# **An Infant Science**

The vast majority of people, wherever they live and whatever their occupation, come in contact with animals in one way or another and have to deal with them. It is obvious that the hunter has to know the ways of his quarry; that the farmer must be aware of the habits of his farmyard animals and of creatures that damage his crops; that the fisherman must know when and where to find his fish and how to outwit them. Even the modern city dweller meets animals: he may want to ward off the cockroaches in his kitchen or he may keep a dog or bird and grow familiar with the way his pet behaves. All over the world, among primitive tribes as well as in modern society, there are those who delight in the observation of animals, and there is a growing awareness of the fact that sharing our world with our fellow creatures is like travelling together—we enjoy being surrounded by other beings who, like ourselves, are deeply absorbed in the adventure of living. There is a growing sense of marvel, and also of affinity.

But man experiences much more than just this sense of awareness of other forms of life; he tends to do more than just look at animals. It is one of his special attributes that man wonders about the world he lives in. He wants to

## FOUR PIONEERS IN BEHAVIOURAL STUDY



CHARLES DARWIN, 1809-1882

Before Darwin treated behaviour, along with structure, as an important part of an animal's equipment for survival, most natural scientists judged animal behaviour by human standards, or ignored it altogether. But Darwin's work on animal and human behaviour, far in advance of his time, paved the way for scientific, objective experiments and observations.



J. HENRI FABRE, 1823-1915

Fabre's importance lies in his having been the first to make detailed observations of animals in their natural surroundings and the first to keep minute and orderly records of what he saw. He spent 40 years watching the bees and wasps in his garden in France, and astonished the world with evidence of how complex the behaviour of insects really is.

see exactly how things happen, and he wants to understand why they happen.

This sense of wonder is at the root of scientific inquiry, and so it was inevitable that the desire to understand the behaviour of animals should lead to the study of animal behaviour. This inquiry—which is still in its infancy—is concerned with far more than just recording interesting incidents of animal life. It tries to find out as exactly as possible "what makes animals tick": why animals behave the way they do. I have spent the greater part of my life at this task, associating with animals in the field and in the laboratory, observing them and studying their responses in a variety of experimental situations. I have, in 30 years or so, seen our understanding of animal behaviour grow considerably. But I know only too well that our science has still a very long way to go. I am only one single member of a guild in which thousands of psychologists, zoologists, physiologists, ecologists and geneticists are jointly building a new science. Most of the questions we ask are still unanswered. Worse, we are not always sure that we are asking the right questions or applying the right methods. We are hardly more than groping to find our way. But these early stages of scientific exploration are fascinating; they give one a sense of adventure, and I firmly believe that many of my fellow men are willing and indeed keen to join me in this adventure. I therefore intend in this book to depart somewhat from the practice of previous volumes in the Life Nature Library—while I hope to be informative, I have laid emphasis on the lines of thought, on the methods of approach applied by biologists in their attempts to understand animal behaviour rather than on the factual information which, over the years, builds up a body of scientific knowledge.

Where do we begin? At the beginning—by asking ourselves: What exactly is animal behaviour? What do we mean by it? The answer cannot be straightforward and simple. Roughly speaking, behaviour is the movements animals make. These involve more than running, swimming, crawling and other types of locomotion. They also comprise the movements animals make when feeding, when mating, even when breathing. Nor is this all: slight movements of parts of the body, such as pricking the ears or making a sound, are also parts of behaviour. And many animals do something akin to our blushing—they change colour, sometimes as a way of concealing themselves from predators, on other occasions when they are aroused to attack or are courting a female. It is difficult to distinguish this sharply from behaviour. And, of course, behaviour can also consist of standing still and looking intently or, perhaps, just thinking—doing something internally that may influence subsequent behaviour.

On the whole, however, we tend to call "behaviour" movement or a change of movement, including the change from motion to absolute non-motion, or "freezing"—in short, what one can directly observe. But even though we may start by studying these observable things, as we observe more closely, and particularly as we apply more analytical methods, we are able to see more and more of the processes that go on inside the animal, and behaviour itself becomes an increasingly vague concept as attention focuses increasingly on the machinery behind it. However, for practical purposes, saying that we are concerned with movements will do.

Animals behave in a bewildering variety of ways; in fact, the range of animal behaviour patterns is as great as that of their many shapes, sizes and colours, which took generations of zoologists to describe and classify. No two species behave exactly alike. A robin can be recognized by its song and also by the

way it feeds on one's lawn, by the nest it builds and by its threat and court-ship postures. And there can be surprisingly many different types of behaviour in one and the same species of animal too. Gulls may feed by plunge-diving for fish or by killing a sick bird or by foot-paddling to drive worms to the surface of a meadow, or even by hawking insects on the wing. Yet the behaviour repertoire of such species is limited—no gull catches a bird the way a falcon does, nor can a robin build an oven-bird's nest. The enormous variety of behaviour repertoires has as yet been described only very sketchily, and the behaviour of most animals is very imperfectly known. But enough is already known to set us wondering about what it all means, to ask questions about behaviour; and this natural progression from description to inquiry leads us deeper and deeper into the subject.

THE next question generally asked by the student of behaviour is: Why does an animal behave the way it does? This seems simple and straightforward enough, but it is really two questions in one—and as we shall see, both are important to the biologist.

Let us say we are watching a dog eat. When we ask ourselves, Why is it eating? we may mean, To what purpose, to what end does it eat; what is the use of eating? One answer, of course, is that it eats in order to survive, or, to put it more specifically, the effect of eating contributes to the dog's survival. This is one aspect of behaviour—and an important one—which we shall deal with later: much of behaviour has survival value. This is of course obvious with eating, but the way other behaviours contribute to survival is not at all obvious and has to be investigated in detail.

However, there is the second question implicit in the one we are pursuing: when we ask why a dog eats, we may also be asking, What makes it eat? In this case we are not inquiring about the effects of its behaviour but about its causes. Now it becomes relevant to know whether or not the dog has been starved, whether it is stimulated by the sight and smell of food, and whether, when it was young, it learnt where and when to seek food.

The study of the survival value of behaviour is now in an extremely interesting phase. Just over a century ago Charles Darwin shook the world with his theory of evolution through natural selection, in which he proposed that the wonderful adaptability of all animals and plants was not due to sudden creation but to a long process of evolution. The present organisms, he said, had through the aeons become what they were through continuous selection of the fittest individuals, allowing these to outbreed the less well-adapted variants. Obviously this theory made it necessary to find out whether the peculiarities of each species really contributed to fitness, particularly those properties which seemed at first glance just "odd" and "improbable". Thus attention focused on the discovery and description of extreme examples of adaptive structures and behaviours. Many fascinating discoveries were made in this post-Darwinian period; one of the most famous is the case of the yucca moth.

The female of the yucca moth is one of the few moths equipped with an ovipositor through which she lays her eggs. This tiny tube is needle-sharp because the moth must thrust it through the wall of the ovary in the yucca flower to lay her eggs inside. Invariably, when she has done this, she collects yucca pollen and pollinates the stigma, an act which ensures that her larvae will have a plentiful supply of seeds to feed on when they develop. Since there are many more seeds than the larvae will consume, the plant is not harmed, and this



C. LLOYD MORGAN, 1852-1936

Although Lloyd Morgan reached his prime 50 years after Darwin, scientists were still trying to interpret animal behaviour in terms of human acts and feelings. Lloyd Morgan helped to put an end to that for ever by showing that one can often find a simpler mental process to explain the act of an animal, and that the simplest explanation may be the right one.



IVAN PAVLOV, 1849-1936

Pavlov's career was centred on the laboratory and the controlled experiment. In a classic test series, he made a dog's mouth water by always giving an artificial stimulus, such as ringing a bell, at feeding time. Soon, he found, the dog's mouth watered in anticipation of food whenever the bell rang. Thus was born the key concept of the conditioned reflex. symbiotic interplay ensures the survival of both plant and insect—without each other, both species would die out.

Surprising as this intricate relationship is, the yucca moth is a true example of insect behaviour—but it also illustrates the trap into which this fascinating and important study fell in the post-Darwinian era. Some men went so far in supporting improbable theories about the survival value of organs, colour patterns and behaviour that they gradually discredited this whole line of research. One well-known and respected naturalist seriously claimed that the bright-pink coloration of the roseate spoon-bill served to camouflage this bird at sunrise and sunset—without trying to consider how the bird managed the rest of the time. It was many years before a more balanced approach and more sophisticated, partly experimental methods at last began to win new adherents to the field—but the new thinking is now paying off handsomely in terms of discoveries that lead us ever deeper into the subject.

There is, for instance, a small fish called the stickleback which habitually builds a tubular nest in the water and, after inducing one or more females to spawn in it, guards it with an intriguing behavioural pattern. It alternates periods of just swimming around the nest with periods of what looks remarkably as though it were fanning it: the fish dips head down, facing the nest, and for as long as 30 seconds appears to direct water at it by moving its fins in a quick, regular rhythm, making forward swimming motions the while with its tail so as to stay in position.

Why does the stickleback do this? A few simple experiments yield an almost absurdly simple answer: it is fanning the nest; it is ventilating the eggs, keeping them supplied with freshly aerated water. If the male is removed, the eggs will die. They also die if the male is allowed to stay and fan but if the nest is shielded with a watch glass. They do not die if the male is removed and replaced by a glass tube through which water is regularly directed at the nest. But it must be freshly aerated water and it must be aimed at the nest; if the tube does not provide water or if stale water is pumped through it, the eggs will not survive.

PROBING into the functional significance of behaviour patterns is like a journey of exploration and discovery; at every step one is faced with surprises. The problem can be approached in two ways. First, one may observe a certain behaviour, as we did with the stickleback's fanning, and ask, What would be the use of this? But one can also look at an aspect of animal life, a pressure of the environment, let us say, like that of being preyed upon; in this case one may ask how the animal deals with this pressure.

Usually, of course, both approaches are applied together. The student begins his research by simply observing, and on the basis of his observations he tries to formulate a hunch as to the most likely purpose of the behaviour he sees. We first conceived the idea that fanning of sticklebacks might ventilate the eggs when we saw that the male's fin movements directed a water jet at the nest entrance. Knowing that growing eggs require oxygen, we put two and two together and promoted our hunch to a hypothesis, which was then tested with a few experiments.

Then, however, we applied the second approach and asked whether just fanning was all that was required. Sure enough, we found that, as the eggs grew and required more oxygen, the amount of fanning increased. We also learned that half-way through the period of parental care the male begins to construct a number of extra openings in the roof of the nest to make ventilation more efficient,

and we saw the significance of the male's exact orientation during fanning, which ensured that the water jet he sent down actually entered the nest.

Black-headed gulls, which nest in large colonies in dunes on the sea beaches, like many other birds take away the empty egg shell each time a chick has hatched. Why do they do this? By considering various possibilities, we thought it most likely that this was useful in concealment, since a piece of shell with its conspicuous white inside lying right next to the chick might serve as a signal to a predator that there was a meal nearby. So we decided to test this hypothesis, and we began our tests with crows, since these birds are the chief predators of young black-headed gulls. We discovered that nests that had pieces of shell lying within eight inches of them were investigated and attacked by crows far more often than those that had no shells. With this significant piece of knowledge, our hypothesis began to have some substance, and we went on to investigate what other defences the gulls had against predators. This led to some fascinating discoveries. For example, we learned that there was a reason for the gulls' habit of all laying their eggs at about the same time. This proved to have a direct bearing on brood survival; birds laying a little before the others, and birds laying a little after, lost their broods much more often to predators.

The habit of nesting in dense colonies also reduced predation, for when we laid out extra eggs in lines running from well inside to well outside the colony, we found that the outside eggs were taken much more often than inside eggs, which were protected because the gulls attacked in force and repelled any predator trying to steal them. We also found, by systematic and prolonged studies, that the gulls' habit of spending nights in non-nesting periods on broad, open beaches was a very effective, if indirect, defence against foxes. Although foxes roamed over the beach as well as over the dunes, they killed many more gulls in the dunes, where they had a better chance to come up on them unawares, than on the beach. Only on exceptionally dark nights did they have much luck in getting at the gulls on the beach.

Thus, by systematic observation and, where possible, by devising an experiment to test whether or not a certain behaviour characteristic contributes to success, the student gradually becomes aware of the intricate adaptability of animal behaviour. He begins to see more and more clearly that behaviour is an essential part of an animal's equipment for survival. Even though we have so far done no more than scratch the surface, a wonderful picture slowly emerges.

First of all, the movements themselves are often incredibly efficient. The cuttle-fish, an inshore squid, can circumvent the defences of shrimps in a very interesting way. As it swims leisurely a few inches above the sandy bottom, it spouts a gentle jet of water at regular intervals through its funnel, aiming down and a little ahead. Every time it does so, the sand in front is whirled up. The function of this becomes clear when one sees the water jet hit a buried shrimp. These shrimps are wonderfully camouflaged, and they conceal themselves even better by lying under a thin layer of sand, which they sweep over their backs with a wide, backward movement of their two antennae. When a cuttle-fish happens to expose a shrimp by whirling up its protective blanket of sand, the shrimp quickly covers itself again. This is its undoing, for the cuttle-fish, which might have overlooked the shrimp had it remained still, detects the movement. It immediately shoots out two tentacles and seizes the shrimp with the sucking discs at their tips.

Not only are the movements themselves nicely adapted to their functions but



## HOW A CUTTLE-FISH SNARES A SHRIMP

Efficient co-ordination of two separate acts in order to get food, even among fairly primitive organisms, is nowhere better demonstrated than by the cuttle-fish. One of its foods is shrimps that lie concealed in the sand on the ocean bottom. As it swims along, the cuttle-fish gently blows away the sand with a jet of water and occasionally uncovers a shrimp (above). If the shrimp were to lie still, it would be passed by unnoticed, but it hastily covers itself up again, and this movement alerts the cuttle-fish, which snatches it up in its tentacles (below).



also their timing, their orientation and their co-ordination with other movements. It is notable that the cuttle-fish does his "sand puffing" only when he is hunting shrimps; to be successful he must aim his water jet at the sand bottom ahead of him; he must at the same time swim in a very special, leisurely way; and he must be ready to strike when he sees a shrimp move. It may seem commonplace, but when you think of it, it is really wonderful that he *does* all this. So if we want to understand how behaviour contributes to success we also have to find out how efficient it is or, looking at it from the other side, what would go wrong if the animal behaved differently, and why the behaviour would misfire. This, however, must await a later chapter.

The quest for the causes underlying behaviour leads to equally fascinating research, though of quite a different kind. We have, of course, known for a long time that, mechanically speaking, behaviour is a consequence of muscle activity, and that muscles on the whole do not contract unless stimulated by nerves. The way muscles work and the way nerves make them contract are the proper study of the physiologist, and a great deal is already known. But rarely is behaviour a matter of an isolated contraction of one muscle. On the contrary, even the simpler behaviour patterns, such as locomotion, are sequences of contractions and relaxations of very many muscles, all well modulated and well timed. In fact, behaviour is almost always a symphony of muscle contractions, with the messages from the central nervous system organized in an orderly manner, and it is this organization we have to understand.

The central nervous system, for its part, does not act entirely on its own accord—it receives stimulation from other sources. What are these sources? Partly they are the sense organs—eyes, ears, nose and many others—which provide the animal with information about the outside world. The sensory processes, therefore, must also enter into our study. But partly, too, behaviour is controlled from within: a hungry animal sets out to feed, and when its sex urge awakens it goes out in search of a mate. We shall have to find out what it is inside the animal that makes it hungry or stimulates its sex urge. And finally, there is the fact that outside stimuli and internal condition interact—i.e., a hungry animal reacts to the food stimuli while a satiated animal does not; outside the mating season, as in winter, most animals are indifferent to the same sex partners that strongly attracted them in the mating season.

There are two major difficulties in this study of the causes of animal behaviour, and unless they are clearly recognized, they can hamper research seriously. The first concerns the subjective experiences of an animal: does it feel anything akin to what we feel when we are, say, angry or sad or amused? The biologist simply does not know and cannot know, and for that reason he does not feel he is entitled to say anything on the subject. Therefore, pursuing a strict and scientifically consistent line of inquiry, he cannot say that an animal attacks "because it is angry" or that it retreats "because it is afraid". He has to express the cause of what we might interpret as anger in terms of processes that can, in principle, be observed and measured just as well as the behaviour itself. In short, he is interested in the machinery of behaviour.

A second possible source of confusion is our failure to distinguish the two meanings of "why". We are apt to say, for instance, that an animal eats because it needs food, that a bird builds a nest because it requires a receptacle for its eggs. Again, we have to go beyond the superficial meaning of the word, and in order to avoid ambiguity biologists are strict about its use. In their language,

"because" refers literally to causes, to events which precede the behaviour and which can be shown to control it.

The confusion arises because we ourselves can, in some way still mysterious to the scientist, think ahead: even before we decide whether or not we shall undertake a particular form of behaviour, we can imagine what the effect of that behaviour will be. Thus we can say, with a certain justification, that the effect of our behaviour controls what we shall do before we have done it. But although many animals do things-such as building a nest, feeding their young, hoarding food-that prove to be useful long after they do it, they do not really seem to have these distant aims "in mind" when they are doing them. Certainly they often show surprisingly little adjustment to abnormal conditions that may arise; in such circumstances their behaviour frequently "misfires". If a young song-bird is accidentally kicked out of the nest and gets chilled, it fails to open its mouth for food when a parent comes and so is neither fed nor brooded-it perishes, simply because the parents cannot cope with this unexpected development; they brood only young that are in the nest and feed only young that gape. What they react to, much more rigidly than we, is the stimuli of the moment. And while it is true to say that the function of feeding the young is to make them grow up-a distant aim-the causes of feeding the young are found in stimuli, external and internal, without which this end would not be reached. We would find out little about such causes if we would content ourselves with assuming that animals, like human beings, plan their behaviour with distant aims in mind.

•HE search for causes is really endless. Because every cause has in its turn a cause, we are led to probe continuously further back in time. In doing so, we find that the life of an animal runs in cycles; behaviour often repeats itself. Periods of feeding alternate with intervals in which the animal, satiated at first, gradually becomes hungry again. Other cycles are on a larger time scale; sexual behaviour in many animals comes only once a year. But when one looks back still further, one comes ultimately to a stage in the life of the animal when it was still growing up, when it was still developing. During development an animal's behaviour changes just as its form does, and the causal organization of this behavioural development determines how the adult shall behave. In order to understand what makes an animal behave the way it does, we must, therefore, do more than study the immediate causes of the self-repeating cycles of behaviour: we must also ask how this fully geared, cycling machinery has become what it is. Although, in practice, research on the behaviour machinery of the full-grown animal necessarily overlaps with studies of its development-for animals, like man, keep developing through adult life-it will be practical to deal with these two fields of research one by one, and behaviour development will not be discussed until Chapter 6.

But the life of one animal is itself a cycle in a series of events that happens on a much larger time scale. Generation follows generation, and through countless generations the animals we know today evolved until they became something else and behaved differently. This, too, concerns us: we have to ask how animals and their behaviour have changed through evolution, how they have become different from each other, and how they have become increasingly efficient. This task differs fundamentally from other kinds of biological study. We can observe the behaviour, and its development, directly in present-day animals, and can repeat these observations, as well as our experiments, as often as we

like. But the behaviour of animals of the past can no longer be seen; we are in the position of historians who have no documents of past events. Nevertheless, as we shall see, there are indirect ways of unravelling the biological past. Also, we can study the evolution which animals are undergoing even now and, on the assumption that the laws of evolution have not changed, apply our findings to what went before.

The study of the causes of behaviour, therefore, embraces three relatively distinct tasks: we need to understand how the behaviour machinery works, how it develops during the life of the individual, and how animals have evolved their behaviour machinery through the generations. All these tasks are now being taken in hand. Yet although thousands of trained researchers are spending all their energy and time on this work and are making good progress, they are constantly discovering how much there is they do not know. The emphasis on the need to confine ourselves to what we can actually observe has, so to speak, boomeranged: we discover that there is so amazingly much to observe. Straightforward observation and description in ever-increasing detail is therefore an important part of our task.

PORTUNATELY we need no longer rely on what we can immediately see and hear; we have now at our disposal the still and cine cameras, with time lapse and slow motion, and sounds can not only be heard but also recorded on tape to be heard again and again, and even analysed in the sound spectrograph. Many refined precision techniques are used in experiment. Tiny quantities of hormones can be assessed; electrodes only a few thousandths of a millimetre in diameter can probe into the nervous systems of living animals; data too numerous to handle are fed into computers which, by doing our sums for us quickly and reliably, free us to get on with our real work: observation and experiment.

The complexity of the research and the variety of phenomena are leading to a high degree of specialization among research workers. Animal behaviour is being studied by people of highly varied interests and abilities. Some study the functioning of parts of the total machinery, such as sense organs or even one particular sense organ, others focus on nerve cells or muscles. Still others disentangle the complicated processes occurring during the development of behaviour. Others again study the way behaviour has changed during evolution. Some prefer to work under controlled conditions in the laboratory, others study animals in their natural environment, and there are those who work in zoos. There are specialists on animal groups or even on single animal species, and there are specialists who compare as many species as they can. In spite of this necessary division of labour, there is among behaviour students of all kinds a growing sense of a common aim, and psychologists and zoologists and physiologists are beginning to join forces in a common effort.

We are still very far from completely understanding the behaviour of animals, but we are beginning to learn how we can arrive at such an understanding. We also feel that our task is urgent. Some animals, such as those we consider pests, are a direct threat to us, to our health and our food supplies; we must know how to keep them in check. Others, such as our cattle and consumable fish, are indispensable to us; they have to be farmed, bred and cropped sensibly. We also have to learn to live and let live—to share our planet with our fellow creatures, and this task of conservation, too, requires understanding. And, finally, since we are really related to our fellow animals, a closer study of their behaviour can help us in learning to understand ourselves.



LOVING SNOW GEESE BRACKET THE SHAGGY HEAD OF KONRAD Z. LORENZ, WHO HAS TRAINED THEM TO THINK OF HIM AS THEIR MOTHER

# Into the Animals' World

Because it is still a young and uncharted science, animal behaviour is approached in as many different ways as there are scientists. Unique as these individual methods may be, they all have a common purpose—to probe ever deeper into the mystery of animal life. In the following pages Life photographer Nina Leen shows the ways in which 10 prominent behaviourists pursue their research.

#### Parent to a Science

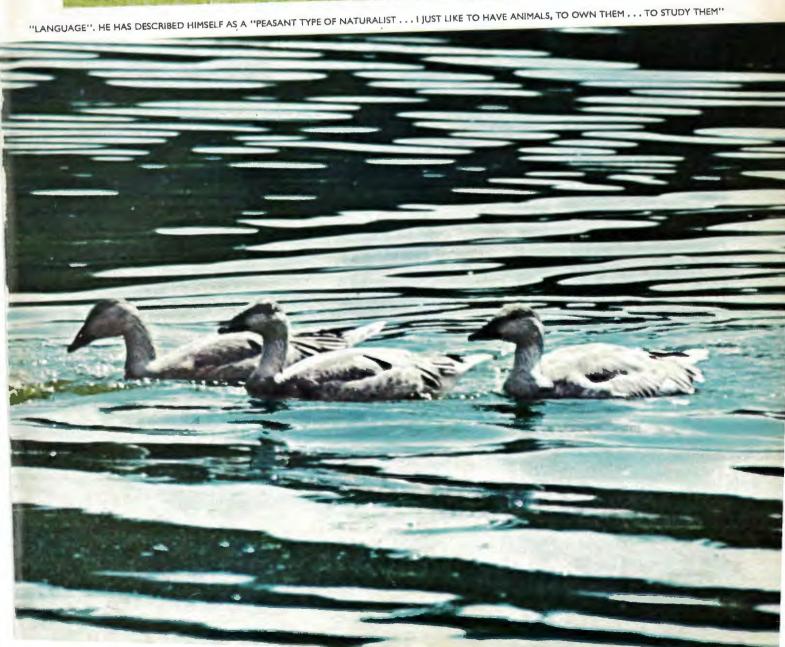
In the early years, two distinct schools of thought divided the science of animal behaviour. Europeans, calling themselves "ethologists", concentrated on instinctive behaviour, observing and testing animals in the wild. The American school of "psychologists" was more interested in what it could learn of behaviour under controlled laboratory conditions. But both sides respected one man, the Austrian Konrad Z. Lorenz, whom Julian Huxley has called "the father of modern ethology". A scientist with a love for all living things, Lorenz laid the groundwork for many of the most important lines of research still pursued today. He never looked at animals in terms of people, as many of the behaviourists had always

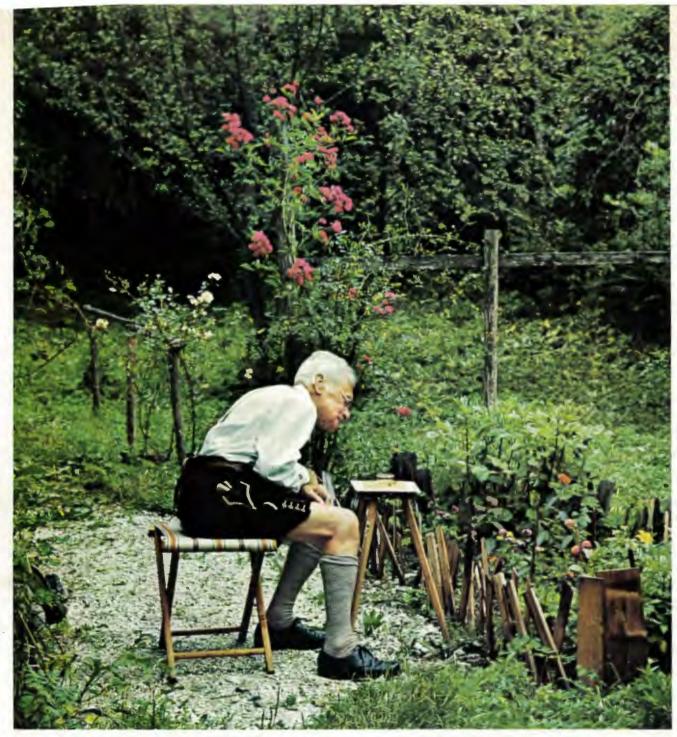
done, but formulated a new school of investigation, based on his conviction that an animal's behaviour, like its physical adaptations, was part of its equipment for survival and the product of adaptive evolution. He proved his point with a wide variety of creatures which he took into his daily life—shrews, frogs, ducks, monkeys, dogs and others, even learning the "language" of some species so that he could approach them on their own level. Among the many basic truths shown by his experiments, all conducted with animals roaming freely in their natural surroundings, were such learning processes as those shown here, where goslings have been successfully taught to accept Lorenz as their "mother".





ACTING THE MOTHER, Lorenz carries food for his brood on the grounds of the research institute he directs in Bavaria. His work with goslings revealed much about the development of early instinctive behaviour.





KARL VON FRISCH TESTS THE COLOUR VISION OF BEES IN THE GARDEN OF HIS AUSTRIAN HOME BY USING YELLOW CARDS TO ATTRACT THEM

#### The Man Who Found That Bees Could See Colours

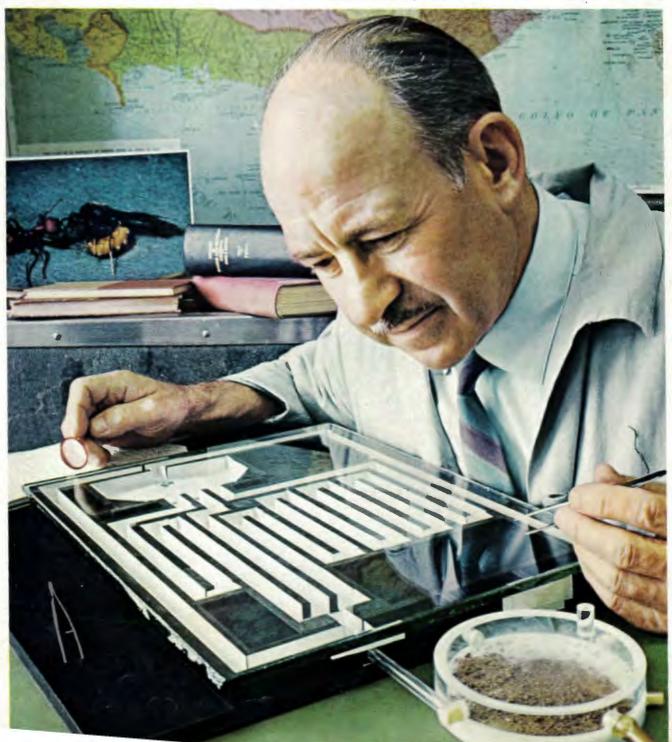
A logical approach to fundamental questions over the years made Karl von Frisch a major force in behaviour studies, particularly in the field of animal sense organs. Half a century ago, for example, he challenged the prevalent belief that bees were colourblind—to believe this, he reasoned, would be to believe that the bright colours of flowers pollinated by bees had no biological significance. By a series of simple experiments with coloured cards, he proved that bees did indeed perceive colours. His further work with a variety of animals, notably many invertebrates and fishes, demonstrated their remarkable sensory capacities, each specifically adapted to the demands of the environment, and often led to conclusions—as in the case of the hearing ability of fishes—that were as fresh as they were revealing.

#### Student of the Clever Ant

Because he is fascinated by the learning ability of ants, Theodore C. Schneirla has combined years of field work with exhaustive laboratory experiments and has become an expert on their behaviour. He studied army ants in the American tropics, gaining detailed insights into the scent stimuli which largely govern their mass movements. Advancing his research at New York's American Museum of Natural

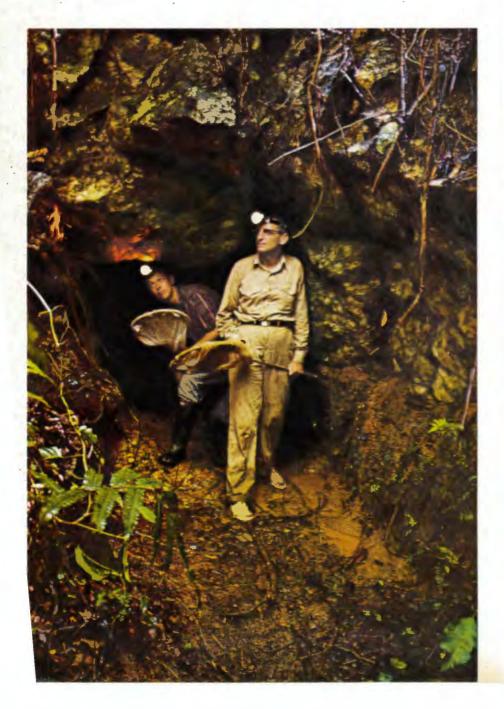
History (below), he devised mazes for testing the more common ant species. In the mazes, ants which have negotiated the corridors to the food are quick to find their way again even when denied an odour trail to follow, thus proving that they have the power to memorize the correct path. They are also capable of applying this learning to other mazes, a feat which places them near the peak of insect learning.

A QUICK LEARNER, THE FORMICA ANT CAN TRAVEL THROUGH A TEST MAZE FROM NEST (RIGHT) TO FOOD WITHOUT AN ERROR AFTER 25 TRIES



#### Prober of an Unheard World

The suspicion long held by scientists that many animals make use of stimuli which are beyond the range of human sense organs was dramatically confirmed in the 1930's by Donald R. Griffin, then a senior at Harvard University. Observing the uncanny ability of bats to navigate in total darkness, Griffin theorized that they might be utilizing their ears rather than their eyes. He took his bats to a laboratory that contained equipment for recording high-frequency sounds, and became one of the first humans to detect the high-pitched squeaks the animals sent out as they flew. These ultrasonic signals bounce off the surface of objects, the reflected sound waves guiding the bats in flight. Since Griffin's discovery of the world of unheard sounds in which bats operate, extensive work has been done not only on the bats' system of echo location but also on similar adaptations in other animals, much of it at the Tropical Research Station of the New York Zoological Society in Trinidad, where these pictures of Griffin were taken.





HUNTING FOR BATS to net and take to the laboratory for study, Griffin and a student assistant, with head lamps lighting the way, emerge from an abandoned mine shaft in Trinidad's dense jungle.



GUIDED BY ECHOES, a fishing bat glides towards a morsel of fish being placed on a wire in a dark testing tank by Griffin. As long as the bait is at the surface, the bat goes right for it,

grabbing it with its claws. But when the wire and the bait are lowered beneath the water, the bat has difficulty, since the surface reflects 99.9 per cent of the echo-location signals.

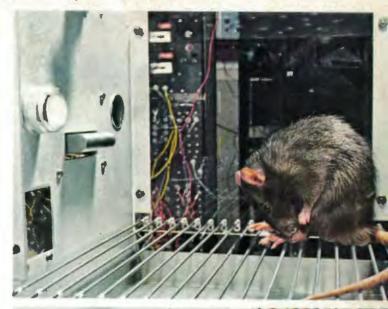


#### An Apostle of Conditioning

An experimental psychologist at Harvard University, B. Frederic Skinner is famous not only for his mechanized tests on animal behaviour, but also for the fearless, controversial conclusions he draws from them. In his experiments he trains pigeons, rats and other animals to perform a variety of unfamiliar acts by rewarding them immediately-a principle known as "reinforcement". Skinner's test animals are completely insulated from the outside world during the experiments; most often he places them in a closed metal box which has sound-proofed walls and ceiling. His mechanically operated tests have been scheduled with such care and are guided by such modern equipment that the tester may leave the room during the length of the experiment, the results being recorded on an electrically operated graph. Unlike most behaviourists, Skinner has no hesitation in applying to humans what he has seen in the laboratory. Thus, he has elaborated his principle of immediate rewards in devising teaching machines for children which lead them from simple questions through increasingly complex ones by constantly encouraging and approving correct answers. He has also expounded his belief that all behaviour can be artificially controlled, in a Utopian novel, Walden Two, where he envisages a land of psychologically conditioned humans living in harmony in an atmosphere free of hate or envy.

A HUNGRY BROWN RAT, with no food in sight, examines a mechanical lever in a Skinner box, here left open for demonstration purposes. The rat in time will learn to press the lever and be rewarded with food, thus "reinforcing" its behaviour.

A BETTER-EDUCATED RAT has been conditioned to push the food lever when a light is on. With the light off (lop), the rat scratches impatiently; then, as the signal flashes on (contro), it lunges at the lever and looks for its reward (bottom).





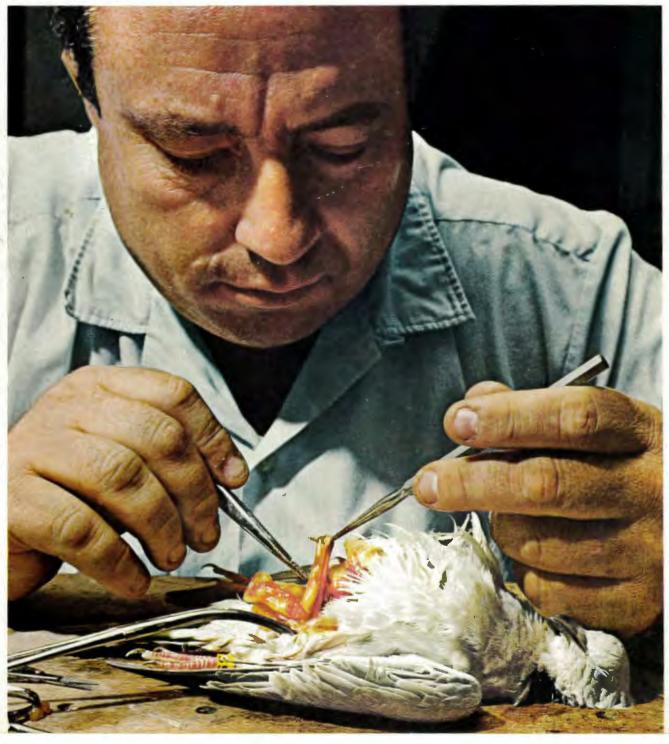


#### In Quest of Causes

In strong contrast to those behaviourists who study many different animals, Daniel S. Lehrman, director of the Department of Animal Behavior of Rutgers University in New Jersey, has devoted fully 15 years to one species alone—the ring-neck dove. He is hunting for a "system of causes" which would explain, step by step, the complex interaction of the effects of hormones, external stimuli and experience

on the development of the dove's behaviour. Thus, for example, Lehrman learned that during the breeding season a female's ovaries and oviducts will enlarge at the mere sight of a male—but less so if the male has been castrated. In countless similar experiments, Lehrmanhas gone even deeper into behavioural cause and effect; but, he says, "Every good experiment has to raise more questions than it answers".

PROBING THE OVARIES OF A FEMALE DOVE, LEHRMAN DISCLOSES THEIR SWOLLEN STATE, INDUCED BY HORMONAL FLOW AT SIGHT OF A MALE





PRESSING WITH A NYLON BRISTLE, HINDE TESTS THE EFFECTS OF HORMONES ON THE SENSITIVITY OF A CANARY'S DEFEATHERED BROOD PATCH

#### The Complexities of Canaries

Another scientist exploring the complex intermeshing of external and internal factors in the behaviour of animals is Robert A. Hinde of Cambridge University. Working mainly with the common canary, he has charted some of the manifold forces that lead to mating, nest building and egg laying. In the course of his studies, Hinde often alters the chemical balance of his test birds, proving

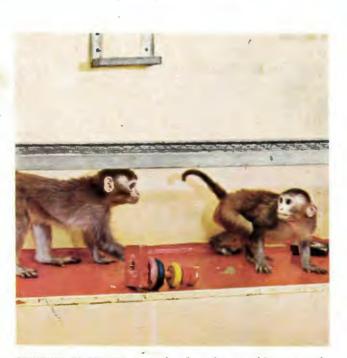
that canary reactions are often dictated by hormones. A female canary, for instance, will begin nest building, a springtime function, at any time of the year if injected with the ovary hormone oestrogen. By documenting scores of similar tests, Hinde has become a world authority on the physiology of reproductive behaviour. A diagram based on his work with canaries appears on pages 94 and 95.



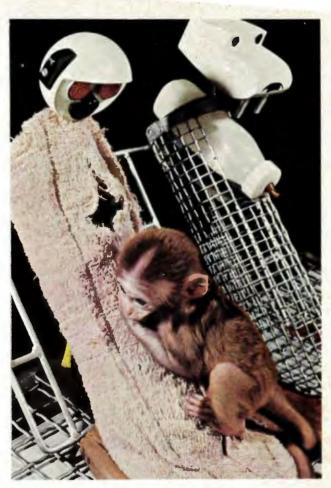
#### An Infant's Vital Needs

Lower animals are not the only ones tested by psychologists in their laboratory experiments. For the past decade, Harry F. Harlow, director of the University of Wisconsin's Primate Laboratory, has been observing the intricate relationship between child and mother as it is manifested in rhesus monkeys. In his tests, each new-born monkey was given access to two artificial "mothers", one a wire frame with wooden face and feeding bottle at breast level, the other roughly the same but with a soft terry cloth covering. The monkeys took milk from both mothers, but as they grew older, they spent more and more time climbing on and clinging to the cloth mother. When faced with an intruder such as a mechanical teddy bear, the monkeys fled to the cloth mother, rubbed against her and then, comforted and unafraid, examined the bear. Similarly, when the monkeys were put in a strange room, they immediately sought out the cloth mother and clung to her for solace before exploring.

Baby monkeys reared without their real mothers or the terry cloth substitutes proved to be incapable of normal relationships with either males or females. As Harlow concluded, the experiments establish the importance of bodily contact in an infant's love and the need for the attention and care of a mother.



CRINGING IN TERROR, a monkey brought up without a mother or young monkeys to play with shows the effect of abnormal upbringing when a youngster its own age is put in its cage.



CUDDLING UP to a cloth-covered mother, this infant rhesus monkey clearly shows its preference for warmth and comfort, despite the fact that it is the wire dummy that gives it food.



EASILY DOMINATED, the same monkey cannot defend itself or engage in play. From these experiments, Harlow learned that contact with other infants was vital to normal development.



PEERING THROUGH A TANK, Eugenie Clark studies a serranoid fish that she captured while scuba diving. This hermaphroditic creature is the subject of many papers by Dr. Clark.

#### Schoolmistress to Sharks

While most animal behaviourists use such familiar creatures as bats, rats, birds and even monkeys in their research, ichthyologist Eugenie Clark has concerned herself mainly with sharks. Now one of the world's leading specialists in shark physiology, she has proved in her experiments that some shark species can be conditioned, like brown rats in a Skinner box, to learn new behaviour patterns in order to get food. In one series of tests conducted at her Cape Haze Marine Laboratory in Sarasota, Florida, lemon and nurse sharks were trained to press their snouts against a square, white plywood target. This rang an underwater bell and produced a piece of fish as a reward. After a six-week training period, the sharks had learned to swim independently to the target and push it whenever they wanted food. Through such behavioural tests it has been shown that sharks are sensitive to underwater sounds and that they can learn to associate these, as well as visual stimuli, with specific situations such as food getting.



NUDGING THE TARGET, a baby shark, having been alerted by a bell that food is to be had, will be rewarded with a piece of fish. In this advanced test, the bell is the behaviour stimulus.

NURSE (SHARK) EMBRYOS, some of which lived on for a week, are removed by Eugenie Clark. Since pregnant sharks do not feed, they are seldom hooked, and finds like this are rare.



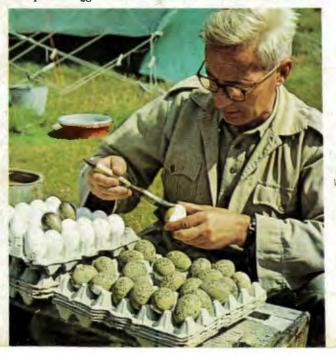


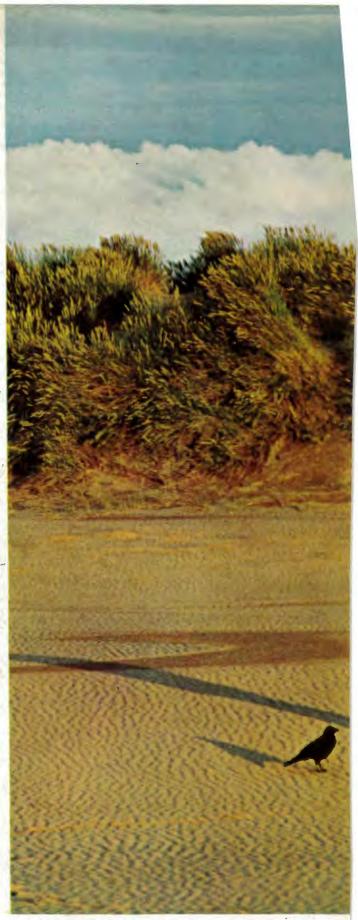
SNIFFING A DEAD TERN, Tinbergen identifies the killer as a fox. Foxes are predators of gulls and, like many other mammals, mark their hunting grounds with strong-smelling urine.

#### An Observant Naturalist

"I like to study animals in their natural environment. I find that during the long hours of observation in the field, I not only learn about behaviour patterns, but I get ideas, 'hunches', for theories, which I later test by experiments whenever possible. Above all, my ideal is to understand how the complex behaviour machinery of each animal helps it to meet the many pressures of its environment." Thus does Niko Tinbergen, author of this book, sum up his approach to the science of animal behaviour. Through the years he has faithfully followed his own particular code for research and study, wandering in the wilds in search of animals at large.

PAINTING CHICKEN EGGS to resemble those of a gull, Tinbergen prepares a field experiment in camouflage. He showed that painted eggs when scattered were hard for foxes to find.





AMONG THE DUNES of Ravenglass in northern England, Tinbergen strolls, trailed by his pet crow. Always intrigued by nature's changing scenes, he keeps his binoculars at the ready.

Mail .





SUCKING UP JUICE, a European hornet stands on the smooth surface of an over-ripe plum. Its socketed antennae, sense organs that respond not only to touch but to scent, helped it to locate the plum.

2

# The Sense Organs: Windows to the World

To be efficient, the behaviour of animals must include the ability to do the right things in the right circumstances. In other words, unless animals carry out the complicated movements we call behaviour at the right moment and in the right place, these will be ineffective. In order to do this, however, they must have information about conditions in the outside world. This information reaches them through their sense organs.

Sensory stimulation is often the starting point of behaviour: a dog sees its master put on his hat and immediately barks in anticipation of a walk, and once outside starts running in pursuit of a scent. Thus he reacts to his environment—and our study of the way behaviour is controlled in animals can therefore logically start with a study of the outside stimuli to which they can respond.

What sort of stimuli do animals receive? First of all, they are not necessarily the same as those to which a human might react. Failure to appreciate this can lead to false conclusions. I once heard of a government official who spent nearly  $\pounds_2$ ,000 on moth-balls to keep birds off the runways of an airport where they collided with jet planes. What he did not know was that birds have a very poorly developed sense of smell—the moth-balls bothered them not at all.

The fact of the matter is that different animals, including man, have different "windows to the world". Some have sensory equipment that in some respects is much poorer than ours; in others, the senses are far superior. There are even animals that react to stimuli which we cannot detect at all—sights or sounds or smells which we could not discover without artificial extensions to our own sense organs. Bees, as we know, see and react to ultra-violet light, whereas we human beings have to transform the ultra-violet rays with special apparatus into the kind of light that we can see.

Once it was realized that animals might have sense organs quite different from our own, it became imperative to explore their sensitivity to outside stimuli systematically and thoroughly. This is a laborious task, but, like all exploration, it is extremely fascinating and rewarding. And the first step in such a study is to find out exactly just what it is in a given situation that an animal is responding to.

KARL VON FRISCH, the famous Austrian zoologist, gave this field of research its initial impetus. His name is rightly connected with his work on bees, but he and his numerous pupils have also done outstanding research on the senses of other animals, particularly on hearing in fishes. One of von Frisch's early papers was simply called "A Fish That Comes When One Whistles"—and indeed he had trained a fish to do just that. However, this was only the beginning; von Frisch also wanted to know why the fish came when he whistled, and his line of reasoning illustrates beautifully the research that studies of animals' senses must pursue.

What stimulated the fish to come to the surface when the whistle was blown? Because we can hear, we might assume that the fish could hear too, and that it was responding to the sound. But the fish might not be able to hear—it might have just seen the movements of the man with the whistle and responded to these. How is one to know? One way is to make the same movements, but without whistling. If the fish does not come, clearly it is not movement alone that stimulates it. Conversely, one can whistle without moving and see whether the fish responds. Or one can block off or remove the sense organ that is thought to be responsible for the fish's behaviour, in this case the inner ear: if it fails to come now it may be assumed that it could hear previously. Once it is established that the fish can hear, one can proceed to explore systematically what exactly its hearing organ can achieve—how accurately it can distinguish between different levels of pitch or how weak the sound can be made before the animal fails to react.

Any response which an animal makes naturally—such as coming for food—can be used as an indicator of behaviour. However, these natural responses are not always convenient to work with and not always as clear-cut as an investigator would like. Therefore he may decide to condition or train an animal to a specific stimulus by presenting that stimulus repeatedly together with a natural one. That is what von Frisch was doing when he whistled every time he offered food to the fish. Another way of conditioning is to flash a light every time one feeds an animal, so that it associates light and food. If it can see at all, sooner or later it will respond to the light alone in expectation that food will be present. This training method, as we shall see, is widely used.

Physiologists like to apply still another method of investigation in higher animals: registering the response to a stimulus directly by electrical means. The core of each sense organ is formed by sensory cells, which are the real receivers

of the stimulus. Such cells are connected by thin nerve fibres with the central nervous system. These nerve fibres are the communication lines which transmit, in rapid sequence to the brain, volleys of chemo-electrical impulses. These impulses, each lasting a thousandth of a second, register on delicate instruments as "action potentials". Any corresponding variation in their firing pattern indicates that the sense organ is responding to the stimulus. Thus, a light flashed into the eye produces changes in the action potentials in the optic nerve, and these will register on a sensitive meter. However, this method of research also has its limitations, as has the training method. For various reasons the action potentials and behaviour do not invariably tell the same story of sensory capability, so the functions of sense organs are best studied with both methods.

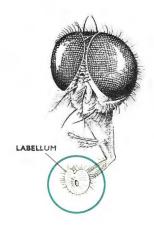
A short review will show the amazing variety of sensory abilities we find among animals. Let us begin by considering the ability to see.

Vision, or responsiveness to light, is one of the five basic senses of the animal kingdom. However, not all animals see the same things. For instance, they are not all sensitive to the same range of the spectrum. We have already noted that bees and many other insects may be sensitive to a wide range of ultra-violet light, but they are far less sensitive to red—in fact, most light that we see as red is invisible to them.

But what about red flowers that are so obviously attractive to insects? Actually, as von Frisch has pointed out, few flowers pollinated by—and therefore adapted to—insects are really red; those that appear red or purple to us reflect a great deal of blue as well, and it is the blue that the insects see. Or consider that popular wild flower, the European poppy. We see it as bright scarlet, but we also observe that it is visited by bees and other insects. A simple test will show that the poppy reflects ultra-violet light which these insects see. We will pick two poppies and flatten them out on a board in a field where poppies grow. One is covered with a filter which absorbs all visible light but admits ultra-violet. The other flower is covered with two filters—one which absorbs all ultra-violet light plus a filter which absorbs all visible light. Both flowers now appear identically black—that is, invisible to our eyes—but the insects will unhesitatingly alight on the first flower, responding to the reflection of the ultra-violet rays.

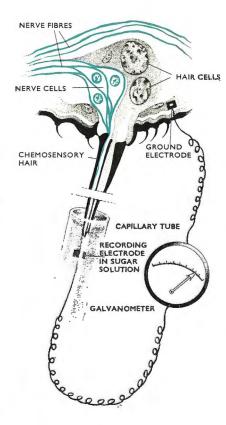
Many other flowers, such as those of the common cinquefoil, reflect ultra-violet too. These blossoms look uniformly yellow to us, but they reflect a lot of ultra-violet as well. However, each petal has a large patch at its base which does not reflect ultra-violet, and so must appear different—certainly darker—to the bees than the rest of the flower.

Another interesting question about the vision of animals is whether they actually distinguish colours within the spectrum visible to them or whether they react only to differences in brightness. This can be tested in the same way that human beings are tested for colour vision—with the difference that animals have to be trained in some way to let us know what they see. Again we use the same technique that von Frisch used in getting a fish to respond to a whistle, but this time we introduce colours as stimuli instead of sounds. Suppose, for instance, we train a test animal to associate food with a red triangle by showing it such a triangle every time we offer it food. Once it has learned this, we then show it other triangles that are identical except that they are blue, green, purple—many colours, along with several shades of grey. If the animal still reacts



### HOW DO WE KNOW THAT FLIES CAN TASTE?

On the end of the blowfly's proboscis is a spongy pad—the labellum—that is obviously used to help it to identify food, because the fly constantly pokes about with it as if testing the edibility of substances. To prove this, however, required a delicate experiment in which one hair on the labellum was wired to an electric circuit. When this hair was placed in a sugar solution, a minute electrical impulse was produced, showing that tastes do register in the fly's nervous system.



to the red triangle, or to a colour close to red, like purple, can we then assume that it sees colour? Yes, we can—almost. There is a chance that the animal is colour-blind and is "faking" colour vision by recognizing the colour as a certain shade of grey. So we make a test for its ability to discriminate between greys. We train the animal to associate food with only one particular shade of grey, then present it with a whole range of greys of varying shades. If it responds to many greys rather than to the particular one it was trained to, then we can assume that its brightness discrimination is not very accurate, and that its initial response in the colour test was indeed a reaction to colour alone. Of course we must make sure that the animal cannot see either ultra-violet or infra-red light, which some of our test objects might give off.

No animal has yet been discovered that can "see" infra-red light with its eyes, but there are other ways of "seeing" than with eyes alone. Infra-red is a form of heat, and certain creatures, notably the rattlesnake and its relatives, have organs that detect it as effectively as though they "saw" it in our sense of the word. In front of and slightly below their eyes, they have two pits which contain a thin membrane, behind which is a cavity filled with air. The membrane is rich in nerve endings—there are 3,500 in each pit, on a surface of three to four square millimetres, which is about 100,000 times as many as humans have on an equal area of skin. Furthermore, these nerve endings are very close to the surface of the membrane, so that all in all a pit viper, as such snakes are called, can sense from a foot and a half away a tumbler of water only a few degrees warmer than the surrounding air. Rattlesnakes will actually strike at such objects, which makes it seem likely that they use this sensitivity to locate warm-blooded prey. And not only do these organs respond to radiant heat but the fact that they are sunk in pits and have so many nerve endings also enables the snakes to detect the direction from which the heat comes. The rims of the pits act as screens for radiation from the sides; they cast shadows which of course vary with the direction from which the heat reaches the pits. These inform the snakes about the direction of the heat source and enable them to strike with great accuracy.

Another point of interest in vision is the extent to which an animal can detect details in its visual field. This is by no means a universal accomplishment: many worms and shellfish, for instance, have what is called a "diffuse light sense" in their skins—they see light only the way we feel warmth. All they can really do is to notice whether it is dark or light; they have at best only very poor means of detecting where the light comes from, let alone seeing objects. Higher animals, by contrast, have developed eyes which contain an optical apparatus. Vertebrates use a lens which projects an image on a retina made up of millions of sensory cells, each of which contributes a tiny part to the total visual image. Insects and their relatives have compound eyes—these have no lenses but are made up of a number of conical tubes called ommatidia, which diverge outwards from the optic nerve to give the insect a wide field of vision. Each ommatidium is insulated optically from its neighbours by a mantle of pigment, each provides merely one point of the visual image, and all these points or dots fit together to provide a mosaic-like picture.

Visual acuity, or the ability to distinguish details, is much greater in eyes equipped with lenses than it is in the compound eyes of insects. For a bee, two dots slightly less than one degree of arc apart will merge together indistinguishably into one, but humans, under favourable circumstances, can dis-

tinguish between dots only some 40 seconds of arc apart, or one ninetieth of one degree, and many birds seem to do even better.

Great visual acuity has, of course, many advantages. It allows predatory animals to see their prey from very far away: insect-eating falcons are able to see individual dragon-flies a half a mile distant, whereas for us the same insect becomes indistinguishable at about 100 yards. By the same token, many vulnerable animals can see their predators from afar. Good vision is generally important in many other ways also, of course. We shall see later, for example, that many birds are able to recognize their partners, their flock mates or their young as individuals, and in many cases this is clearly a matter of their recognizing these others of their species by sight.

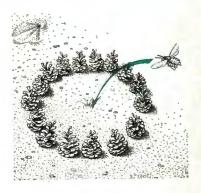
PROBING still deeper into the qualities of vision, we find that much more is involved than mere distinction of quality or quantity of light and discrimination between objects. What, for example, about moving objects? This is an interesting thought: to the element of discernment it adds the element of time. It means that an animal must be able to register differences in the moment of stimulation between cells or groups of cells in the retina. A cine-film is a good illustration of the problem. We know that the pictures we see on the screen do not really move but consist of a series of different still images, each of which falls on a slightly different spot on our retina than its immediate predecessor. The illusion of movement is produced because one element of the retina is able to convey information of the exact moment it was stimulated to other cells that are then stimulated in turn. Thus a constant flow of information and stimulation is set up which in its sum adds up to a picture of movement.

To be able to do this, it is clear that there must be cross-connections between the sensory cells—and indeed, such cross-connections are present in enormous profusion. In insects they are found in the ganglia, or nerve centres, that lie immediately behind the eye. In higher animals, not only are the nerve cells immediately in front of the sensory cells interconnected but also other cells that lie deeper down in the nervous system.

But there is even more to movement than that: what about speed of movement? Clearly this is important—and indeed animals at times do react differently to objects that move at different speeds. Often they can even discriminate between a smooth movement and a wavy or an irregular one. How the nervous system achieves this, however, is as yet unknown.

Another complex aspect of vision is the distinction and recognition of shapes. It is quite easy to train a bird or a mammal to respond to a circle and to ignore a rectangle—I have myself derived much enjoyment from studies of such form discrimination in wasps. The female digger-wasp, who stocks her burrow with insects she has killed as food for her larvae, clearly has this ability. The question is, how does she manage to find her way back from some distant hunting ground to her own burrow in a large colony? I soon found that these wasps remembered the arrangement of small landmarks such as pebbles, pine-cones and tufts of grass around their burrows. Knowing this, I trained wasps to recognize a circle of pine-cones which I laid out around the entrance. When such a wasp went foraging, I moved this circle a foot or so. The result was that when she returned she searched vainly for her burrow in the centre of the ring of cones, ignoring the real entrance which was in plain view. In subsequent tests, I offered her a choice between a circle of dark stones and a triangle or an ellipse of pine-cones. Although she could distinguish the stones from the cones

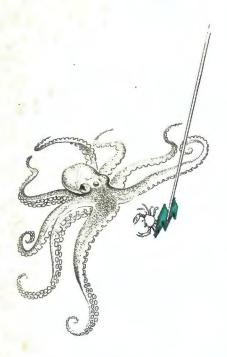






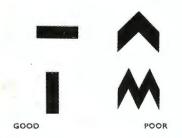
THE CONFUSED DIGGER-WASP

A digger-wasp always memorizes the landmarks around its burrow so that it will be able to find its way back. In an experiment to test this, Dr. Tinbergen surrounded a burrow with a ring of pinecones (top), and the wasp immediately learned to recognize it. But when the ring was moved a foot or two (second drawing), the wasp was unable to find its burrow just outside the ring. When the pine-cones were arranged in a triangle and a decoy ring of pebbles was made (third drawing), the wasp chose the pebbles, proving that it was their arrangement rather than the cones themselves that the insect was responding to



#### WHAT THE OCTOPUS SEES

Experiments with octopuses have revealed the interesting fact that they can distinguish between certain shapes but not between others. This was tested by fastening each of the four shapes below to a stick and presenting them, with crab attached (above), to attract the octopus. The animal quickly learned to associate these shapes with food. The next step was to introduce a mild electric shock to the vertical bar (below, left) but not to the horizontal one. The octopus soon learned to tell them apart and to avoid the electrified one. However, it never did learn the difference between the inverted V and the M. Is this due to lack of intelligence on the octopus's part? See the diagrams on the opposite page for the answer.



perfectly well, as I knew from other tests, she went to the stone circle—just because it was a circle.

This same matter of form discrimination has been studied intensely in a very interesting experimental animal, the octopus. Like all the cephalopods, the octopus has highly developed eyes, in many respects similar to the lens eyes of vertebrates. It distinguishes well between shapes and can easily be trained to come forward, preparing to feed, when specific shapes are shown. It has no difficulty in telling a vertical from a horizontal rectangle. However, it gets confused when presented with two oblique rectangles, one held at right angles to the other, or with a V-like and a W-like figure. It looks as if in shape recognition a process is involved in which the vertical and horizontal projections of the different shapes are compared to each other—as if some kind of central nervous scanning of the retina takes place.

Sense organs that respond to touch, to pressure or to other mechanical action are an important part of the basic sensory equipment of most animals. In their simplest forms, they occur in the skin, where they are obviously useful in maintaining a close contact with the surrounding environment. But mechanical stimuli of other kinds are used for many other, far more specialized purposes. By the tension of some muscles, by the laxness of others, by the position of his bones, tendons and joints, a human being gets a constant stream of enormously detailed and useful information about his posture and his movements—as is the case with all higher animals, which have highly complex sense organs in their muscles, tendons and joints. Insects, which have an external skeleton, have other arrangements for the same purposes. Pads of sensory hairs and groups of minute dome-shaped organs are often found at the joint of a leg segment. In the normal position these hairs touch the next segment in such a way that any bending of the joint will move or bend the hairs slightly, triggering a response in the sensory nerves.

The organs sensitive to touch report mechanical stresses due to gravity on the insect's body and allow it to perceive its own weight, or even that of a load when it stands, and to feel when it hangs upside down. Web spiders use this same ability, but with a different mechanism, to locate an insect caught in their web: pulling with their legs at the strands, they can feel the direction which offers the most resistance.

Staying right side up in their world is a problem common to all animals, and here, too, the sense of touch and pressure is involved. Ingenious modifications of the touch organs are used to determine the direction of gravity. In vertebrates, this is accomplished by one or more tiny, hard, pebble-like bodies, called otoliths, in the inner ear. Heavier than the surrounding tissue, the otoliths rest on a cushion of sensory hairs, to which they are attached by a layer of mucus. When the animal is tilted the hairs are bent in one direction or another, and this acts as the stimulus. In many crustaceans the otolith is not formed by the animal itself but consists of a grain of sand that the animal picks up and inserts every time it sheds its shell. Alois Kreidl, a resourceful Austrian zoologist of the 19th century, demonstrated the function of this grain of sand in a most ingenious and interesting fashion. He put a shrimp in an aquarium on a bed of iron filings instead of sand. When it moulted, the unfortunate animal ended with a grain of iron in its gravity organ, and when a strong magnet was held over it, it swam upside down.

Some aquatic insects keep their balance in the water in still another way.

They carry next to their bodies a small supply of air, held in place by a coat of water-repellent hairs. The spaces between the hairs are not large enough to let the air escape, but they do permit direct contact between the air bubble and the surrounding water. With an "air pocket" like this on each side of its body, such an insect can tell if one side is tipped down, because the side that is deeper in the water will be subjected to a very slightly increased pressure. This compresses the air in the bubble, permitting the water to press slightly farther into the pocket; sensitive hairs detect this and relay the information to the insect that it is no longer horizontal.

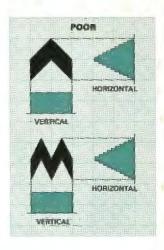
Insects also depend on sensory hairs for other kinds of information—picking up minute vibrations in the water, for example. A water bug, Notonecta, finds its prey this way. Hanging upside down from the surface, it uses the hairs on its long, delicate legs to detect ripples sent out by other tiny swimmers or struggling insects which have fallen into the water. In an aquarium, Notonecta can be stimulated to swim towards a thin wire held on the water surface and vibrated gently so as to send out little ripples. It is amazing how accurately these insects can aim for the source of the ripples by this seemingly primitive mode of orientation, and this without the aid of any visual guide.

The whirligig beetles have gone one better than Notonecta. They are surface swimmers, and as they glide about on ponds they rest their feelers just on top of the water. These feelers are equipped with pads of sensory hairs which detect not only surface ripples made by other moving insects but even the presence of motionless objects such as rocks or floating pieces of wood nearby—the water bug apparently has the ability to register the echoes of its own ripples bouncing off these obstacles.

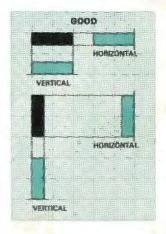
The principle of echo location is carried to extraordinary lengths by the finest specializations of the mechanical senses we know: the organs of hearing. Hearing itself is already astonishing enough, and it may be appropriate to pause here for a few words about it. What we recognize as "sound" is actually the creation of pressure waves in a medium like air or water by some kind of movement. If a tuning fork is struck, its ends will vibrate and this vibration affects the surrounding air, sending rapidly alternating waves of high and low pressure out into the room. When these waves hit a membrane like the ear-drum, it will vibrate also, and these signals, sent to the brain, are recognized as sounds. The diaphragm in a telephone receiver is simply a vibrator, sending sound waves to our ears; so is a radio loud-speaker.

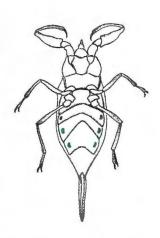
Nor all ears are membranes. Mosquitoes hear with plumes on their antennae. Many locusts have "ear-drums" on their legs; nocturnal moths often have them on the sides of their bodies. In general, insect ears are far less elaborate than the ears of vertebrates; for one thing, they seem unable to distinguish pitch. Yet they are very sensitive to differences in sound intensity, and they utilize to the full the rhythmic properties of sound pulses. The males of the grasshopper Ephippiger perform a rhythmic staccato song to attract females: this song can be successfully imitated with sounds of any pitch within their range of hearing, but only when these sounds either begin or end abruptly. A tape recording of a long, smooth whistle elicits no response whatever from the females, but if the tape is cut in two just at the peak of the sound, thereby breaking it off abruptly, and the two parts are linked by a piece of blank tape, either of the two halves will make the female approach.

Sensitivity to the various parts of the sound spectrum differs for different in-



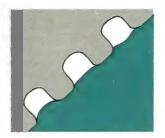
It is not lack of intelligence that handicaps the octopus, but limitations of its eye, which can scan an object vertically and horizontally to measure its dimensions rather than its precise shape. To see what this means to the octobus, it is necessary to make projections of the four objects. In these graphs each dimension is measured by the number of small background squares that any part of one of the objects covers. For example, the very top of the inverted V covers only 1 square. At its centre it is 20 squares wide, and at its bottom it again covers only I square. A horizontal projection of this comes out as a triangle (in colour), I square wide at its top, 20 wide in the middle and decreasing again to I square at the bottom. Wherever the V is measured vertically it is 10 squares thick, and thus the vertical projection is a rectangle, also 10 squares thick (shown in colour). The same is true of the M; its projections are identical with those of the V, and the two are indistinguishable to the octopus. However, the projections of the two other shapes (below) are different, and the octopus can tell them apart.





#### TELLING UP FROM DOWN

The adult water scorpion, Nepa, determines its position in the water by means of small holes on its belly. The openings of these holes are covered by membranes, which are pushed in or out very slightly by expansion and compression of air in the holes—according to how deep in the water the holes are. In the enlargement below, the upper hole, near the scorpion's head, is subject to less water pressure than the lower one, near its tail. The slight disturbance of the membranes covering the holes informs the scorpion that it is headed up towards the surface.



sects—and some can hear in the ultrasonic range. Just as bees can see ultraviolet light, moths can hear ultrasonic sound—an adaptation to detect their enemies the bats, whose calls are largely ultrasonic.

Vertebrates, for the most part, hear very well. Even the fishes, which were thought until fairly recently to be quite deaf, not only have a well-developed hearing sense but also communicate by sounds. Frogs and toads, many reptiles, and of course birds and mammals, all produce a bewildering variety of sounds without which the countryside would seem very desolate indeed. Most of these sounds act as social signals, and most of them indicate a good ability to discriminate pitch.

The champions of hearing, by any standard, are the bats. Bat sounds long went undetected because they are pitched two to three octaves above what we can hear. Very few human ears can detect air vibrations with frequencies higher than some 20,000 per second, and the average limit of human hearing is down near to 14,000 cycles. Bats, however, produce and hear sounds of up to and over 100,000 vibrations per second. Moreover, these sounds are very loud: if we were able to hear them, they would sound like the scream of a jet fighter at close range. To a number of bats flying around on a calm, still summer evening, and to the unfortunate moths which can hear them and must try and avoid them, the evening is anything but calm. It is an inferno of constant shrieking, each bat emitting a series of screams in extremely short pulses of less than a hundredth of a second in duration.

What is important to the bat is not the sound but its echo: bouncing off obstacles like trees, walls and even flying insects, this keeps the bat informed, as sonar does a submarine, of things in its way and food on the wing. This echo-location device has evolved in different bats in different ways—some send out a wide, scattered beam, others a narrow one which can be changed in its direction and thus used as a scanning device. We know that the mechanics of this involves the bats' ears, mouth and, in some species, nose, because if any of these are blocked, they fly "blind". But how the bats' ears and brains process the information they receive from the echoes is still a mystery—their auditory apparatus must be of great complexity.

Whales use a similar sonar system in the water. It has long been known that whales could hear—readers of Moby Dick will recall that sperm-whales must be approached very quietly—and it is also no news that they make sounds. British sailors called one particularly articulate species, the arctic beluga whale, the "sea canary". But the full story was not revealed until World War II, when hydrophones, developed for the detection of submarines, picked up the amazing variety of under-water noises which are produced by whales and dolphins. We know now that at least some whales can emit ultrasonic sounds as high as those of bats, although we still do not understand how they produce them, since they have no vocal cords. We know also that they use echo location for avoiding obstacles and for finding prey, and that they have a vocal "language" for social communication.

Further investigations like those already conducted with porpoises in the Marineland aquaria of Florida and California may reveal still other aspects of whale life. For instance, it may explain the puzzling phenomenon of mass strandings and deaths of whales in shallow water. For many years nobody could understand why these huge creatures sometimes came into shallows, got stuck there and died of suffocation when the weight of their bodies, no longer

supported by the water, made it impossible for them to inflate their lungs properly. Now it has been pointed out that strandings occur almost always on gently sloping sandy or muddy bottoms, precisely the places where the coastline would fail to give exact echo-location information such as the whales would get on steeper rocky coasts.

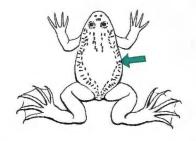
Still very mysterious are the lateral line organs possessed by many fishes and some frogs. These are made up of pits or grooves arranged along the body surface, each containing rows of sensory cells. From each cell protrude protoplasmic "hairs" which respond to the slightest movements of the surrounding water—such as might be caused by the approach of a prey or another fish. The hairs are extremely sensitive and, like ears, can receive information from distant objects. Because of their great sensitivity, excessive stimulation may be actually painful—many territorial fish ward off intruders with strong beats of their tails which, without touching them, may be as effective as direct blows.

Just as all sound- and echo-locating devices are basically mechanical, the qualities of smell and taste are often lumped together as the chemical senses. Smell is generally used for preliminary examination of things, sometimes at a distance; taste for things actually touched, as food is tasted when it is in the mouth. The distinctions between smell and taste blur when we consider the chemical sensitivity of the lower animals, but very many of them do have a chemical sense for distance perception and another for the final check of food before it is swallowed.

It comes as no surprise to learn that many animals have better chemical sense organs than we have and that they use them in quite a different way. Even among our close relatives, the mammals, we cut a poor figure. The world of smells in which a dog must live would be bewildering to a human—a good tracking dog can follow a single scent through a mixture of other scents with uncanny certainty. Mammalian predators use smell extensively for tracking their prey; and the preyed-upon to avoid their hunters. One animal less well endowed may even make use of a superior nose belonging to another. It is a common sight in the African savannah to see baboons and impalas travelling together, the impala profiting from the baboon's keen eyesight, the baboon from the impala's sense of smell.

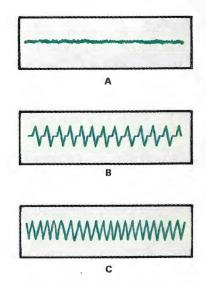
Most commonly—and quite logically—the sense of smell in vertebrates is located near the front end, in the nose. This may be supplemented by another sensing device known as Jacobson's organ, common among many reptiles. Jacobson's organ is actually a small cavity in the head; it has no external opening, but opens into the roof of the mouth. Whether it should be called a tasting or a smelling organ is difficult to say, emphasizing again the fact that these two senses overlap somewhat in most animals, since they both depend on chemical analysis. Jacobson's organ is lined with sensing cells which "smell" by responding to molecules in the air. The reason a snake constantly flicks out its forked tongue is that it is testing the air, collecting a small sample on its tongue, which is then brought back into the mouth and inserted into Jacobson's organ for analysis. Newts have no such tongues but, being amphibians, have evolved noses that can be used both in the air and under water.

A sense organ which is entirely alien to us is associated with the curious electric "battery" found in some fishes. The fact that certain species, like the electric eel of South America, can deliver powerful electric shocks as a means of defence against predators and of stunning prey has long been known, but it



#### TELLING FRONT FROM REAR

The sides of the African clawed frog are equipped with "lateral buds", shown above as small specks. These are pit-like organs lined with microscopic hairs which bend in response to movements of water along the frog's body. The buds "fire" impulses into the nervous system, and the rate of firing varies according to whether the surrounding water is moving from front to rear along the frog's skin, standing still or moving from rear to front (graphs A, B and C respectively, below). So sensitive are the buds that they can also detect slight disturbances in the water made by insects and wrigglers, which the frog can catch even when blindfolded.



is only quite recently that scientists have realized there is more to the electric organs than that. They are now considered to be extreme specializations of much more common organs which create very weak electric currents and are used to locate obstacles and prey. In other words, the "sixth sense" possessed by such fishes is a high degree of sensitivity to electrical fields.

An outstanding example of this is an African fresh-water fish, Gymnarchus niloticus, which has a set of muscles in its tail that have lost the power to contract. Instead, they send out a continuous stream of weak electric discharges, at a rate of about 300 per second. During each discharge, the tail is momentarily electrically negative with respect to the head of the fish. Thus the fish generates in its environment a two-poled field of electric current, and it can sense weak disturbances in this field. The sense organs are located in and near the head and consist of pores in the thick skin, which itself is non-conducting. These pores lead into jelly-filled channels. At the bottom of these channels are found groups of sensory cells which have elaborate nerve connections with the brain. It is possible to train such fish to discriminate between a non-conducting object, such as a piece of glass suspended in the water, and an identically shaped conducting object, such as a porous tube filled with a salt solution or with acid. These objects distort the electric field around the fish in different ways, and the fish can feel these differences on the surface of its body. The physiology of these sense organs is still not quite known, but their extreme sensitivity is already clearly proved.

With this apparatus, *Gymnarchus* cannot detect fish that are more than four inches away from it. However, distance is not particularly important, since these fish live in densely populated and turbid waters where visibility is very poor—also they are nocturnal.

This brief review cannot possibly provide more than a glimpse into the fascinating world of the senses. There are certainly more sense organs than I have mentioned. Some marine animals, for instance, respond to slight differences in salinity. Other animals can detect differences in the humidity of the air; bees use this ability to find their way to the nectar in a flower, and lizards to find their way to water. Many animals perform feats of orientation that still baffle the scientist. No one has yet been able fully to explain homing in birds or the migration of marine fishes. And there are many lower animals in the sea that apparently sense differences in the tides, spawning only during spring tides, or full moon and new moon tides. How they can tell which is which we do not know—perhaps they register subtle fluctuations in pressure, which would be greatest during spring tides.

And what about perception that goes beyond the senses that we know? This is called extrasensory perception, and it is an issue blurred by various factors, of which imprecise terminology is one. If one defines a sense organ as any organ that provides an animal with information about the outside world, there is per definition no such thing as extrasensory perception. On the other hand, if one applies the term to perception by processes not yet known to us, then extrasensory perception among living creatures may well occur widely. In fact, the echo location of bats, the functions of the lateral line in fishes and the way electric fishes find their prey are all based on processes which we did not know about—and which were thus "extrasensory" in this sense—only 25 years ago. There is no point in quarrelling about a term—what we can all agree on is that we must continue our studies of the animal's windows to the world.



ALTHOUGH MOST SPIDERS RELY ON TOUCH FOR THEIR INFORMATION, THE TARANTULA DEPENDS ON ITS BEADY EYES-ALL EIGHT OF THEM

### Senses: Means to an End

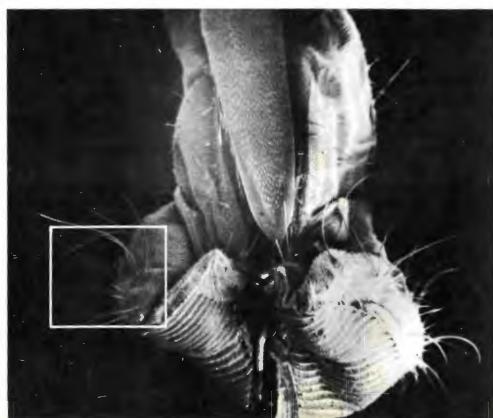
All animals, from the lowest on the evolutionary scale to the highest, manifest behaviour of some sort. Though all share one world, all may be said to live in different worlds, since each perceives best only that part of the environment essential to its success. Thus, how an animal behaves has much to do with what its sense organs are and whether these are few or many, simple or complex.

### Feelers for Smelling, Hairs for Tasting

Although among most animals the head serves as the repository of the major sense organs, there are many in which some or all of these organs must lie elsewhere—either because the head is too small to contain them or does not exist, or because another

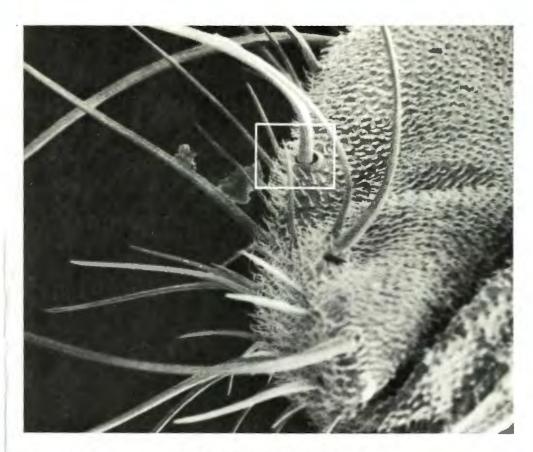


1 Tasting food with the sensory hairs on its feet, a house-fly lets down its elephant-like proboscis and begins to feed. The square shows the area of the proboscis examined in ever finer detail below.



2 Magnified 75 times, the proboscis is shown to have two lobes. The fly eats by pressing the proboscis against food, particles of which are drawn up through pores and the cavity between the lobes. structure represents a better place for them to be. The headless mussel has developed eyes and tentacles for tasting that lie around the edge of its shell. Some sea snails carry their eyes on their backs, tubeworms have them on the tips of their tentacles.

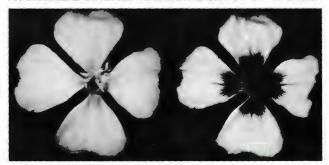
Grasshoppers hear with organs on their legs or abdomens. Many moths and butterflies smell with their antennae. Flies taste with countless hairs on their legs and must first step on their food (below) in order to become sufficiently stimulated to eat it.



3 In a further magnification, the area marked off by a square in the previous picture becomes a forest of sensory hairs, which, like those on its feet, enable the insect both to taste and feel its food.



4 Never before seen with such depth of focus, a single sensory hair, magnified here almost 2,600 times by the new scanning electron microscope, rises from its rounded, hollow socket like a sturdy column.



WHAT THE BEE SEES differs from what man sees, as these pictures reveal. In each panel, the flowers are the same, but the ones on the right have been photographed through an ultraviolet filter to show patterns normally visible only to the bee.

#### Beyond the Senses of Man

As far as the senses go, the world is not as it seems. Perception must vary from one kind of animal to another, since the sense organs rarely, if ever, have exactly the same range. Take man and bee. Because the human eye reacts to light waves of only a certain length, man fails to respond to the shorter and longer waves of the optical spectrum. The bee is not so hampered—at least as far as the shorter waves go -and can actually see ultra-violet. Thus, to the bee a flower may display a pattern etched in ultra-violet (left) that impels the bee towards the nectar. But should the flower be red, the bee would see it as black, simply because its eyes do not register the longer light waves. At the other end of the visible spectrum, where red becomes infra-red, man goes "blind" himself, yet a creature like the diamondback rattler (below) has its own way of perceiving it.



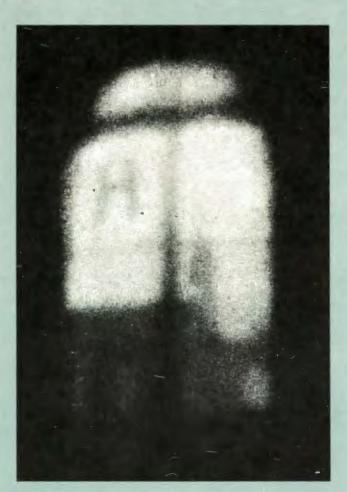
THE SCALY HEAD of a diamond-back rattlesnake exhibits uncommon sense organs—a pit beneath each eye that enables the snake to detect its warm-blooded prey through infra-red radia-

tion. Containing numerous, tightly packed nerve endings, the pits respond to heat but not to light, and thus let the diamond-back locate food in the dark, when it usually does its hunting.



WITH A BURST OF POWER of the kind used to kill its prey, an electric eel lights up more than 200 neon bulbs. Set off here by handling, the discharge usually occurs only after a fish swim-

ming into the electric field around the eel's body causes a disturbance which affects sensory pits in the eel's head. These tell the eel where the fish is, how big it is and whether to fire.



TAKEN THROUGH GLOW-WORM'S EYES, these photographs suggest more about insect vision than they in fact show. The first, made in 1891 by the Austrian physiologist Exner, is of a



window, with a letter R pasted on it, and a steeple; the second, made 27 years later, is of a man. Both are, at best, approximations of the images as registered by the insects' retinas.

#### The Sense of Sight—New Light on an Ancient Subject

Among different animals, different senses dominate. In birds, sight does; in most mammals, smell and hearing do. Fishes can be said to rely upon smell and touch for information about their environment; most insects upon smell and taste. Man uses all these senses, but again, as with other animals, one sense dominates, and this sense, of course, is sight.

Because he leans on sight so heavily, man naturally enough has long tended to consider the world in a visual way; not only has he assumed that most other animals depend on their eyes more than they actually do but he has also assumed that they see the way he does. That accounts for the numerous experiments made with cameras and insect eyes—investigators

thought that if they could take photographs through the eyes, they might see the world as an insect does. Nothing could be further from the truth. What photographs like the ones above really show is not what the glow-worms might have seen, but what the camera saw. How such images would have been processed by the brains of the glow-worms—and how, therefore, they would have been seen by the insects—is simply not known.

Misconceptions about vision can be attributed not only to human bias but to incomplete and often inaccurate information about the different kinds of eyes in the animal kingdom. Man's understanding of even his own eye has been amazingly slow in com-



THE ACTUAL FACETS OF A GLOW-WORM'S EYE—not seen in the old photographs opposite—show up here in a 1963 photograph of a young woman by the science photographer Roman

Vishniac. To prepare the eye, Dr. Vishniac had first to clear away all nerves and muscles with tiny needle-like spines from a fresh-water sponge, a task that took about 18 hours to finish.

ing, and for centuries was based upon the false notion, first propounded by the ancient Greeks, that the lens captured the image and that the retina (the true photo-receptor) nourished the lens and conveyed to it, from the brain through the optic nerve, a mysterious power called the "visual spirit". Not until late in the 16th century was the Greek view seriously challenged, by the Swiss anatomist Platter, who proposed that the lens captured light instead and distributed it over the retina. The German astronomer Kepler suggested in 1604 that the image was somehow "painted" on the retina. A few years later a Jesuit friar named Scheiner offered dramatic proof of this—in peeling away the opaque layers at the

back of the eye, he actually laid bare an image, a faint, fleeting record of what the eye had been taking in at the moment its owner had died. When, late in the 19th century, it became possible to fix such an image on the retina with chemicals and produce something called an optogram, the notion of the eye as a pin-hole camera gained wide acceptance and persists today. Such a notion, however valid, does nothing to explain what happens to the image once it has fallen on the retina, a fascinating problem that is only just beginning to be solved. Some of the startling discoveries made to date are depicted and explored on the following pages—in several instances for the first time anywhere outside scientific journals.

# The Anatomy of Vision

ONE: THE IMAGE ON THE RETINA

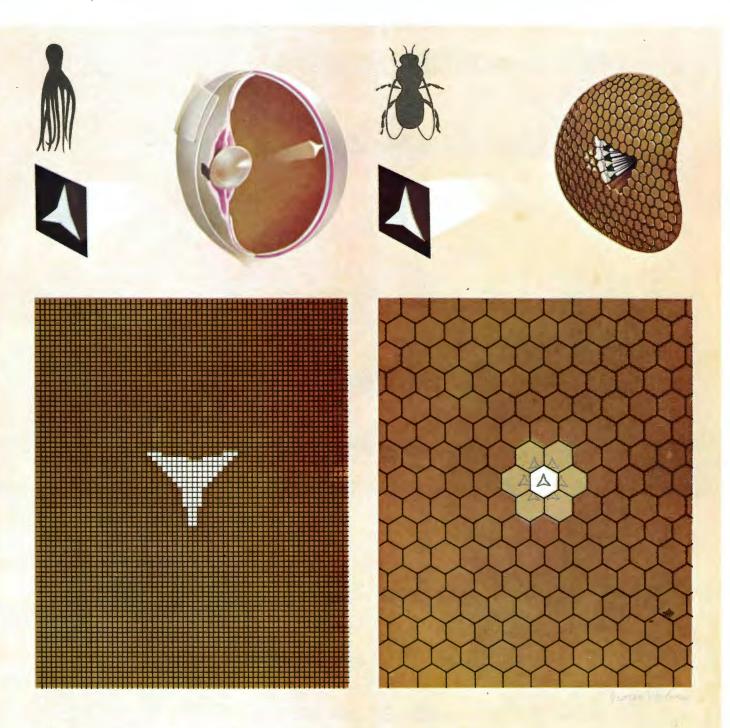
It may never be possible to show exactly what any animal actually sees. But as the paintings on these and the following pages demonstrate, it is possible to show in a schematic way not only what the image falling on the rear wall of the eye or retina may look like in various animals but also how the retina transforms this image into visual information of use to the brain in initiating behaviour.

The eye alone, of course, never sees: the brain sees. What the eye does in its most basic role is to register light. To this end, all eyes, from the simplest to the most complex, have in common light-sensitive cells. These cells, thousands of them packed together, form a sensitive screen in the retina. Light striking this screen excites each cell individually, and together the light-stimulated cells form a mosaic-like pattern, an image of what the eye is looking at.

This, the first major step in the process of vision, is the subject of the paintings at the right. What the animal will ultimately see (shown on the following pages) depends on how its retina and brain process the mosaic. Here are shown the three kinds of image-forming eyes that have evolved in the animal kingdom, each looking at the same starlike shape from the same distance. The paintings at the bottom are enlargements of the light-sensitive portion of each eye on which the image is recorded. In the first two, the tiny squares represent the individual receptors; in the third, the facets do.

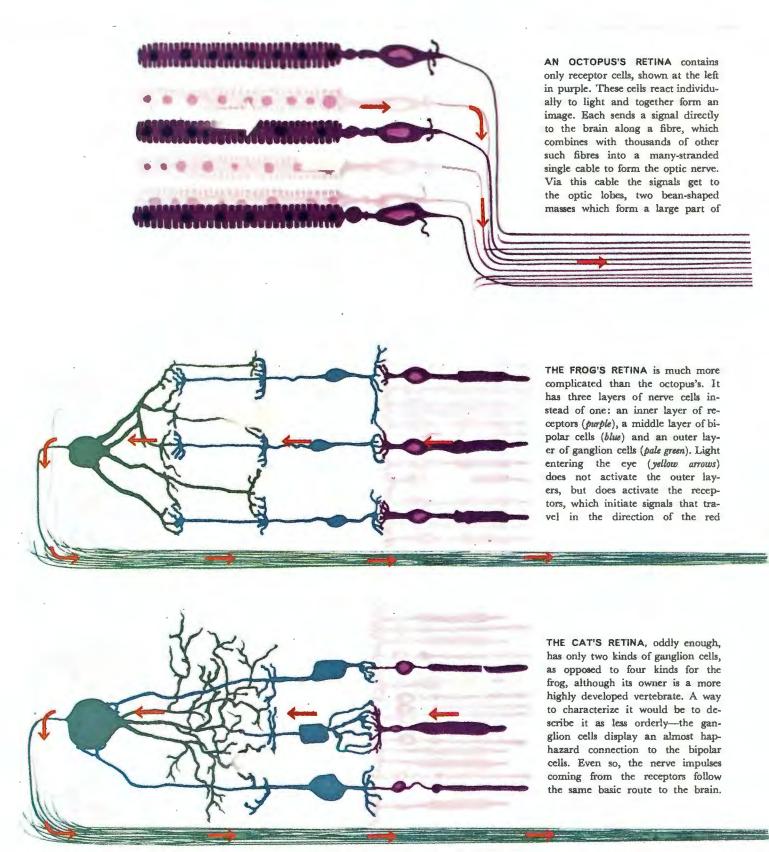


THE HUMAN EYE, which stands here also for the eyes of other vertebrates, is like a camera, with a diaphragm (the iris) to regulate the amount of light passing into it through the pupil, an elastic lens to focus the light, and film (the receptors of the retina) to record the light. Although far from perfect optically, it is superior to the eyes of many other vertebrates. The human eye is characterized by its receptors, some 130 million tightly packed rods and cones which connect to about one million optic nerve fibres. The image they form (above) shows a remarkable fineness and appear as one piece when reassembled in the brain, although in fact it is a mosaic on the retina.



THE OCTOPUS EYE, the most advanced visual apparatus of any found among the invertebrates, has evolved independently of the vertebrate eye, yet, with a few obvious differences such as a rectangular pupil and two protective coats instead of one, it shares many of its basic features. Here again the eye operates on the principle of a camera. However, the image, as registered by the receptors (above), is smaller—because the eye itself is smaller. It is also much less precise, not because of any inability of the muscle-controlled lens to focus clearly, but because the receptors are fewer in number and proportionately bigger—and thus produce a coarser mosaic.

THE INSECT EYE—the so-called compound eye—consists of many tiny units, each of which may be said to be an eye in itself, since each has its own lens and light-sensitive cells connected to the brain. These little "eyes" may number from less than 12 in some cave-dwelling insects to more than 28,000 in the dragon-fly. Because of their tapered shape, they face outwards in slightly different directions, and thus each takes in a different part of the scene. The painting above shows how the facet aimed directly at the starlike shape receives the complete image, while the surrounding facets receive only part of it—a result of their not being aimed exactly at the star shape.

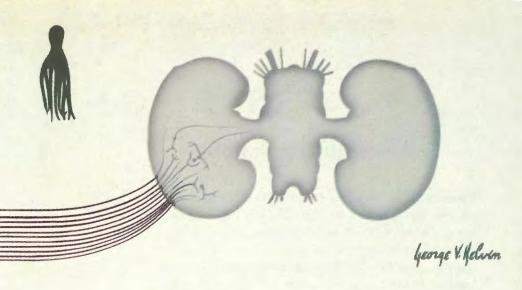


#### VISION, TWO: THE EYE AND THE BRAIN

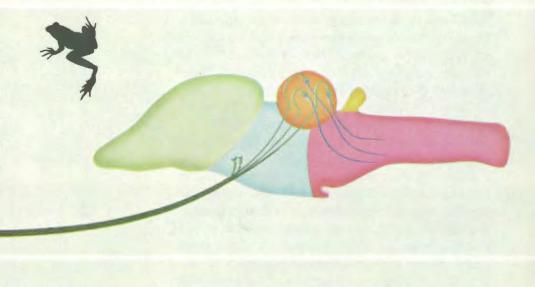
The recording of an image on the retina, as has already been shown, is but the first step in vision. The second step involves getting the image to the brain in useful form. These diagrams show in broadest

outline how this is accomplished in an invertebrate (an octopus) and two vertebrates (a frog and a cat). The octopus has a relatively simple retina, consisting of a single layer of receptor cells which transmit visual information directly to the brain for processing. The frog and the cat—in fact, all vertebrates—

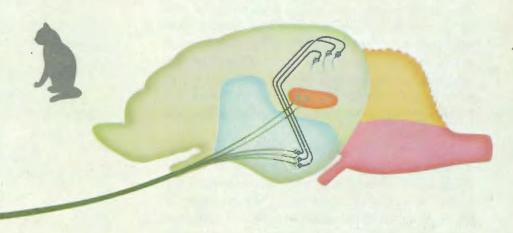
the octopus's brain. Here the signals, or visual information, are processed and, in ways as yet unknown, put to use by the octopus. The octopus is able to see remarkably well because of the high development of its eyes and central nervous system. It can also distinguish between shapes, which, considering the limited amount of visual interpretation that the average invertebrate can make, is amazing.



arrows—back through the bipolar and ganglion cells and via the optic nerve to the brain. Reflecting the importance of speed to the insect-eating frog, nine-tenths of the visual information gets processed right in the retina and is then forwarded directly to a reflex centre in the brain (orange), where it is acted upon almost at once. Is it any wonder that the frog has been described as a living catapult?



But something different happens to the impulses when they reach the brain. Only one-tenth go to a reflex centre like that of the frog. The other nine-tenths connect to cells in a kind of relay station (dotted circle, blue), before being sent on for final processing to the cerebral cortex. This arrangement would apparently give the cat a broader choice in responding to what it sees than the reflex-dominated frog.



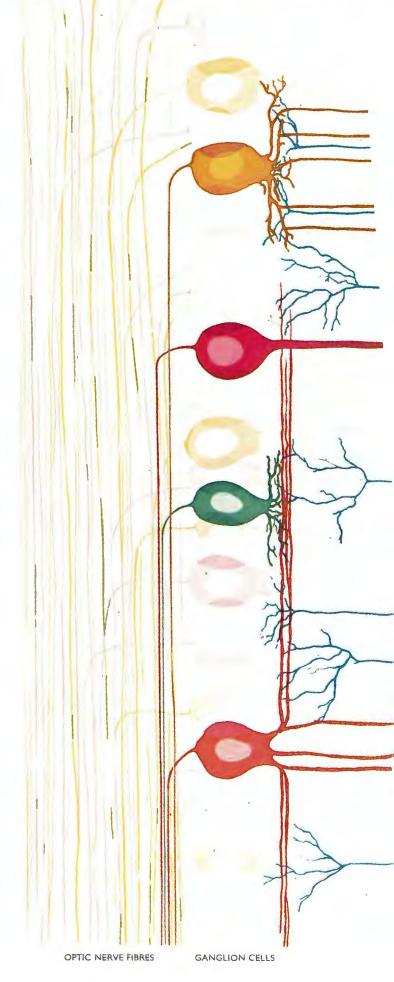
have much more complicated retinas, made up of three separate layers of nerve cells. Light entering the eye passes right through the cells of the first two layers, without affecting them, on its way to the receptors at the back. Here it triggers nerve impulses —electrical signals which pass from the receptors to the bipolar cells for initial processing and then on to the ganglion cells for further processing, and finally along the fibres that form the optic nerve to the brain for still further processing. Some details of how this processing is carried out in both the retina and the brain are shown on the next pages.

#### VISION, THREE: LAYERS OF THE RETINA

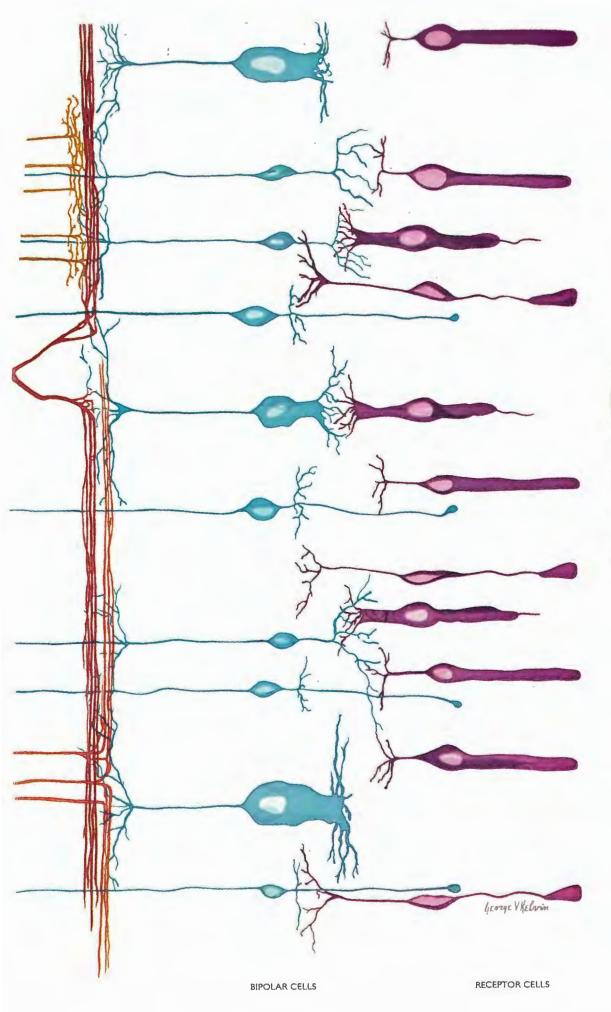
The vertebrate retina is characterized by its complexity. The painting on the right is a highly magnified cross-section of a frog's retina, showing the three layers of cells already described: receptors (purple), bipolar cells (blue), and the ganglion cells (various colours). The receptors are the only cells sensitive to light; the bipolar cells are essentially links between the receptors and the ganglion cells. However, their linkages vary—some of them connect with one receptor, some with several; some of them meet the ganglion cells half way, others send fibres almost to the bodies of the cells themselves. These variations in linkage are believed to make possible the first step in processing the visual information, much as the wiring in radio controls the nature of the signal which travels through it.

There are even greater differences of size and of structure among the ganglion cells than among the bipolar cells. The type shown in red, for example, is relatively scarce but has a huge network of farreaching branches which connects up with a great many bipolar cells and thereby enables it to collect information from a large area of the retina. Although the orange type connects with bipolar cells at two levels, it receives information from a more restricted area. The tan type, which also connects to the bipolar cells at two levels, is more numerous than the orange type but receives information from an even smaller area. And the green type, the most numerous of all, receives information from the smallest area.

The effect of this complex circuitry is astonishing: it permits the four kinds of ganglion cells to take the visual information coming from the receptors and to analyse it in four different ways. The red type, for example, seems to fire only when there is a decrease in light—a dimming or darkening of whatever the eye is observing—and thus presumably it conveys to the brain information about large, dark shapes. The orange kind is believed to respond to fairly big moving objects, and the tan to smaller moving objects with curved or pointed edges, such as insects or the tips of wind-tossed grass. The green is activated only by abrupt, contrasting edges of light and dark.



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The enlarged portion of the frog's retina at the left in colour is, in reality, infinitesimally small; so small, in fact, that it would easily fit into the tiny square in the drawing of the frog's eye above, with plenty of room left over.



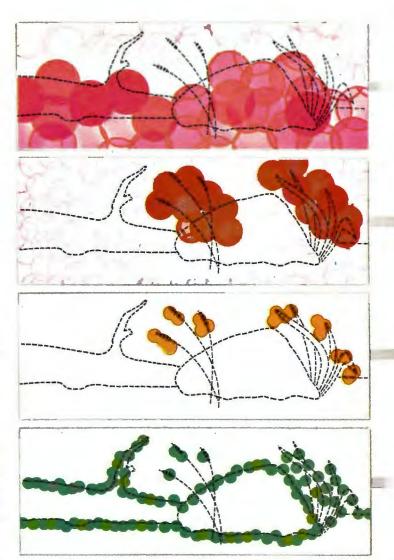
#### FROG GANGLION CELLS

Red ganglion cells, largest and least numerous of the four kinds, are affected by dimming; they respond only to darker parts of the swamp scene, such as shadows. Although it is known where they terminate, it is not yet known how the connecting brain cells react.

Orange ganglion cells, called "event detectors", become activated when movement occurs in the frog's visual field. Here they respond to the swaying reeds and the grass.

Tan ganglion cells are set off by very small, moving objects with convex edges, like the tips of the cat-tails and grass, and also insects—hence their name: the "bug detectors".

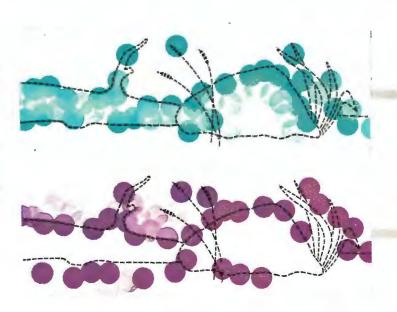
Green ganglion cells, the so-called "edge detectors", react to sharp edges, either lighter or darker than the background. They are shown here outlining the swamp scene. As in the red cells, the response of the connecting brain cells has not yet been determined.





#### CAT GANGLION CELLS

The retina of a cat contains only two kinds of ganglion cells. One kind, shown here in blue, responds to increases in light. The other, shown in purple, responds to decreases. In short, as long as the light falling on individual receptor cells in the retina is changing, one or the other kind of ganglion cells will fire. A steady rate of firing is ensured for the cat by a constant, almost imperceptible tremor in its eye. This tremor causes the image to flick to and fro on the receptors, and these, in turn, react to the changing intensities of light falling on them.



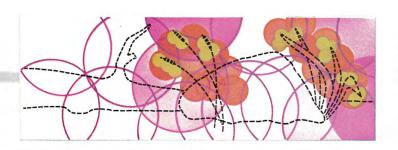


CAT AND FROG WILL SEE THIS SCENE DIFFERENTLY

#### VISION, FOUR: THE FINAL PROCESSING

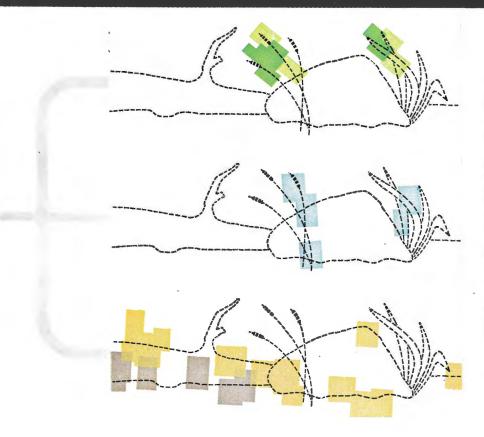
We have been talking for six pages about visual processing. What is it? It can best be explained by taking what has already been learned about the four kinds of ganglion cells in the frog's retina and applying it to an actual scene. How these cells might respond to the rock, log and grasses in the land-scape above is shown at the left. How cells in the frog's brain might react to the visual information sent from the retina is shown directly below. The same

thing can be done for a cat (lower half of both pages), which, by contrast, has only two kinds of ganglion cells but many more kinds of brain cells concerned with vision than the frog has. The diagrams for both cat and frog, showing the responses of hundreds of cells at one time, are abstracted from readings made in the laboratory, with electrodes so fine that they could be inserted into single nerve fibres in the optic nerves and brains of living animals.



#### FROG BRAIN CELLS

In the frog's brain, impulses coming from the "event detectors" and the "bug detectors" end up being processed together by large brain cells (pink circles), which provide a brand new kind of visual information. What happens to the impulses of the other two kinds of cells at their terminals in the brain is unknown, and thus cannot be depicted.



#### CAT BRAIN CELLS

In the cat's brain, hundreds of different kinds of cells sort out the visual information relayed from the retina. Only three kinds are shown here. The cells in the first two diagrams are concerned with the movement of long, narrow shapes-like that of the waving grasses. Their responses, as these diagrams show, differ slightly from each other. The responses of any other similar cells will also differ, since each cell works on the same visual stimulus from a slightly different angle. Altogether they provide a detailed view of the movement of the grass blade. It is thought that this kind of multiple processing by the brain makes the cat's vision a much more supple and subtle process than the frog's.

The third diagram illustrates brain cells that fire on receipt of information pertaining to edges—either darker edges (coloured brown) or lighter edges (coloured yellow). All the cat's brain cells are depicted as being rectangles because they actually respond to areas of this shape in their field of vision.



A WELTER OF LURES surrounding a black bass indicates the lengths to which lure makers will go—hoping to stumble on what attracts a bass. If this could be determined scientifically, then a supernormal lure could be designed that might stimulate the fish into biting every time.

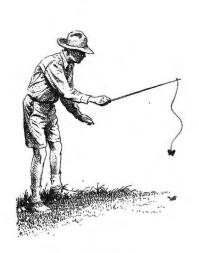
3

## Stimuli and What They Do

When I am engrossed in a book or thinking about tomorrow's work, I may fail to hear the clock in my room tick. Yet if you were to ask me whether the clock had stopped, I would switch my attention to it and probably hear it tick very clearly.

Everyone has experienced this kind of thing, and if you stop to think about it the obvious conclusion is that one does not always make use of all the information one's sense organs can provide. Something very similar is true of animals. Early in this century, a famous scientist, Carl von Hess, concluded that all honey-bees are colour-blind: when he took them into the laboratory and confronted them with two lights, they always went to the brighter of the two, regardless of the colours used. The conclusion seemed valid enough—after all, the bees were reacting just like colour-blind people, who discriminate between brightnesses rather than colours of light.

But was it really a valid conclusion? Karl von Frisch, at that time a young research worker, did not think so. For all the great respect and admiration he had for his senior colleague, he had still greater respect for the adaptedness of living organisms—he felt there must be some function in the bright colours of



THE SEXUAL RESPONSES
OF THE GRAYLING BUTTERFLY

In an effort to learn more about how male grayling butterflies respond to females, Dr. Tinbergen and his colleagues worked out some ingenious experiments. These were all based on the male's well-known habit of flying up in pursuit of a passing female and utilized different kinds of "female" models made of paper and presented to the males like lures at the end of a fishing rod. Details of the experiments are shown on the opposite page.

the flowers. To prove this, he conducted a series of experiments with bees in their natural environment, out in a field where they were actually foraging. Instead of lights, he presented them with pieces of cardboard of various colours and also of different shades of grey. The results were clear-cut and convincing: foraging bees did respond to colours, especially to yellow and blue. The bees tested in the laboratory had not been foraging; they had been trying to escape, and in this "motivational state" they became oblivious to colour and reacted only to the brighter light.

We know now that this is only one example of a very widespread phenomenon. Like the professor sitting in his study with the ticking clock, animals do not necessarily use all the potential information about the outside world which their senses are able to give them; what they do use depends on what they are doing at the moment. Therefore, if we want to understand fully how external stimuli help to control an animal's behaviour, we must do more than investigate what they can respond to—we must find out what at any given moment they actually do respond to. Once again, we must go beyond the seemingly obvious and probe our subject in depth—in this case, exploring in depth the animal's world of external stimuli.

It is rather remarkable that this has been done so rarely. Yet even on the basis of the relatively few experiments undertaken since we started concentrating on this field, some extremely interesting phenomena and problems have been noted.

The grayling butterfly offers an excellent case in point in its sexual pursuit of a female. Males of the species often rest on the bark of trees or on the ground in arid, sandy areas. They are beautifully camouflaged, and it is often rather startling to see one fly up, as it were, out of nowhere—which they do whenever a female flies by. If the female is willing to mate, she will alight; the male then settles near her and starts his ground courtship. But a female that is unwilling flies on, and the male, after following her a few yards, abandons her and settles down to wait for another.

What makes a male fly at a female? This was the key question, and it led us through an amusing sequence of experiments to a rather surprising answer.

Simple observation in the natural habitat gave us the clue to our own line of testing. We soon saw that it was not just the female of the species that stimulated the graylings to rise but also a large variety of other insects ranging in size from small flies to butterflies much larger than the female graylings. We even saw the hapless males rise in pursuit of birds up to the size of thrushes. More striking still, we saw them pursue falling leaves of various sizes, shapes and colours—and not only were leaves pursued but sometimes the shadows they cast on the ground, and even the shadows cast by the pursuing males themselves.

All this bewildering variety of objects which the male graylings apparently took for females of their species suggested two things to us: first, that visual stimuli were important; and secondly, that chemical stimuli were not, for scent could be ruled out on the grounds that the direction of the flights was independent of the wind.

But if the decisive stimulus was a visual one, how to find out what factor of vision—size, shape, colour, action or a combination of any or all of these—was responsible for the graylings' behaviour?

We first prepared a number of paper dummies of butterfly shape which we attached with a yard of thin thread to the end of a slender, three-foot pole. With these "fishing rods" we could make the dummy butterflies do almost

anything we wanted, and in our initial series of experiments we made them dance in the air towards a male. This invariably elicited a vigorous response, so we set about elaborating the test still further.

We now prepared a large number of dummies, grouped in series, in which one particular characteristic at a time was varied. One series, for example, consisted of dummies which were identical in all respects except colour. In another, colour and size were constant but the shape varied; in still another it was size that changed. Armed with our rods and our various dummies, we roamed over the countryside searching for male graylings. Whenever one was found, the dummies would be presented, always in a standardized way—i.e., moving in the same way, approaching from the same distance, under similar lighting, with the same speed, etc.—at regular intervals and in irregularly varied sequence. This was an attempt to present to each male all the models under roughly the same circumstances and to record how effectively each model elicited his sexual pursuit response. By doing this for one series after another, we could express the stimulating effect of, say, various colours, shapes, sizes and so on in the percentage of occasions on which a model actually elicited a response.

We ran some 50,000 tests of this nature, using a large number of males found in their natural habitats. It was clear at once that the exactness of the imitation of the female was not an important factor. Even when we glued the wings of a real female on to a dummy, we got no more response than was elicited by a dummy coloured a uniform brown. Dummies of all different colours, in fact, all got a response, but some seemed more effective than others. Curiously enough, however, it was not the natural brown of the female that worked best. Black was even better, and gradually it became clear that the darker the colour of a dummy, the more effective it was. This was confirmed with a series of dummies of various shades of grey: white was least effective, and black was best.

Now what about size? We had made a series of dummies ranging from onesixth the diameter of a normal female to four and a half times normal size. Male graylings rose in pursuit of all these, but much to our surprise, the larger dummies were more effective than those which were the size of an average female.

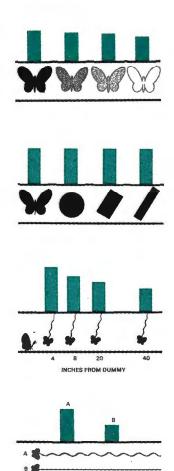
So we had established three things: movement was important, dark colours worked best, and the bigger the dummy, the better the response. Now what about the effects of shape?

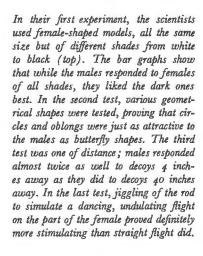
SHAPE, it developed, seemed of little importance. We offered many dummies of different shapes but with the same surface area—long rectangles, butterfly shapes, circular shapes. The long rectangles were the least effective, but we found that this was not because of the shape, but because they moved differently from the other shapes—they did not flutter as well.

So the next thing we studied was the type of movement. This we did by making the same model move in different ways. As anticipated from earlier tests the dancing movement was twice as effective as a smooth and regular movement.

Finally, we tested the effect of distance. The same dummy was made to dance at varying distances from the males. We tried this with many dummies, both "good" ones and "poor" ones, and we found that the nearer the dummy was to the male, the more responses it got.

Putting all this together gave us a much better understanding of why we had seen males follow birds, falling leaves, shadows and all those many other things which seemed so different from a grayling female. Shape mattered little to the males, nor did colour—what was important was bigness, darkness of tone, near-





ness and a dancing activity. But how did all this add up for the male; in short, how did it say "female"?

The matter seemed inexplicable in human terms, and so we had to consider the possibility that the male graylings "recognized" females in a way quite different from the way humans do. To us, recognition is very often the result of a yes-no decision of some kind: we look at something dancing past and say to ourselves, "this is a female" or "this is not a female". But the butterflies showed no such clear-cut decision. They showed instead a graded scale of responses, as if many of the dummies were to them, let us say, 75 per cent female or 50 per cent female—and the frequency of their responses depended upon the quantity of "femaleness" of the object attracting them.

This opened up an entirely different line of thought—we realized that we had to think not just in terms of stimulation but of quantity of stimulation. Both a white and a black butterfly stimulate a male, but the black one stimulates him more strongly than the white one. And we discovered, as we pursued this new line of thought, how curiously automatic this response to strength of stimulation can be. For example, we found that a white dummy, although known to be less stimulating than a black one, would none the less elicit the same number of responses from the males if it was presented from a shorter distance than the black dummy. Similarly, the effectiveness of a white dummy, or a relatively ineffective small dummy, could be boosted by making it dance. So a deficit in one type of stimulus could be compensated for by an increase in another kind of stimulus, however different in kind it might be. It seemed that all the stimuli contributed in a quantitative way to a "pool of stimulation" which caused the grayling to respond.

ANOTHER striking thing was that some properties of the female, such as its colour, did not contribute to this pool of stimulation at all. Did this mean that the males were colour-blind? This was hard to believe—like bees, they feed on flowers whose bright colours would seem to have some function in attracting them. We decided to offer our series of coloured dummies to graylings at a time when they were feeding—and lo and behold, they behaved very differently: they reacted almost exclusively to yellow and blue models. Furthermore, they did not react at all to grey models, showing that they did have true colour vision.

In other words, in the case of the grayling butterfly, whether or not it is stimulated by a coloured object or merely by the darkness of an object depends on what it is doing at the moment. Or, to put the matter in more general terms, the condition of the male decides which part of the outside world it will admit to its pool of stimulation.

Clearly, it would be interesting to see if other animals reacted in this same automatic way. This has been done by studying a variety of behaviour patterns in a number of subjects.

One of these is the feeding behaviour of a large, carnivorous water beetle known as *Dytiscus marginalis*. This beetle preys on fish, aquatic insects, tadpoles and worms, and also occasionally eats carrion. The surprising thing about *Dytiscus* is its clumsiness. Though it has well-developed eyes and obviously good vision, it does not swim straight at its prey; in fact, it does not seem to be able to see it at all. Yet when it is near a prey animal it does show, by changing its normally quiet swimming into a kind of frantic, irregular thrashing, that it has become aware of it. Just what is the stimulus that prompts *Dytiscus* to pursue and devour its food?

We can check this in several ways. First, we can show it a tadpole enclosed in a test tube which we put into the water nearby. The beetle ignores the tadpole completely; it does not even show its frantic swimming movements when it touches the glass. However, if we sew the tadpole into a little bag of cheese-cloth which hides it completely from sight, the beetle responds vigorously: it either grabs the bag with its forelegs and begins to chew it up or, if it happens to swim past under the bag, it immediately dives to the bottom and swims around in irregular searching movements below. The same response can be elicited by taking water from a tank in which tadpoles have been swimming and squirting it into the beetle's tank.

Obviously, when it is feeding, a *Dytiscus* responds to a chemical stimulus—it smells rather than sees its prey. Yet when it is crawling about on land it uses its eyes to good effect to avoid obstacles, even at a distance and even if these are placed behind glass. By the same token, when it is flying the *Dytiscus* beetle is able to see bodies of water: it often alights on glass, on cars or on other shiny surfaces which it mistakes for water. We can only conclude that a feeding *Dytiscus* just does not use its eyes—here, too, the sensory "input", as it is called, is admitted only in part.

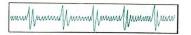
This conclusion that an animal does not at any particular moment use all the information its sense organs receive raises an interesting problem: what happens to those stimuli which it does not use? To put it in a slightly different way: when *Dytiscus* is swimming around in bright daylight in search of food, its eyes are stimulated by light; we would expect this input to be carried by sensory nerves to the central nervous system, which, through motor nerves connected with the muscles, would then cause the feeding movements. Yet in a foraging *Dytiscus* the visual stimulus is not translated into movement; its feeding movements are unaffected by what it sees. Somewhere along the line between the eyes and the motor centres that control feeding behaviour, the input received by the eyes must be "censored" or suppressed. How is this done?

To answer this question, we have to progress from observation and study of the intact animal to a direct investigation of what is going on inside it. This can be done in various ways. For instance, it can be done in larger animals by sinking extremely fine electrodes into a nerve centre to register the very weak electrical currents generated by external stimuli. Experiments of this kind have been carried out on cats, with an electrode sunk into a nerve centre located directly behind the ear. When a metronome was made to click near the cat, it was possible to see what the cat heard—quite literally, for every time the metronome clicked the nerve centre "fired" and the "action potentials" accompanying the impulses were recorded on the instruments.

Now the cat was shown a mouse. Not surprisingly, its interest at once concentrated on the mouse. But at that same instant, the action potentials registering on the meter disappeared! Yet the metronome was still clicking as before. The cat, however, was now oblivious to what previously it had heard clearly; it had managed somehow to shut out the noise.

Neurophysiologists describe this phenomenon as "gating"—it is as if a gate were opened or closed, either admitting or stopping the flow of information. What is admitted or stopped seems to be determined by what the animal is doing or intending to do—by its motivational state. Where and how sensory information is stopped in such cases is largely unknown; the example of the cat's ear may or may not be typical.





#### TUNING OUT A STIMULUS

To avoid utter confusion, animals must be able to choose among a great number of sights, sounds and other stimuli pouring into their nervous systems, and select the ones that are most useful to the needs of the moment. A cat sitting quietly will hear the ticking metronome behind it. But if it sees a mouse, the sound of the metronome will no longer register. This can be proved by putting an electrode in the cat's head, wiring this to a meter and observing the response to the regular ticking of the metronome (graph, above), which disappears (graph, below) when the mouse runs by.





The cat with the metronome and then the mouse, and *Dytiscus* with the swimming tadpole are reacting to specific stimuli which they select out of a wide range of things assaulting their sensory organs—and these stimuli are sufficiently important to be examined on their own. We call them "sign stimuli". Selective response to sign stimuli is a widespread phenomenon; just exactly how widespread we do not know, and more systematic investigations of the total stimulus situations to which animals react are certainly needed. It is interesting that many animals, even the higher forms, show selective responses to sign stimuli before they can have gained experience with them. This has for instance been studied in detail in newly hatched chicks of the herring-gull.

Normally, as soon as they are hungry, these chicks peck at a red patch near the tip of the lower mandible on the yellow bills of their parents. It is this red patch which very particularly elicits the pecking reaction—a yellow bill without the red patch stimulates only a quarter of the responses that a red-patched bill evokes, and patches of other colours score somewhere in between. Even when one presents the chicks with an array of uniformly coloured bills, all get the same response—except a red bill, which is twice as effective. Yellow, the natural colour of the parents' bills, scores no higher than white, black or blue. But a chick will peck at a red cherry, and I was even told of one case when a fully grown young gull ran up to a little girl at the seashore and pecked vigorously at a "very red scab" on her knee!

This is what we call "misfiring"—an animal's behaviour may go off under inappropriate circumstances and so fail to attain his proper goal. Such misfires often indicate that an animal is responding to a sign stimulus. When songbirds feed a much larger cuckoo chick in their nest while ignoring their own, their behaviour misfires. Our knowledge of sign stimuli makes us understand why this happens: despite the fact that the cuckoo looks so different from the birds' own young, it does provide the part that matters, a particularly large gape showing the brightly coloured mouth and throat that stimulates the parent to feed it. The cuckoo chick, therefore, survives because the song-bird's behaviour is misfiring. By the same token, a moth displaying big "eyespots" on its wings survives because these "eyes" stimulate the song-bird to fright—they alone are the effective stimuli, however different the rest of the moth may be from a predatory mammal or bird.

The study of stimuli has its eminently practical side, too. In northern Sweden, a valuable salmon fishery was threatened with extinction when a hydroelectric project changed the water level, the vegetation, even the speed of the current in the river the fish habitually spawned in. Under the new conditions, no spawning took place—until a behaviourism student was called in for consultation. He found that the salmon required stretches of gravel in which they could bury their eggs; and not only that, but gravel of a special kind, with stones approximately walnut-sized. Artificial gravel beds were thereupon laid in the river, and this simple measure proved to be all that was needed to save the salmon, and thereby the livelihood of the local fishermen.

The possibilities of applying our growing knowledge of stimulus situations in other fields are obviously great, but to date they have hardly been explored. In most cases where they have been tried, however, they have shown great promise—distress calls of their species, for instance, are much more likely to drive birds away from airfield runways than are moth-balls, and for that matter they have been effective scarecrow substitutes not only in this situation but also

in orchards and grain fields. The U.S. Department of Agriculture, for example, has made significant progress in the use of sex and food attractants both to locate and to control destructive insect populations like the gypsy moth in New England and the Mediterranean fruit-fly in Florida.

Most of the experiments on sign stimuli have been carried out with dummies whose design was based on the natural object—the assumption being that the natural object would be the most strongly stimulating one. With this as the standard, the dummies could then be varied in a number of ways to answer the question, How is the object recognized? But once behavourism students began to think in terms of the stimulating effect of single characteristics such as colour, shape and so on, it was natural that they should begin to make the dummies vary beyond the limits of the normal object. Thus, as we have already seen, the grayling male was not by any means most strongly stimulated by dummies of normal female size, but large models were better, while black dummies were more effective than the naturally coloured brown ones. In other words, we have found we can improve on nature; we can provide "supernormal stimulation".

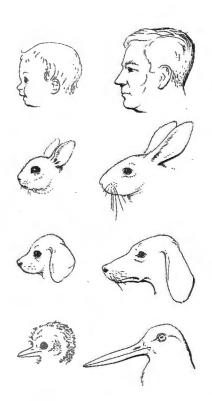
Several such cases have been well studied. Gulls and other birds, if offered the choice between an egg of normal size and an outsize egg, will prefer the latter—only to find that in spite of frantic attempts they cannot even sit on it. Herring-gull chicks, as we have seen, peck at the red spot of the bill of their parent—but further tests showed that this was not a colour stimulus alone but also a matter of contrast. They also pecked at dummy bills showing strongly contrasting patches, like very white on very dark or vice versa. And probing still further, we found that the chicks responded to the shape of the bill: a thin bill was more effective than a thick bill.

With all this information in hand, we decided to try another improvement on nature, so we made a thin rod coloured red, on which we painted three sharply defined white rings. To human eyes this did not look like a good imitation of a herring-gull's bill at all, yet the chicks aimed 25 per cent more pecks at it than at a real herring-gull's bill!

This phenomenon of supernormality may well be more widespread than we realize. For instance, it is possible that many song-birds are not merely willing to feed a young cuckoo but simply love to feed it, just because the cuckoo offers such an enormous and inviting gape. And the curious fact that several species of hawk moth caterpillars have not one but two eye-spots on each side of the body may have a similar explanation: to the song-birds that prey on them this supernormal arrangement may be more frightening than a normal set of eyes.

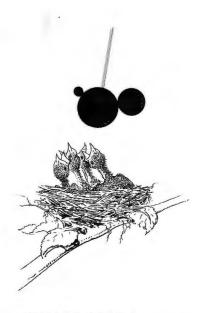
Can any of this be applied to man? Since it is not always easy to experiment on our own species, we know less of ourselves than of some animals—but there are many indications that we, too, are sensitive to supernormal stimulation. Many of the animals in the widely beloved cartoons of Walt Disney have "supernormal" baby-faces. Artists painting or sculpting the human body also exaggerate certain aspects deliberately. And what about our responses to lipstick? And our taste responses to salt, to sweet, to hot? What about our response to the flavour of alcohol? It might be worth-while investigating such matters in the same way as we are investigating animals.

Studying the sign stimuli in greater detail, we soon begin to see that neither are they as simple as they appear to be nor is the response of the animal to them, as we might think, as automatic as the response of a slot machine to the weight of a coin. The following story shows how complex a seemingly



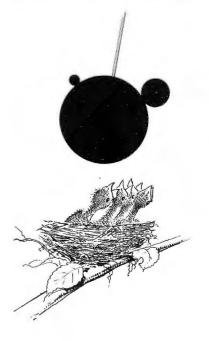
#### THE APPEAL OF AN INFANT

Does the "baby" look of a baby arouse parental instinct? There seems to be evidence that it does. In the drawing above, the human baby, the bunny, the puppy and the chick all have features, or sign stimuli, that stir up parental feelings: short faces, prominent foreheads, round eyes, plump cheeks. The angular, elongated faces of the adults on the right do not awaken the same feelings. Parental response in humans extends not only towards children but also towards such popular baby substitutes as pets and dolls.



#### WHERE IS THE HEAD?

Another of Dr. Tinbergen's experiments was aimed at testing visual discrimination in baby thrushes. By presenting the models shown here, he found that they would gape at things that didn't look anything like mother thrushes, but that they nevertheless had an excellent idea of the proper size relationship between a parent's head and body. In the drawing above, for example, the babies gaped to the left towards the small "head" because it seemed the proper size for the "body". But when a larger "body" was presented (below), they switched and gaped at the middle-sized "head", identical with the one they had previously ignored.



simple stimulus can in fact be. Young thrushes, at the age of about 10 days, begin to direct their gaping at the head of the parent bird. It can be easily shown with dummies that the young birds do not react to any specific details of the parent; rather, any slightly moving object close to and above the nestlings makes them gape. Now, let us probe this situation a bit further.

If we use a flat circular disc as a dummy—something that has no top or bottom but will look the same no matter how it is turned—we shall find that the nestlings will gape at its highest part, the part where the parent's head normally ought to be. But if we add a protuberance to the disc, this becomes the head, even if it is placed near the bottom of the disc where no normal head should be. This does not work for any protuberance. Shape does not seem to matter, but size does; and this is most interesting—it is relative size, not absolute size, that counts. If the "head" is almost as large as the "body", apparently it does not seem like a head and is not as effective as a smaller head would be. This is tested by presenting a disc with two "heads" of different sizes. The nestlings will gape at the most appropriate one, stretching towards the larger of the two heads if they are attached to a large body, and to the smaller one if they are attached to a smaller body.

Such "relational" or "configurational" stimuli seem to be the rule rather than the exception. Relations in space give rise to recognition of form; relations in time to recognition of movement. Both types of relations may be extremely complex. How are sensory data so integrated as to make possible the visual recognition of an individual human face or the aural recognition of a particular melody? So far, no one has been quite able to analyse such matters; yet somehow they are accomplished.

We began this chapter by considering what seemed to be a rather simple problem: to which outside stimuli does an animal actually react? We end it on a note of great complexity. We have seen that not all the information which the sense organs can provide is used, that part of the "input" that goes into the animal is somewhere rendered ineffective, depending on what the animal is doing. We have further seen that even the simpler kinds of effective input, the "sign stimuli", are really products of an integrative activity of the animal—in responding to a shape it does more than just sum up the activity of the separate sensory cells; it compares and relates them. So if we want to compare the animal to a slot machine, we may do so—but we must recognize that it is a slot machine of great complexity, in which each coin, or stimulus, causes intense and complicated activity inside it. This becomes even more evident when we realize that the effectiveness of a stimulus depends not merely on the stimulus itself but also on the state the animal is in. And as we shall see, this state changes continually.

Yet, amazing though these perceptual processes are, what the animal finally achieves seems to be much more primitive than what humans do, for, as we have seen, animal behaviour "misfires" much more strikingly than our own behaviour does. But in evaluating this, we must not forget that most of the misfiring occurs when we disturb the normal environment. However risky it would seem to rely on sign stimuli, the actual risk is not great, and we have to admit that the system works remarkably well. Nor should we think too highly of our own behaviour. An observer from Mars who saw an old spinster kiss her Pekinese might well consider this a striking example of misfiring, and could we honestly say that he would be very wrong?