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CHEMICAL SENSES. The distinction between a sense of smell (olfaction) and a sense of taste (gustation) cannot easily be made in many animals. *Chemoreception*, or chemical sense, is a useful inclusive term that also indicates the most important property of these two senses: the capability of identifying chemical substances and of detecting their concentration. The term chemoreception has the added advantage that it allows the inclusion of an often forgotten, but important and varied group of receptors within the body: the internal chemoreceptors. These are similar to external chemoreceptors, but are concerned with monitoring the concentration of a number of substances in the body fluids. Strictly speaking, virtually every nerve-cell functions as a chemoreceptor, in that it reacts specifically to substances released by other nerve-cells. While many internal chemoreceptors play a role largely restricted to visceral regulation (for example, carbon dioxide receptors located in the walls of the carotid arteries and aorta are involved in the nervous control mechanisms of blood circulation), others are important in registering levels of HORMONES that reach the BRAIN, and in detecting nutrients in the blood.

Compared with many animals, human beings have a rather reduced sense of TASTE AND SMELL. For this reason we tend to underestimate the role of the chemical senses in determining the behaviour of numerous animals. Chemoreception was certainly the first sense to develop in the course of EVOLUTION. Primitive organisms are critically dependent on the right kind of chemical environment for survival and reproduction. As soon as motility evolved, chemical sensitivity capable of directing such behaviour towards life-supporting surroundings must have conferred powerful SURVIVAL VALUE. The behaviour of present day lower organisms is still often restricted to *chemotaxis*, i.e. movement controlled by chemoreception. The bacterium *Escherichia coli*, for example, is known to be attracted by and to migrate towards sources diffusing oxygen, glucose, galactose, serine or aspartic acid. There are however, GENETIC mutants of the bacterium that are not responsive to one or other of these substances. This indicates that specialized receptors, probably in the form of chemically specific sites on the outer membrane, are responsible for this sensitivity. Similarly the unicellular protozoan *Amoeba proteus*, is selective as to what it engulfs, digests, and incorporates into its cytoplasm. The feeding behaviour is released by certain proteins, basic dyes, and salts.

Chemoreception is similarly widespread among the multicellular invertebrate animals. An example is the much studied sea hare (*Aplysia*, a marine mollusc that feeds on a single species of seaweed). If sea water that has been in contact with this seaweed is injected into a corner of an aquarium containing sea hares, they immediately crawl to that point. Recording the electrical activity of nerve-cells demonstrates that those receiving input from the tentacles are responsive to diluted extract of seaweed: the chemoreceptors are thus located on these appendages. How the chemical recognition of a particular seaweed is achieved is not understood, and several test substances not characteristic of the specific seaweed also lead to excitation of these nerve-cells.

Many species of starfish (Asteroidea) feed on sea urchins (Echinoidea), and many of these move away when a starfish approaches. This response must be chemically elicited. Interestingly, in one such predator–prey pair, the sea urchin *Strongylocentrotus* is not bothered when the predatory starfish *Pycnopoda* is already feeding, and is thus not on the prowl. Whether the starfish does not release the warning substance in this situation, or whether chemicals escaping from the injured prey inhibit the escape response, is not known.

Hydra littoralis, the small freshwater coelenterate, is a classical subject for chemosensory studies. It catches its prey with its tentacles, kills it with its *nematocysts*, veritable miniature poisoned arrows, and then contracts the tentacles towards its open mouth and ingests the prey. This latter part of the feeding behaviour is released quite specifically by a small protein constituent called gluthatione. Other species of coelenterates respond in a similar manner to gluthatione, but some respond specifically to other substances, such as proline and leucine.

Many stationary marine organisms go through a larval phase in which they are mobile, and form part of the plankton. When the time comes to become sessile they choose the permanent site by chemical criteria. The larva of the common barnacle (*Balanus balanoides*) prefers to settle on slate that has been impregnated with an extract of adult sedentary barnacles, as opposed to slate that has not been so treated. The active component of the extract does not lose its potency even when exposed to the extreme heat of 200 °C, or to concentrated sulphuric acid. It is thought that a very stable protein is present in the cuticle of arthropods, and that the receptors suspected of being involved in the recognition of this substance are located on the antennae of the larvae.

In a variety of insects chemoreception has developed to pinnacles of sophistication. Here it is also possible to draw a distinction between olfaction and gustation, in the sense that some of their chemoreceptors are specialized for the detection of very low concentrations of substances, whereas others only respond to high concentrations. The olfactory receptors are generally situated on the antennae, and in some insects these have developed to be veritable scent-molecule sieves. They are studded with thousands of porous sensory hairs, each containing a thin protrusion of a sensory cell which sends its *axon* directly to the insect's brain. A remarkable example is provided by the antennae of the males of many moths, the silk moth (*Bombyx mori*) being one of them. The females have an abdominal gland that secretes a scent. This is carried down-wind, and when detected by the males causes them to move upwind (see TAXES) until they reach the source. By this means the females can attract males over distances of several kilometres. In the silk moth the substance secreted by the female is a polyalcohol called bombykol. Because of the striking effect it has on the behaviour of the male it is called a PHEROMONE, by analogy with hormones circulating in the blood. When it reaches the sensory cells it causes them to become electrically activated. These in turn send nervous messages to the brain, where the detection of the pheromone is registered, and causes the behaviour already described. From experiments it is known that the relevant sensory cells react only to bombykol and not to other related chemicals. In contrast the olfactory sense of other insects is more general. Honey-bees (*Apis mellifera*) for example, can be trained to distinguish a number of different scents. Correspondingly, their antennae carry receptors that are responsive to a variety of substances.

Contact chemoreceptors, analogous to taste receptors, are found on the *tarsi* (feet) and mouth-parts of insects. Those located on the tarsi of the blowfly *Phormia regina* are hairs with perforated tips, and contain the processes of several sensory cells. One of these responds to salt solutions, another to sugar solutions, yet another to pure water (a fourth does not respond to chemicals, but is sensitive to the bending of the hair). These receptors control the extension of the fly's *proboscis* (sucking tube).

In vertebrates the olfactory sense is also specialized for the detection of low concentrations of chemical substances, typically ten thousand molecules per millilitre of air or water. It is mediated by sensory cells lining more or less extensive patches of nasal mucous membrane. The area they occupy is a fairly good indicator of the olfactory capabilities of a given species. The sensory cells are ciliated, the *cilia* forming a great tangle embedded in a layer of mucus. A species of average olfactory capabilities possesses some hundred millions of receptor cells, each of which sends off a nerve axon. The axons make up the olfactory nerves, and these terminate in the olfactory bulbs, brain centres in which the neural information about smell undergoes complex processing. The size of the bulbs is a good guide for the assessment of the olfactory capabilities of a species. Secondary nerve fibres carry the higher order olfactory information to other parts of the brain.

Recordings of the electrical activity of olfactory cells in many species of vertebrates have revealed that they are of a generalized type; that is, each cell responds to a wide variety of substances, either by being inhibited or by being activated to various degrees by each of them. Each receptor appears to have its own sensitivity spectrum to scents. In contrast, behavioural studies done in man suggest that there are about seven primary scents: ethereal, camphorous, minty, floral, musky, putrid, and pungent. The results from these two types of research cannot be easily reconciled, and it is fair to say that the mechanism of the sense of smell is not completely understood. This also applies to the processes involved in the chemical recognition of scent molecules as they reach the receptor cells.

As to the multifarious role of olfaction in the behaviour of vertebrates a few examples must suffice. After MIGRATION, Atlantic salmon (*Salmo salar*) return to their native river where they spawn; they are guided by the smell of the local water to which their IMPRINTING occurred as fry. If, at the fork of a stream, they head into water that does not carry the native scent, they let themselves drift downstream until they perceive it again, and try an alternative course. Minnows (*Phoxinus phoxinus*) and many other fish that live in a school scatter hurriedly as soon as they smell an injured member of their own species, perhaps one mauled by a pike (*Esox lucius*). A specific warning substance contained in the skin seeps out through the wounds of the victim and triggers this fleeing response. Some birds, contrary to widespread belief, can smell quite acutely. Vultures (Cathartidae) are thought to locate carrion by smell. Kiwis (Apterygidae), being nocturnal, also seem to locate food by its scent. Voles (*Microtus*) distinguish individuals of their own local variety from those of other varieties by their odour. Male rhesus macaques (*Macaca mulatta*) identify females in heat through a specific sexual pheromone which is secreted by the vagina during the receptive phase.

Some vertebrates, including certain mammals, possess an additional olfactory organ known as *Jakobson's organ*. In lizards (Lacertidae) and snakes (Serpentes) it is located within cavities with two openings to the roof of the mouth. The animal appears to introduce scents into these cavities with the tip of its forked tongue. In other animals, e.g. the golden hamster (*Mesocricetus auratus*), these organs, also known as *vomeronasal organs*, are located within the nasal cavities. If the nerve supplying the organs is cut in male hamsters, their sexual behaviour is markedly impaired. Destruction of the olfactory mucous membrane proper does not have such an effect. This suggests that the male's vomeronasal organ is specially adapted for the reception of sexual smells produced by the female.

The gustatory sense of vertebrates, like that of insects, is sensitive to high concentrations of chemicals (typically billions of molecules per millilitre of water) and is mediated by sensory cells located within the mouth and in some animals also by receptor cells located in the gill cavity, or on the body surface. The receptor cells themselves are clustered within structures known as *taste buds*. Only a fringe of hair-like processes protrudes into the open through the narrow neck of an enveloping structure. The buds, of which a domestic cat (*Felis catus*), for example, has some fifteen hundred, occur in groups within structures known as *papillae* which can be seen on the tongue with the naked eye. Three types of papillae can be distinguished on the human tongue: *folliate*, *fungiform*, and *vallate*. The vallate types are restricted to the base of the tongue, while the two former types predominate respectively on the edges and on the tip of the tongue. Man appears to interpret the taste of substances with reference to four basic taste qualities: salt, sweet, sour, and bitter. The sensitivity to these qualities is not evenly distributed over the surface of the tongue. The tip is more sensitive to sweet, the base to bitter, while areas particularly sensitive to salt and sour lie between. However, the basic tastes are not strictly associated with stimulation of one or the other type of papillae, as experiments in which single papillae are stimulated with small drops of chemical solutions show.

While the taste of some substances relates reasonably well with their chemical nature, for example all sour-tasting substances are acids, it does not do so in other cases. Bitter-tasting substances, for example, are a very heterogeneous group of chemicals. Most sweet-tasting substances are chemically similar, i.e. sugars; but some do not conform to this rule, such as lead and beryllium salts, or the well known artificial sweetener saccharin. Salty taste is generally associated with inorganic salts, but some of them do not fit this rule. Magnesium salts, for example, are perceived as bitter by human beings.

Electrophysiological recordings from single fibres of the lingual nerve of rats give results that do not agree too well with the existence of the four basic tastes deduced from behavioural experiments. A fibre, for example, may respond markedly to one salty substance (sodium chloride), but not to another (potassium chloride). Another one responds to acids as well as to some salty substances, and so forth. How this information is sorted out in the olfactory centres of the brain is not well understood.

Certain human individuals cannot taste very specific substances. A fairly common case is the inability to detect the bitter-tasting compound phenylthiocarbamide and some closely related substances. This inability is inherited, and is interesting because those taste-blind to

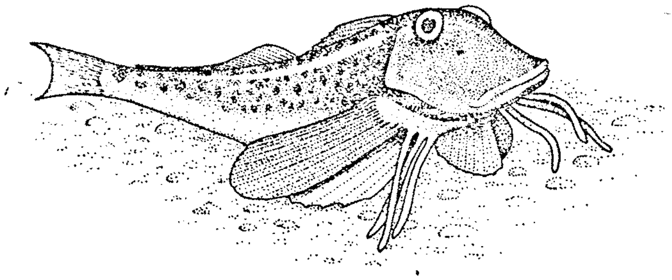

Fig. A. The North American sea-robin (*Prionotus*).

phenylthiocarbamide can still taste other bitter substances. Similarly other animals seem to perceive certain substances differently from us. Saccharin, a substance that tastes sweet to us, seems to taste somewhat bitter to rats (*Rattus norvegicus*). Quinine, a compound that tastes exceedingly bitter to human beings is hardly tasted by pigeons (*Columba livia*), even though they can taste other bitter substances.

The sense of taste is, of course, mainly concerned with FOOD SELECTION and choice of drink. Rats made salt-deficient will preferentially choose food or drink containing sodium chloride. Rats will also learn to avoid food with a specific taste if previously they have been made ill by consuming it. Fish are interesting in that many of them have taste buds on the body surface. The North American sea-robin (*Prionotus*), portrayed in Fig. A, even has specially modified pectoral fin rays, the tips of which are studded with gustatory receptors. The fish samples the substrate with its fin rays, and responds to the taste of food by digging with its mouth. Mouthbreeding cichlid fish (Cichlidae) appear to distinguish their own and foreign fry by taste: the latter may be snapped up by a parent fish, but they are then spat out again. J.D.

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