in their relation to the pattern.

Now it seems very difficult to conceive that such facts as these are susceptible of a physiological formulation. Thus the image as cast on the retina of the dog is not a fixed one, affecting always the same retinal elements; it varies enormously and hardly remains constant from one moment to another. Obviously the individual retinal cell, with its individual nervous connection with the cortex, counts for nothing *per se*; any particular retinal element may form almost any point in the retinal image; it is only its position relative to other stimulated elements that gives it any significance, and that significance is a constantly changing one. In other words, what really matters in visual perception is the whole, the pattern, irrespective of what particular retinal elements are stimulated. Somewhere the retinal mosaic must be organized into a whole or pattern, and it seems inconceivable that this can be a purely summative physiological process. From the physiological point of view the relation between stimulus and response must be mediated by chains of neurones extending between the receptor organ and the effector, and each stimulated receptor cell must contribute its own individual impulse. There seems no way of imagining how a pattern, a whole, can be formed, if the physiological formulation is true, and yet it is essentially to patterns and not to a mosaic of physiological stimuli that the animal responds.

Here is a good illustration from Lashley [14] of the impossibility of a summative or connectionist explanation of perception. Speaking of human vision, he writes,

> "with the eye fixed and a pattern moved across the field of the macula, the same reaction (*e.g.* naming the object) may be elicited at any one of a thousand points, no two of which involve excitation of exactly the same retinal cells. To say that a specific habit has been built up for each of the possible positions is preposterous, for the pattern may be one never before experienced. The alternative is that the response is determined by the proportions of the pattern and, within the limits of visual acuity, is independent of the particular cells excited. This means that, not only on the retina, but also in the central projection, there is a constant flux of stimulation such that the same cells are rarely, if ever, twice excited

by the same stimulus, yet a constant reaction is produced. The activity of the visual cortex must resemble that of one of the electric signs in which a pattern of letters passes rapidly across a stationary group of lamps. The structural pattern is fixed, but the functional pattern plays over it without limitation to specific elements" (pp. 158–9).

We seem to be justified then in treating perception as something different from physiological stimulation, and the clearest sign of perception is response to wholes, patterns, images, Gestalten, or, in most general terms, relations. Under the heading "relations" we must include temporal as well as spatial relations, as will be shown later on.

The word stimulus has been very much abused. When a male bird responds with characteristic behaviour to the sight of a female of the same species, it is hopelessly wrong to describe the female as the "stimulus" to the action, for by stimulus should be meant merely the physical action on the retina and nervous system of the male of the light rays reflected from the female. But what the male really responds to is his own perception of the female seen in relation to his own needs ; a treatment of the facts in terms of perception seems to be called for.

In dealing with an animal's responses, particularly to a visual field, it seems then that we have to do with reactions to perceived situations, or patterns, or relations, and not with the bare physiological effects of a constellation of physical stimuli. Only in artificial experimental conditions is the animal subjected to pure or simple physical stimulation, and even then it is probable that the animal organizes its sensory field in some way in conformity with its normal experience and its normal needs, and reacts to the stimulus as representative of some normal or usual perceptual situation.

We may accept then the fundamental thesis of the Gestalt theory, which is that "instead of reacting to local stimuli by local and mutually independent events, the organism reacts to an actual constellation of stimuli by a total process which, as a functional whole, is its response to the whole situation" ([13], p. 80).

We have seen in the course of this book that on the executive side behaviour shows a certain spatio-temporal wholeness, exemplified clearly in all cases of conative or directive behaviour, and also in all examples of long-range cycles of behaviour. Such behaviour may be analysed into constituent parts ; separate reflexes can be distinguished by analytical artifice ; but analysis lets slip the essential thing, namely the continuity and directedness of the action taken as a whole, which is given its full weight in our direct or organismal method (see Chapter I). In the same way, we have to recognize in the perceptual field a wholeness or unity which is destroyed by physiological analysis. Both in the perceptual field, then, and in the responses of the animal, we have essentially to do with spatio-temporal wholes, and not with mere summations of the parts which may be distinguished by analysis.

This general truth, of fundamental importance in the study of behaviour—and, we would add, for biology generally—is well expressed by R. H. Wheeler in the following passage from his textbook of psychology :

> " We may propose the law that any reaction of the . . . organism-as-a-whole is a unified response made to a total situation of some kind, and if to a specific detail, always to that detail in relation to other details. We may call this total situation a stimulus-pattern or arrangement of stimuli. . . . The reaction of the organism-as-a-whole is a pattern-reaction, or configurational (i.e. Gestalt) response, and is not composed of isolated movements or a combination of discrete movements. Neither is it composed of discrete habits, instincts and wishes. It is an organized unit, and we call it a configurational response to emphasize the fact that it is, *first*, a response to a total pattern of stimuli, and *second*, that it is not a summation of discrete responses to discrete stimuli " ([15], p. 77).

The " law of the whole " is true also of development [16]. In Chapter VI it was shown that in the development of executive behaviour we have to do with a process of differentiation *within a whole* ; this same law holds good of development on the perceptual side. Careful study, particularly of the psychical development of the child, has shown that at first the perceptual field is very generalized, and gradually becomes differentiated, as maturation and learning progress. There are not present at the beginning a number of isolated sensory impressions corresponding to the simple physical stimuli impinging upon the baby's sense organs. As Koffka [17] says :

> " It is not the stimuli the psychologist takes to be simple, because they correspond to his elementary sensations, that are most influential in the behaviour of a baby. The first differentiated reactions to sound are aroused by the human voice whose stimuli (and ' sensations ') are very complicated indeed. For instance, . . . between the first and second month the infant reacts to the human voice with a smile, at first without differentiating between a friendly, neutral, or scolding voice. This differentiation occurs in the fourth or fifth month, when a smile is the reaction to friendly or inviting speech, while angry words evoke crying and general symptoms of discomfort " (p. 147).

As the baby grows up, its perceptual field becomes richer and more differentiated, more objects are attended to, as their significance, especially in relation to the baby's own needs, becomes clearer. We find this same enrichment of the perceptual field, this same differentiation, taking place in all cases of learning, as new objects come to stand out as indicators of the goals pursued.

The subject of animal perception, on which I have touched in this chapter rather lightly, is admittedly a difficult one, and much more work must be done, especially on the lower animals, before any clear-cut generalizations can be safely put forward.

One or two points, however, seem to be fairly well established. We have of course no means of knowing the nature of the perceptual field in any animal, save by inference from its behaviour, and the problem is to discover what are the significant features in its perceptual world to which it makes significant responses, i.e. responses related to the main aims of its life, self-maintenance, development, reproduction. Obviously an animal's perceptual world may be very different from ours, and the probability is that it is much less differentiated than ours, much less articulated. Also the lines of articulation may be differently drawn.

The observations of Volkelt, Bierens de Haan and others indicate that animals may respond not to objects which to us seem clearly differentiated and conspicuous, but to perception-complexes, or linkages of ill-differentiated objects, and particularly to such complexes and linkages as are usual or normal in the animal's experience. Thus the effective perception leading the Octopus to pounce on its prey is the normal complex " crab running on the bottom."

In the second place, the normal succession of events appears to be an important factor in response. In Nature " coming events cast their shadow before," and the organism takes advantage of this uniformity of sequence through anticipatory or proleptic response. Thus for *Piscicola* (see p. 33) the normal sequence of events is disturbance of the water, approach of a fish, attachment to the fish, and *Piscicola* responds to the first element in the normal procession of events by an action which has reference to the events which are likely to happen next—its response is anticipatory or proleptic. We have seen many examples of such response, and it is a common feature in many types of " conditioning " or learning by association.

Another general point about the perceptual field in animals is that the focal points of attention, the features to which response is made, depend very much upon the *needs* of the animal, and shift as these needs change. To a hungry animal food becomes of absorbing interest, and every indication or sign-stimulus of food is eagerly followed up ; the satiated animal on the other hand is indifferent to food or signs of food. So too an animal on heat may be blind and deaf to all perceptions save those leading to successful mating.

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CHAPTER X

PERCEPTUAL WORLDS AS FUNCTIONAL

In the introductory chapter I said that we must think of each individual animal as living in its own perceptual world, which is separate and distinct from that of any other individual. No doubt, as Leibniz said, each individual mirrors the same reality, but as the points of view are different, so the perceptual worlds also are different. As there is a diversity of creatures, so also is there a diversity of private perceptual worlds. And the constitution and content of these worlds depend upon the nature of the animal, and vary with its needs and interests. Each animal selects from the possible perceptual environment only those features that are significant in relation to its life and ignores the rest. In this sense each animal makes its own world of perception.

In this supplementary chapter I propose to develop, in the light of some recent investigations, the thesis presented in summary fashion in the above paragraph, which is reproduced with some modification from p. 178 of the original edition.

It is necessary first of all to introduce and define the concept of *valence.* The word itself I have borrowed from the English translation of Lewin's papers [1], but I have used it [2] in a somewhat wider sense than was intended by Lewin. I call *valent,* or possessing valence, those objects, or characters of objects, and those events, in the perceptual world of an animal, in respect of which it shows behaviour. " Valent " means, in effect, perceived, attended to, responded to, in the particular situation considered. It has, quite definitely, a psychological connotation.

Instead of qualifying as *valent* such features and events as elicit response, we might call them significant or meaningful stimuli. But to this course there are two objections. First, the word stimulus is, strictly speaking, a physiological concept, and should accordingly be used only in connection with the physiological treatment of behaviour, which I here reject; secondly, the word significant might be taken to imply that the animal is consciously aware of the significance or meaning of the object or event to which it responds, and this we are by no means entitled to assume without definite proof. (In the earlier chapters of this book I have used this somewhat ambiguous word, and I have also employed the expression "sign stimulus." Both seem to me now objectionable, and better replaced by a neutral terminology.)

Simple observation shows us that the actions of animals have for the most part a definite objective; they aim towards some specific "end-state," and cease when this is attained. We may judge from the nature and course of the action, and from the end-state in which it culminates and ceases, what its objective is. Accordingly we can properly speak of avoiding responses, feeding responses, mating responses, and so on, because they have—visibly and objectively—a course and an end-state which show us clearly at what they are aimed. At the same time, we can infer from the character of the action the kind of valence possessed for the animal by the objects and events in relation to which its action is carried out. We may speak therefore of food-valences, danger-valences, mate-valences, parent-valences, offspring-valences, and so on.

A word of explanation is necessary here of the use of the expression "end-state," instead of the more usual word "end." The distinction is one drawn by Stout [3], who points out that the word "end" as used in relation to directive or conative process is ambiguous and may mean one of two things. "It may mean either (1) actual satisfaction of conation, or (2) the conditions of satisfaction as they appear to conative consciousness before the satisfaction is actually and completely attained" (p. 123). For the word used in its first meaning he substitutes the expression "end-state" or "terminus," confining the word "end" to its second meaning "as *object* of conative consciousness—the conditions of satisfaction as apprehended by the subject before actual attainment." The distinction is an important one. In instinctive behaviour generally, unless it is illumined by experience, we have no warrant for saying that the animal consciously pursues an end ; we can only say that its action is directed towards a specific end-state. The determining factors lie in the impulse, and not in the apprehended goal. Instinctive action is therefore directive but not consciously purposive, in the sense of being determined by an end or goal.

Returning now to the question of valence, it is a fact that, as a rule, only those objects and events are valent which, in the normal life of the animal in its normal or usual environmental conditions, possess biological significance. This is a general statement, for which much evidence can be adduced, but I shall not attempt to justify it here—limitations of space forbid. In any case biological significance is not part of the definition of valence. What is more important for our particular purpose is the fact that valence is largely relative to the needs, drives and " interest " of the animal ; it is not a quality inherent in the object or event and inalterable ; the same object may have quite different valence according to the psychological situation, or, rather, different characters of it may lose or acquire valence according to the dominant need or drive of the moment. Evidence of this is presented below.

The important thing to realize is that the animal's perceptual world is essentially a practical or functional one. The animal attends to, perceives, and shows behaviour in respect of, only those events, objects, and characters of objects that are at the moment functionally important to it, those about which it is impelled *to do something* ; only these have valence for it. All other features of the environment, which come within its sensory range, constitute what we may call the neutral background of action, and in so far, and at such times, as they are not responded to or dealt with in any way, they must be regarded as not perceived, as having no valence.

I can best develop this thesis, which I regard as of fundamental importance for the understanding of animal behaviour, by referring to some concrete examples, and I shall take first Kirkman's illuminating observations [4] on the behaviour of black-headed gulls (*Larus ridibundus*) towards their eggs.

Kirkman has shown that, according to circumstances, its own egg may be treated by a gull (1) as something to be incubated, (2) as something to be eaten, (3) as something to be rolled back into the nest, or (4) it may be ignored altogether, may be treated as part of the neutral background.

If the bird is broody and the egg is in the nest and intact, it will be incubated. Many other objects, very roughly resembling the egg in size and smoothness of contour, but not necessarily in appearance, will, if placed in the nest, be treated as *functionally equi-valent* to the egg, i.e. they will be brooded. If a gull returning to its nest finds one of its eggs with a gaping hole in it, made by some marauding gull intent on sucking, it will forthwith complete the sucking of the contents, even though the embryo be far advanced. Generally speaking, for the gull an egg with a conspicuous hole in its side, whether its own egg or another's, whether inside its nest or outside, is " something to be sucked " ; it has food valence. An intact egg in another bird's nest has similar food valence.

If an egg, its own or another's, is placed close to the nest of a sitting bird, it will roll it back into the nest—it is " something to be retrieved." Later experiments by Kirkman [5] demonstrate that the gull may also roll into the nest various egg-shaped or other-shaped objects, which are treated as functionally equi-valent to the egg..

The egg or egg-equivalent however loses its " retrieving " valence if it is more than a certain distance from the nest. For every black-headed gull there is a maximum distance from the centre of the nest, be it 1 foot, 1½ feet, or more, beyond which the egg or eggs put outside are completely ignored. They cease to exist for the bird. It may walk over or by them several times in the course of an hour or more and yet be blind to them ; they have become "just part of the landscape."

It is clear from these experiments that the valence of an egg changes according to the psychological situation ; we may infer also that for the gull there is no such thing as " an egg," but merely something, which according to circumstances is to be incubated, or retrieved, or eaten. The " egg " may be ignored entirely ; it may pass out of the perceptual field, be treated as part of the neutral background. If the gull could form concepts and use words, it would have no concept of " an egg," and no word for it, but it would have separate words for the egg-object in different situations. For us " an egg" is recognizable as such in all situations, it is a continuing object, retaining its identity; not so for the bird.

A beautiful example of the changing functional valence of one and the same object (as it appears to us) according to the *needs* of the animal concerned is afforded by the observations of Brock [6] on the behaviour of the hermit crab *Pagurus arrosor* towards its commensal anemone *Sagartia parasitica.*

In its normal state the *Pagurus* inhabits a gastropod shell which it carries round with it as a protective "house," and this house always carries upon it one or more *Sagartia,* which have been planted on the shell by the hermit crab.

If all the anemones are removed from the house of a well-fed *Pagurus* it will search round for one, and when it finds it will tap and stroke it to induce it to lose tonus and loosen its hold on the bottom; it will then swing it up and press it against the shell until it adheres. The anemone has in this case its normal valence as "something to be placed on the house." If however a *Pagurus* which has been long deprived of food, but possesses its normal equipment of *Sagartia,* can find nothing better, it will feed on a *Sagartia* supplied to it, especially if this is injured, so that its juices diffuse out. In these circumstances, *Sagartia* has lost its normal valence and has acquired food valence. In the third place, if the *Pagurus* is removed from its house, and is given no suitable substitute, it will attempt to treat a *Sagartia* as a house, trying to press its soft tail into the slight hollow of the pedal disc. In this case the *Sagartia* has house valence.

What we perceive as a continuing object and call a *Sagartia* is not such for the hermit crab; it is something which, according to circumstance and need, is to be planted on the shell, to be eaten, or to be treated as a house. A "*Sagartia*" has a purely functional valence for the crab, and this valence changes with the specific need of the crab, caused by a specific deviation from the normal state.

Let us try to discover, with the aid of Brock's experiments, just what *Sagartia* is in the perceptual world of *Pagurus,* in different circumstances.

There is some evidence that *Pagurus* may form a vague visual image of a *Sagartia,* but this image must be extremely ill defined, for it is not distinct from that of other objects of very roughly the same size and shape. Brock's work shows however that the hermit crab finds *Sagartia* mainly by its sense of smell ; it can discover the anemone even when hidden from sight under a layer of small stones. Other species of anemone also exercise a similar attraction. Once *Pagurus* has found and established contact with a *Sagartia* the smoothness and convexity of the anemone's surface is the essential valent characteristic which elicits the stroking movements. A *Pagurus*, if previously excited by a chemical stimulus from a *Sagartia*, will stroke and tap the smooth rounded surface of an inverted watch-glass, and attempt to overturn it ; but once it overturns the watch-glass and tests the concave side it abandons it. On the other hand, a plasticine model of a *Sagartia*, even after it had been rubbed with *Sagartia* juice, was dropped very quickly, presumably because its surface was not smooth enough.

These facts clearly indicate that *Sagartia* does not exist as a specific and individualized object in the perceptual world of *Pagurus*. What a *Pagurus* looks for when it is robbed of its anemones is not *Sagartia* as a specific object, but " something " possessing certain characteristics, such as a particular smell, a certain size and shape, a certain smoothness of surface. Other objects possessing one or more of these characteristics may be treated, at least to begin with, in the same way as a *Sagartia*. *Sagartia* comes nearest to being an individualized object for *Pagurus* in its capacity of " something to be placed on the shell," but even here, other anemones, and, in certain circumstances, even smooth, convex hard objects may elicit attention and at least the preliminaries of planting behaviour. That only *Sagartia* as a rule can be successfully planted on the shell depends to a considerable extent upon the co-operation of the anemone.

We note that it is the specific need of the *Pagurus* that determines the search for an object with special characteristics valent in this connection. The *Pagurus* lacking a *Sagartia* on its shell is attuned to seek out " something " to satisfy this need, and it will attend to particular qualities or valences, and only to such qualities, namely' those characterizing the object which is normally placed on the shell. Failing discovery of the normal object, other objects possessing one or more of these qualities will arouse attention. It is need that causes these qualities to become valent; in other circumstances they are indifferent or neutral.

When another need is dominant, as when the *Pagurus* is hungry, food objects become highly valent; it seeks out objects having food valence, attends to and responds to a valent characteristic which *Sagartia* has in common with other edible objects. So too when the need for a shell is exigent and no shell is available, *Pagurus* tests all objects of suitable size and movability, including *Sagartia*, in its search for the appropriate valent characteristic; as *Sagartia* presents, when detached, a slightly hollowed-out foot, the *Pagurus* may attempt to treat it as a substitute house.

We see then that the needs of *Pagurus* essentially determine what characteristics of objects shall be valent; it will seek out and attend to only such objects as possess characteristics which are valent in relation to the dominant need of the moment; its perceptual world at any moment (i.e. the world to which it responds, the objects and events that have valence) is strictly correlative with its needs. Any object which presents valent characteristics similar to those of the normal object which it seeks in satisfaction of a need will be treated, at least to begin with, as functionally equivalent to the normal object. Further, it will be seen that valent objects are characterized mainly by their functional possibilities, by what can be done with them. Thus, according to its needs, the *Pagurus* seeks, quite generally, (1) something that can be picked up and fixed on the shell, or (2) something that can be used as a house, or (3) something to eat. *Sagartia* fills the first requirement better than anything else, but it may in certain circumstances also be used to satisfy the other two needs. It is highly improbable that the *Pagurus* recognizes it as the same object in all three cases.

The analysis of this interesting case may serve to warn us against a very common error into which it is easy to slip when considering the behaviour of animals. We are apt to assume, without the least warrant, that an animal's perceptual world—the world in respect of which it shows behaviour—is essentially similar to our own. Thus we are liable to take it for granted that, as *Sagartia* is a perfectly definite and specific object for us, it must be so for a *Pagurus*. We can guard against this error to some extent by considering the sensory limitations of the animal in question, but this is not the whole story ; it is not so much a question of what an animal *can* perceive, but of what it does in practice attend to and respond to.

Careful investigation and analysis is required before we can determine what characteristics of objects and events are valent, and in what circumstances, for a particular animal, before we can establish the schema of its perceptual world. And this is a pre-requisite for a rational treatment of animal behaviour from the psychological point of view. The case of *Pagurus* and *Sagartia* illustrates the fact that valence is relative to needs. I shall give now an example showing how valence is dependent upon the waxing and waning of the reproductive drive, and for this purpose I select the interesting story of the reproductive cycle in the three-spined stickleback (*Gasterosteus aculeatus*) as it emerges from the work of Leiner [7], Wunder [8] and Craig Bennett [9].

In the late spring, when temperatures are rising, the male puts on his nuptial livery, and moves into shallow and quiet waters, generally those with a sandy bottom. Here he proceeds to construct a nest. In shape it varies somewhat, but is more or less tubular, built in a depression of the sand. He removes the sand with his mouth and collects vegetable débris, bits of stems and roots and leaves, sticking them together with a glutinous secretion produced by the kidneys. He may cover the tube with sand. According to Craig Bennett the presence or sight of a ripe female is a stimulus towards the building of a complete nest. We note that at this particular stage of the reproductive cycle débris suitable for making a nest acquires valence, which it did not possess before, and also that unusual material, such as hair and yarn, may be functionally equi-valent with the normal, being utilized in the same way in the construction of the nest.

The male stays by the nest, fanning it with the enlarged pectoral fins, and driving away all intruders from a territory extending a few inches round the nest. Anything that moves within this area is attacked, including an immature or a spent or even a ripe female. Any ripe female however which approaches and carries out certain characteristic movements [10] is courted by the male, and induced by him to lay a batch of eggs in the nest. He darts backwards and forwards between her and the nest, in a sort of dance, displaying his bright colours. He enters the nest and smears it with kidney secretion. He may nibble at her and gently jostle her towards the nest. The female then pushes her way into the nest, lays her eggs in the middle and quickly passes through to emerge at the other end. The male follows her through the nest, fertilizing the eggs, and when he comes out he chases the female away. Her valence has suffered a sudden change; from an object to be courted she has become an object to be repelled.

When the eggs have been laid and fertilized the male stands guard over them until they hatch in 10–12 days, and he takes little if any food during this period. He constantly fans the nest in such a way as to cause a current of water to pass over the eggs, and without this aeration the eggs will not develop properly. He may open little holes in the nest, which facilitate the aeration. He repairs the nest if it is disturbed, and puts back any eggs that fall out. He removes any dead eggs or eggs attacked by fungus. If all the eggs die he will break up the nest and build another.

Towards the end of the brooding period, when the eggs are ready to hatch, he makes big openings in the nest, which facilitate the escape of the young. When the young hatch and fall out of the nest or wander from it, the male picks them up and puts them back. He may also retrieve young fry of other fish if found near his nest. He guards the shoal of young fry for two or three days; then they lose "to be guarded" valence, he becomes indifferent to them, or he may even eat them—they have acquired food valence in his eyes. The fostering behaviour of the male is elicited by the complex nest-with-eggs. A nest in which no eggs are laid is guarded for some days but it gradually loses valence, is deserted and another made. A nest from which the young have hatched becomes an indifferent object, and the material of it may be stolen with impunity by another male. Eggs laid by a female, as occasionally happens, outside any nest, are not treated by the male as objects to be guarded and fostered ; on the contrary, he eats them. But eggs just fallen out of the nest are things to be retrieved. Valence of either nest or eggs is therefore dependent on their normal association with one another. And the eggs must be live eggs ; dead eggs are removed from the nest. Such is the normal course of events. Specially to be noted is the waxing and waning and alteration of the valence of partner, nest and young, as the cycle progresses.

We have seen from these few examples, which could easily be multiplied, that valence is relative to needs and drives, and generally to the psychological situation as a whole, including in this certain spatial or Gestalt relations, such as we have discussed in the previous chapter. As illustrating further the changing valence of an object in relation to the psychological situation as a whole we may refer back to the case of the Yorkshire Terrier and the towel, described on pp. 13–14.

In the higher animals at least, valence may be relative, not only to needs and drives, but to " interest." I can best explain what I mean by describing an actual case. On one occasion I was taking my fox terrier Gina up the garden, playing ball with her. When we approached a pile of wood where previously she had hunted for voles, she ran up to it, dropped her ball, and went nosing round the wood in typical hunting fashion, " feathering " with her tail. When I threw the ball for her she paid no attention ; it had lost all valence, gone out of her perceptual field ; her attention and interest were diverted to the vole hunt. This interest in voles was not determined by need—she does not eat the voles she catches—any more than her interest in the ball. No doubt both interests are based upon instinctive propensity, but the special valence of the objects and places which excite behaviour arises from previous experience.

The practical or functional nature of an animal's world is demonstrated with particular clearness when we consider the objects which it " handles " with its paws or feet or mouth—the objects which Tolman [11] appropriately calls " manipulanda."

After Gina had learnt to retrieve a ball and cast it down at my feet for me to pick up and throw for her again, other objects of manageable size began to acquire the same valence ;

on a country walk she would bring to me stones, pine-cones, sticks and broken boughs of moderate size, in the expectation that I would throw them for her. In course of time an astonishing range of objects came to be treated by her as functionally equi-valent to a ball—an orange, a gooseberry, a bottle cork, a raw potato, a box of matches, a wooden cube, a clean dry bone, and even a rubber boot-sole and a long-handled brush [12]. These objects have nothing in common in appearance or shape or smell, and it is clear that the dog does not confuse them with a ball. But they have in common their moderate size and pick-up-ableness, so that they can be used as functionally equi-valent to a ball. It is their *functional* value, functional valence, in relation to the dog's intention at the moment, that makes them stand out in the dog's perceptual field, focusing her attention upon them.

The same principle of functional equi-valence is illustrated by another acquirement of Gina's. As already discribed (pp. 142–3) she learnt to retrieve pennies thrown a short distance away, bringing them back to receive in exchange a reward of cheese or other tit-bit. Pennies thus acquired valence as a means towards food. This *means* valence rapidly spread to other coins, ranging in size from a sixpence to a half-crown, and also to a variety of small objects, such as a bottle cork, a brass hook and a box of book matches. The basis of functional equi-valence in this case was the small size of the objects concerned. It is noteworthy that a cork may be brought to one either as an object to be thrown and retrieved, having ball-valence therefore, or as a means towards cheese ; the two actions, bringing an object to be thrown and bringing it for cheese, are easily distinguishable, for Gina will not give up the means object until cheese is forthcoming, while the ball object is readily surrendered.

A bone has generally food valence for a dog, provided it is not completely bare and dried up, when it may be used as a plaything. But often, especially when it is fresh, the dog will bury its bone. This burying behaviour is usually exhibited only towards food objects, but observations on a Toy Yorkshire Terrier have shown me that certain other objects also will elicit an attempt at burying them [13]. This particular bitch, if there is some object in her bed or on her chair which is in her way, will go through the typical motions of burying it, nosing imaginary earth over it. The general formula which covers normal burying of food is " something not wanted now " ; this may sometimes be widened to cover " something not wanted here."

Klüver, who in his valuable book, *Behaviour Mechanisms in Monkeys* (1933) emphasized the importance of establishing the range of equi-valence of " stimuli," has given in a recent paper [14] some interesting examples of functional equivalences, of which I shall quote one.

" In studying the ability of monkeys to utilize objects as ' tools,' " he writes, " I found that certain *Cebus* monkeys were capable, for instance, of obtaining a piece of banana beyond reach by means of a stick. In such a situation the same animals also made use of a variety of other objects : a sack, a towel, a newspaper, branches of a tree or strips of bark, a meshed wire, a wire ring, a rope, a leather belt, a bottle brush, a floor brush, a fern leaf, a steel strip, a string, a toothpick, a dead mouse, a live rat, a live guinea-pig, and a carrot " (p. 94). A truly astonishing array—anything in fact which it was remotely possible to use or attempt to use for the purpose. It will be remembered that Köhler's chimpanzees also employed all sorts of objects as stick-equivalents to draw in food (see above, p. 156).

In this chapter I have sketched in merest outline the view, which I believe to be illuminating, that an animal's perceptual world is essentially " practical " or " functional," that it attends to and perceives only those objects and events which are of practical importance to it, about which it can or must do something. I should add that a very similar view is expressed by J. von Uexküll and his school in their " Umwelt " theory [15].

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