

---

## THE SENSES IN PERSPECTIVE

---

LOUW FEENSTRA  
JOHANNES BORGSTEIN

---

**ABSTRACT.** In this paper we explore the similarities and dissimilarities between the various human senses and those of a variety of animals and even plants. To the original five senses a number of "sixth senses" have been aggregated; the sense of equilibrium, the vomeronasal organ and, according to some, the immune system and even language. The cells themselves respond to an amplitude of external stimuli, and science has come to view 'perception' as any system used to acquire knowledge. We might define a sense as: the assembly of a sensor that transduces incoming energy into another form, collected by some part of the central nervous system that transports it and feeds it in an altered state into some part of the brain that is able to 'recognize' this. Senses do not function in isolation, but the 'sensors' or 'receptors' are connected to a system of (re)action, with which it forms one unitary system making some meaningful activity possible.

---

**KEY WORDS.** Senses, sense-organs, perception, knowledge system, reaction system, stimulus, transduction.

---

*Nous sommes des ectodermes*  
Paul Valéry, *L'Idee Fixe*

We are immersed in a vast and chaotic chemical electromagnetic soup of which our senses detect only a narrow spectrum—as much as is necessary for survival.

Anonymous

Each of us lives within the prison of his own brain. Projecting from it are millions of fragile sensory nerve fibres, in groups uniquely adapted to sample the energetic states of the world around us: heat, light, force, and chemical composition. That is all we ever know of it directly; all else is logical inference.

V.B. Mountcastle\*

### INTRODUCTION

The long-term management of patients with hearing loss and deafness, disturbances in equilibrium, loss of the sense of smell and diminished taste facility must eventually lead to an interest in senses '*An sich*'. We explore in this paper the similarities and dissimilarities between the various human senses and those of a selection of animals and even plants.

Traditionally it was maintained that man is endowed with the five senses: vision, hearing, smell, taste and touch. To these a number of "sixth

senses" have been aggregated at various times: the sense of equilibrium, Jacobson's organ, also called the vomeronasal organ and, according to some, the immune system.

Other species of the animal kingdom have developed different senses, some of which do not exist in humans (see table 1), while similar senses may have in other species a different range of action (see table 2). Some specific sense-like reactions have even been described in the kingdom of plants.

To discriminate between bodily systems that belong to (the) senses and those systems that do not has become increasingly difficult as science has gradually come to view 'perception' as any system used to acquire knowledge, where 'knowledge' is rather loosely defined.

For a starting definition of a sense we will use "any specialized part of a living organism that is able to react to some specific stimulus."

A structure without senses implies a configuration that is not able to react to any specific stimulus. Such a structure would not be an 'active' living thing (a comatose body would still respond to stimuli), though it might possibly be a living organism in a more dormant form, like a spore, or some 'sleeping' bodies like, for instance, a not yet active grain of seed or an encapsulated bacterium. Even these structures must respond to certain stimuli or they would not revert to more active forms. Thus one might in general say that a structure without reactions is "dead as a doornail<sup>1</sup>."

Science makes a distinction between stimuli that reach sense-organs from outside the body and those from within the body itself. Senses belonging to the former type are called exteroceptive senses, the latter enteroceptive or proprioceptive senses.

In most if not all *biomedically* oriented books on perception the description of a sense is usually causally and materialistic formulated as:

it asserts that perceptual experience depends on the operation of the nervous system, with no requirement for the involvement of some noncorporeal force. Perceptual experiences is a functional property of brain processing, constituted of neuronal and physicochemical activity, and embodied in, and inseparable from the active brain. Once generated from neural events, the higher order mental patterns and programs have their own subjective qualities and progress, operate and interact by their own causal laws and principles which are different from and cannot be reduced to those of neurophysiology<sup>2</sup>.

We might define a sense more or less as the assembly of a sensor (some specialized cell system) that transduces incoming energy into another form, picked up by some part of the central nervous system that transports it and feeds it in an altered state into some part of the brain that is able to 'recognize' this. Generally it is considered that senses do not function in

isolation, but that their 'sensors' or 'receptors' are somehow connected to some system of (re)action, say a motor organ, with which it forms one unitary system making some meaningful activity possible.

Even unicellular systems clearly are able to react to some stimuli and therefore might also have one or more 'senses' at their disposal, although they do not have the neurological system of the more complex organisms.

The most fundamental problem organisms face is to maintain the conditions suitable for their continued existence and functioning. Homeostasis refers to the process by which feedback information is used to maintain a constant state of certain basic conditions such as temperature, water content, or position. In many cases, the feedback information is sensory in nature, informing the organism about its external environment<sup>3</sup>.

One might argue that if indeed the activities of collecting information and reacting thereon are in essence a 'sense', the individual cells of any multi-cellular organism also contain 'senses' as they are able to exchange information with neighboring cells and sometimes with cells, organs and different tissues across some distance. This is the stance taken by some immunologists.

Within this definition, language also may be considered a sense, as it allows us to collect information about our environment and react to this. Much of human life as we know it would be impossible without the abstract symbolic thought processes engendered by language.

#### LIMITS

The senses are the links to the external world, the organism communication channels if you like. Environmental events that fall outside the range of sensitivity of the sensory channels will simply not be experienced, cannot be experienced. Science has allowed us to detect some of these events indirectly by using instruments, since we cannot integrate them into our perceptual universe. Some instruments amplify energy, making weak signals strong enough to stimulate the senses, as a microscope amplifies vision. Other instruments convert energy that is outside the normal bounds of the senses into a form that is within perception, as a Geiger counter that processes information about the presence of radioactivity.

There is furthermore an interesting discrepancy between the limits of awareness and the limits of bodily reaction to some specific stimuli. It has been shown, for instance, that animals, including man, react on some specific pheromones (volatile chemicals) that reach the vomeronasal organ while unable to notice consciously those volatiles<sup>4</sup>.

The limits of action or the scope of the different senses of humans is not the same as those of other animals (see table 2). Different species have

access to different kinds of information. Essentially, animals and humans have different 'environments'. Members of different species interact with their (own) physical and biological worlds in ways that reflect their own unique requirements and capabilities. Stated differently, "although all animals inhabit the same *physical* world, their *perceptual* world may differ radically<sup>5</sup>." Even in man, the common idea that we share a common perceptual environment is little more than a collective hallucination.

#### DIFFERENTIATION

Classification of senses may be conveniently based on the different nature of their specific stimulus. It does not seem necessary to present an exhaustive list of all the senses, but it might be helpful to give a brief overview. It should be noted that while most sense-organs can be stimulated in more than one way, each has only one specific stimulus. For instance, pressure on the eyeball, cutting of the optic nerve and electrical stimulation of some parts of the cerebral cortex may all lead to some light-like experience. However, the stimulus most specific for any sense organ is the one that uses least energy. For the eye, the specific stimulus is 'visible' light (if we may be permitted a mild circular argument).

The specific stimulus usually is described in physical or chemical terms (see table 1). Sometimes a specific reaction of a living structure to some specific stimulus is noticed while the specific sense has not been named or is not (yet) known. Pseudoplasmodia of the cellular slime mould, *Dictostelium discoideum*, for instance, have been shown to migrate in thermal gradients away from a temperature several degrees below that of their acclimation temperature, but how it achieves that is not clearly understood<sup>6</sup>. Similarly, a homing pigeon can find its way over hundreds of miles of unknown territory.

Another possible classification of the senses makes use of the proximity of the perceiver to the object of perception. Touch and taste are then called the 'near senses'. Volatile chemicals from an odorous substance are diluted with distance, so smell often works more effectively for substances in the vicinity of the nose and might be called an 'intermediate sense'. Seeing and hearing are far, or 'distance senses'. They can pick up information originated as far away as distant galaxies, making possible to observe objects located in the past. They provide advance warning of approaching danger and guide the search for desired objects at a distance<sup>5</sup>.

#### VISION

Light is one of the stimuli most utilized for obtaining information, as many organisms live where light is available at least some of the time. Light is a

distinctive stimulus in that its intensity, direction, frequency and polarization can all convey useful information. Most animals obtain information about objects in their environment from reflected sunlight, but some are able to generate their own light.

Physically light is just a form of electromagnetic radiation. Since virtually all matter essentially consists of oscillating electrical discharges, electromagnetic energy exists in abundance. Any animal that can sense electromagnetic radiation benefits in several ways. First, electromagnetic radiation travels very rapidly ( $3.10^8$  meters per second in a vacuum) so information may be picked up from distant sources with minimal delay. It also tends to travel in straight lines, so that images retain important geometrical characteristics of the object that reflected the radiation to the eyes.

Light visible to the human eye has a frequency of about 300 nanometers (violet) to 700 nm (red). Whether this range is fortuitous or not is debatable, for in principle other portions of the electromagnetic radiation might equally well have been used to bridge the distance between perceiver and objects. Other frequencies might have disadvantages, and most of the energy in the ultraviolet range for instance is absorbed by molecules in the earth's atmosphere (mainly nitrogen and oxygen) and consequently rarely reach the objects in our environment. Light is also useful as a medium of information about the world because it interacts with the surface molecules of many objects, in the form of reflection and absorption. This allows light to convey information not only about the presence and absence of objects but also about the structure of those objects and their surfaces.

Longer wavelengths interact differently with solid objects with sizes relevant to living systems, and penetrate opaque objects rather than being reflected by them, thereby warming them.

The human eye is able to see from a minimal intensity of about  $10^{-6}$  candelas per square meter, to the maximal intensity of about  $10^7$  candelas per square meter, above which there is risk of damage to the eye. The human's eye therefore has a scope in the range of  $10^{13}$ .

Eyes being extensions of the brain are placed in the skull near such organ. The eyes of predators are placed in front of the head to give a better depth perception, while prey animals tend to have their eyes placed more laterally on the skull for a wider angle of vision.

Light falling on the retina preserves the spatial structure of the object from which it is reflected. This image falls on some of the rods and cones, the two major classes of photoreceptors of the retina. Animals with a preponderance of rods are more active at night, while those with more cones during daylight. The human eye, having both rods and cones resembles a camera with two different kinds of film at once. Each rod and cone gauges the amount of light that hits its receptive retinal field,

together resulting in separate neural messages passed on to a network of so called collector cells of the retina. The output of the collector cells provides the input for the retinal ganglion cells. These in turn signal the outcome of their processing by generating action potentials, brief electrical discharges carried by their axons. All these axons together make up the optic nerve.

The optic nerve is composed of the orderly bundled axons from all the retinal ganglion cells. In the same methodical fashion the axons travel to the nuclei within the central nervous system and thence to the cortex of the occipital brain where they terminate in specific regions.

Vision is able to *detect*, picking out objects from their surroundings. It is able to *discriminate*, distinguishing one object from another; thus we are able to *identify*, recognizing the object that is seen. To delineate an object it has to have contrast, i.e., there must be a detectable difference between the amount of light reflected by the object and its surroundings. In addition we notice the form, which may be defined as the spatial arrangement of an object. Once perceived, the information must be processed, so that the organism is able to respond to the information, and sometimes become consciously aware of it.

Structuralistic approach treats perception as an analytical process, decomposing complex forms into small, simple elements. The gestalt theorists' approach by contrast stresses the grouping by organizational properties into figures. Contemporary thinking endorses the multiple spatial channel theory, i.e., detection of any spatial target depends on responses generated in a set of visual cells tuned to contours of a particular size and orientation. Each set of cells is responsible for the ability to see targets over some range of sizes and orientations<sup>5</sup>.

#### OTHER VISUAL SYSTEMS

Light-reception organs come in a wide range of sizes and designs, from the simple organelles of single-cell organism to the highly complex mammalian eye. Photosynthetic bacteria move toward optimal light intensities but most bacteria must use the energy of kinokinesis, as they are too small to develop light receptors that have directional specificity.

Plants also obtain information about their environment from light, in addition to obtaining energy for photosynthesis. The higher plants seem to have at least two sensory photoreceptor pigments: photochrome and one or more unidentified blue-light receptors.

Most animals, at least the arthropods, mollusks, and vertebrates have a similar type of photopigment (rhodopsin) for light detection.

Different photopigments that absorb light most efficiently in different regions of the spectrum are used. These photoreceptor pigments have been incorporated into specialized sensory structures with a variety of

designs during the course of evolution. The photoreceptors of vertebrates are fundamentally different from those of arthropods, which are sensitive to the polarization of light.

The simplest eyes are pigment cup eyes and pinhole eyes of simple invertebrates. More sophisticated designs employ a lens that changes the direction of light by refraction, or use reflecting elements to direct light from onto a specific receptor cell. The compound eyes of both crustaceans and insects consist of a hexagonal array of elements that project light from a particular direction onto the appropriate receptor cells although there is a great deal of variation in the details of how the different systems function<sup>3</sup>. All vertebrates have single-lens eyes of similar structure, with the exception of a few cave-dwelling species that have been in the dark for so many generations that the unstimulated eye function has been lost entirely. In mammals the cones include several types, each containing a different photoreceptor pigment that confers sensitivity to different parts of the light spectrum.

The number of receptor cells an organism might have variances between one in unicellular algae to 130 million in humans.

The visual capabilities of different species vary greatly. The visual field may diverge from 60° for algae, 169° for humans to 180° for fish (and almost 360° in the wily chameleon), while the resolution varies from 0.004° in the eagle, 0.01° in humans to 60° with algae. The threshold ranges from a radiance of 10<sup>8</sup> photons per second / square meter x steradian (shrimp), 10<sup>10</sup> photons per second / square meter x steradian (humans) to 10<sup>14</sup> photons per second / square meter x steradian (nautilus)<sup>3</sup>.

The polarization of light is used by bees and a few other flying insects for location and orientation.

The importance of vision in the interactions of organisms is further indicated by the fact that boundaries exist between major ecological zones in the relatively homogeneous environment of open water based on the presence or absence of enough light for vision. Marine ecologists identify three such fundamental depth zones, each containing its own species. The shallowest, the *euphotic* zone extends to a depth of <140 meters, where sufficient light still penetrates to support photosynthesis. The next zone, the *mesopelagic* appears to be determined by the depth to which sufficient sunlight penetrates to support vision, which is <1000 meters. The third zone, the *bathypelagic* zone receives no useful light from above and the organisms within it do not make daily vertical migrations<sup>7</sup>.

Mesopelagic animals generally have large, well-developed eyes, are bioluminescent and have bodies that are transparent, reflective, or countershaded. Bathypelagic animals have poorly developed eyes, little bioluminescence and non-reflecting bodies that strongly absorb blue light and thus look black, brown, or red when illuminated with white light<sup>7</sup>.

Mantis shrimp and some vertebrates can detect ultraviolet light beyond the human visual range using a photoreceptor with a peak sensitivity to light at wavelengths of around 350 nm <sup>8</sup>. The *Neogonodatylus oerstedi*, a marine crustacean has at least four types of photoreceptor for ultraviolet light that are located in cells of the eye known as R8 cells. These photoreceptors are maximally sensitive to light of wavelengths 315, 330, 340 and 380 nm. This indicates a remarkable color-vision system that may be unique and useful in their habitat; the top few meters of water in tropical coral reefs, making the colors perhaps even more vibrant than we could perceive them <sup>9</sup>.

Camouflage is another testimony to the extent that predators employ vision to locate and identify their prey. Four fundamental steps in effective camouflage are identified: (1) *color resemblance* to the background; (2) *countershading* which uses absorptive pigmentation and reflection to destroy the natural patterns of brightness that would otherwise reveal the shape of the organism; (3) *disruptive coloration*, which uses high-contrast color patterns to interfere with perception of the true outline of the organism of its motion; (4) *shadow elimination* which modifies the form or orientation of the organism.

#### NON-VISION REACTIONS ON LIGHT

Light and dark has immediate effects on sleep and wakefulness in mammals. Bright light has immediate alerting effects in diurnal mammals whereas darkness promotes sleep. On the other hand, bright light induces sleep and darkness increases wakefulness in nocturnal mammals. These responses to changes in light conditions appear to be mediated by the superior colliculus and the pretectum region independently from cortical vision and circadian rhythms. The eyes seem to release impulses to different areas of the brain with different effects.

In addition to the well-described specialized light receptors there exist a variety of evidence that many organisms possess poorly characterized responses to light that are not mediated by any known receptors. In animals this is sometimes referred to as dermal light sense or extra retinal photosensitivity <sup>3</sup>.

#### INFRARED ORGAN

Some animals have organs that are sensitive for infrared light <sup>10</sup>. The larvae of the beetle *Melanophilia acuminata* can only develop in freshly burnt wood. Forest fires are approached by the beetles in large numbers from distances of up to fifty kilometers. The beetles do not use olfactory or auditory cues to detect forest fires but a paired thoracic pit infrared organ, situated next to the coxae of the middle legs. These organs consist of an infrared sensillum reacting in the wavelength range of 2.5 micrometers to 4  $\mu$ m. which corresponds to the emission maximum of a forest fire. An

intensity of only 0.06 miliwatts per square centimetre is sufficient to cause twitching of their antennae. The spheres of the pit organ consist of organic molecules that have stretch resonances near 3  $\mu\text{m}$ . and thus absorb strongly near this wavelength. Infrared absorption is converted into heat within fractions of a millisecond. This heating will cause a change in sphere volume that probably induces a deformation of the dendritic tip.

Infrared organs have also been observed in some species of snakes, crotalid and boid snakes, where infrared radiation warms up a thin membrane innervated by fibres of the trigeminal nerve. These act as true thermoreceptors, while those of the *Melanophilia* act according to a photo-mechanical principle.

#### HEARING

The ear is sensitive for vibrations, transmitted through some elastic medium such as air or water, causing tiny collisions among the molecules in that medium. These travel as waves of alternating high and low pressure accompanied by back-and-forth movement of the medium in the direction the wave is propagated. Close to the sound's source, the movement of the medium resembles the flow of an incompressible fluid with no elastic properties. It is useful to distinguish between this *near field behavior* and the *far field behavior* of true sound, although there is often a significant transition region in which both properties are important. The boundary between the two is usually at a distance from the source on the order of the wavelength of the sound. This distinction is similar to the one between vibration and sound. The sound wave spreads outward from the source of vibration constituting acoustic energy. The speed with which these waves travel is about 340 meters per second in air and 1 500 meter per second in water. Like the human eye the human ear can handle energy levels that can differ by a factor of at least  $10^{13}$ . The limits of the ear for sound levels are on the one hand the threshold of hearing of approximately 20 micropascals at 1 000 Hertz and on the other hand the threshold of pain.

Frequency is the measure of how rapidly a sound wave oscillates. It is usually measured in Hertz, which is one complete cycle per second. Pitch is the perception of a fundamental frequency of vibration that produces harmonics in the sound. Frequencies above the range of human hearing, about 18 000 Hz. are called ultrasonic, while those below the range of about 20 Hz. are called infrasonic. The actual mixture of frequencies generates a multidimensional perception of timbre or quality.

The region of the sound spectrum responsible for conveying human speech runs from 150 Hz. to 8 000 Hz.

Sounds travel through and are intensified by the auricle and the auditory canal, together forming a kind of a directional microphone. Reaching

the eardrum and on to the ossicular chain that transfers the airborne vibrations into fluid vibrations of the inner ear.

Within aquatic surroundings water borne vibrations can travel without any hindrance into the fluid containing inner ear of an aquatic animal. Air borne sounds, however, pushing directly against the fluid containing inner ear would be reflected, and lose about 99 per cent of their acoustic energy. The middle ear is therefore thought of as nature's evolutionary device to compensate for this energy loss when reptiles first moved from an aquatic environment to land. The middle ear thus acts as an acoustic impedance transformer between air and fluid by the combined action of the surface area differences between the drum and the oval window (the entrance to the fluid system of the inner ear), the lever action of the ossicular chain and the buckling motions of the tympanic membrane.

The inner ear in turn transforms the incoming vibrations into electrical potentials thereby analyzing the original sounds into their component frequencies. The potentials take the form of neural impulses within the auditory nerve that contains about 50 000 individual fibres. The nerve branches into several different pathways that eventually reconverge within the auditory cortex in the temporal lobe. These various pathways process different aspects of auditory information. They contain neurons whose response properties enable us to specify where sound is coming from and other neurons to identify what the sound is long before it reaches consciousness.

The range of hearing acuity or sensitivity in animals is not the same as that of humans<sup>11</sup> (table 2). Other aspects of the hearing of different species, like the acuity of sound localization, the ability to hear that a sound has changed in frequency and the ability to dissolve different frequency components of a complex sound or background noise differ also.

The humans ear can discriminate sound intensities (to tell whether one sound is louder than another) that differ by about one to two decibels. Small mammals and birds may require two or three times larger differences for intensity discrimination.

The information-processing principles originally identified by gestalt psychologists for vision have close analogies in auditory sensation. For example, the synchronous onset of two sound frequency components is interpreted as indicating that they belong to the same event. This strategy helps allocate different sound components appropriately to different sound sources which often exist simultaneously.

The most important kinds of general information concern the direction and distance to the source and the nature of the acoustic environment between transmitter and receiver.

Hearing is the first leg in the hearing-language-speech triad that allows for spontaneous development of language, only found in man.

## OTHER HEARING MECHANISMS

## ECHOLOCATION BY BATS

Field observations and behavioral experiments with echolocating bats document remarkable, sometimes seemingly impossible, skills at detecting, localizing and discriminating the nature of targets by echoes of emitted sounds. Using either CF/FM or FM sounds (CF=constant frequency; FM=frequency modulated sounds) in ways adapted to different echolocating conditions, and using different mechanisms of information processing, bats behave as if they can construct a full acoustic image of nearby objects in space by the echoes of each pulse. Ingenious behavioral experiments have led to a number of interesting and controversial models of how they might be obtaining the necessary information. Neurophysiologic experiments with both CF/FM-and FM-emitting species have revealed neural organization and functional specializations associated with each echolocation strategy<sup>12</sup>.

## ULTRASONIC HEARING BY FISH

*Alosa sapidissima*, an American shad, a species of clupeid fish, can hear sounds higher than the usual 2–3 kHz. sounds that teleost fishes usually hear. It is able to detect sounds up to 180 kHz. They are thus able to hear the “normal sounds that fish hear” and also ultrasonic clicks of one of their major predators, echolocating cetaceans. Ultrasound detection is probably not widely found among fishes, although it has been shown that cod, *Gadus morhua*, can detect 38 kHz. signals. Clupeid fishes have a unique ear structure in which a pair of thin air-filled tubes project from the swim bladder and terminate in air chambers that are connected with the utricles of the inner ear. The ability of clupeids to detect ultrasound may be an example of convergent evolution, for moths and other insects also have auditory systems capable of detecting the ultrasonic sounds of predators. Shad readily detect echolocating pulses of dolphins and, like moths, the response to the detection of such sounds is escape behavior. It is possible that the ability of clupeids to detect ultrasound is a preadaptation that evolved before there were echolocating predators. All extent clupeids share the auditory specializations of the ear, and fossil clupeids are known from the Lower Cretaceous period (130 million years ago), long before odontocete cetaceans evolved in the Oligocene epoch (25–38 million years ago<sup>13</sup>). The larger sea mammals, such as whales, also communicate in frequencies in the infrasound levels, undetectable by most other animals.

## SMELL

Olfaction is the most primitive of all the senses. The ability to detect chemical substances in the environment exists in all organisms, from the humble amoeba and its single celled cousins, to the most complex mammal.

Smell conveys signals about the environment (food, drink, cosmetics, sexual and mating possibilities, danger like fire and poisonous food, etc.) and it is accountable for most of the flavor of food and drinks. When someone loses his smell everything tastes insipid. Indeed, the flavor of food depends largely on smell.

In humans three specialized neural systems are present within the left and right nasal chambers; the main olfactory system with the cranial nerve I (N.I), the trigeminal somatosensory system with the cranial nerve V (N.V) and the terminal nerve with the cranial nerve 0 (N.0). The N.I mediates odor sensations, the N.V mediates through both chemical and nonchemical stimuli somatosensory sensations including those of burning, cooling, irritation and tickling. The coolness of menthol and peppermint are mediated by N.V, as for example, are the sharp sensations induced by ammonia vapors and various acids. The function of N.0, a ganglionated neural plexus that spans much of the nasal mucosa before traversing the cribriform plate to enter the forebrain medial to the olfactory tract, is unknown in humans. In some rodents disruption has been found to alter reproductive behavior <sup>14</sup>.

Most animals rely more on smell than humans do. A mole's nose, for instance, allows this animal to live in the dark confines of underground burrows, with virtually no need for eyes. Smell plays an enormously important role in the social lives of many animals. Many mammals send and are able to receive at least two dozen different types of odor messages, ranging from distress signals to age appraisal. For animals, mate selection and identification are often mostly governed by odor. Typically, the females of these species will emit sensuous scents, called pheromones, from specialized glands and these scents can be detected by potential mates. It has been proposed that this system continues in man, but as we are unable to rationally perceive these scents, they function below conscious level—seemingly irrational attractions must be rationalized and justified.

The stimuli for smell are *volatile*; a substance that smells must give off molecules to its surroundings; air or water as the case may be. Like appropriate stimulation reaching the eye and ear, smell also consists in an aggregate of information from several different objects. Inhaled air contains odorant molecules donated by a large variety of surrounding objects. The olfactory system is able to segregate this mixture into its constituents and its fluctuations in time. One prerequisite for smell is that the volatile molecules must be fat-soluble, for the receptor cells in the nose that capture volatile molecules are surrounded by lipid materials.

## THE VOMERONASAL ORGAN OR ORGAN OF JACOBSON

The vomeronasal organ in humans looks like two small pits, about a centimeter up from the nostrils, with tiny openings in their centers that are about 0.1 millimeters across. It consists of a pair of tiny dents on both sides of the nasal septum on top of the vomer bone. While its function in man is speculative, there is ample evidence that in other mammals this structure is clearly a sensory organ, playing a key role both in sex and other social interactions between animals. In rats, mice, hamsters, prairie voles and possums the vomeronasal organ is used to detect tiny amounts of pheromones. The organ is entirely distinct from the nose's main sensor for airborne chemicals, the olfactory epithelium, which detects everyday scents. In humans, the vomeronasal organ's sensitivity to steroids in skin extracts depends on the sex of its owner, suggesting in our species some role in subliminal sexual signaling

## MECHANICAL STIMULI (TOUCH, MOVEMENT, GRAVITY)

Arthropods usually detect stimuli through the movement of innervated hairs formed and protruding outward from the cuticle. These cuticular hairs may be coupled to various types of mechanical stimuli either by their mechanical properties or through contact with other structures. Spiders also have slit sensilla in their cuticles that provide sensitivity to deformations. Displacement of the substrate over only one nanometer may be detected.

Vertebrates are most sensitive to the mechanical stimuli that are detected by hair cells. These are the receptors in the lateral-line system in fishes and amphibians and in the organs of hearing and equilibrium in vertebrates. The hair cells' name is derived from the cilia projecting from the distal end of each cell. Bending the cilia in one direction leads to a strong excitation of the cell, while bending in the opposite direction produces a weaker inhibition of the ongoing activity. In most cases the cilia are in contact with a structure that moves under a specific type of stimulation. In the simplest case this type of structure is a gelatinous projection or cupula that sticks out into a flowing fluid to couple the flow to the cilia of several hair cells. In a steady flow the displacement will be approximately proportional of the flow velocity and the hair cells will become velocity detectors. However, in a changing flow the thickness of the boundary layer will vary, changing the force acting on the cupula. The cells then become sensitive to acceleration. Hair cells can thus function to obtain either information about the flow pattern over the body surface, as in the lateral-line system, or information about the acceleration of the animal, as in mammal semicircular canals. If the cilia are attached to an object that differs in density from the surrounding fluid, a gravity detector

is produced, which is at the same time sensitive to acceleration of the sense organ.

Fish and aquatic forms of amphibians can readily detect the relative motion of any solid object within a few centimeters of their bodies from the flow produced around the object acting on the lateral-line system. The hair cells on the surface, called free neuromasts, respond to a flow over the surface with sensitivities in the order of 1 millimeter per second. Most fast and persistently swimming fish have some of their lateral-line hair cells enclosed in canal organs that respond to local pressure differences proportional to acceleration of the fluid. The lateral-line system usually contains organs oriented in different directions so that the direction of stimulus flow can be resolved. The wide variety of lateral-line geometries can be understood as providing different speed-of-response and sensitivity trade-offs as well as directional and frequency specificity. Lateral lines seem to be more extensively developed in fish that live in the darkness of caves or the deep ocean. Lateral-line organs function at frequencies below 100 Hz. and match the frequencies of vibration of the animals during locomotion. The lateral-line system probably functions mainly to detect and localize obstacles in the environment along with prey, predators, and conspecifics.

Pressure sensitive organs, coined dome pressure receptors, have been found in the *Alligator mississippiensis* and other alligators' snouts, allowing those animals to sense tiny movements at water level if their heads are half emerged in the water. It has been shown that this sense-organ was probably already present some  $195 \times 10^6$  years ago during the Jurassic period<sup>15</sup>.

Interestingly, the *Heterocephalus glaber*, an almost blind rodent that lives underground, has mechanoreceptors attached to its incisors and to its few existing bristle-like hairs on an otherwise almost naked skin. This animal has well developed smell and mechanoreceptors, while its vision is almost non existent and its hearing restricted primarily to the low frequencies that are easily transmitted through soil. The cerebral cortex corresponding to the sensory systems of this animal are entirely different from those of its relatives and are specifically related to touch<sup>16</sup>.

Near field effects also occur in air. It has been demonstrated that near-field acoustics serves as an essential component of the dance communication of bees. In it the signal is transmitted by air-particle oscillations in the near field that are generated by wing vibrations. The effective range of such signals is limited to a few millimeters. Similarly, in the fruit fly courtship includes a song transmitted by wing vibrations at 166 Hz. that is detected by particle motion in the near field.

Solids are distinguished from fluids in having a tendency to return to their previous shape after undergoing a small bend or twist. They can thus

support a variety of transverse waves as well as the compression waves of sound. Any of these vibrations can provide organisms with information. In fact, many insects do use them for communication and they may be the primary mode of transmitting information within the nests of social insects. Solids are also distinct from fluids in that they support tension, which provides the restoring force for spider webs. The web-building spiders probably use substrate vibrations for a wider variety of information-gathering purpose than does any other animal. These spiders detect, identify, and localize prey caught in their webs mainly by its vibrations.

Information is often provided by forces that arise from direct mechanical contact with an object. Animals and even some plants make use of tactile information.

Touch does more than aid object identification. It also plays a major role in development and in social interactions. It has been shown in monkeys that touch deprivation early in life stunts growth, both physical and social<sup>17</sup>. In a way, touch can be construed as the most reliable of the sensory modalities. Where the senses conflict, touch is usually the ultimate arbiter. Imagine reaching out to grasp an object that you see, only to find nothing there. After the initial astonishment, you'd probably decide that it was your visual system that had been misled—touch, in other words, seems more trustworthy than sight<sup>5</sup>. Touch sensations can arise from stimulation anywhere on the body's surface. Indeed, the skin can be characterized as one large receptor surface for the sense of touch<sup>18</sup>. The skin on the human hand contains thousands of mechanoreceptors (sensitive to mechanical pressure or deformation of the skin), as well as a complex set of muscles to guide the fingers as they explore the surface of an object. The mechanoreceptors play a key role in analyzing object detail such as texture; the muscles make their major contribution when grosser features such as size, weight, and shape are being analyzed<sup>19</sup>. The hand and the finger pads convey the most useful tactile information about objects. In this respect, the hand is analogous to the eye's fovea, the region of the retina associated with keen visual acuity. As in foveal vision, touch acuity is best when the fingers move over the object of regard.

The distinct perceptual qualities produced by the tactile stimulation corresponds to some physical property of objects, i.e., the shape, the smoothness or roughness and the firmness. The skin contains different sorts of touch receptors which are not evenly distributed over the body. Females appear to be more sensitive to light touch than males. Surface temperature depends on the difference between the temperature of the touch organ and the object<sup>5</sup>.

## OTHER HYDRODYNAMIC SENSORY SYSTEMS

Hydrodynamic sensory systems have evolved many times in aquatic animals and not only as the fish's lateral line system. Rats, seals and sea lions use their whiskers for active touch discrimination, and probably for obstacle avoidance. These whiskers are heavily innervated by slowly and rapidly adapting afferent fibres that respond to tiny deflections of the hair shaft. Seals, *Phoca vitulina*, have a high sensitivity of their whiskers. They can detect water velocity at speeds as low as 245 micrometers per second, which in turn is several orders of magnitude below the water-particle velocities measured in the wake of a swimming fish of about 22 cms. in body length. Therefore the whiskers of harbour seals form a hydrodynamic receptor system with a spectral sensitivity that is well tuned to the frequency range of fish-generated water movements<sup>20</sup>.

Some birds also make use of hydrodynamic sensory systems. In a series of very elegant experiments it was shown that the sandpipers, *Calidris canutus*, living worldwide in coastal intertidal areas, are able to detect their favorite hard-shelled prey even when buried in sand beyond the reach of their bills<sup>21,22</sup>. They use as prey detection mechanism a large array of Herbst corpuscles (sensory organs that can measure the acceleration due to changes in pressure), that involves the perception of pressure gradients that are formed when bills probe in soft sediments in which inanimate objects block pore water flow. Repeated probing in soft, wet sediments allows red knots to induce a residual pressure build-up of sufficient strength to detect the pressure disturbance caused by a nearby object. The cyclic process of shaking loosely packed sand grains followed by gravitational settling into a closer packing, leads owing to insufficient drainage of the sediment, to a locally increased pressure disturbance that is 'pumped up' at each shake.

## IMMUNE SYSTEM

The immune system itself may in many ways be viewed as a sense organ, giving the brain information about things happening inside the body, much as the eyes and ears give external information. The chief agents of this sense organ are the cytokine molecules that are produced by the immune cells when microbes enter the body. These molecules help in the defense of the body against invading micro-organisms, but they also act on the brain and behavior. Micro-organisms influence sleep, an exclusive function of the brain. Given that the immune system acts as a sense organ it should have connections to the brain, either directly via the circulation, or along the vagal (and probably other) nerves.

There are close links between the brain and the immune system. Different moods may increase or decrease the activity of immune cells, sometimes for long periods of time—the humors of primitive Greek

physiology. Very basically, simple measures as sleep and expressing your feelings are good for your immune system while depression, chronic stress and insomnia are bad. The brain and the immune system exchange information via circulatory and nervous tracts; a kind of information exchange that is being studied within the framework of psychoneuroimmunology. The placebo effect is probably also mediated via these mechanisms

#### QUORUM SENSING

Quorum sensing or the control of gene expression in response to cell density, is used by both Gram-negative and Gram-positive bacteria to regulate a variety of physiological functions. In all cases, quorum sensing involves the production and detection of extracellular signaling molecules called autoinducers—a system analogous to olfaction. While universal signaling themes exist, variations in the design of the extracellular signals, the signal detection apparatuses, and the biochemical mechanisms of signal relay have allowed quorum sensing systems to be exquisitely adapted for their varied uses. It has been shown that quorum sensing modulates both intra- and inter-species cell-cell communication, and it plays a major role in enabling bacteria to architect complex community structures.

Autoinducer signals elicit specific responses from akaryotic hosts. It seems clear that bacteria communicate within and between species, and that eukaryotic hosts talk back<sup>23</sup>.

Autoinduction was first described in the marine symbiotic photobacterium *Vibrio fischeri*<sup>24</sup>. This organism, which colonizes the light organ of certain marine fish and cephalopods, expresses bacterial luciferase and thus luminescence when present in high concentrations in the light organs of the fish. It regulates expression of genes encoding bioluminescence in response to population density. The autoinducers are N-acyl-L-homoserine lactone (NHL) molecules which, owing to their size, passively diffusible nature, and the properties of the Gram-negative cell wall, are present in equal concentrations intracellularly and extracellularly. When the NHL-producing bacteria in the environment have reached a sufficiently high concentration, with the NHL signal molecules exceeding a threshold concentrations (about 10 nmol/L) these autoinducers bring about the quorum response of bioluminescence through bacterial luciferase production. The autoinducer binds to an NHL-responsive transcriptional activator called LuxR, which in turn binds TNA polymerase and initiates transcription of the *lux* operon after binding to a promoter element. The *lux* operon consists of several genes including LuxI—the autoinducer synthase. Thus after activation of the *lux* operon the basal levels of audioinducer rise

substantially in a true positive feedback loop since the autoinducer synthase is also transcribed <sup>25</sup>.

In animals and plants, membrane-permanent signal molecules, including steroid and brassinosteroid hormones, nitric oxide and methyl jasmonate, are well established as important regulators of development, cell differentiation and metabolism. Considering the widespread occurrence of such diffusible signals in eukaryotic organisms, it is not entirely surprising that prokaryotes also employ membrane-permeant signal molecules. It has become clear that a diverse collection of Gram-negative bacteria produce acylated homoserine lactone (HL) derivatives that function in cell-cell communications. Bacteria utilize acyl HLs to monitor the density of cells within their own population in a process called 'quorum sensing'. Each cell in the population produces a low basal level of the diffusible acyl HL via the activity of an acyl HL synthase, usually a member of the LuxL family of proteins. As the bacterial population density rises, the concentration of the acyl HL also increases. At a sufficiently high population density, in essence a bacterial quorum, the accumulated acyl HL interacts with a receptor protein, usually a member of the LuxR family of transcription regulators that acts to control a specific constellation of acyl HL dependent genes. In different bacteria, the basic mechanism of acyl HL regulation is conserved but the target genes are extremely varied. The first acyl HL quorum sensor to be fully described was that of the marine bacterium *Vibrio fischeri* that regulates bioluminescence (*lux*) gene expression. However, acyl HL quorum sensors in other bacteria regulate a range of functions including virulence genes in *Pseudomonas aeruginosa*, conjugal transfer in *Agrobacterium tumefaciens*, swarming motility in *Serratia liquefaciens*, and antibiotic production in *Erwinia caratovora* <sup>26</sup>.

#### CONCLUSION

All living cells and organisms, be it bacteria, plants, fish, amphibians, reptiles, birds, mammals or others have one or more specific ways to react with their surroundings, with others and within him/her or itself. For that they make use of a variety of organs—called organelles in unicellular organisms—that are more sensitive than other parts of their bodies for some specific or less specific clues that may be described in chemical or physical terms. These organs or organelles may somewhat loosely be called senses. Historically in the western world five senses have been distinguished, i.e., vision, hearing, smell, taste and touch. Obviously humans have more than the five basic senses, i.e., they possess the sense of equilibrium and the vomero-nasal organ, without taking into account the extreme complexity of intercellular communication which drives everything from cell division to differentiation. Many animals have simi-

lar senses to those found in man, but with a different physical or chemical spectrum. Moreover, some animals and plants have other different senses at their disposal, not available to us, sensitive to other stimuli, and still definable within physical or chemical "language".

Although humans may continue to live without properly functioning senses, usually by the help of instruments and/or other humans, animals in their natural habitat usually quickly die, unless they find themselves in a protected environment, like a cave.

It seems highly probable that (properly functioning) senses or sense like organs enable the living organism to continue living and to preserve the species to which it belongs.

The senses are a prerequisite of life itself, and each species has senses at its disposal that seem to be adapted to, or in harmony with, the way it lives within the environment in which it is placed.

TABLE 1

Stimulus and the belonging sense, reaction, response or effect within animal or plant

STIMULUS	SENSE/REACTION/RESPONSE
heat flow, thermal stimulus	thermoreceptor (infrared organ), klinotaxis, tropotaxis
light	organ of vision, eye, photoreceptor (infrared)
sound	organ of hearing, ear
change in magnetic field	sense of direction
change in electrical field	electroreceptor
change in field of direct current	galvanotaxis
gravitation	statolith
change in posture	organ of equilibrium, muscle spindle
angular acceleration	semicircular canals, sense of rotation
change in external pressure, touch	lateral line organ, organ of touch
tissue injury	nociceptor, pain
chemicals (olfactory-, taste-, gustatory stimuli)	chemoreceptors, chemotaxis, olfaction, taste, smell, organ of Jacobson (vomeronasal organ)

TABLE 2

**The range of sound frequencies audible to various species at a fixed intensity of 50 dB<sub>SPL</sub> (in kHz)**

ANIMAL	LOWER LIMIT	OPTIMUM	HIGHER LIMIT
Fish	0,05		1
Amphibians	0,1		4
Reptiles	0,01		5
Birds	0,75	2-4	12
MAMMALS	0,1		150
Human	0,02	3	18
Elephant	0,02		6
Horse	0,20		22
Dog	0,2		36
Cat	0,125		60
Rat	1		59
Moth	18	30	120
Bat	7	10-30	100
Seal	0,5	1-40	58
Dolphin	0,4	20-100	145

## NOTES

- \* V. B. Mountcastle. "The view from within: Pathways to the study of perception," *Johns Hopkins Medical Journal* 1975; 136: 109-31
- 1 Alston WP. *The Reliability of Sense Perception*. Cornell University Press. Ithaca and London. 1993
- 2 Sperry RW. "Mind-brain interaction: mentalism, yes; dualism, no," *Neuroscience* 1980;5:195-206
- 3 Dusenbery DB. *Sensory Ecology. How Organisms Acquire and Respond to Information*. WH Freeman and Company, New York. 1992
- 4 Sobel N, Prabhakaran V, Hartley CA, Desmond JE, Glover GH, Sullivan EV, Gabrieli JDE. "Blind smell: brain activation induced by an undetected airborne chemical," *Brain* 1999;122:209-17
- 5 Sekuler R, Blake R. *Perception*. McGraw Inc. 3rd edition. 1994
- 6 Whitaker BD, Poff KL. "Thermal adaptation of thermosensing and negative thermotaxis in *Dictyostelium*," *Exp Cell Res* 1980;128:87-93. Quoted in Dusenbery DB, 1992
- 7 Lythgoe JN. "The ecology of vision," Oxford, England: Clarendon Press. In Sekuler R and Blake, 1994
- 8 Marshall J, Oberwinkler J. "The colourful world of the mantis shrimp," *Nature* 1999;401:873-4
- 9 Douglas RH, Partridge JC, Dulai K, Hunt D, Mullineaux CW, Tauber AY, Hynnninen PH. "Dragon fish see using chlorophyll," *Nature* 1998;393:423-4
- 10 Schmitz H, Bleckmann H, Mürtz M. "Infrared detection in a beetle," *Nature*. 1997;386:773-4
- 11 Fay RR, Popper AN (eds.) *Comparative Hearing: Mammals*. Springer handbook of auditory research. Springer Verlag. New York, 1994
- 12 Grinnell AD. "Hearing in bats: an overview," In: Popper AN, Fay RR. *Hearing by Bats*. Springer Handbook of Auditory Research. New York, Springer Verlag, 1995:1-36
- 13 Mann DA, Lu Z, Popper AN. "A clupeid fish can detect ultrasound," *Nature*. 1997;389:341
- 14 Doty RL, Mishra A. "Olfaction and its alteration by nasal obstruction, rhinitis, and rhinosinusitis," *Laryngoscope* 2001;111:409-23
- 15 Soares D. "An ancient sensory organ in crocodilians". *Nature* 2002;417:241-2
- 16 Catania KD, Remple MS. "Somatosensory cortex dominated by the representation of teeth in the naked mole-rat brain," *Proc Nat Acad Sci* 2002;99:5692-7
- 17 Harlow HE, Harlow MK. "Learning to love," *Scientific American* 1966;54:244-72
- 18 Sherrick CE and Cholewiak RW. "Cutaneous sensitivity," In K Boff, L Kaufman, J Thomas (eds.). *Handbook of Perception and Human Performance*, vol.1. New York 1986: Wiley-Interscience. Pp.12.1-12.58
- 19 Roland PE, Mortenson E. "Somatosensory detection of microgeometry, macrogeometry and kinesthesia in man," *Brain Research Reviews*. 1987;12:1-42. In: Sekuler R & Blae R. 1994
- 20 Dehnhardt G, Mauck B, Bleckmann H. "Seal whiskers detect water movements," *Nature* 1998;394:235-6
- 21 Piersma Th, van Gils J, De Goeij P, van der Meer. "J. Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution," *J Animal Ecology* 1995;64:493-50422  
Piersma Th, van Ales R, Kirk K, Berthoud H, Maas LRM. "A new pressure

sensory mechanism for prey detection in birds: The use of principles of seabed dynamics?" *Proc R Soc Lund. B* 1998;265:1377-83

23 Basle BL. "How bacteria talk to each other: Regulation of gene expression by quorum sensing," *Current Opinion in Microbiology* 1999;2:582-7

24 Nelson KH, Platt T, Hastings JW. "Cellular control of the synthesis and activity of the bacterial luminescent system," *J Bacterial* 1970;104:313-22

25 Hartman G, Wise R. "Quorum sensing: Potential means of treating gram-negative infections?" *The Lancet* 1998;351:848-9

26 Fuqua C, Greenberg EP. "Self perception in bacteria: Quorum sensing with acylated homoserine lactones," *Current Opinion in Microbiology* 1998;1:183-9