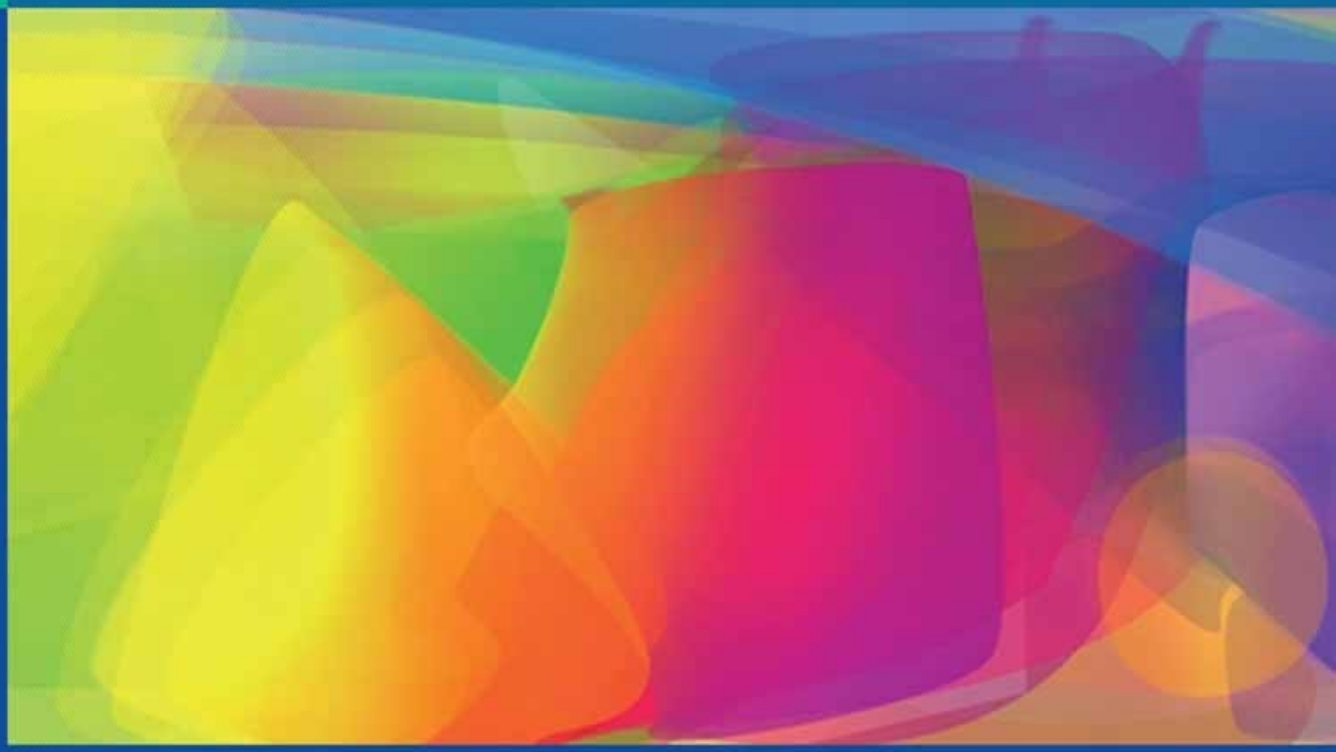
Friedrich G. Barth · Patrizia Giampieri-Deutsch
Hans-Dieter Klein *Editors*

Sensory Perception

Mind and Matter



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Mind and Matter

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Prologue

This book is about *sensory perception* in a very broad sense. It aims towards the strengthening of existing bridges and the building of new ones between a wide range of disciplines traditionally separate from each other and considered to be hunting in their own different woods. The gaps between the search for the molecular mechanisms at work in sensory cells or the brain of a fruit fly and the examination of cognitive functions and capabilities in man are indeed obvious, as are the differences between the psychophysics of color vision and neurophilosophy. We are confronted with differences in regard to both the level of complexity of the systems examined and the procedures applied to analyse them.

However, despite of all these differences there are commonalities as well. The most eminent ones are the sensory systems and the brains themselves. Without them there would neither be neurophilosophy nor molecular neurobiology, which has included the so-called lower animals like flies and bees and snails into its research most successfully. Such animals may vastly differ from us humans. At the same time they share with us a surprising number of the basic properties of living organisms. These include brain functions like learning and memory and even quite advanced cognitive abilities which only a few years ago no one could have expected to find in bees, birds, or dogs.

Our book is meant to provide at least a glimpse at some of the many exciting modern developments in the study of sensory perception, both technical and conceptual. At the same time we are aware of the fact that in terms of evolution the story we would like to illuminate from various points of view

is a very old one. *All living organisms* rely on information on their outside and inside worlds. Without such information proper behavior ensuring survival and procreation is impossible. It should therefore not come as a surprise to find sensory mechanisms of remarkable refinement even in bacteria and single celled protozoans.

In higher animals evolutionary selective pressures have led to a fascinating diversity of sensory and nervous systems. Eyes, ears and noses as well as many types of sense organs providing information alien to our human experience represent the windows of the brain to the outside world. They are the interfaces between an organism's environment and its behavior. As a rule all these windows are highly specialized filters. They provide the individual organism with the information on a small fraction of the physical world only. This small fraction, however, is the biologically relevant one, both in space and time.

We humans are no exception to these general rules. To explain and understand the mechanisms of information processing and the generation of meaning by our brain has been given attention for more than 2 000 years. A particular incentive for this long-lasting search may have been the fact that we do have subjective conscious experiences associated with brain activity and that we are able to describe them verbally. Unfortunately one has to admit, that despite all the brilliant advances of the modern molecular and cellular neurosciences higher functions emerging from the complex activity of systems of many neurons cannot be explained yet at the level of brain function.

Sensory perception, the topic of the present book, provides access to both the sciences of the brain and the sciences of the mind. We are convinced that classical questions of philosophy and psychology referring to perception and mind will benefit from an understanding of the insights of modern neurobiology into the mechanisms of sensory processing in animals and humans. Likewise neurobiology can and indeed should profit from a central task of philosophy, which is to keep or make terminology and concepts clear, thereby increasing their unifying power. Also, in the age of biology and in view of the overwhelming importance often attributed to it, it may be wise trying to see biology in a still larger context. This seems to be particularly relevant for functional brain research which despite its fascinating advances clearly demonstrates the present limits of biological reasoning.

Unfortunately*, perception and consciousness* have often been conflated in philosophy (as in every day language). Both neuropsychological studies of brain-damaged patients and *subliminality* studies have now led to a revision of the common assumption that perception and consciousness of perception are always inseparable. Studies of subliminality have in addition demonstrated that controlled investigations into unconscious conflicts, unconscious affect, and unconscious anxiety are possible.

Sensory perception is functionally related to an organism's reactions. The range of issues addressed by the present book therefore includes *free will,* which, defined as libertarian free will, implies free actions, unconstrained and uncaused by any physical process, and has been a topic of hot debates recently. Libertarian free will is incompatible with the concept of the physical world as a closed causal system. The more sophisticated approach of the compatibilists rejects libertarian free will and is supported by a long philosophical tradition inaugurated by Aristotle more than 2000 years ago.

There is currently no consent regarding the answer to the question whether the sciences involved in the study of sensory perception are autonomous enterprises which

can interface with each other and exchange their results, or whether the findings of, say, psychology, should be reducible and indeed reduced to findings elaborated by the neurosciences. The current philosophy of mind again raises the traditional metaphysical questions but certainly requires empirical answers that only the experimental sciences can provide.

Our book strives to bring together the neurosciences with psychology, which speaks the language of cognitive experiences and with philosophy, which has been thinking and arguing about the meaning and origin of consciousness since its beginning. The debate about the possibility to explain mental phenomena neurobiologically will still have to continue for a while. The editors of this book are convinced, however, that in any case we need a patient interdisciplinary discourse between neurobiology, psychology and philosophy if we aim at an in depth understanding of the many fascinating facets of sensory perception and their relation to brain functions and cognition. Leading experts have written chapters for our book as food for thought and reflection which hopefully will contribute to promote such a discourse and also point to the big gaps still to be bridged. Some of the contributions may also help to overcome the deep rooted bias of humans to overemphasize the uniqueness of their brains and increase the awareness of the impossibility to decouple the "mind" from evolutionary biology and the question of biological fitness.

We are very grateful to the University of Vienna (in particular the faculty of Life Sciences) and the Austrian Academy of Sciences which were the main sponsors of a very successful and stimulating international symposium held in Vienna in 2008 on the same topic. This symposium initiated the idea of publishing the present book. We also thank Springer Verlag Wien New York for the help and guidance received during the preparation of this book.

Wien and Lofer, January 2011
Friedrich G. Barth
Patrizia Giampieri-Deutsch
Hans-Dieter Klein

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Basic mechanisms in sensory systems

Introductory remarks

Senses and sensing are a characteristic property of living beings. From bacteria and unicellular protozoans all the way to vertebrates, primates and man there is a need of information on what is going on inside and outside the body in order to maintain homeostasis and to properly behave in the organism's own and specific environment. Although plants do have sensing as well, it is the heterotrophic animals which have a particularly intimate relation with their habitat. The reason is their need to spend a considerable amount of time and effort to move around in search of energy pre-packaged in the bodies of other organisms, be they plants or animals. Their highly developed sensory systems (like their muscular and nervous systems) reflect the particular demands resulting from their dependence on information about the static and in particular the dynamic properties of environmental conditions. Most sensory systems are indeed particularly well adapted to respond to dynamic rather than static stimulation.

The study of sensory systems has come a long way and made innumerable fascinating discoveries. The scope of what we want to understand is enormous and ranges from the molecular mechanisms at work when a sensory cell takes up a stimulus and turns it into a nervous signal to the old problem of what the activity of sensory systems tells us and other animals about the physical reality of the world. In this section of our book four experts address basic mechanisms of sensing, starting with processes at the cellular and molecular level and ending with the intriguing problem how the distributed organization of our brain and the lack of single loci for integrated percepts goes together with the coherent wholes we experience.

1. Sensory transduction

Stephan FRINGS of the University of Heidelberg outlines the first steps of perception, that is the ways how sensory cells detect stimuli of different forms of energy and transform their properties to electrochemical signals which are sent to the central nervous system and its brain. As will be seen there are a number of commonalities among the primary processes regarding key cell structures and transduction processes in cells serving mechanoreception, vision, and chemoreception. Obviously, questions of the sensitivity and selectivity of sensory cells and sensory organs, as treated in this chapter, are highly relevant for an understanding of what we and other animals perceive.

2. Hearing

In his chapter, Geoffrey MANLEY of the Technical University Munich deals with vertebrate hearing. He traces the evolutionary history of hearing back to the fishes and draws our attention to parallel developments in reptiles and birds. Not only are the major improvements of the hearing organs per se highlighted but also the changes and specializations of the brain pathways devoted to hearing pointed out. As so often seen when taking a comparative approach the human sensory system is not the culmination of evolution; instead, even more spectacular specializations are found in many other species reflecting the importance of hearing in their species-specific normal behavior.

3. Vision

Kristine KRUG of Oxford University introduces the reader to the principles of function found in primate vision. The emphasis is on the brain and the ways in which it transforms patterns of activity received from the eye and representing patterns of local contrast in the visual field to signals directly related to perception in the higher areas of the visual cortex. As has been known for a while various parameters of the visual stimulus like color, shape and motion are processed in parallel in different cortical areas. Experimental evidence will be provided that links the activity of individual neurons in the brain to visual motion and depth perception.

4. The binding problem

Finally, Wolf SINGER of the Max Planck Institute for Brain Research in Frankfurt /Main takes us a step further into the functional principles of our brain, stressing that even the most complex cognitive features need to be explained on the basis of neurobiological data. Evolution, the most important determinant of perception, is itself considered as an adaptive cognitive process and given particular attention as the source of our a priori knowledge of the world which to a large extent determines what and how we perceive. Despite all the exciting advances made by brain research during the last decades there are still substantial gaps in our understanding of the brain's operations. Thus a major issue still is the neuronal basis explaining the qualia of our subjective experiences, including awareness and self-consciousness. Different from previous concepts, parallelity, reciprocity, and distributedness turned out to be the principles dominating the brain's cortical connectivity. There is much less linearity and hierarchy than previously assumed and no single site onto which all information is converging to allow coherent interpretations of the world and our obviously coherent perception integrating the many different aspects of an object. An exciting hypothesis proposes a solution of an enormous problem: How are the activities of the many neurons distributed widely in the cortex and subcortical areas bound together to a particular representation? As is explained in *Wolf Singer's* chapter the temporal synchronization of oscillatory activity of widely distributed neurons, that is convergence in time rather than space, may be a key factor solving the binding problem and giving perceptions access to consciousness. **FGB**

Sensory cells and sensory organs

1

Stephan Frings

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Abstract

Animals possess sensory organs that collect information and convey this information to the central nervous system. This introductory chapter outlines how sensory cells perform their task of detecting adequate stimuli and how they produce electrical signals that encode information for the brain. In the course of animal evolution, the specific transduction mechanisms that operate in the various sensory cells have been optimized under intense selective pressure. The results of this process often include extreme sensitivity for the adequate stimuli and efficient signal amplification. To illustrate different solutions to the problem of detecting and encoding complex information, the sensory modalities of touch, vibration detection, hearing, vision, and olfaction are briefly introduced on the levels of key cell structures and transduction molecules. Pain perception is described as a sensory modality with very special features that differ fundamentally from those of other modalities. Thus, polymodality of sensory cells, modulation by the immune system, and suppression by endorphins represent characteristic properties of the pain system, linked to its unique protective function. This chapter is designed to direct the reader's attention to some central points of the topic. It does not deal with the subject of sensory detection in a comprehensive way. It rather highlights a set of particularly important aspects of sensory transduction that may be of interest for the interdisciplinary approach followed in this book. Questions of sensitivity, selectivity, and adaptation in sensory cells are directly related to the mode of perception that defines our view of the world. Inasmuch as our sensory organs have been shaped by evolution, our perception of reality is the consequence of evolutionary forces and constraints as well.

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1. Introduction

The process of sensory perception begins when sensory cells detect stimuli in the environment. Light acts on photoreceptors, sound on mechanoreceptors, and odorants on olfactory receptors – all highly specialized cells of eyes, ears, noses that are exposed to the outside world. The sensory organs we have today are the result of millions of years of adaptation to the needs of animals in their struggle to survive. This is an important point, as all sensory systems fulfil a clear and vital purpose: the survival of an individual and the continuance of a species. There is no luxury in sensory organs; we do not perceive unnecessary things. Humans do not perceive the Earth's magnetic field because no selective pressure has ever favoured the development of a magnetic sense in the evolutionary line leading to the hominids, while such pressure did bring about an acute sense for magnetic fields in migratory birds. Thus, our specific set of sensory organs serves the vital functions of finding food, finding mates, and avoiding predators. Consequently, we are not equipped to perceive the world as it is, but we are able to survive in it (see also Chapter II, 6 by FG Barth).

This selective development of sensory organs began early in evolution, in the precambrian age, more than 550 millions ago. The oldest fossils of larger animals with robust shells date from the cambrian age, 500–550 millions years ago, and some of these animals clearly had eyes (Conway Morris 1998). In fact, eyes have probably already been used for about 300 million years, when cambrian predators like *Anomalocaris* were searching the bright and shallow seas for animals to eat, using eyes which resembled those of today's insects. And prey organisms in turn had to develop some means of perceiving an approaching *Anomalocaris* as early as possible, and to get away before it was too late. Trilobites, for example, started into the cambrian age already with well developed eyes. Although probably one of the favourite foods of *Anomalocaris*, they outlived the cambrian predator and became one of the most successful group in animal evolution (Fortey 2000). Thus, predatory animals challenged animals of prey to acquire a decent set of sensory organs, or else to perish. This enormous selective pressure has continued over millions of years, and it continues today in the intricate scenarios of co-evolution between the hunter and the hunted. It has produced eyes, ears and noses of almost unimaginable sensitivity, in fact, a sensitivity that has reached physical limits: A single photon, the movement of one atom, or a single odorant molecule can be detected by sensory cells of some animal species. This beautifully illustrates the power of evolution. Evolutionary processes can optimize living systems right to the state of absolute perfection: It would not help to develop a photoreceptor that detects less than one single photon. In fact, such a cell would be useless, as it would respond to absolute darkness. The single-photon response of vertebrate photoreceptors indeed represents a sensory system driven to perfection by the relentless forces of evolution. One of the fascinations of sensory physiology is to witness how perfection has been achieved in the various sensory organs.

2. How sensory cells work

It requires a multitude of different sensory cells to carry out all our vital functions. The brain has to be informed on every relevant detail so as to be able to coordinate these

functions in a sensible way. The spectrum of information acquired by the brain is quite dazzling. The posture of the body, its supply with nutrients and oxygen, the state of the cardiovascular and digestive systems, as well as the body temperature and ion concentrations are constantly monitored by various types of sensory cells. Information about objects in the environment, their shape, colour, chemical composition, their distance and movement are collected and conveyed to the brain. This steady and complex flow of information is then integrated and used to generate expedient behaviour. However, the brain itself can only process information which is encoded in a language that consists of electrical discharges, termed action potentials. The task of a sensory cell is to convert the relevant stimuli into this language – a process that is called transduction. Transduction differs greatly between light-sensitive cells and cells that detect mechanical stimuli. But a few common principles can be outlined that illustrate the working of all sensory cells (Fig. 1).

The pivotal components of each sensory cell are specific sensory molecules that are contained in specialized cellular structures like cilia, microvilli or other membrane structures. Sensory molecules are highly specialized for their particular stimulus. If it is the right stimulus – the adequate stimulus – then the cell will respond even to very weak stimulation. The sensor may also respond to other stimuli, but not with high sensitivity. Thus, we may see stars with our photoreceptors at night in our bedroom in absolute darkness when we bump our eye against the edge of our wardrobe, thus receiving a strong mechanical stimulus. But the identity of a sensory cell and, indeed, of the entire sensory modality is defined by the *adequate* stimulus which elicits the sensory response; the ability of dim light to stimulate a sensory response defines a photoreceptor.

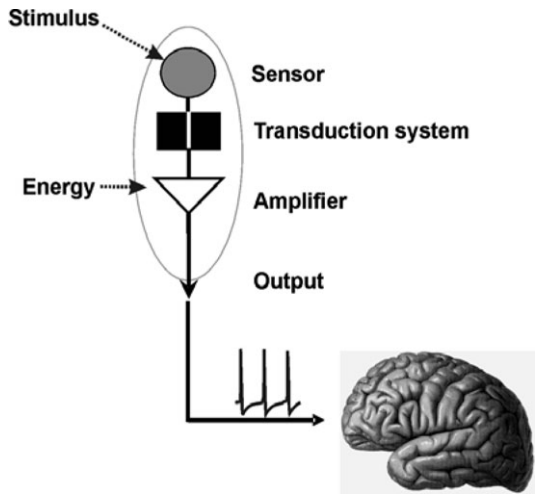

Fig. 1 Functional components of a sensory cell. An adequate stimulus acts on the cell's sensor, a structure specialized for the detection of this stimulus. The sensor triggers a transduction system which generates a chemical or electrical signal inside the cell. An amplification process increases the signal strength, using metabolic energy to boost the cellular response that is elicited by the stimulus. Finally, an output signal is generated in form of a series of electrical action potentials (spikes) that inform the brain about the detection of the stimulus

Following the uptake of the stimulus the next functional step is the transduction of the sensory signal – meaning the conversion of the extracellular stimulus into an intracellular signal. All cells operate with a certain repertoire of intracellular signals. These may be chemical or electrical signals which trigger the cell's internal responses to stimulation. There is only a limited number of such signals. Roughly ten different chemicals and basically four types of electrical signals carry such signals within all cell types of the body. In sensory cells, the sensor molecule must actuate at least one of them – for example a calcium signal or an electrical depolarization. In most cases, this task is fulfilled by ion channels residing in the plasma membrane of a sensory cell. Ion channels are proteins that can trigger both chemical and electrical signals, because ions – like the calcium ion

Ca^{2+} – can enter the cell through ion channels These ion channels are termed transduction channels as their job is to start the transduction process. Once they are activated by the stimulus, the cell can start to process the sensory signals.

Sensory transduction virtually always includes a step of signal amplification. If the adequate stimulus consists of only a few photons or a few molecules of odorant, not much energy is fed into the sensory cell. However, this little energy must be converted into a robust output signal, usually a series of electrical potential changes that can be conveyed to the brain for analysis. The difference in energy between the input and the output of a sensory cell is added to the sensory signal, thereby amplifying it. Different sensory cells have developed different amplification strategies. Not surprisingly, the most effective amplification strategies known are operating in sensory cells with high detection sensitivity.

Transduction of the stimulus energy to a first cellular response is followed by a process called encoding. Encoding leads to the generation of an electrical signal that contains the sensory information. Ideally, *all* aspects of the stimulus would be translated into the electrical code. Stimulus intensity, stimulus duration and other relevant parameters should be encoded in such a way that the brain is able to extract all this information by analysing the action-potential activity received from a sensory cell. The duration and shape of action potentials are uniform and therefore not useful for coding. The sensory information must, therefore, be encoded in the number of action potentials and in the time between them This coding principle is called frequency modulation (FM). It is a very reliable method of information coding, as we know from the excellent quality of FM-coded music and speech in radio transmission. Thus, the final task of a sensory cell is to convert the amplified sensory signal into a message encoded in a frequency modulation that is then read out and deciphered in the brain, a process that leads in most cases to perception.

3. Touch, medium flow and mechanosensitive hairs

Touching things or being touched is arguably the most basic sensory experience. Even *Paramecium* is able to register touch when it bumps into an obstacle. And, what is more important, it can properly respond to this experience. It stops, then swims backwards for a short distance, readjusts its heading, and continues to swim in the new direction – apparently to bypass the obstacle and to continue on its way. This is quite a remarkable accomplishment for a single-cell organism, and it illustrates that the processing of touch information is almost as old as life itself. Today's complex animals use all kinds of specialized structures to feel even the slightest touch. One of the most successful developments for this purpose was the combination of a hair-like structure and a sensory cell. Imagine a hair shaft, delicately suspended in a soft, elastic membrane, able to move into any direction upon the slightest touch, and connected at its base to the dendrite of a sensory cell and its sensor structure. If anything touches this hair, a force will act on the sensor and start the transduction process (Fig. 2A). We find touch-sensitive hair-like structures on the surface of insects which are able to detect with these highly-sensitive mechanoreceptors air currents that may indicate an approaching mate or predator. The combination of hair-like structures and sensory cells has been employed throughout evolution and works perfectly well in higher animals. The motile whiskers of rats are a

good example. The animals can feel their way in the dark by probing their environment with their whiskers. If anything touches these hairs, sensory cells at their base are activated. Physiologists think that the input from all whiskers is integrated by the animal's brain to form an image of objects that surround the rat's head – that the rat "sees" with its whiskers. While we do not sport whiskers ourselves, we have a less sophisticated form of the hair – sensory cell combination: the hair-follicle receptors. Each hair on our forearm is equipped with a sensory cell that picks up each movement of the hair and hence contributes essential information to the touch sensation of our skin.

Although touch is such a basic, omnipresent sensory modality, we do not know much about the transduction mechanisms in mechanoreceptor cells. We know that our skin contains at least seven different types of mechanoreceptors apart from the hair-follicle receptors, and we have a good idea what they are there for. Some detect vibrations, others the touch intensity or the speed of an object moving along our skin. However, we do not know how the mechanical stimulus is converted into an output signal. The main reason for this ignorance is that our touch sensors are hidden in the skin and very difficult to study. Fortunately, one of biology's most popular model organisms, the nematode worm *Caenorhabditis elegans*, lends itself also to studies of touch reception. These animals respond to a gentle touch with an evasive movement that can be triggered by each of its six touch-sensitive cells. The underlying transduction mechanism was examined with immense effort by Martin Chalfie over a period of almost thirty years (Bounoutas and Chalfie 2007). It turned out that the transduction channel of the

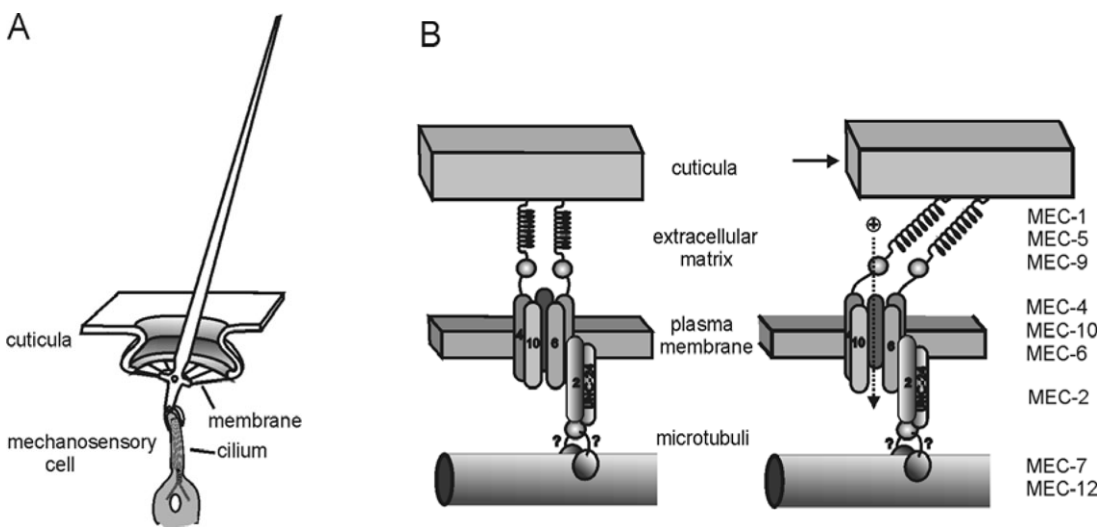

Fig. 2 Mechanosensory cells. **A** The combination of a hair and a sensory cell allows insects to detect medium flow signals like wind with extreme sensitivity. The deflection of a hair that is supported by a membrane is converted into a mechanical stimulus detected by a mechanosensory cell (modified from Müller and Frings 2009). **B** Model of the mechansosensory transduction channel that operates in the touch receptor of the nematode worm *Caenorhabditis elegans*. The channel consists of several proteins that are coassembled in the plasma membrane of the mechanosensory cell. It is tethered to the microtubule system inside the cell and to the cuticula outside of the cell. When the cuticula moves upon being touched, the transduction channel is pulled open and allows cation current to flow into the cell. This channel is an example of a multi-protein complex – in this case made of multiple MEC proteins (modified from Frings 2009)

touch-sensitive cells is a protein complex in the sensor membrane, connected to the cuticula, the skin of the worm (Fig. 2B). When something touches the cuticula, the transduction channel is pulled open and causes an electrical signal. Thus, the worm operates its touch receptors by linking the transduction channel to the cuticula, just like the insect links its mechanoreceptor cell to a hair-like structure. Conceivably our touch receptors also work with such tethered transduction channels – but this is not yet known. Despite the manifold tasks that touch receptors perform in our lives, from explorative, tactile activity to social signalling, we know little about how they work. In fact, our sense of touch is the least understood of all our senses despite its fundamental importance. Maybe the worm can help us here.

4. From vibration detection to hearing

For many animals the perception of vibrations is even more important than touch sensation. Being touched by a predator marks the moment when it is often too late to escape. Vibrations, on the other hand, travel over some distance and can alert the animal well before the predator can strike. Vibrations in water or soil are caused by animals moving around. They spread into the surroundings and warn every animal that is able to detect them. It is therefore not surprising that both fish and land animals have developed sensory organs for the detection of vibratory signals. Some of the vibration sensors found in animals are almost incredibly sensitive. Cockroaches possess inside their legs sensory organs that consist of a tiny horizontal membrane supported in air by a ring of sensory cells. Whenever the slightest vibration travels along the ground where the cockroach sits, the membrane will itself vibrate and stimulate the sensory cells. These will then transmit the information to the animal's central nervous system and brain, which will initiate an appropriate flight response. The astonishing finding about this vibration detector (the subgenual organ) is that it responds to vibration amplitudes in the range of 0.2 nm – the diameter of two hydrogen atoms. This is a movement on the scale of thermal vibrations, the trembling and shivering of all small particles, including atoms and molecules, that is caused by heat. All particles of the substrate the cockroach sits on wobble about in that range – even without any vibrations caused by another animal. Does the cockroach detect thermal vibrations? Probably not, because the animals leg averages the thermal movements of a large number of particles. Moreover, its vibration detector responds with that extreme sensitivity only to a particular frequency range of substrate vibrations. The vibration detector of the cockroach is most sensitive for frequencies around 1.4 kHz. We can envisage a cockroach sitting on the kitchen floor. If anybody enters the house, the vibrations spreading from each footstep contain a 1.4 kHz component. The cockroach picks them up and runs for cover.

A particularly successful strategy to detect mechanical stimuli was realized in fish that need an early-warning system just as urgently as insects do. It led to the development of a multi-purpose mechanoreceptor, a cell type that is used in vibration detection, in hearing and in the sense of balance, one of the pivotal achievements of animal evolution: the hair cell (Fig. 3A). Hair cells possess a tuft of hair-like extensions or villi on one side – termed stereovilli – and a device for activating neurons, a synapse, on the opposite side. If anything deflects the "hairs", the synapse will activate neurons which will then conduct the information to

the brain. Fish use hair cells in their lateral line organ, a canal along each side of the fish's body with many openings to let water enter the canal lumen. Driven by pressure differences between individul openings, minute volumes of water enter the canal and deflect the stereovilli of hair cells. Fluctuations of the water flow, caused by other fish or by any currents and eddies, will thus produce sensory signals in the lateral line organ. With its lateral line organ the fish is able to collect information about what is going on around him – even in murky water or at night when vision is limited or impossible. But fish also use hair cells for keeping balance as they swim. They have an intricate fluid-filled bony structure, the vestibular organ in their heads, which uses hair cells to measure any movement of this fluid relative to the canal's wall that occurs upon acceleration of the body. Moreover, some hair cells in the vestibular organ are specialized to measure the position of the body relative to the Earth's gravitational field – a sensory information that allows the fish to swim upright. Finally, sound waves travelling through water cause vibrations in various parts of the fish, including the swim bladder and the skull. These vibrations are translated by a system of small bones into medium flow inside the inner ear which in turn stimulates hair cells. Thus, the fish depends on the signals obtained from hair cells at various parts of its body in many ways. As evolution proceeded from fish through amphibians and reptiles to mammals, hair cells remained important. Today, our vestibular organ allows us to walk upright, and the hair cells detect medium flow in our organ of Corti in the cochlea of the inner ear (Fig. 3B).

As we analyse airborne sound (see also Chapter I, 2 by GA Manley), we are still interested in the three basic parameters: the amplitude (perceived by us as the loudness), the frequency (perceived by us as the pitch), and the direction to the sound source. Of course, our ear is adapted to detect and to analyse airborne sound, vibrations in form of pressure waves travelling through the air. We pick those signals up with our outer ear and channel them towards the eardrum which is set into motion by the sound waves. This motion is transmitted by the three tiny bones of the middle ear (malleus, incus, stapes) to the cochlea, a bony tube that houses the organ of Corti (Fig. 3 C; see also Fig. 6 in Chapter II,6). The human cochlea has the form of a snail-shell with three turns. In this way, its lumen has sufficient space for the organ of Corti which is about 3 cm long. Along its entire length, hair cells are positioned in four rows, numbering approximately 3000 in each row. The cells sit on a tissue, the basilar membrane, which has a very particular property: it is stiff at the bottom of the cochlea and floppy at the top of the snail-shell. Mainly as a consequence of this gradient in stiffness, the basilar membrane responds to sound in a peculiar way: If a high-pitched tone enters the ear, it is the stiff bottom part of the organ of Corti that vibrates most. Conversely, if we hear a low-pitched tone, the upper, floppy part of the basilar membrane vibrates most. When we play a triad on the Piano, three distinct sections of the organ of Corti are set into vibration, one vibrating with the lowest tone, one with the middle tone, and one with the highest tone. All other areas of the basilar membrane remain almost motionless. The important point here is: the frequency information contained in a sound is converted into spatial information, a phenomenon termed tonotopy. In this way, the cochlear covers the entire frequency range that we can hear: 20 Hz at the top of the snail-shell and 18 kHz at its base. Wherever the basilar membrane vibrates, it stimulates the local hair cells. To obtain information about the frequency of the sound, the brain simply has to look which of the hair cells along the organ of Corti were

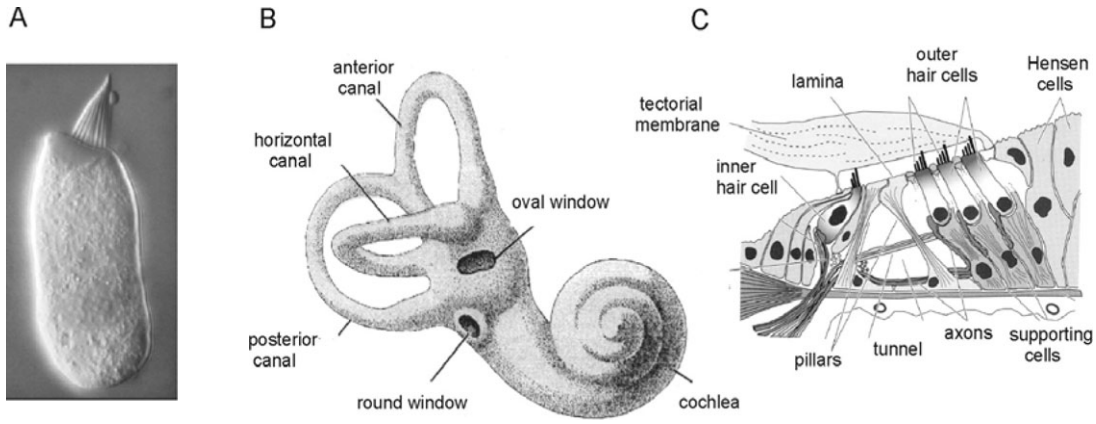

Fig. 3 Vibration detectors. **A** A hair cell isolated from the inner ear of a frog. The hair bundle on the apical pole consists of about 50 mechanosensitive stereovilli. The length of the individual villi increases from left to right; the structure with the spherical tip is the so called kinocilium, which is not mechanosensitive. **B** Schematic drawing of the inner ear showing the three canals of the vestibular organ that aid spatial orientation and balance, and the cochlea that mediates hearing. Sound enters the inner ear from the middle ear through the oval window and leaves via the round window. The inner ear houses hair cells for the detection of acceleration (vestibular organ) and for the analysis of sound (cochlea). **C** The organ of Corti is a sensory epithelium inside the cochlear coils. Hair cells are aligned in four rows, with 3000–4000 cells per row. The organ of Corti vibrates with the incoming sound; high frequencies (18 kHz) cause the largest vibrations near the oval window, low frequencies (20 Hz) near the top of the cochlea. The three rows of outer hair cells sense local vibrations and amplify them by shaking the tectorial membrane. The inner hair cells pick up these amplified vibrations and activate neurons which convey the auditory information to the brain (modified from Fain 2003)

stimulated. Each position corresponds to a frequency. The tonotopic organization of the cochlea and its precise tuning to the individual frequencies of our auditory world is endlessly fascinating to sensory physiologists, and it is by no means completely understood.

Thus, loudness correlates with the intensity of hair-cell stimulation, and frequency with the position of the hair cell along the organ of Corti. The third parameter, the direction to the source of the sound, can only be derived from the comparison of the two sensory signals generated in left and right ear. When the sound comes from the right, it hits the right ear with full intensity, but it is muffled when it reaches the left ear after having travelled through the head. Thus, there is directional information in the difference of the sound pressure levels (perceived as loudness) at the two ears. Moreover, the sound will arrive at the left ear a small fraction of a second later than on the right. This time-difference can be analyzed by the brain with amazing accuracy. Finally, the highly asymmetrical shape of our outer ears can help us to decide whether a sound comes straight from the front or straight from the back, in which case there are no differences in loudness or timing.

The sensitivity of our hearing is amazing, but the accuracy and sensitivity of hearing in many animals far surpasses ours. Especially nocturnal predators like owls, bats or leopards have driven the detection and evaluation of acoustic information to the extreme. While these animals have optimized their ears with respect to position, size, structure, and motility, the common basis for the extraordinary performance of all hearing systems is the exquisite sensititvity of hair cells. The stereovilli of hair cells respond to the

slightest mechanical stimulus, even to movements that are much smaller than the diameter of a single stereovillus. How is that possible? If looked at from the side, the tuft of about fifty stereovilli tapers from one side of the cell to the other (Fig. 3A). The top of each stereovillus is connected to the side of the next longer neighbour by a protein filament termed tip link. But no tip links connect sideward to the stereovilli of equal length. In this way, the entire tuft of stereovilli is organized to move unisono, as one unit, whenever a stimulus pushes it along the tapering axis. Any movement along this axis will elicit a response with extreme sensitivity. Physiologists have employed ingenious methods to study the hair-cell response and found that the tip links are likely to be directly connected to ion channels. The slightest dislocation of the stereovilli stretches the tip links and pulls the ion channels open which, thus, act as transduction channels. They conduct potassium and calcium ions into the hair cell and trigger a cellular response that eventually leads to action potential generation in the neurons that are attached to the hair cell. When researchers examined the relation between the movement of stereovilli and the cellular response they saw their phenomenal sensitivity and found an intriguing image to illustrate it: Deflection of the stereovilli out of their resting position by 0.003° was sufficient to cause a cellular response (Hudspeth 1989). To appreciate what this means, we can envisage a stereovillus as large as the Eiffel tower, 300 m high; deflecting such a giant structure by 0.003° would cause its tip to move by no more than the width of a thumb (20 mm). In the real world, the tip of the stereovilli must move only 0.3 nm to cause a sensory response, the diameter of 3 hydrogen atoms. Thus, hair cells show a similar sensitivity to mechanical stimulation as the vibration detectors of the cockroach discussed in the previous chapter.

5. Vision

There is an amazing diversity of eyes in the animal kingdom (Land and Nilsson 2002). Eyes may be small inconspicuous spots in the skin, they may be huge, complex structures that make up more than a quarter of an animal's body, or they may look like huge globes of transparent glass waved about on thin stalks like some magic lantern. Animals may use the physical principles of diffraction or reflection, absorption dichroism, circular dichroism, frequency dispersion and light polarization to extract information on the visual world, and the depth of analysis by visual systems is really astounding. In fact, a recent theory on brain evolution suggests that the strongest impetus of early brain evolution was the wealth of information provided by eyes and the fundamental advantage for any species that was able to process that information – first came the eye, then the brain (Gehring 2002).

In all animals, the sense of vision (see also Chapter I,3 by K Krug) is mediated by a single family of proteins – the opsins. Animal opsins are not light-sensitive themselves. But they can house light-sensitive molecules, chromophores, which change their structure when hit by light of adequate wavelength (perceived by us as colour). In our eye, retinal is the chromophore. The combination of opsin and retinal is called rhodopsin, and some rhodopsins respond best to light seen as blue, others to light seen as green or red. When a chromophore is illuminated, it absorbs light, changes its structure and, hence, kicks the opsin molecule into an active state – the chromophore switches the opsin "ON". This is the start of vision. The activated rhodopsin is able to generate cellular signals that, in turn, can cause a cellular response. Sensory cells that possess rhodopsin and respond to illumination are called photorecep-

tors – light-sensitive sensory cells. They operate in all animal eyes, irrespective of their principle of construction. A photoreceptor provides the information that it is hit by light, a rather basic quality of information that simply distinguishes "bright" versus "dark". More useful information can be gleaned from the combination of a photoreceptor with a pigment cell that absorbs light but does not produce neuronal information itself (Fig. 4A). Such a combination tells the animal from which side the light comes, a message that may help to escape into the right direction. The interpretation of shadows and the position of light-obscuring objects is much improved when many photoreceptors are placed into a pit or even into a chamber with a small opening (Fig. 4B). In such an eye, the shadow of the predator will black out some of the photoreceptors while others stay illuminated. With the appropriate neuronal equipment, an animal can derive the form of an object from this shadow. The final addition to the eye is a lens, a translucent piece of tissue that focuses the image of an object onto an array of photoreceptors and at the same time increases the light flux by widening the hole for its access.

In our eye, the back wall is covered with about 150 million photoreceptors which together with many other cells form the light-sensitive retina. The lens is composed of translucent cells which have lost practically all large organelles which would be in the way of light entering the eye. The cells in the lens have developed a sort of low-key mode of life without nucleus and mitochondria, doing not much more than staying clear. They can live for many years in that quiet state, and they must prevent at all costs the aggregation of proteins, which would cause turbidity and a reduced optical quality of the eye. A special protein, crystallin, prevents aggregation and keeps our lenses clear, usually up to old age. What we see is projected by the lens onto our retina, where a sharp image is formed, just like on the film (or chip) of a camera. The retina converts this image into a pattern of electrical activity. This involves considerable processing inside the retina. Eventually, the information about our field of view is delivered to the brain by approximately two million neurons, the ganglion cells of the two retinae. Through a relay station, the thalamus, the information reaches the primary visual cortex in the back of the brain where the process of visual perception begins (see also Chapter I,3 by K Krug).

The eye is the only human sensory organ where a considerable amount of information processing already takes place before entering the brain circuits that eventually generate perception. The retina is a neuronal network made up of different cell types (Fig. 4C). The network performs operations which are characteristic of brain function. This is not surprising considering the fact that the retina is a developmental derivative of the brain. *Convergence:* In most parts of the retina, highly sensitive photoreceptors (so called rods) respond to minute light intensities, corresponding to a flux of 10–500 photons per second. More than 100 individual rod photoreceptors may converge onto a single target neuron. This convergence increases the chance that the target cell is activated even at very low light intensities when only a few photoreceptors detect a light signal. The incoming signals are added up to generate a stronger activation in the target cell. However, convergence reduces spatial resolution, as the output of the target cells represents the averaged activity of the entire area of the visual field covered by the converging photoreceptors. Convergence does, therefore, not occur where high spatial resolution is required. In the small central spot of the retina specialized for high spatial resolution, the fovea, there is no convergence; instead, each photoreceptor is connected to its own target cell.

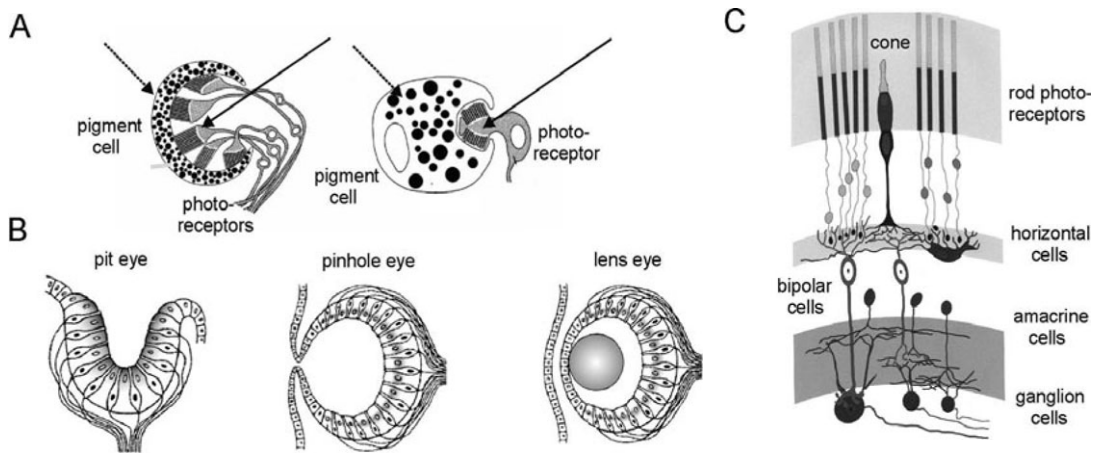

Fig. 4 Photoreceptors and eyes. **A** The combination of photoreceptor cells with pigment cells yields information about the position of the light source. The pigment cells shield the photoreceptors from the left side, so that only light coming from the right side can be seen. **B** Directional information is improved when a set of photoreceptors sits inside a pit eye. A pinhole eye produces an image on the retina, a light-sensitive tissue with many photoreceptors. Each photoreceptor can generate one point (one pixel) of the image. A translucent lens projects a sharp image onto the retina, thus strongly improving the optical quality of the eye (modified from Land and Nilsson 2002). **C** Photoreceptors in the retina pass their sensory signal through bipolar cells on to ganglion cells, which in turn send action potentials to the brain. Horizontal cells and amacrine cells connect these three cell types horizontally and enable the retina to perform complex signal processing

Lateral inhibition: One of the most important properties of a clear image is a pronounced contrast. On the level of the retina, contrast means that the activity of photoreceptors clearly marks the edge of a dark image; those on the bright side are active, those on the dark side are not. In fact, the retinal network exaggerates this difference in activity: The activated photoreceptors send an inhibitory signal to the less active ones in their vicinity, suppressing their residual activity and, hence, increase the perception of contrast.

Direction-selective activity: Perceiving motion is a complicated task for the visual system. In the retina, certain target cells of photoreceptors only respond when the image moves from right to left, but do not respond to other motion directions. Others are specialized to movements into other directions. These cells ("starburst cells") collect inputs from many other retinal cells and perform some kind of computation that results in direction selectivity – the neuronal basis of motion vision.

Colour contrast: In addition to the highly-sensitive rod photoreceptors, our eye possesses three types of cone photoreceptors with distinct wavelength specificities: "blue" cones, "green" cones, and "red" cones. These photoreceptors are concentrated in the fovea and mediate daylight colour vision. To extract and perceive colour information, the brain evaluates the relative activation of the three cone types; each wavelength in our spectrum of visible light corresponds to a discrete relation of activity in the "blue", "green", and "red" cones. In the same way as contrast is important for black-and-white images, colour images are only clear if they have good colour contrast. The retina employs the principle of lateral inhibition to increase the contrast between wavelengths corresponding to green and red, as well as to

blue and yellow. Thus, colour vision is aided already by network computation in the retina.

Classification: Whenever possible, the brain operates by parallel information processing. The retina splits the visual information into two main channels: One contains the information on colour and form of an object, the other has the information about its localization and its movement. These two classes of information go separate ways through the brain; only after the analysis has been completed, they rejoin to allow the perception of an object as a whole. Thus, when visual signals leave the eye, they are already processed and prepared for further analysis in the brain.

6. Olfaction

Smelling something usually triggers an emotion (see also Chapter V,18 by R. Juette). We may find an olfactory stimulus agreeable or unpleasant. We may even experience craving or revulsion; but we seldom are indifferent towards an olfactory stimulus. Smelling seems to inevitably come with hedonic judgement. Unlike the skin, the ear, and the eye, the nose forces us to make a decision about an object that we examine by its odour. We have to decide whether the object is good for us or bad. Some of these hedonic responses are even genetically fixed. For example, the smell of a carnivorous predator makes us uneasy. In the zoological garden, even on the safe outer side of the fence, most of us feel the hairs on our necks stand on end when we smell lions or wolves. This kind of response it not learned, it is inherited from our ancestors. Even one-day old babies smile when they are offered a sniff of banana or vanilla scent, but they display disgust or start crying when challenged with the smell of rotten eggs. Thus, without having learned anything about food yet, babies know how to distinguish a "good" smell from a "bad" one. The smell of burning wood and grass has an alarming effect on almost every land-living animal, irrespective of prior experience. A rare exception seem to be humans, as tens of thousands of years of barbecuing our meat seems to have abolished the negative connotation of the smell of fire. In addition to congenital decisions on odorous objects, we learn to associate odours with the quality of objects all through our lives. We memorize olfactory experiences together with what they mean to us, and sometimes we can remember even after decades, how something or someone smelled – and whether we liked the smell or not.

Chemically speaking, the odorants which cause the perception of odours form a complex mixtures of volatile compounds, each at a different concentration and with a different smell. The aroma of coffee consists of about 800 individual odorants. We are unable to identify – let alone name – individual odorants within this mixture, nor are we interested in doing so. The relevant sensory signal for us is the impression that this unique combination makes on our olfactory system, and the pleasant feeling it generates. The total number of odorants present in our olfactory world cannot be established. We are constantly exposed to the smell of people, animals, plants, earth, cars, factories, perfumes, indeed an endless variety of olfactory objects, each of them exuding their individual combination of odorants. And whenever we try to put a number to the diversity of odorants, a chemical factory or a new strain of bacteria creates new odorous compounds – and our number will be obsolete. For the purpose of the present discussion, I take the variety in our olfactory world as unlimited.

How can a sensory system cope with such an endless number of different stimuli? Twenty years ago, Linda Buck and Richard Axel, then at Columbia University, discovered that mice possess a large gene family that encodes 1000–1300 different odorant receptor proteins (Buck and Axel 1991). This is by far the largest gene family in the genome. Dogs have roughly 900, humans 400 odorant receptor proteins. The receptor proteins are exposed to the inhaled air by olfactory receptor cells, tens of millions of which make up the olfactory epithelium at the ceiling of our nasal cavity (Fig. 5A). These cells are neurons which carry a tuft of sensory cilia, and each individual cell expresses only one odorant receptor gene. When the right odorant hits the sensory cilia, it binds to the receptor protein and induces a sensory signal that is sent to the brain. Since we have only 400 odorant receptors, each of these receptors must be able to bind not only one type of odorant but thousands of different odorants (otherwise our olfactory experience would be limited to 400 different odour molecules only). Physiological experimentation has shown this very clearly. Each olfactory receptor cell can be stimulated by many different odorants. But what kind of message is delivered to the brain by a sensory cell that does not clearly distinguish between individual odorants? When the brain receives action potential activity from an olfactory receptor neuron, this could mean: "I have detected something that may be amyl acetate *(banana)* or possibly limonene *(peppermint)*, but – depending on the concentration, which I do not know – it could also be isovaleric acid *(sweat)* or acetophenone *(almond)*." The brain cannot derive any reliable information from that kind of fuzzyness. Obviously, the read-out of a single olfactory re-

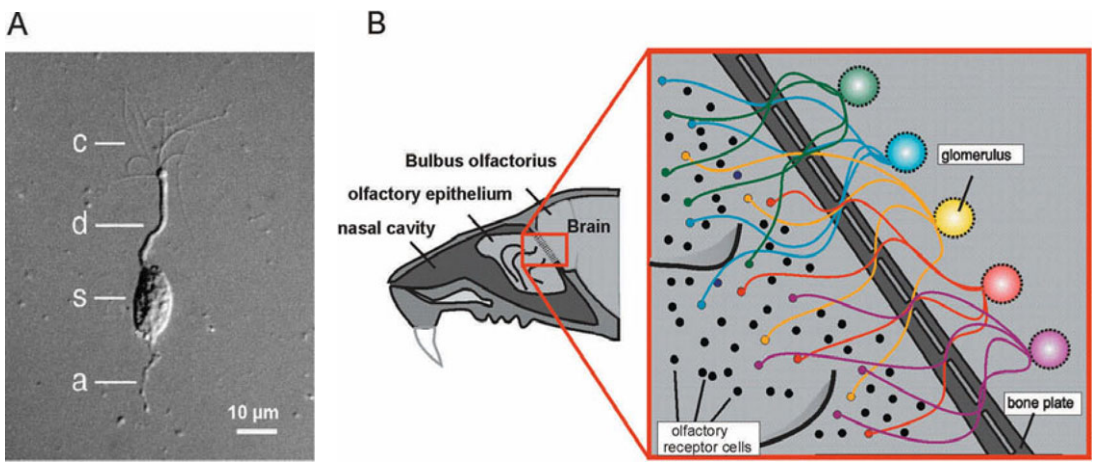

Fig. 5 Detection and sorting of olfactory information. **A** An olfactory receptor cell isolated from the olfactory epithelium of a frog. A dendrite (d) leads from the cell body (soma, (s) to the tissue surface where it carries a tuft of sensory cilia (c). The cilia present odorant receptors to the inhaled air and transduce the chemical information into a cellular signal. Output signals travel as action potentials along the axon (a) to the brain. (modified from Kleene and Gesteland 1981) **B** The mouse has approximately 1300 different odorant receptors, but only one type is expressed in each individual olfactory receptor cell. Cells with the same odorant receptor send their axons to the same spot in the olfactory bulb of the brain; cells with another receptor target a different spot. These spots are called glomeruli, and receive several thousand axons from cells expressing the same odorant receptor type. During a sniff, the activity of all glomeruli generates a spatial pattern that encodes the olfactory information for further processing by the brain (modified from Waldeck and Frings 2005)

ceptor cell does not identify an odorant for the brain. However, the olfactory system is very good at identifying odorants, although it operates with fuzzy receptors. The principle of information coding must be different.

Odour discrimination is a combinatorial process; the sensory information is contained in the combined activity of many sensory cells. This can be understood if one considers that each of our 400 odorant receptors has a slightly different structure and hence a preference for a slightly different group of odorants. Consequently, the set of receptor neurons activated by one odorant differs gradually from the set activated by another odorant. Instead of looking at the response of a single receptor neuron, the brain analyzes the *pattern of activity* that results from the fact that some receptor neurons respond and others do not. In mice, such odour-induced activity patterns can be visualized by modern brain imaging methods. This is possible because all olfactory receptor neurons with the same type of odorant receptor send their axons to the same spot in the brain, a glomerulus in the olfactory bulb (Fig. 5B), while neurons with a different receptor target a different glomerulus (Mombaerts 2006). Several thousand axons of cells with the same receptor converge onto a single glomerulus. If these cells are activated by an odorant, the combined cellular response at the level of the glomerulus is strong enough to be recorded in a brain-imaging experiment. So, a response of the olfactory bulb to an odorous stimulus is seen as the "lighting up" of several glomeruli as they are activated, while other glomeruli remain quiescent and dark. The current notion of olfactory encoding holds that olfactory information is transformed into a map of glomerular activity, a spatial code for the quality and intensity of an odour. How this map is read out by higher levels of the brain, how it is translated into perception, hedonic assessment, and memory, are exciting research topics still at an early state of understanding.

7. Pain

Pain is usually perceived as an experience that inflicts diseased or wounded people as an abnormal occurrence that causes agony and makes us suffer. Such a negative view of pain mostly results from the experience of chronic pain, long-lasting distress that may accompany inflammation or almost any kind of lesion. The physiological concept of pain is quite different. For the physiologist, the pain system provides its own sensory modality, just like hearing or vision, but specialized on stimuli that are strong enough to cause damage to our body. Such noxious stimuli are an every-day occurrence, they alarm us when the coffee is too hot to drink, when we step on a drawing pin on the floor, or when the way we lie in bed obstructs the blood flow into our hand. By warning us, the pain system constantly protects our body from damage. A striking illustration of the beneficial role that the pain system plays in our lives is the fate of people who are unable to feel pain. Patients with congenital insensitivity to pain have normal touch perception, but do not feel pain. Because they lack the alarm function, they are at constant risk of suffering damage, as they bite their tongues, break their fingers and toes, or touch hot objects, all without being alerted to the danger they are in. In severe cases, these patients may also have psychological problems, being in a continuous state of withdrawal, reminiscent of autism. The observation that these patients tend to scratch off their skin absentmindedly and are indifferent towards the wounds they inflict on themselves, promot-

ed the hypothesis that in some of them the lack of pain perception prevents the maturation of the sense of self, the awareness of personal identity. Apparently, the pain system enables us to perceive the boundary of our body, an experience that may be necessary to develop an appropriate sense of what belongs to our person and what does not.

Noxious stimuli are detected by a set of sensory cells called nociceptors. These are neurons that have their sensory endings in the skin, in joints, muscle, and in inner organs, and they convey nociceptive signals to the central nervous system. The working of nociceptors differs in several ways from that of hair cells, photoreceptors or olfactory receptor cells. Firstly, they have a relatively low sensitivity – they respond only to stimuli strong enough to destroy living tissue. Secondly, a single nociceptor is often able to respond to several different stimuli, for example to heat exceeding 50 °C, to mechanical stimulation, and to acids. This "polymodal" behaviour points to the fact that the pain system generates a signal that primarily has to alert us to a critical situation independent of its cause. Informing us precisely about what happens to our body, whether the affected part suffers a burn, a cut, or contact with a corrosive chemical, seems to be of secondary importance. The pain system does not have to be specific but rapid. It has to provide an intense danger signal that can elicit protective behaviour as fast as possible – before tissue damage becomes too severe. A third fundamental difference between the pain system and the other senses is its intimate relation to the immune system. Whenever we suffer a cut in our skin, the immune system springs into action. Cells in the wounded area release signalling molecules that recruit immune cells to come to the aid of the local immune response. While the skin tissue is slowly repaired, the aroused immune system detects and removes bacteria and other harmful material, thus preventing a spread of the infection throughout the body. This process is termed inflammation, and it is accompanied by four standard observations: *rubor,* a reddening of the tissue caused by increased blood supply to the wounded area; *calor*, a local increase of tissue temperature; *tumor*, a local tissue swelling that occurs when the wall of blood vessels allow serum to leave the blood stream and enter the tissue during the recruiting process; and *dolor*, increased pain sensitivity. This sensitization to noxious stimuli is important as it prevents us from touching the inflamed tissue and makes us shield it from contact with anything. Sensitization is based on the ability of the immune system to change the response characteristics of nociceptors: Under the influence of inflammatory mediators, the nociceptors respond more intensely to a noxious stimulus than they do in intact tissue. We experience an amicable slap on the shoulder, that would usually cause us no pain, as quite painful when our skin is inflamed by sunburn. Thus, the immune system tunes the sensitivity of the pain system in the interest of the repair of damaged tissue.

A fourth and very striking difference that distinguishes pain perception from all other sensory modalities is the brain's ability to shut down the entire sense of pain in situations where pain perception or pain-driven behaviour may be counterproductive to survival. Pain suppression helps animals to escape a predator even after they have suffered horrible wounds like the loss of a limb. Humans also report this loss of pain perception. People who were severely wounded in car accidents or in battle report that they did not feel any pain during the first state of shock. The perception of severe pain started only later. This reflects a temporal cut of the information line. The brain presses a *veto* button and prohibits the entry of pain information. The most important site of this *veto* function is the spinal cord. Here, nociceptors

pass the nociceptive information to the central nervous system through synaptic connections with spinal cord neurons. These synapses are targets for the brain's pain suppression system: The brain analyzes the situation during an assault on the body and may decide that pain perception is momentarily less important than efficient flight behaviour or, alternatively, the stabilization of vital functions like blood pressure. Under these conditions, a signal descends from the brain into the spinal cord, reaches the nociceptor synapses, and shuts them down by releasing endorphins onto them – self-made pain killers that derive their name from a fusion of "endogenous" and "morphins". Endorphins prevent the synapses from handing over the pain signal to the central nervous system and, hence, uncouple the nociceptor system from the system of pain perception. Thus, although the nociceptors scream out their message about a serious wound, the message is not heard by the brain because the critical synaptic junctions are blocked by endorphins. Pain perception can thus be functionally and anatomically separated from the nociceptive system; pain perception is an activity of the brain, not an activity of nociceptors. In medicine, the functional separation of the two systems is achieved by analgetic drugs like morphin, a substance produced by the opium poppy *Papaver somniferum*. Morphin mimics the brain's *veto* function as it binds to the nociceptor synapses in the spinal cord and prevents the passage of the nociceptive signal to the brain (see also Chapter III,11 by R. Weissensteiner et al.).

8. Synopsis

This brief introduction to sensory cells and sensory organs was designed to illustrate a few fundamental aspects about the first steps of perception: the detection of stimuli and the initial information processing that produces useful signals for the brain. The first point to consider is that sensory organs exist only for stimuli relevant for survival. Consequently, our senses enable us to perceive only a particular segment of reality. The close link between perception and survival has shaped the sensory organs and has sometimes driven their effectiveness to the physical limits. In these cases evolution has come to an end. Sensory cells have developed various sensors to detect the adequate stimulus at low intensity; specialized structures present the sensor to the outside world. Stimulation leads to transduction: The sensory cell has to translate the stimulus first into an intracellular signal, and eventually into a neuronal output signal in the shape of action potentials. On their way to the higher levels of processing in the brain, the sensory signals are sorted and spatially segregated. This allows rapid, parallel processing of information as it is channelled towards the final step of sensory function, perception.

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