Sensory perception: adaptation to lifestyle and habitat

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Abstract

Sensory perception is a biological phenomenon and should be treated as such. It has a long history, beginning in the early stages of the evolution of life. Even bacteria depend on information gained about their outside and inside world. Basic mechanisms of sensing have indeed already been invented by the simplest organisms. Among the rich diversity of extant sensory systems are quite a few unknown to man. They give animals access to experiences alien to humans. A prominent characteristic of all sensors and sensing is their selectivity for the biologically relevant and their capacity to ignore most of the potential stimuli actually present. This implies that sensors and sensory systems are windows to the world with an extremely limited but well tuned transparency. They have not evolved to provide abstract truth but rather to achieve fitness (survival and reproduction). The intimate relationship between sensory systems and the habitat and lifestyle of a particular animal species is a logical consequence of this.

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1.

Introduction

The study of sensors and sensory perception addresses a large range of questions. The search for answers has mainly been driven by a particular interest in our own human perceptions. However, neurobiological findings are often most fascinating where they refer to creatures different from ourselves as humans and living with strange senses in sensory worlds alien to our own.

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After a short introduction to some fundamentals this chapter will focus on a few select issues, viewed from a zoologist's point of view, and implying that an understanding of our own brain substantially depends on an understanding of what is going on in animals. There are sensors approaching perfection in the animal kingdom and sensors stimulated by forms of energy humans cannot perceive, such as ultrasound, infrared radiation, and electric fields, to name only a few. The principles of operation in many animal sensors represent interesting alternatives to established ways in which physics is applied to solve a sensory problem. While all these animal sensors are worthy of study in their own right they also shed light on our own human particularities. Like all creatures humans are a product of evolution. No sensory systems came from heaven but rather have evolved by a process of trial and error and by going through simple, progressive stages.

Senses and sensory perception have a *long history*. All forms of life depend on information about their exterior and interior worlds. There is no behavior which would make sense without such information which also provides a basis for motor control. In what follows we focus on the outside world, commonly referred to as the environment. However, it is important to stress that information about the inside world, the invironment, is of crucial importance as well. It is needed to guarantee homeostasis – by controlling body temperature and blood pressure, by keeping the osmotic balance right and by ensuring the proper regulation of metabolic processes. Feedback systems maintaining stable equilibria rely on a corresponding wealth of sensors looking into the organism and controlling its functions. Most sensors respond more strongly and promptly to changes of stimulus conditions than to constant conditions. In other words, organisms are much more interested in knowing about the dynamics of the physical and chemical conditions than their static conditions, which underpins both the relevance of the homeostasis concept and the importance of knowing about changes when executing behavioral programs. Sensory systems make closed-loop real-time control of behavior possible.

In biological sensing the goal *is never abstract truth but fitness*, which entails an organism's capacity to survive and to reproduce, and in more practical terms its ability to orient and to communicate, to move around, to escape from predators and to find prey and a mate.

With all this in mind the wealth of sense organs and sensory capacities found in the animal kingdom is not surprising. Sensory capacities already exist early in the evolution of life, for example, in bacteria, even archaea, which have stretch sensitive cell membrane channels important in keeping the osmotic balance (and internal pressure) right. In unicellular, eukaryotic protozoans like the ciliate *Paramecium*, one already finds highly developed sensory responses to mechanical (like touch) and other (like chemical) stimuli. There are even de- and hyperpolarizing receptor potentials and a sophisticated sensory guidance of oriented swimming behavior that exist despite the absence of any neuron or nervous system (Eckert 1972; Eckert et al. 1972).

Highly effective solutions of sensory problems have thus been found very early in the history of life, and many of the basic mechanisms seem to have been passed on to animal taxa positioned much higher in the phylogenetic tree, including humans. A sensory cell translates the properties of a stimulus into the language of the nervous system. Membrane channels regulating the ion flux across the sensory cell membrane are at the core of *sensory transduction* which describes the processes converting the different forms of stimulus energy to changes of the membrane potential. The membrane potential in turn decides on the occurrence (number and frequency) of nerve impulses sent to the next neuron and / or to the central nervous system. As expected there are variations in the molecular structures and functions which respond to different stimuli like light, sound, touch, and chemicals. However, there are also striking similarities across the animal kingdom and even between different sensory modalities. The diversity of animal sense organs serving the same stimulus modality (form of stimulus energy), such as vision or hearing or chemoreception, is not so much due to the diversity of the transduction processes but to that of the non-nervous structures (e. g. optical apparatus of eyes, sound transforming structures in ears, etc.) first picking up the stimulus from the environment and channelling it to the sensory cell proper, which typically is not directly exposed to the stimulus impinging on the body. The specialist defines these processes as *stimulus transformation* which differs fundamentally from *stimulus transduction* and represents the largest playground and richest soil for biologically applied physics. Here we most readily find proof for the adaptedness of biological sensors to the particular needs of the behavior of a particular species living in a particular habitat. Here a perfect match between sensory filters and the behavioral task is often found in the finest structural and functional details.

Plants have sensory capacities as well. They sense, for example, light, temperature and gravity. However, being autotrophic organisms able to convert solar energy into biomaterials such as sugars and fats by way of photosynthesis and typically living in the same spot for a lifetime, a plant's relation to the environment is much less demanding than that of an animal. *Animals are heterotrophic*, feeding on the energy pre-packaged in the bodies of other organisms. Typically, animals have to run around and search for sources of energy (in the last instance always provided by the plants, the primary producers) and a mate. Their highly developed muscular, sensory, and nervous systems have to be seen in this general context. Interestingly, animals that hardly move at all, such as filter feeding sponges, often look plant like. Their sensory capacities are comparatively limited and some of them appear like plants to the non-specialist and still carry erroneous plant names, like the sea anemone (a coelenterate) or sea lily (an echinoderm).

In the following a few examples will illustrate the intimate relationship between the properties of sensory systems and the environment and lifestyle of animals. The selectivity of sensory systems will first be shown by looking at stimulus transformation way out in the sensory periphery. Subsequently filter properties and selectivities of the brain will be considered. All along the way behavior will be the reference needed to understand the biological significance of particular senses.

2.

Sensory periphery – physics, behavior, and ecology

2.1 Color vision

Sense organs are often called the windows of the nervous system to the outside (and inside) world. Although this is true in principle, the main issue here is that the transparency of these windows is very limited. Not only does a sense organ respond to a particular form of energy only – an ear to acoustic but not to electromagnetic waves, and an eye to electromagnetic but not to acoustic waves – but even within its modality it usually selects a small fraction only. To give an example: The wavelengths of light seen by animal eyes are roughly between

300 nm and 800 nm (0.3 to 0.8 µm). This is only a tiny fraction of the wavelengths of extant electromagnetic waves, which cover a range of more than 20 powers of ten, from gamma waves at the short wavelength (high frequency) end to radio waves at the long wavelength (low frequency) end. Even within the small range seen by animals, significant differences in sensitivity are found which can often be related to ecology and behavior.

One of the best known among such cases is the honeybee (*Apis mellifera*, Hymenoptera). The overall width of its spectrum of visible light is the same as in humans, but it is shifted by about 100 nm towards the short wavelength side. This implies that honeybees don't see light that we perceive as red but do see light in the ultraviolet (also known in other insects, fish and birds) which is beyond our short wavelength limit in the violet. Therefore to honeybees the colors of flowers look different from what we see (Fig. 1). For them the petals of a corn poppy flower (*Papaver rhoeas*) which are magnificently red for us would be black were it not for the reflection of ultraviolet radiation which we do not see. For bees and other insects the petals appear ultraviolet, a color alien to us. Similarly, the reflections of the flowers of the marsh marigold (*Caltha palustris*) could not be more yellow to our human perception. However, they reflect both in the yellow and in the ultraviolet range of wavelengths so that the bee sees a color referred to as "bee-purple". Of course we do not know what the color experience of a bee actually is like. However, behavioral and other evidence shows that they can certainly distinguish between different bee colors. The behavioral benefit that ensues from this lies in their ability to distinguish between the flowers of different species. This is the basis for effective pollination of the plants visited and an indispensable part of the "food for pollination deal" between insects and plants. Often flowers bear guide marks to the food (nectar, pollen) which are seen by the insects, because no ultraviolet is reflected by them. Because humans are ultraviolet-blind these guide marks, which are conspicuous to bees, do not exist in our visual experience.

Fig. 1 Color vision. The flower of the corn poppy (*Papaver rhoeas*) shown above, appears red to humans but "ultraviolet" for honey bees and other insects. The flowers of the marsh marigold (*Caltha palustris*) shown below, appear yellow to humans, but to a honey bee they appear in "bee purple". (photographs by author)

To be sure, wavelength and color are two different things. Color is the analyzed wavelength. Although it correlates with the input from sensory cells, it is the product of its integration in the central nervous system. Light of a certain wavelength is colorless. Its subjectively perceived color only exists in our minds and those of the bees and of other animals. However, particular spectral sensitivities of the photoreceptor cells (their wavelength selectivity) are the basis for a particular kind of color vision and the differences such as those between bee and man.

Contradicting our intuition, *the* color vision does not exist. Whether color is seen or not to a large degree depends on the behavioral context. In the bee it is mainly related to the flower visits, but not to visual motion detection, which is a "colorless" operation. Even when visiting flowers, chromatic patterns can only be resolved by the bee at very close range when it already sits on the flower or hovers above it, due to the limited spatial resolution of the bee's compound eye (Hempel 2001, 2002). Other properties of the eye add to the selectivity of the "sensory windows" in the periphery. One of them is the regionalisation and heterogeneity often found in insect (and other) eyes (Kelber 2006). A particular part of the compound eye may be specialized for a particular purpose such as polarization vision (see below) or pursuing a mate, or the distribution of the frequency of the occurrence of photoreceptor cells of a particular spectral type may change between the dorsal and ventral eye.

2.2 Polarization vision

When sunlight is scattered within the atmosphere or reflected from shiny surfaces like those of water or vegetation, it is partially polarised. Such polarised light represents a source of spatial information for many animals. Amongst these is again the honeybee, of which Karl von Frisch (1949) first showed that the polarisation pattern of the sky can be used as a compass cue for orientation, even if only a small patch of sky 10° to 15° wide is seen (von Frisch 1965). Only a small fraction (up to ca. 6 percent) of the bee's compound eye serves the acquisition of compass information from the sky's polarisation pattern (Wehner and Strasser 1985; Wehner and Labhart 2006). The relevant ommatidia look skywards and form the eye's so-called dorsal rim area. In bees the polarisation compass works exclusively with photoreceptor cells which have their peak sensitivity in the ultraviolet; it is therefore monochromatic and color-blind (von Helversen and Edrich 1974).

More recently another case of orientation using polarized light has been found in a spider (Dacke et al.1999). *Drassodes cupreus* (Gnaphosidae) has polarizing filters built into specialized secondary eyes (its posterior median or PM eyes) which look dorsally to the sky but do not form images because they lack a lens (Fig.2). The cornea of these eyes acts like a mere window. The light reflected from the tapetum makes these eyes appear brilliantly blue and is polarized in the direction of the eye's long axis. The built-in polarizer blocks light polarized perpendicular to the eye's long axis. The resulting preference for a particular e-vector orientation in each PM eye and the divergence of the preferred axes of the two PM eyes by 90° form the basis of the polarization analysis of the skylight which is thought to serve the spider when orienting itself home to its burrow after foraging trips. Remarkably, the spider's activity peaks shortly after sunset when the skylight appears particularly strongly polarized to its PM eyes. The main points of the story are the following then. Lacking a lens the stimulus transforming non-nervous optical structures of the PM eyes integrate over a large visual field. Another non-nervous structure, the tapetum, provides the polarizing filter. A comparison of the sensory input from the right and left PM eye will be needed at a higher stage of integration in the central nervous system when using it for polarization navigation (and not mixing up light intensity with direction of polarization). Nevertheless the selectivity and filtering in the periphery is a perfect example of elegantly applied biological physics, which makes the job of the central neurons considerably easier.

Drassodes belongs to a group of spiders with a tapetum of the secondary eyes de-

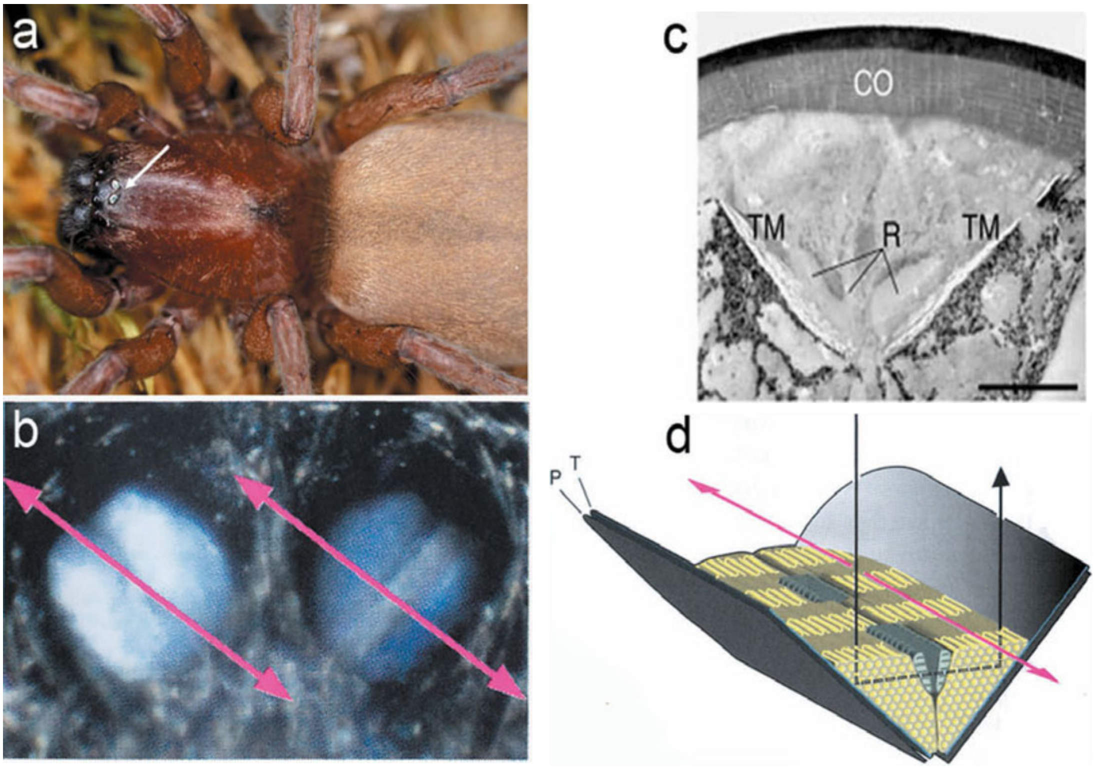

Fig. 2 Polarization vision. **a** The ground spider *Drassodes cupreus* (body length about 1.5 cm). **b** The two posterior median eyes viewed from above under plane-polarized light with the angle of polarization indicated by red arrows. The light reflected from the tapetum is polarized in parallel to each eye's long axis by a polarizer in the eye which is the reason why the right eye remains dark. **c** Section through eye showing its cornea (CO), the two flat mirrors formed by the light reflecting tapetum (TM), and the receptive segments of the visual cells (R). Scale bar 20 μm. **d** Arrangement of the so-called canoe-shaped tapetum (T) (the built-in polarizer) and the visual cells of the retina (yellow and green); black arrow indicates path of light through the eye; red arrow shows direction of polarization parallel to the tubular receptor cell microvilli which implies maximal sensitivity (light absorption). (*a* photograph by Jorgen Lissner; *b, c*, and *d* from Dacke et al. 1999)

scribed as canoe-shaped. The name describes the two flat mirrors forming an angle of 90 to 100° between them which the tapetum consists of (Homann 1928, 1951; Dacke et al. 1999). It is possible that the strange shape of the tapetum serves as polarizing optics in other spiders as well.

2.3 Vibration detection

Most spiders live in a world of vibrations (Barth 2002).They not only use substrate or web vibrations as guides to prey but also actively communicate using self-generated vibratory signals during courtship and male competition. This has been studied in details in the Central American spider genus *Cupiennius* (Ctenidae) (Barth 1997, 1998, 2002). These spiders are wandering spiders which do not live in a web. Instead their vibratory communication with a prospective mate and the detection of prey generated vibrations occur on their dwelling plants (e. g. bromeliads) where they hide in retreats between the leaves during the day and come out to court and prey at night (Fig. 3 a). As in all sensory systems a fundamental problem is to detect and recognize the biologically meaningful signal (vibration) among a lot of background noise. In the given case the background vibrations of the plant due to abiotic sources contain very low frequencies only (below 10 Hz) at the time of the nocturnal activity of *Cupiennius*. Both the courtship and prey generated vibrations (e.g. vibrations produced by a cockroach crawling around on the dwelling plant) contain significantly higher frequency components (male and female courtship signals: main components around 100 Hz and 40 Hz, respectively).

In accordance with this the sensitivity of the vibration sensors on the spider legs is low at low frequencies up to 10 to 30 Hz and increasingly high at higher frequencies, where the vibration amplitude of the tarsus (last segment of the leg) is as low as 10^{-2} to 10^{-3} µm at threshold (Geethabali and Barth 1982; Molina et al. 2009) (Fig. 3b, c). The vibration sensor has prominent high pass characteristics. Although the unusual shape of the threshold curve makes sense from a behavioral and ecological point of view, its origin has for a long time remained enigmatic. Most recently it could be demonstrated

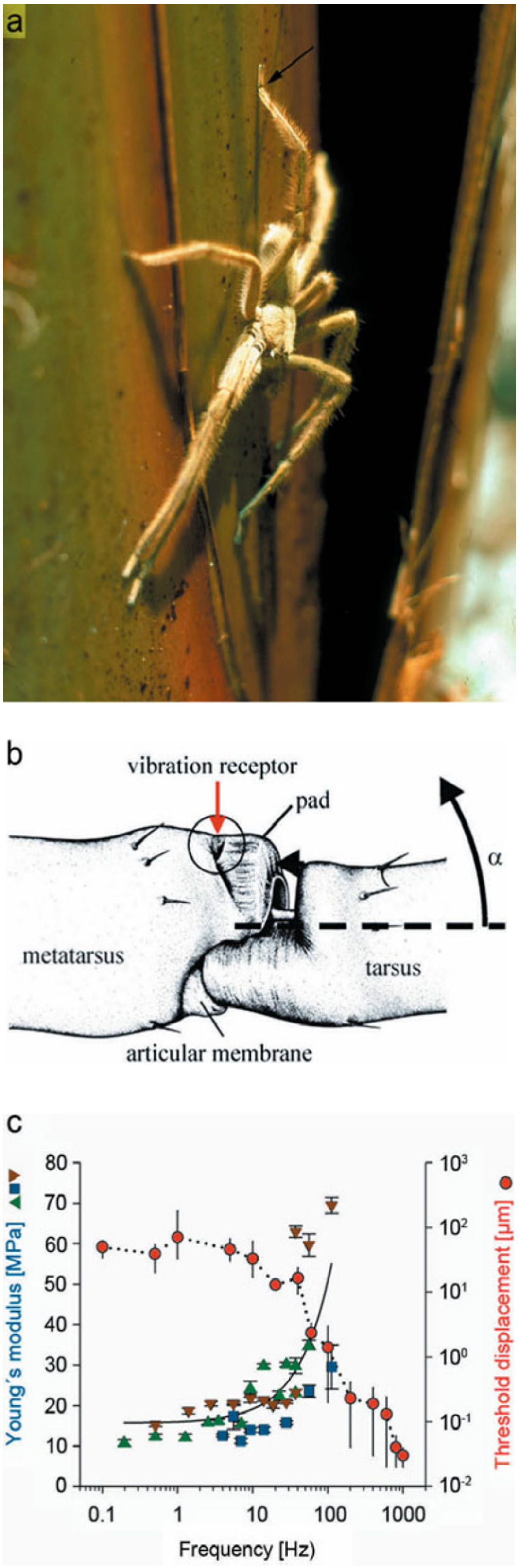

Fig. 3 Spider vibration sensor. **a** A male of the wandering spider *Cupiennius salei* sitting on the pseudostem of a banana plant; arrow points to location of vibration sensor found on all legs. **b** Functional morphology of natural stimulation of the vibration sensitive organ (see red arrow) by the upward movement (see long curved arrow) of the leg's last segment (tarsus), and the subsequent introduction of force (arrowhead) into the cuticular pad which eventually leads to a compression of the vibration sensitive slits making up the organ. **c** Young's modulus (for scaling see left y-axis) of the cuticular pad seen in *b* and tarsal threshold displacement (for scaling see right y-axis) necessary to elicit a nervous response as a function of stimulus frequency. (*a* photograph by author; *b* modified from Barth and Geethabali 1982 with permission, Springer; *c* modified from McConney et al. 2007, with permission, Royal Society)

that the material properties of a tiny cuticular pad in front of the organ perform the function. Again a non-nervous stimulus transmitting structure way out in the sensory periphery forms a highly selective filter enhancing the signal to noise ratio.

The pad works as follows: When the spider's plant is vibrated the tarsus (last segment of the leg) is moved up and down thereby pushing against the distal end of the metatarsus (the second last leg segment). More precisely, it pushes against the cuticular pad in front of the vibration sensor. According to micromechanical measurements using atomic force microscopy (McConney et al. 2007) the pad material has viscoelastic properties. Its stiffness (Young's modulus of elasticity) increases rapidly beyond frequencies of ca.10 to 30 Hz. This implies that vibrations containing higher frequency components are passed on to the sense organ with increasing efficiency (decreasing energy loss). The graph describing the frequency dependence of Young's modulus nicely mirrors the electrophysiologically determined threshold curve (Fig. 3 c). The correlation seems perfect (Fratzl and Barth 2009). In order to see whether it also reflects a causal relationship we made the pad stiffer by cooling it. The predicted increase in sensitivity could indeed be demonstrated even with temperature drops like those occurring naturally (Vogel 2008; Vogel and Barth 2011). Remarkably, this finding nicely links a small cuticular pad on the legs to both behavior and ecology. When the night active spider *Cupiennius* leaves its retreat after sunset, temperatures are lower than during the day. Its vibration sensors are, therefore, more sensitive just at the right time and for the biologically relevant signals.

As in the other cases presented, the biological application of physics seems perfect and reflects the biologically relevant stimulus patterns in surprising detail.

3.

Senses and the brain

To summarize, it has become clear by now that sense organs are windows of very limited transparency and that, therefore, the sensory worlds animals (including man) live in are extremely limited compared to physical reality. A major source of the filter properties of sense organs are their auxiliary structures and the processes of stimulus transformation. They contribute substantially to peripheralize information processing, to keep out improper stimulation from the nervous system and to concentrating on what is biologically important. We have also seen that there are many more senses in animals than the five classical ones traditionally attributed to humans. Apart from quantitative differences between the physical properties of stimuli and what we experience, there are also qualitative differences. Electromagnetic waves are experienced as colors, pressure waves as sound; color, sound, odor etc. are all mental constructions which do not exist outside the brain. What we experience as the outside world is to a large extent the experience of ourselves. There is good reason to assume that this situation is also true in non-human animals.

We now enlarge the picture by including a few aspects pertaining to the central nervous system where the information provided by the sense organs is integrated and analyzed, ignored or stored (as memory), and where the decisions are made about what to do or not. It will become even more evident that sensory signals take on a meaning only in the light of behavior and habitat. In the brain there is again alot of weighting and filtering of information. Often there is even a surprisingly influential control of the sense organs by the central nervous system which to a large degree then tells them what to sense and what not.

3.1 Perception as an active process

A few examples will show that sensing is not the result of mere passive accumulation of inevitable sensory stimulation, but that instead it is often a remarkably active process.

The water bug *Notonecta glauca* (Hemiptera) has a regionalized eye with ommatidia specialized for the detection of the polarization of light located ventrally. This is different from the honey bee with its dorsal rim area, but makes sense as well. The water bug does not use the compass information contained in the polarization pattern of the sky above, but detects water bodies below by the light reflected from their surface, even when flying under low light conditions at crepuscular times. Such light, reflected from the air-water interface, is horizontally polarized and the photoreceptor cells ventrally in the compound eye are arranged in a way that leads to maximum sensitivity for just that horizontally polarized light. More precisely, the receptor cells are sensitive to UV light and their microvilli (which contain the photosensitive pigment) optimally oriented for the reception of horizontally polarized light. The biological background is explained below (Schwind 1983).

Although bound to water for most of the time, *Notonecta glauca* flies in search of new habitats. On such dispersal flights it exhibits a remarkable behavior of active sensing and use of physics (Schwind 1983, 1984, 1991). When descending on to the water surface the bug abruptly tilts its long body axis upwards for a moment before diving into it. The tilt is such that the polarization sensitive ventral eye area forms an angle of 53° with the water surface. This behavior turns out to be very clever because as the Scottish physicist David Brewster (1781–1868) revealed, at an angle of incidence of 53° at the air-water interface the light reflected from the surface is maximally linearly polarized (and the angle between the reflected and the refracted light 90°). The water bug seemingly checks the presence of the water surface according to its polarization properties. Unpolarized light does not elicit the bug's tilting response even when it is much brighter. The bug can be fooled, however, by an artificial surface reflecting light like a water surface prompting it to crash. Whereas in *Notonecta* the diving behavior is only elicited by ultraviolet light, it is the blue or green range in other aquatic insects that prompts a plunge reaction (Schwind 1995).

3.2 Three dimensions out of two

There is ample evidence that our human perceptions are to be understood as active processes, with the brain as interpreter. Our perceptions to a large extent are inventions of the brain, although at the same time the brain is at the mercy of the sensory organs. Two examples shall make this point clear.

The first is the perception of two-dimensional pictures in three dimensions as seen in Salvador Dali's painting of his sister Anna-Maria (1925) (Fig. 4). The projections of the more distant windows onto the retina of our eyes obviously are smaller than those of the closer windows. Nevertheless our brain interprets these windows to be of the same size, using logical rules in the unconscious which it has incorporated during evolution and the individual's early experiences. Two-dimensional drawings with lines converging in a way exemplified by Dali's painting, an increasing density of contours and other characteristics make the brain instantly convert the two-dimensional scenery into a three-dimensional one (see also Fig. 5c). Biologically, the illusion makes more sense than would the physical truth of two-dimensionality, and this is not only true when looking at pieces of art. The subjective size constancy provided by the brain is biologically speaking highly relevant, and may indeed be life

Fig. 4 Three dimensions out of two. Painting by Salvador Dali (1925) showing his sister Anna-Maria. (Salvador Dali "Bildnis meiner Schwester, 1925" / CR Foundation Gala – Salvador Dali/VBK Wien 2010)

saving when, for instance, an enemy is not misinterpreted as tiny and harmless just because of its distance from its potential prey.

The well known Necker cube (Fig. 5a), named after the Swiss crystallographer Louis Albert Necker, who first presented it as early as 1832, is a line drawing of a cube in isometric perspective with the parallel edges of the cube drawn parallel and so not showing which line is in front or behind, where lines are crossing. The drawing is ambiguous because there are two possible perspectives which flip back and forth. The brain obviously tests both hypothetical perspectives but finds no clue to help it decide for one or the other. Interestingly, the view said to be preferred by the majority is the more common one from above, with the corresponding cube face in front. The Necker cube is often used to support arguments against naïve realism. Indeed, the cube we see is not even there but created by our brain out of 12 lines drawn in two dimensions.

Another well known illusion supporting our main point is the Kanizsa triangle (Fig. 5b). Again the visual system interprets parts of a picture in a way that seems to make sense, although they are not actually present. Gaetano Kanizsa was an Italian psychologist who presented a "triangle" consisting of illusionary contours in 1955 (Kanizsa 1955). Such illusions are used to support the Gestalt theory of perception. Interestingly, in a similar manner honeybees see "what is not there" under similar conditions (see Chapter II,7 by M Giurfa).

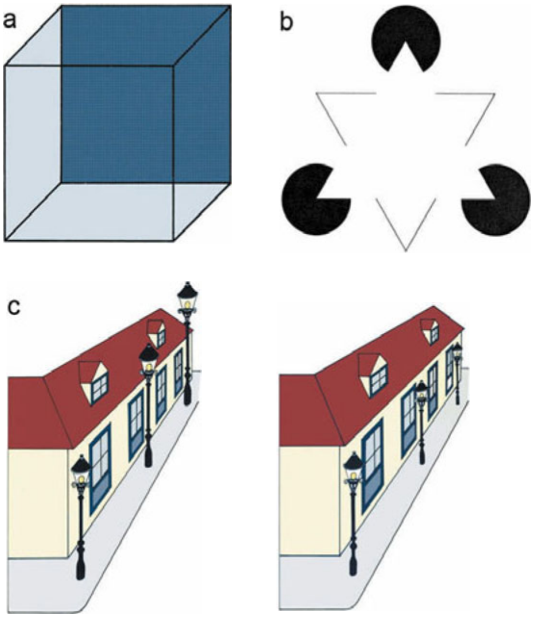

Fig. 5 The brain's active role in perception. **a** Necker cube; **b** Kanizsa triangle; **c** street scene. See text for further explanation. (modified from Barth 1989, with permission Wissenschaftliche Gesellschaft an der Universitaet Frankfurt)

3.3 Efferent control

The water bug is a particularly impressive example of active sensing, though there are many other examples. When we turn and look at something of special interest or focus our attention to the conversation at the neighboring table in a restaurant, this is also active sensing (and at the same time narrowing the sensory field of "view") and telling the sensory systems what to see and hear.

3.3.1 Nervous

The non-specialist may be surprised to hear that the central nervous system not only receives input from the sensory organs but also controls that input. In the vertebrate visual system, for example, there are more efferent than afferent nerve fibers.

Efferent control of sensory organs now seems to be the rule rather than the exception. One of the most striking examples is the circadian change in sensitivity of photoreceptor cells. In the horseshoe crab *Limulus* a circadian oscillator activates efferent fibers in the optic nerve at night. The anatomical and physiological changes induced by them result in an increase of the retina's sensitivity by roughly five orders of magnitude (Batra and Barlow 1990). Adaptations of organisms to planetary periodicities, clock induced daily and seasonal changes, are universal, reflecting the evolution of life under the influences of these temporal changes. As in the case of *Limulus* vision at night is made possible in many other animals by endogenous clock-induced adaptations (Fleissner and Fleissner 2006). As early as 1864 F. Leydig observed rhythmic changes in insect eye structures in constant darkness, indicating that they are endogenous and not induced by changing exposure to light. Among the most intensively studied cases is the scorpion *Androctonus australis*, a night active scorpion (Fleissner and Fleissner 2001, 2006). Its visual sensitivity is also controlled efferently: Due to the activity of efferent neurosecretory fibers its median eye sensitivity changes by three logarithmic units in a day-night rhythm even at constant darkness.

Yet another case is the efferent control of hearing in mammalian ears by the modulation of the basilar membrane motion (Cooper and Guinan 2006). Efferent olivo-cochlear neurons innervate the *outer* hair cells in the cochlea (Fig. 6). Although these cells are not the ones sending information about acoustic stimuli to the brain, they contribute substantially to what the *inner* hair cells tell the brain. Olivo-cochlear neurons control the sensitivity of the peripheral auditory system using the outer hair cells as mechanical effectors whose mechanical activity (contractions) enhances the sound-induced vibrations of the basilar membrane (on which both the outer and inner hair cells sit) in particular frequency ranges. The effect is a remarkable increase of the ear's spectral resolution and, therefore, its ability to distinguish between frequencies. In technical terms one would say that the frequency filter has become much narrower (corresponding to a narrowed spatial range of vibration along the basilar membrane). Latest findings point to the presence of an additional mechanism mediated by the olivo-cochlear neurons which is an inhibition of the mechanical basilar membrane response (Cooper and Guinan 2006).

3.3.2 Hormonal

We primarily associate hormones with the control of metabolism, development and growth, and reproduction, but less with nervous activity. However, there is close interaction between the endocrine and the nervous system. In invertebrates the majority of hormones are indeed neurohormones, secreted by specialized neurons. However,

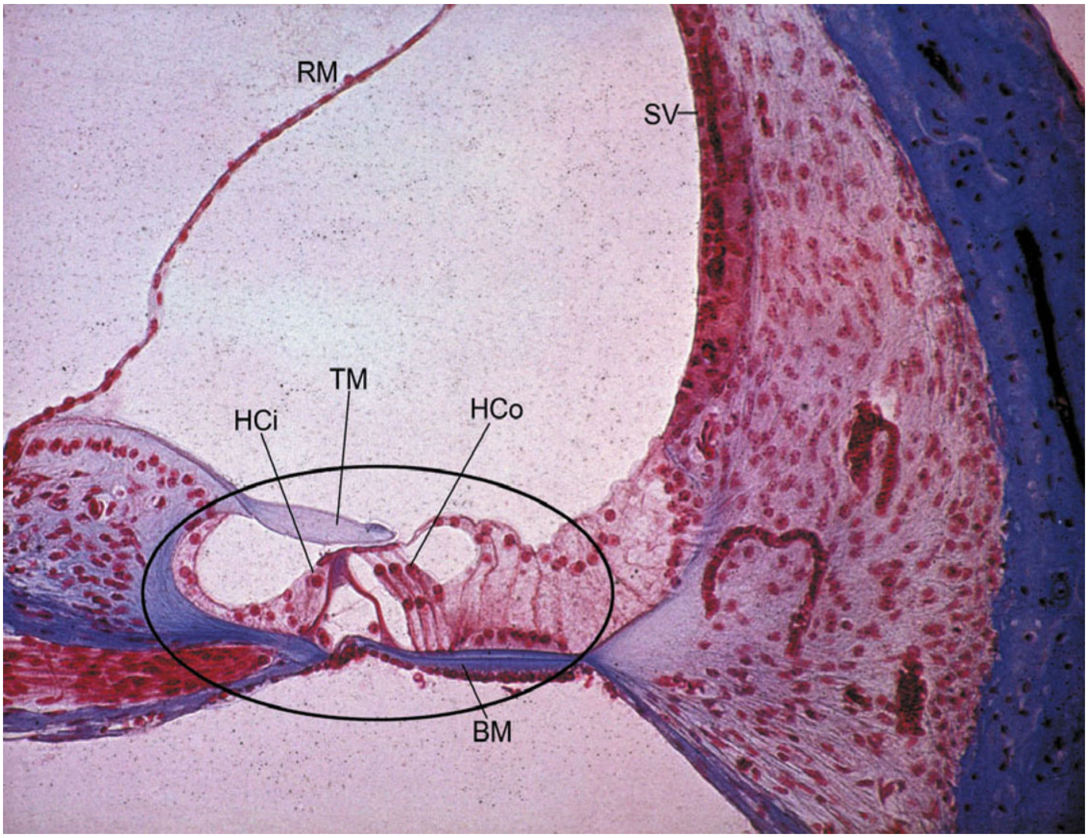

Fig. 6 Mammalian inner ear. Histological section showing details of the sensory apparatus in the cochlea of a guinea pig (*Cavia*). HCo, outer hair cells; HCi, inner hair cells; TM, tectorial membrane; BM, basilar membrane; RM, Reissner membrane; SV, stria vascularis. See text for explanation. (modified from M. P. Kage, W. Nachtigall 1980 Faszination des Lebendigen, Herder Verlag, with permission, M. P. Kage)

here attention shall only be drawn to an additional dependence of sensory input: Hormonally induced state changes in an organism are often paralleled by changes in the responsiveness of sense organs to internal and external stimuli.

Thus changes in olfactory and auditory sensitivity have been known to fluctuate across the female menstrual cycle (Navarrete-Palacios et al. 2003). Olfaction is most sensitive around the time of ovulation and significantly less so during other phases of the menstrual cycle. Similarly, the visual sense changes in color discrimination during the menstrual cycle (Eisner et al. 2004; Giuffre et al. 2007).

Weakly electric fish (Gymnotiformes) have a peculiar sense for the electric fields they produce themselves by their electric organ discharges (EOD). The pulsed self-produced electric fields are used for orientation and communication, and to this end the weakly electric fish have electroreceptor organs widely distributed over their body surface. They detect changes of the field due to objects of either higher or lower conductivity than that of the surrounding water. In the so-called wave-type fish the EOD has a sinusoidal time course and is discharged at a frequency which is under hormonal control and higher in males than in females and juveniles (Fig. 7). By the application of testosterone the discharge frequency can be lowered experimentally. The electrosensors are closely tuned to the fish's own EOD frequency, and this tuning is mediated by steroid hormones which shift the receptor's best frequency according to the EOD discharge frequency (Bass and Hopkins 1985; Zakon 1987, 1998).

3.4 Sensory maps

How is the outside world encoded in sensory signals represented in the brain?

3.4.1 Filtered sensory information is projected onto maps

Of such maps the most familiar is the "somato-sensory homunculus" on the gyrus postcentralis of our cerebral cortex. This map allocates tactile sensitivity (more precisely its spatial resolution) of different skin areas to different brain areas. Areas with high tactile sensitivity like our lips or thumbs correspond to particularly large cortical areas which form kinds of central nervous foveae supporting the concept of filters matched to particular functions. Corresponding maps are found for the other senses like vision and hearing as well.

To qualify as a map the spatial relationship of the position of a stimulus in the sensory space has to be reflected by the position of corresponding neurons on the map. The tactile map then is a topographically ordered, though distorted, representation of the environment, and is called somatotopic. Most likely these maps (termed retinotopic in the case of vision) play a particular role in oriented behavior. However, the map does not always reflect the location of a stimulus source in space. In the acoustic system it is the frequency corresponding to its tonotopic representation in the cochlea. In the barn owl, for example, which uses its acute sense of hearing to localize prey in the dark, the map represents nervously "calculated" values like time of arrival differences or sound intensity differences between the two ears (Konishi 1986, 2003; Wagner et al. 1987). As in the sensory organs the most behaviorally relevant aspects of a stimulus receive particular "attention" and space in the central nervous map (like tactile stimulation of lips and thumbs, echolocation frequencies of bats, relevant time differences in owls etc.).

3.4.2 Different from what a geographical map suggests, the sensory maps laid down in the central nervous system are not always static phenomena.

Change may not only occur depending on the intensity of usage; to use or not to use parts of the receptive field of a sense organ substantially influences the degree of its central nervous representation (Fig. 8) (Jenkins et al. 1990). A map´s position may routinely change depending on behavior and on other stimulus modalities (Sparks 1988). In the monkey (*Macaca*) eye movements induce a shift of midbrain auditory receptive fields of neurons involved in the orientation towards an acoustic stimulus from the left to the right Colliculus superior. This tells us that these sensory maps are organized according to motor coordinates; the auditory neurons use oculomotor coordinates. The absolute position of the goal (a loudspeaker in the experiment) is less important than its position relative to that of the eyes.

3.4.3 An exciting aspect of sensory maps in mammals is their multiplicity

The various senses have not just one but from five to 15 representations in the brain. Each of these multiple maps represents specific invariants of a stimulus, which may also differ in their relationship to behavior and

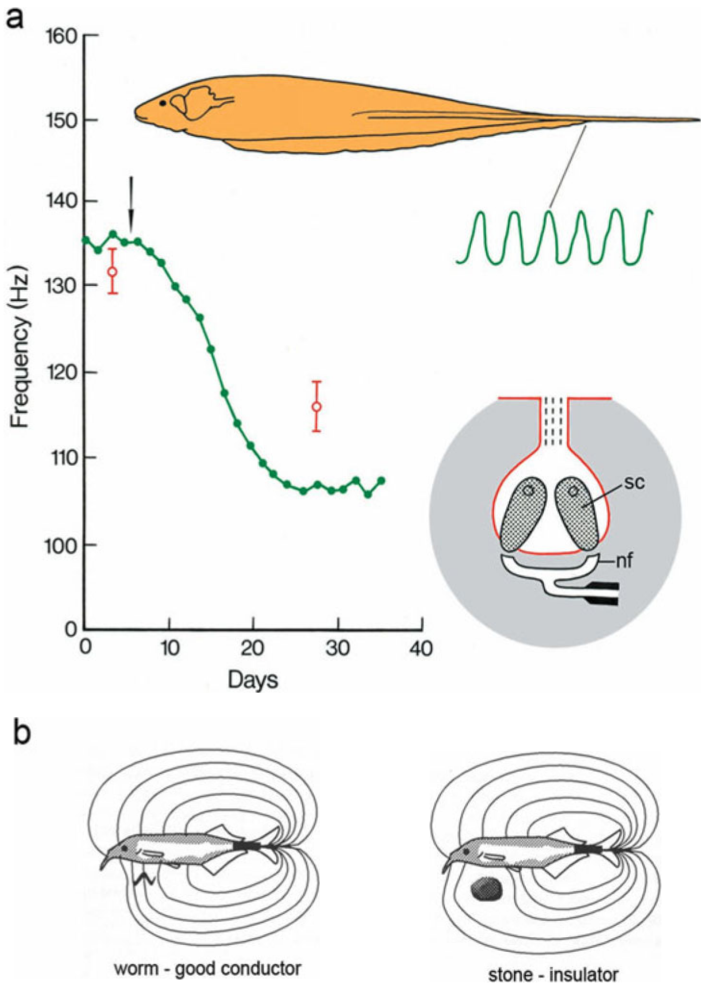

Fig. 7 Efferent control by hormones. **a** Drop of discharge frequency of the electric organ following the application (black arrow) of dihydrotestosterone in a female weakly electric fish (*Sternopygus*). Values in red show simultaneous drop of the frequency to which the electroreceptors are tuned. The oscillation drawn in green below the fish represents the electric discharge of the the electric organ located in the tail region. Inset: the electroreceptor, the so-called tuberous organ, in the skin of the fish; sc, sensory cells; nf, nerve fibers. **b** Schematic drawings showing how an object changes the electric field produced by the fish depending on whether it is a good conductor (left) or an insulator (right). (**a** modified from Zakon 1987, with permission, Elsevier; **b** from von der Emde 2001, with permission, Springer)

thus have different meaning (like one eliciting a shift of one's view, the other affecting emotions). This is best studied in the visual system. Importantly, the stimulus pattern is taken apart and its individual parameters like shape, color and motion are processed separately by the brain. As Semir Zeki (1992) put it: "There is no single central area, to which all other areas would report exclusively, neither in the visual nor in other sensory systems." This type of parallel processing can be nicely demonstrated using non-invasive methods to monitor brain activity and also by studying the often very specific and limited mental deficits of stroke and other patients (Zeki 1992).

The fact that properties of the outside world have parallel representations in the brain, both on the sensory and the motor side, has significant implications. (i) One is the *binding problem*, that is the question of how the representations all come together again and how the holistic nature of our experiences can be explained. One major explanation refers to the temporal synchronization of neurons widely distributed in the brain (see chapter I, 4 by W. Singer). (ii) The other implication is that the older concept of a sequence from sensation to Gestalt to idea is replaced by a model of multiple parallel functions, in which all parts of the brain dealing with the same function cooperate.

4.

Evolution and adaptedness – Darwin's legacy and a few clarifications

Having pointed often to the fit between sensory systems on the one hand and behavior and environment on the other some thoughts on "adaptedness" shall be added in this final section. Adaptedness, an uncommonly used term, focuses on being adapted instead of on the historical process of becoming adapted; it addresses the present role of sensory systems or parts of them and their utility to the individual organism. Throughout this chapter I had in mind process based fitness, convinced that a particular trait of a sensory system can only be classified as an adaptation or adaptedness if its function is identified.

Of course there is no escape from evolutionary thought when we try to understand the emergence of adaptedness and its relation to environmental selection pressures. However, the statement by Theodosius Dob-

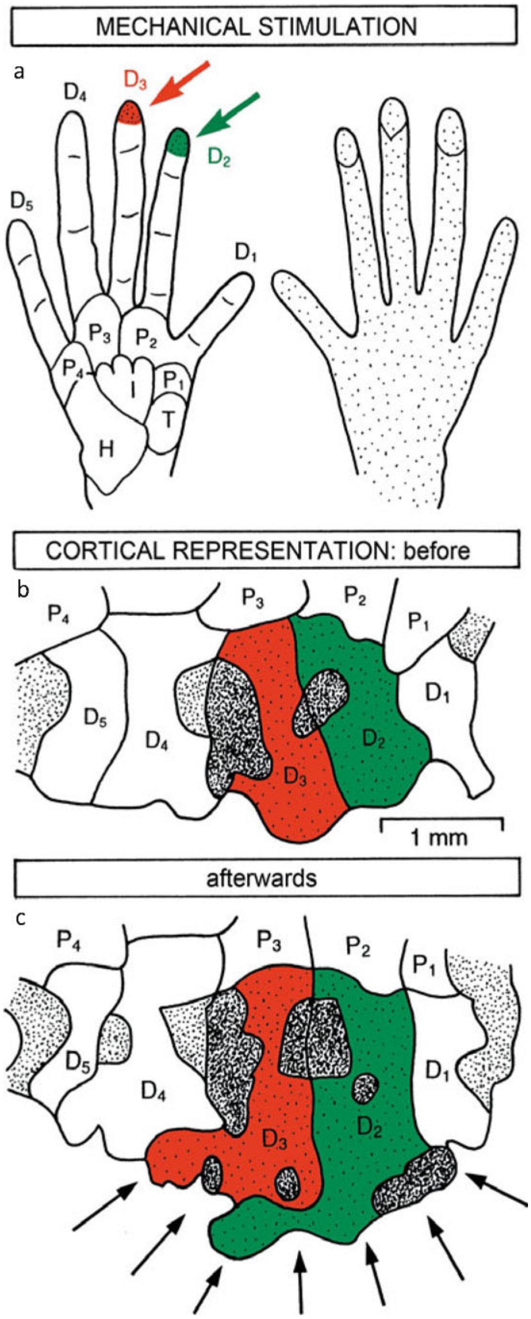

Fig. 8 Sensory maps. **a** Activity-dependent plasticity of cortical representation of an adult owl monkey's hand following continued tactile stimulation of digits D2 and D3. **b** Normal representation of the individual fingers in the somatosensory cortex preceding selective stimulation. **c** After several months of selective stimulation the central nervous representations of the stimulated fingers are enlarged. (modified from Reichert 2000, after Jenkins et al. 1990)

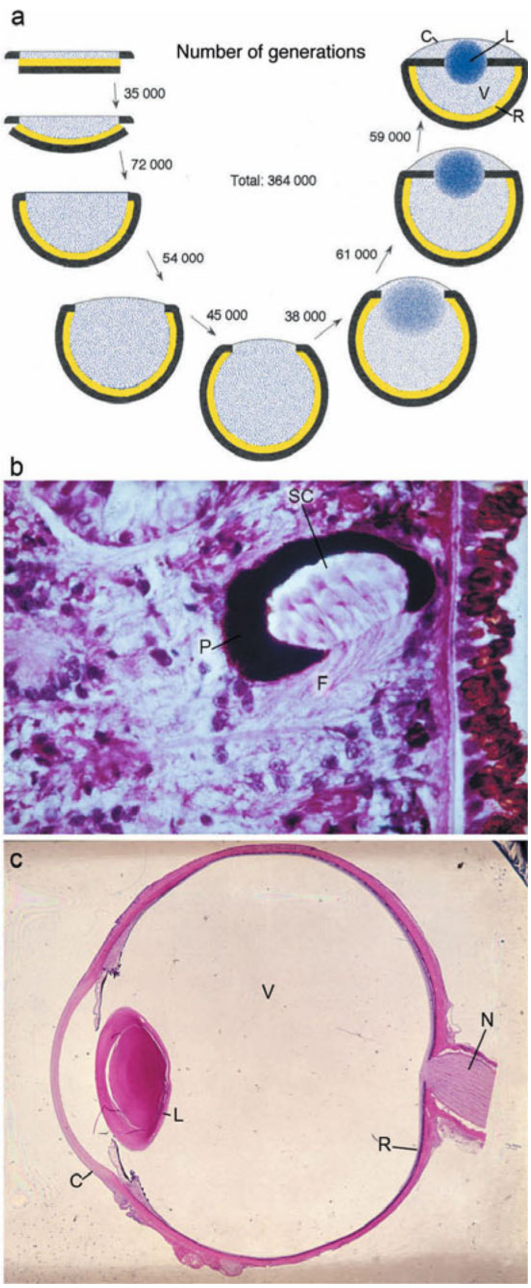

Fig. 9 Evolution and adaptedness. **a** Stages of a modelled sequence of eye evolution starting with a light sensitive flat patch (yellow: photoreceptor cells; blue: protective layer; black: dark pigment). The sequence ends with a focused lens eye characterized by a large invaginated retina (R), a small aperture and a spherical lens (L) with high refractive index and a focal length equal to the distance from the retina. C, cornea; V, vitreous body. The numbers represent generations estimated to be necessary to accomplish the steps between the stages. **b** A simple pigment-cup eye of a flatworm (*Planaria*) located slightly below the body surface. Sensory cells (SC) are seen inside the pigment cup (P) and their axons (F) leaving it. **c** Section through a mammalian camera-type lens eye (mouse). C, cornea; L, lens; V, vitreous body; R, retina; N, optic nerve. (**a** from Land and Nilsson 2002, with permission, Oxford University Press ; **b** and **c** from author)

szansky (1973) that "Nothing in biology makes sense except in the light of evolution," is short sighted and too often quoted carelessly and without reflection. With the same justification one can say that "no aspect of life can be understood without consideration of its physiology; the variants in a population should primarily be understood as physiological experiments" (see also Turner 2007).

In his "Origin of Species" (1859) Charles Darwin was puzzled by the refinement of the human eye. He wrote "To suppose that the eye with all its inimitable continuances could have been formed by natural selection, seems, I freely confess, absurd in the highest degree". How could such impressive design come about without a designer? Following the stringency of logic in his theory of natural selection, however, Darwin concluded (bravely, considering the biological knowledge available at his time) that "Reason tells me that if numerous gradations from a simple and imperfect eye to one complex and perfect can be shown to exist, each grade being useful to its possessor . . .; if further the eye ever varies and the variations be intended . . .., and if such variations should be useful . . .. under changing conditions of life, then the difficulty of believing that a perfected complex eye could be formed by natural selection, though insuperable by our own imagination, should not be considered as subversive of the theory." As it turned out much later it is not subversive at all. Even the habit of disguising lack of knowledge by saying that there were millions and millions of years for a countless number of small steps of improvement needs revision. In their pioneering study Nilsson and Pelger (1994) presented evidence that there need only be 2 000 sequential modifications by one percent in length, width, or protein density to turn a flat patch of light sensitive epithelium into a focussed camera-type eye, provided there is continuous selection for improved spatial vision. Under a few conservative assumptions the authors concluded that the process may be very fast and could indeed have been accomplished in less than 400 000 generations, even with changes from generation to generation of much less than 1 per cent (Fig. 9) and of course without the need for "intelligent design". Assuming one year for the sequence of generations the authors concluded that the formidable vertebrate type of eye may have evolved within less than half a million years, which helps greatly in explaining the rapidity of eye evolution during the Cambrian Explosion (see also Land and Nilsson 2002).

Recent data from Darwin's finches, the true emblems of evolution, underline the surprising speed at which evolution may occur (Grant and Grant 2006). A species of Darwin's finches in a population on one of the islands of the Galapagos archipelago evolved smaller beaks within two decades, this major shift even having occurred within just one generation. When the large ground finch (*Geospiza magnirostris*) arrived on the island of Daphne Major in 1982, the medium ground finch (*Geospiza fortis*), long-time resident on this tiny island, evolved a smaller beak as a result of competition for food. With the smaller beak the finches were more suited to small seeds whereas the much larger newcomer finches with their stronger beaks were mainly interested in the larger seeds. In this way competition among the two species was reduced. In difficult times such as a drought (as in 1977) or unusually rainy weather (as in 1984–85), which are episodes of strong selection, either the large and tough seeds or the small and soft ones are predominant. Under such circumstances the surviving birds and their offspring tend to be bigger with larger and stouter beaks or smaller beaks (better adapted to eat smaller seeds), respectively. Evolutionary biologists refer to this phenomenon as character displacement (Grant and Grant 2006). Obviously natural selection not only operates over vast periods of time but sometimes the evolutionary course of diversification can be directly observed within one or two generations only. The story of the finches also tells us that the identification of an adaptation relies on the identification of function which in turn needs the determination of the specific selection pressures at work. These do not work single-sided, but also depend on the animal's interaction with them. There is a wise saying that "Structure without function is a corpse, function without structure is a ghost." (Vogel and Wainwright1969). The two have to be brought together by integrative biology to include knowledge of the intact and behaving organism.

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