First publ. in: The Oxford Companion to Animal Behaviour / ed. by David McFarland. - Oxford [u.a.] : Oxford Univ. Pr., 1987. - S. 498-501. - ISBN 0-19-281990-9

SENSES OF ANIMALS. The environment in which an organism lives varies over time and space. Even the most primitive organisms show some capacity to react individually to temporary or local conditions, so that the biochemical processes that underlie their life and replication can adjust and persist. Most animals have a marked ability to adapt behaviourally. However, behavioural adjustment can only be achieved if the animal can assess the state of the environment. It is the function of special mechanisms known as the senses, or more accurately as sensory systems, to provide this monitoring of the environment and to transform and process the information acquired so that it can control or steer the behaviour in an adaptive manner (see ADAPTATION).

The state of the environment is characterized by spatial and temporal variations of physical and chemical energy. It is these variations that the senses respond to. Potentially there is an infinity of environmental variables that could be sensed. Information about many of them would not contribute appreciably to the adaptiveness of behaviour, and since developing and operating a sensory system demands energy, each species has evolved responsiveness to only a selection of stimuli. Human beings, for example, can sense neither ultra-violet light nor magnetic fields.

How does one find out what stimuli animals can sense? In the first instance behavioural observations give clues. The flatworm *Planaria* is found under stones in streams. If one removes the stones they move away to hide under another stone. This suggests that they can sense light. Simple experiments using a torch with planarians kept in an aquarium in a dark room soon confirm this: they consistently avoid light and seek darkness.

Anatomical peculiarities also give clues. Animals that have eyes are likely to sense light. Indeed, if one examines *Planaria* with a magnifying lens one can see two dark, cup-like structures, one at each side of the head, that look very like eyes. Further experiments with a miniature torch soon confirm this. The light-avoidance response is released when light falls on these 'eyes', but not when it falls elsewhere on the body. Surgical removal of the eyes renders the animals completely unresponsive to light. Simple reasoning about environmental demands upon animals can also be a guide. Species that live in deep caves never encounter light and might thus be expected not to be able to sense it. And indeed, certain cave-dwelling fish (Amblyopsidae) and shrimps living in caves (Palaemonidea) have been found to be blind.

Often, however, such straightforward methods are not sufficient. Naturalists in the eighteenth century investigating the ability of bats (Chiroptera) to fly in complete darkness without colliding with obstacles were not able to deduce what sense they were relying on. Actually, they discovered that plugging the bats' ears disrupted their ORIENTATION, but as no sounds could be heard they did not know how to interpret this finding. Development of advanced acoustical equipment during the Second World War led to the solution of the riddle. The bats emit ultrasounds that are inaudible to us, but to which their own ears are exquisitely sensitive, and they make use of the ultrasound echoes to orientate.

Similarly, sophisticated equipment and formal experiments were necessary before it was possible to conclude that pigeons (*Columba livia*) are capable of perceiving the polarization plane of light, that is the vibration plane of light waves. In the LABORATORY hungry pigeons were placed in a circular chamber, and were rewarded with food grains for pecking small discs which were placed along the walls of a chamber aligned with the polarization plane of an overhead light source. If they pecked discs not so aligned they received no food, and were punished by having to sit in the dark for a period of time. From time to time the polarization plane of the overhead light source was turned to a new, unpredictable position, thus making a different set of discs the correct ones, i.e. the ones that would yield food on being pecked. The pigeons soon learned to observe the polarization plane orientation and began to choose the correct discs more often than by chance. Control experiments were necessary to prove that the increased rate of correct choices was not due to some unintentional cue other than polarization, such as brightness patterns, apparatus noise, and so forth.

Human beings are unaware of the polarization of light (except under rather special circumstances), and so it is difficult to imagine that to a pigeon, and indeed to many other animals that are sensitive to this stimulus, the sky must appear as an intricate design, since its light is polarized in a complex patterned way that is linked with the position of the sun.

Experiments such as these show that animals are responsive only to selected sets of stimuli, but that the selection can differ from species to species. Rattlesnakes (*Crotalus*) and some boas (Boinae) detect infra-red radiation with specialized pit organs, which can be seen in Fig. A as small depressions located between the nose openings and the eyes. By means of these organs they can sense small prey from a distance of 1 or 2 m and attack it. Certain fish can sense electric fields, pigeons are sensitive to changes in atmospheric pressure, many insects see ultra-violet light, some mammals are colour-blind, birds may see more colours than we do, certain moths can hear ultrasound, rodents can smell odours that are imperceptible to us, and so forth. This diversity is explained by the fact that each species has a different NICHE, and that,

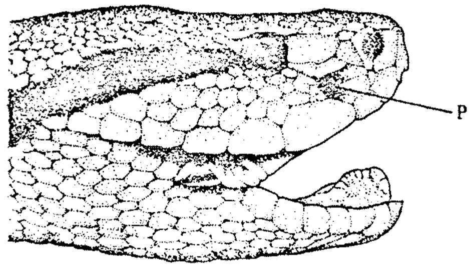

Fig. A. Head of a rattlesnake showing the pit (P) which is sensitive to infra-red radiation.

accordingly, one or the other sensory capability contributes more to make its behaviour adaptive in its particular conditions of life.

A consequence of this diversity is that the often asked question of how many senses there are cannot be answered meaningfully. Even if we restrict ourselves to human beings there are difficulties. The sense of balance, for example, can arguably be subdivided into senses of angular acceleration associated with the *utricular* and *saccular maculae*, all located in the inner ear. Both are doubtlessly mechanoreceptive senses in that they are responsive to MECHANICAL forces, but then, so is the sense of touch and, strictly speaking, also the sense of HEARING, in that sounds are mechanical waves. Some arbitrariness is unavoidable, but according to the type of stimulus energy that they are sensitive to, the senses can be classified as VISION, hearing, mechanical senses, CHEMICAL SENSES, temperature sense, (see THERMOREGULATION), and ELECTROMAGNETIC SENSES. Even so, one important sense, PAIN, is difficult to fit in, because it is sensitive indiscriminately to strong thermal, chemical, and mechanical stimuli.

So far we have been considering senses that are responsive to stimuli originating in the environment. However, in higher animals most organs are not directly exposed to the outer world. Rather they exist in an environment that is internal to the organism, the *milieu intérieur*. The state of this internal environment is subject to variations. For example, with physical exertion the content of oxygen in the blood falls and that of carbon dioxide rises. If injury is to be avoided such deviations require adjustment, through either physiological or behavioural responses, in our example perhaps by an increase of the breathing depth and rate (see HOMEOSTASIS). Internal (*enteroceptive*) senses of the chemical, thermal and mechanical variety, of which human beings are only dimly aware, ensure the necessary monitoring and initiation of corrective action. The internal stimuli, such as stomach distention, blood sugar level, level of HORMONES, that play such an important role in the MOTIVATION of behaviour are all, of course, mediated by these senses. Enteroceptive senses function to coordinate physiological and behavioural responses into an adaptive whole. SEXUAL receptivity of a female cat (*Felis catus*), for example, is only reproductively significant if it is synchronous with ovulation; the rise in the blood of a sex hormone triggers both.

Similarly, temperature sensitive neurones located within the hypothalamus and the spinal cord (see BRAIN) of vertebrates are crucial for the regulation of the body temperature. In birds, for example, the former area appears to be involved with blood circulation and plumage adjustments while the latter controls shivering and panting.

In higher animals the coordinated action of many body structures is involved in behaviour. For example, usually a number of muscles control the flexion of a given leg joint, and a number of leg joints are involved in even such a simple behaviour as walking. Effective walking can only be achieved if the nervous system has continuous information about the state of these structures. The degree of flexion of the knee joint in one leg clearly is important for the correct adjustment of the tension of the muscles in the other leg if balance is to be maintained. Special, so-called *proprioceptive* sense organs, associated with muscles, joints, and tendons, provide just that information.

Sensory systems. We now turn to the structures that underlie the sensory processes, the sensory systems. They are made up of components subserving three different functions: *transduction*, *transmission*, and *processing*. In higher multicellular animals the structural elements of sensory systems are discernible as specialized cells or groups of cells; in lower, unicellular animals the same functions are carried out by more or less recognizable cell organelles. What follows refers mainly to vertebrate animals, but similar even though usually correspondingly simpler structures and mechanisms are found in invertebrate animals.

The stimulus transduction is achieved by receptors. These cells or *organelles* convert, or better, translate the stimulus energy impinging on them into a standard form of signal-code. In higher animals these are usually sequences of nerve cell *action potentials*, and the code transduction is usually such that the more intense the stimulus, the higher the frequency of action potentials. Receptors are specialized according to the stimuli, the type of environmental energy, that they react to. Accordingly the physico-chemical processes that mediate the transduction vary a great deal: light receptors of the visual sense, for example, contain pigments that are modified chemically by the light they absorb, mechanoreceptors mediating the sense of touch undergo electrochemical changes as a consequence of the deformation of their membranes, and so forth. It is, however, characteristic of all receptor cells that, as a stage of the translation, they convert the stimulus energy changes into a graded electrical potential, known as the *receptor* or *generator potential*, that is proportional to the stimulus intensity.

Receptors may occur singly or in clusters. The temperature receptors of mammals are distributed in a variable fashion over the body surface, with differing densities. The temperature sensitivity of a given area is related to that density. Exploration of the skin with small heating and cooling probes reveals that there are discrete sites sensitive to either cold or warmth. The snout area is often highly sensitive, and indeed it has the highest density of these warm and cold spots. The cold receptors have been identified anatomically on the skin of the nose of cats. They are thin nerve endings that are embedded in the basal layer of the epidermis (outer layer). The identity of warm receptors is uncertain.

Receptor cells can also occur in clusters, and are then often associated with accessory structures that can be of considerable complexity, and which aid the stimulus reception, or even the transduction process itself. In the eyes of vertebrates the cones (actually three different types of cones) and rods of the retina, which contain light sensitive pigments, are the only actual receptor cells. Other structures, such as the pupil, the lens, and so forth, are only accessory structures that enable the formation of an image on the retina. The receptors proper, plus such additional structures, form what is called a sensory organ.

The organization of such sensory organs often contributes much in expanding the basic capability of receptor cells, that is, in coding the relevant stimulus energy into proportional neural messages. This is illustrated by the organ of hearing, the *cochlea* situated in the inner ear (the outer ear and middle ear have largely supporting functions). The receptor cells are hair cells that react in a proportional manner to bending of their hairs. They are arranged in such a manner in relation to auxiliary structures that each hair cell is only stimulated by tones of a certain pitch, and transduces the sound energy associated with that pitch.

The conversion of generator potentials into sequences of action potentials is achieved by the receptor cells themselves in the case of primary receptors, or by follower nerve cells after mediation by synapses in the case of secondary receptors. The next stage is the transmission of the coded information. The response organs, muscles and glands, that are responsible for actual behaviour are as a rule situated some distance away from the receptor structures. The information acquired by these receptor structures has, therefore, to be conveyed to the effector organs. However the transmission is rarely direct. Rather the sensory information proceeds first to the so-called sensory projection areas, more or less discrete parts of the brain, where it is processed. Sensory nerves, which are bundles of nerve cell *axons*, form the first transmission channel. Through them the sequences of action potentials, which encode as an ensemble the qualitative, spatial, and temporal characteristics of stimulus patterning, reach the brain. There they are relayed by further neurones, whose axons make up the central sensory tracts or pathways, to the projection areas themselves.

By introducing finely sharpened needles that are insulated except for a tiny area of the tip (microelectrodes) into the sensory nerves or tracts of anaesthetized animals, we get some information about the way in which the sensory information is being transmitted. The tips of these microelectrodes pick up the electrical potentials associated with the neuronal impulses, and, when amplified, they can be made audible with a loudspeaker or visible with an oscilloscope. If we apply this electrophysiological technique to the optic nerve of a cat, and stimulate the corresponding eye with a fine pencil of light, we find that a given axon responds with an increased action potential frequency to illumination of only a particular small spot of the retina. Typically it gives off a burst of impulses at the onset of the illumination and then settles down to a steady medium rate, becomes totally silent at the ending of the stimulus, and then recovers to a low firing rate during darkness. Sensory systems are generally particularly responsive to stimulus changes, less so to steady stimuli, and often they are also spontaneously active in the absence of any stimulation. If the light being shone on the cat's retina is made to change colour we may find that the neuronal unit only responds to red light, not to green or blue. If we sample further axons in the nerve (there are approximately half a million of them) we find that each of them responds to light shone on a particular spot of the retina. The response may be to only red, green, or blue light, or it may be indiscriminate. Visual scenes are thus represented by a time-varying mosaic of action potentials travelling through individual fibres of the cross-section of the optic nerves.

Results from experiments like this can sometimes throw light on the sensory capabilities of an animal. For a long time psychologists maintained that cats were colour-blind. They could not train them to distinguish colours. Physiologists however, on the basis of the information just described (i.e. the presence of colour coding visual axons), maintained that they must have COLOUR VISION, and indeed, with improved CONDITIONING techniques, psychologists have come to the same conclusion: cats do see colours.

Finally, we must consider the information processing function of sensory systems. This takes place mainly in the sensory projection areas we mentioned earlier, although some of it occurs at each of the transmission relaying sites, such as the sensory nerve nuclei of the midbrain, or the dorsal horn of spinal grey matter, or, as in the case of vertebrate vision, in the retina itself (apart from the receptor cells, it also contains neurones forming a highly complex network).

The nerve cells of the sensory projection areas often receive the coded mosaic of nerve impulses coming from the receptors in a map-like fashion. For example, touch of the various body parts is relayed to corresponding regions of the *somatosensory* cortex of the forebrain such that there is a distorted representation of the body: the sensory *homunculus*. The face and hands of this representation are oversize, corresponding to the greater touch sensitivity of these body areas, which is related to the greater density of touch receptors in the skin. Typically for any sense there are several such representations. Touch is represented clearly twice on the forebrain cortex, and once on the cerebellar cortex, and less clearly several times more in other brain areas. The projections should not be thought of as equivalent. In the case of vision, for example, the visual cortex is concerned mainly with recognition of shapes while the visual midbrain deals with information about the location of stimuli in the visual space. Neural pathways usually interconnect such multiple projections, enabling information exchange.

How is the sensory information processed? Microelectrode recordings from neurones in these projection areas provide some insights. In the visual system a first stage is represented by line detection neurones. They only fire in response to a bar or strip of light falling onto a certain point of the retina with a particular orientation. They do so because they receive the joint input from several aligned units from the same retinal area. In the next stage neurones combine the inputs from several of these line-detecting units, and are responsive to correspondingly more complex patterns, and so forth. In the auditory system, where the processing proceeds in an analogous way, neurones have been found in squirrel monkeys (*Saimiri sciureus*) that respond specifically to the different calls that these primates make during SOCIAL encounters. They respond uniquely to quite complex sound patterns, representing stimuli that are known to influence the animal's behaviour.

Not all the information that an animal is capable of receiving is useful at all times. Accordingly, one finds quite frequently that depending on the behavioural context, sensory information that is potentially available is disregarded. The grayling butterfly (*Hipparchia semele*) reveals marked colour preferences when it visits coloured dummy flowers in search of food. This indicates a good colour DISCRIMINATION ability. None the less, in an experiment in which males pursue dummy coloured female butterflies dangled from a fishing rod they behave as if they were completely colour-blind. In this sexual context the male grayling butterfly just does not attend to colour cues, only to brightness: the darker the model the better. Similarly, touch stimuli on the snout of a resting cat have no particular consequence, at best perhaps some withdrawal or licking behaviour. But when the same cat is hunting, the snout becomes highly sensitive, and the slightest touch releases biting. It is as if the motivation of the cat directed its ATTENTION to these particular stimuli in preference to others, a sort of optional stimulus selectivity.

While sometimes the direction of attentiveness, as in the above examples, makes FUNCTIONAL sense, in other cases stimulus selection may be due to the fact that the brain simply cannot deal with the wealth of information that floods into it and has to ignore some of it. Rats (*Rattus norvegicus*) that have learned to distinguish visual patterns (say a white square from a black circle) illustrate this, for on closer examination they are found to have mastered the discrimination only on the basis of a partial stimulus feature, and to have disregarded other distinctive cues. In our example some might choose the brightness difference, others the shape difference, but none both.

Some stimuli in the environment recur repeatedly, but may prove unimportant for the adaptiveness of the behaviour of an animal Thus they need not be attended to. The process of HABITUATION represents an additional stimulus selection mechanism that deals with this situation. For example, a colony of black-headed gulls (*Larus ridibundus*) nesting near to an army gun range did not react to the firing noise. However, when a rocket was launched for the first time the birds panicked in response to the hiss. Some days later, however, they ignored this noise too.

The phenomenon of attention implies that at one or more levels of the sensory system, higher centres of the brain must be able to influence the flow and processing of sensory information at lower levels. So-called *centrifugal* or *efferent* neural pathways to virtually every relay station, sometimes even to the receptors themselves, have been described, and may in fact be those mediating such attentional control.

There remains to be considered how the highly complex networks of sensory systems are put together during the development of the individual. There is no doubt that GENETIC information plays a crucial role. An example is provided by Siamese cats which have a single gene mutation (i.e. a sudden and relatively permanent change of a gene) that produces a rearrangement of the nerve cell connections in the visual system. Because of this, information from both eyes does not converge as it does in cats that have the normal genes. The result is that Siamese cats have deficient depth vision (their well-known squinting is a by-product of the neural fault). On the other hand, it can also be shown that experience is important in organizing sensory systems. Kittens that are brought up in horizontally or vertically striped cages develop visual cortex neurones that respond exclusively to horizontally or vertically oriented line patterns respectively. In normally reared kittens these neurones, as an ensemble, respond to lines of all orientations. Of course, when animals learn to recognize very specific stimuli, such as their mate or offspring, we must in any case assume that sensory mechanisms are being modified by experience (see LEARNING). J.D.

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