

Sensory Ecology and Neural Coding in Arthropods*

Martin Egelhaaf, Roland Kern and Anne-Kathrin Warzecha

Lehrstuhl für Neurobiologie, Fakultät für Biologie, Universität Bielefeld,
Postfach 10 01 31, D-33501 Bielefeld, Germany

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Arthropods live in almost any conceivable habitat. Accordingly, structural and functional specialisations have been described in many species which allow them to behave in an adaptive way with the limited computational resources of their small brains. These adaptations range from the special design of the eyes, the spectral sensitivities of their photoreceptors to the specific properties of neural circuits.

Introduction

Organisms can be found in almost any habitat, however harsh it may appear to humans. Since organisms are the outcome of a long evolutionary process, they are generally conceived to be adapted by natural selection to their respective environments. These adaptations manifest themselves in all sorts of structural and functional specialisations. Of course, also the behaviour of animals as well as the underlying neuronal machinery are subject to evolution. The variety of behavioural specialisations might be particularly obvious in arthropods. Since there are so many more different arthropod species as compared with any other phylum – more than $\frac{3}{4}$ of all animal species are estimated to be arthropods! – arthropods can be found almost everywhere ranging from the deep sea to the most lofty mountains. Accordingly, structural and functional specialisations are particularly obvious in this phylum.

Although it is quite easy to term a structural characteristic of an animal or a particularly conspicuous behavioural trait a ‘functional specialisation’, it is usually much harder to demonstrate that such a specialisation can really be regarded as an adaptation. Obviously, a specialisation represents

an adaptation, if it is necessary for solving a particular task which can otherwise not be solved. This is hardly ever the case, as there might be usually other solutions to the task. We may only understand the significance of functional specialisations, if we realise that no animal species can live everywhere. Rather any environment is likely to be structured in a characteristic way, thus constraining the sensory input an animal can expect to receive during its lifetime. Moreover, since animals normally operate under closed-loop conditions, their own movements determine to a large extent the dynamical properties of their sensory input. Hence, at least in principle, it is possible for an animal to make reasonable predictions concerning the structure and dynamical properties of its sensory input signals. With this in mind, we may conclude that a specialisation can be regarded as adaptive, if it makes use of the special features of a particular habitat to reach a solution which is comparatively simple from a computational point of view, but which only works under special conditions. Animals are usually no general purpose systems but have to operate only under a limited subset of possible conditions. Hence, this so-called ‘ecological constraint’ provides the chance to be able to do extraordinary things with even a small brain and thus, on the whole, quite limited computational resources.

However, the behavioural performance of animals does not only depend on the specific characteristics of their habitat but also on constraints imposed by the neuronal hardware: Neurons have specific computational capabilities owing to their biophysical properties: Neurons receive their input

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Reprint requests to Prof. M. Egelhaaf.
Fax: (0521) 1066038.
E-mail: Martin.egelhaaf@biologie.uni-bielefeld.de

either directly from sensory cells or often from many interneurons. The synaptic input of a neuron is 'integrated' by the dendritic tree and then, possibly, transformed into a sequence of action potentials. Dendritic 'integration' has been regarded for long as a kind of passive summation of synaptic input. Only recently voltage dependent ionic channels have been found in the dendritic membrane of neurons in almost all systems investigated in this regard (see e.g. Koch, 1997; Regehr and Tank, 1994; Mel, 1994). Hence, complex computations can be accomplished even by individual nerve cells, although there are only few examples where the functional significance of these complexities could be established (e.g. Sobel and Tank, 1994). Despite their complex computational capabilities, neurons are noisy elements as a consequence of stochastic cellular processes, such as transmitter release and the opening and closing of ionic channels (e.g. Allen and Stevens, 1994; Hille, 1992). Consequently, the reliability of information processing is eventually limited by a host of noise sources.

Finally, what can be achieved by nervous systems is limited not just by the layout of the environment at a macroscopic scale but also by physics at a microscopic scale. For instance, the spatio-temporal resolution of visual systems is limited by the nature of light, which may impose severe constraints on the way visual systems are built as well as on the time scale on which behaviour is possible.

The present paper will dwell upon all these aspects which need to be taken into account, if we want to understand why animals process information in the way they do. Most of these aspects are not exclusively relevant for arthropods but for animals quite generally. However, it is often in arthropods that the significance of these aspects can be assessed particularly well. We do not intend to present a comprehensive review, but just present *selected* examples to illustrate the general points we want to make. All examples were chosen in the realm of vision. We start by giving some examples where animals appear to make use of the special spatial layout and temporal properties of their stimuli, in order to use them as efficiently as possible to extract the behaviourally relevant information. Then we turn to those physical and neuronal constraints that eventually limit what can be achieved at all by animals.

How to Make Efficient Use of a Predictable Environment?

Animals that live most of the time in basically the same environment or perform particular tasks only in certain situations can, at least in principle, make use of this predictable environment to find relatively low-level solutions to seemingly high-level tasks. We select only three relatively well-analysed examples where this parsimonious computational strategy might be particularly obvious.

Adaptive eye design to life in a flat world

Animals living in an absolutely flat world can make various predictions about the outside world from the geometry of the situation: (i) All objects that do not rise above the horizon, are smaller than the observing animal itself (and thus most likely harmless), whereas objects which cross the line of horizon are larger (and, at least if moving, potentially dangerous). (ii) The ground surface is mapped onto the ventral part of the retina in such a way that objects are seen the more ventral in the visual field the closer they are. Hence, the retinal position of the base of the object relative to that of the horizon is thus a reliable, monocular cue to the distance of an object (for review, see Zeil *et al.*, 1989). Since an object of a given size appears under a smaller viewing angle if it is further away, the angular resolution might be expected to increase in those parts of the eye which look at regions close to the horizon of the visual environment.

Certainly, the flattest of all environments is the water surface. There are various animals that live at the water surface and make use of the specific geometry of this situation. Examples are water-striders which live on the water surface (Dahmen, 1991) and water bugs which hang from the surface and look at it from below (Schwind, 1980). However, also land animals are known which live in a fairly flat world. A variety of crab species living on sandy beaches or in mudflats are particularly well-analysed examples in this regard (Zeil *et al.*, 1989). Although amazing structural specialisations in eye design have been found which are characteristic of each of the different animal species (see e.g. Land, 1990), all of them have one feature in common: The acuity is largest in those parts of the eye which look at the horizon. From this acute

zone, the resolving power then gradually decreases along the eye's vertical axis (Schwind, 1980; Dahmen, 1991; Zeil and Al-Mutairi, 1996). Especially in crabs, comparative studies have shown that this specialisation in eye design can be regarded as an adaptation to the life in a flat environment, as there are no such pronounced acute zones in crab species which live in more complex visual environments, such as mangrove thickets or rocky shores (Zeil *et al.*, 1989). Finally, in the water bug *Noto-necta* which hangs from the water surface, the spatial resolving power of the eye decreases from the region looking at the horizon in such a way that an object of a given size, such as a prey, is viewed by approximately the same number of ommatidia irrespective of its distance (Schwind, 1980). Therefore, in those animals living for most of their lives in a flat world with its well-defined spatial characteristics, eye design has been well adapted to make particularly efficient use of this specific situation.

Adaptive spatial sensitivity distribution in compensatory optomotor systems

The diurnal hawk moth, *Macroglossum stellatarum*, feeds like hummingbirds. It hovers in front of flowers while sucking nectar. Due to its high energy demand, the animal has to visit up to 1500 flowers a day, thus spending much of its time in searching for appropriate food sources (Pfaff and Varjú, 1991). During every visit of a flower, the hawk moth is confronted with visual environments which are characterised by similar spatial layouts: The frontal part of the visual field is covered by the flower which is, due to the limited length of the animal's proboscis, relatively close to the animal – at least closer than most structures of the environment seen by the more lateral parts of the eye.

The spatial sensitivity distribution of the optomotor system that helps to stabilise the hawk moth's position in front of the flower against disturbances caused, for instance, by a gust of wind appears to be specially adapted to cope with this situation. Displacements of the animal go along with displacements of the retinal images of the environment. These retinal image displacements can be employed by the animal to control compensatory movements in order to stabilise its position in front of the flower. In general, retinal image

displacements can be decomposed into a rotational as well as a translational component. The translational component of the retinal image displacements induced by self-motion of the animal strongly depends on the distance to objects in the environment, whereas the rotational component does not. This suggests that in normal feeding situations of the hawk moth where objects in the lateral part of the visual field are more distant than in the frontal part, the rotational component is much less contaminated by the translational one in lateral parts of the visual field than in frontal ones. Interestingly, the spatial sensitivity distribution of the optomotor system of the hawk moth helps to detect the rotational image displacements without much interference from the translational components, because the optomotor system is most sensitive to rotational motion in the lateral parts of the visual field. Likewise, translational retinal image displacements can be detected better in the frontal visual field than in its lateral parts, which, in a typical feeding situation, is covered by the nearby flower (Kern and Varjú, 1998). Neurons have been found in the hawk moth's nervous system that partly reflect these functional specialisations (Kern, 1998). In conclusion, the hummingbird hawk moth represents an example of an animal that takes advantage of the fact that its visual environment is to some extent predictable in certain behavioural contexts. Waterstriders are another example of animals which exploit specialised spatial sensitivity distributions of their control systems compensating for translational and rotational self-motion, respectively, to stabilise their position relative to their environment (Junger and Dahmen, 1991).

Adaptive sensitivity distribution in systems detecting the polarisation pattern of the sky

Many arthropods can detect a basic property of light which normally remains invisible to us: the plane of polarisation. Polarised light is widespread in nature and provides an animal with a great deal of additional visual information, if the plane of polarisation can be sensed. It has been discovered long ago for a variety of invertebrates, most notably for bees and ants, that these are not only able to sense the plane of polarisation, but that they can use the global polarisation patterns in the sky

as a compass (Frisch, 1965). Subsequently in many species photoreceptors were found to be highly sensitive to the plane of polarisation: The visual pigment is a dipole and as such exhibits maximal absorption when the plane of polarisation of incident light is parallel to the long axis of the molecule. When the visual pigment molecules are aligned in parallel in the membranes of the microvilli, as is the case in specialised photoreceptors in certain insect species, the photoreceptor gets sensitive to the plane of polarisation (for review, see Waterman, 1981). However, the existence of photoreceptors sensitive to the plane of polarisation does not explain how the *global* pattern of polarisation in the sky can be evaluated and used for visual navigation. It merely shows that the information is provided by the sensory system.

Originally it was thought that insects could use the knowledge about the polarisation pattern in the sky to perform some kind of three-dimensional geometrical construction and to derive from such constructions the position of the sun and, thus, their orientation with respect to the sun. Since the polarisation pattern in the sky changes during the day with the elevation of the sun, the animal would also have to know the time of day and year. Such an all-inclusive solution to the problem of navigation by the polarisation pattern in the sky would be a daunting task for any system, not to speak of insects with their tiny brains. Fortunately, there are simpler, though slightly imperfect ways to solve the problem: Bees and ants use a simplified and stereotyped template of the celestial polarisation pattern. While the actual pattern changes with the elevation of the sun, the insect's internal representation of this pattern is 'hard wired' and stays in place (for review, see Rossel, 1989; Wehner, 1997). In a specialised region in the dorsal part of the eye the photoreceptors are sensitive to the plane of polarisation of the incident light and are aligned in a specific pattern. If the difference of the summated output of these retinal analysers of the two eyes is taken, a maximal overall response is achieved when the animal is aligned with the solar/antisolar meridian. As the animal rotates about its vertical body axis, the match between the polarisation pattern and the sensory filter deteriorates systematically. In this way, no mistakes in orientation are made, irrespective of the time of day, if the polarisation pattern in the sky

as seen by the animal is symmetrical about the solar/antisolar meridian.

What About Animals which Do Not Live in a Very Predictable World?

All the above mentioned adaptations to a predictable structure of the environment are indeed fascinating because they reveal how nature made efficient use of this predictability and in doing so found parsimonious solutions in terms of computational expenditure to solve often quite complex tasks. However, there are many other animals which appear to live in much less constrained environments – but, nevertheless, seem to perform quite well. Since these animals cannot resort to the strategy to adapt their visual analysers to a predictable environment, one might envision that these animals should rely, in some way, on more expensive computational strategies, thus, requiring larger nervous systems. As far as one can tell, there are no indications that this is the case.

Think, for instance, of the common Calliphorid flies, which are widely used to study the neuronal mechanisms underlying visual orientation behaviour (for review, see Hausen and Egelhaaf, 1989; Egelhaaf and Borst, 1993a). Quite related Dipteran species can be found in often vast numbers all around the world in habitats ranging from sheepwalks in the Australian outback to apartments in European cities. Obviously, the spatial structures of these environments do not have much in common with each other, and it is hard to see what features the animal should be able to rely upon when trying to 'make any prediction' that can be used to reduce the computational expenditure of the sensory mechanisms by which relevant information about the environment is gathered. In particular, blowflies often appear in environments, such as the abovementioned apartment, which came only lately into existence and thus into the reach of flies. Hence, flies might have had hardly a chance to adapt phylogenetically to this particular sort of environment. Consequently, many Calliphorid flies appear to be generalists which can well survive in almost any kind of visual environment. Nonetheless, their brains are not bigger nor more complex, at least on the basis of their gross morphology, than those of the above described specialists. In this context, it should be noted, that apart

from adaptations in the structure of the eye or the most peripheral processing stages in the nervous systems, we hardly know, apart from exceptions, anything about the computational principles in both specialists and generalists. Hence, all statements in this regard are quite preliminary and basically reflect our ignorance.

Generating Predictable Sensory Input by Active Behaviour

In the examples given above, the visual input was predictable, because of the specific and well-defined geometrical layout of the respective visual environment. However, this is not the only possibility how a highly predictive visual input comes about. If the animal is not conceived as viewing the outside world passively, but is actively moving in a specific way, additional information may be available (for review, see Land and Collett, 1997). Only two, quite different examples will be given, where active behaviour of the animal is required to allow it to acquire relevant information of the outside world and, thus, to be able to solve a particular computational task.

Adaptive design of a visual pathway designed to chase after rapidly moving targets

The first example shows that it might be necessary to behave in a specific way in order to solve a biologically highly relevant problem, i.e. the problem of finding a mate. Flies show virtuosic aerial pursuits in their mating behaviour in which males chase and catch females (Land and Collett, 1974; Wagner, 1986). While chasing, males fly underneath their target and keep it fixated in the dorsal part of the visual field. Since these pursuit manoeuvres belong to the fastest visual guided behaviours that can be observed, there must be an accurate and rapid system for piloting the chasing male. Sex-specific specialisations have been found in male flies at various levels of the visual pathway, ranging from the retina (Hardie *et al.*, 1981; Hardie, 1986) to the output level of the visual system (Hausen and Strausfeld, 1980; Strausfeld, 1991; Gilbert and Strausfeld, 1991). The male-specific specialisations are discussed to be part of the control system mediating chasing behaviour.

Most conspicuously, all these specialisations concern the dorsal part of the visual field: The

male-specific neurons at the output level of the visual system have their receptive fields in the dorsal part of the visual field. Moreover, in a restricted region of the dorsal frontal eye there is a zone of particularly high acuity (Hardie *et al.*, 1981). Interestingly, chasing males fixate on their target with just this acute zone (Land and Collett, 1974; Wagner, 1986). Since the female is seen against the sky, its contrast is much larger than if it would be seen against the ground. A high contrast of the target might be particularly important from a signal detection point of view, if it is taken into account that, depending on the distance between male and female fly, the retinal image of the female may only cover few ommatidia and thus stimulate only a small number of photoreceptors. The problem of detecting the female may get even worse, as due to the high velocities both males and females often assume during chases, the target may spend only a few milliseconds within the receptive field of a given photoreceptor. The specific arrangement of photoreceptors in the acute eye zone can also be interpreted to enhance the sensitivity of the male for detecting small objects, because here not only 6 but 8 photoreceptors with largely overlapping receptive fields and the same spectral sensitivity converge on the same second-order neurons. From all these specialisations it appears that male flies may be only able to perform their rapid and virtuosic chasing behaviour, as long as they fly below the chased female in order to keep its contrast high and thus detectable against the background.

Active vision in order to extract information about the spatial layout of the environment

Various insect species have been shown to acquire information about the spatial structure of their environment by active, more or less periodic movements. For instance, locusts perform periodic sidewise movements of their body, thereby viewing the world from a range of vantage points. They were shown to use the information gained by these active movements to estimate the distance to a target before they accurately leap upon it (Sobel, 1990; Collett and Paterson, 1991). Different kinds of active movements are frequently observed in various hymenopteran species, such as bees and wasps. They perform systematic flight manoeuvres

when they leave their nest or a newly discovered foodplace. They do not depart by taking a straight flight course. Rather they turn around to face the place they are leaving and fly backwards in a series of continually increasing arcs (Zeil, 1993a,b; Zeil *et al.*, 1997). There is good evidence that the animals acquire through these systematic flight manoeuvres information about the location of the goal in its environment. They store this information in some way and use it to recognise their goal when they return. Rather than performing sidewise movements as locusts do to estimate their distance to a target, bees and wasps tend to pivot around the goal, thereby fixating on the goal with roughly the same retinal area. In this way the objects in the surround move relative to the goal in a well-defined way. Simple geometrical analysis of this situation reveals that pivoting generates distance information relative to the goal rather than relative to the animal as sidewise movements do (Collett and Zeil, 1996). Whereas, in the latter case, the movements of the animal are purely translational, they also contain a rotational component in the former case.

While it is fairly obvious that these animals induce quite specific spatio-temporal properties of the time-dependent retinal images, it is not clear so far, in which way the visual system and, in particular, the mechanisms evaluating these motion patterns operate. In any case, information about various spatial aspects of the visual environment of an animal appears to be acquired with relative ease, if an appropriate strategy of moving actively is adopted.

Constraints Imposed on Any Adaptation by Physics and by the Neuronal Hardware

So far, we discussed examples of structural and behavioural specialisations which might be regarded as adaptations to particular ecological niches. It is important to note in this context that most of these adaptations are only required because there are principal constraints set by the physical nature of light as well as by the available neuronal hardware. Some examples of such constraints will be given here.

Size limits of eyes due to the physical nature of light

The physical nature of light imposes constraints with respect to both the minimal size of eyes and

thus their spatial resolution as well as their dynamical properties (for review, see Kirschfeld, 1976; Land, 1981). Mainly two properties of light are important in this regard:

- Light is quantal in nature, i.e. there is a minimum unit of energy capable of being detected. The quanta emanating from a light source are randomly distributed in time. The stochastic nature of light is particularly obvious at low light levels, since the signal-to-noise ratio of signals decreases with a decreasing amount of available light. This requires that all computations such as movement detection that involve the comparison of brightness differences sensed by different photoreceptors depend on the absorption of at least as many photons as are necessary to obtain a statistically reliable estimate of the average brightness in the receptive field of the different receptors. At low light levels, reliable estimates can be obtained, at least in principle, by either spatial pooling of the output signal of a number of photoreceptors thereby sacrificing spatial resolution, or by smoothing out the membrane potential fluctuations elicited by the absorption of single photons by temporal averaging, thereby reducing the temporal resolution of the visual system. Indeed, in motion vision systems quite commonly light is pooled from a larger area of the eye when it gets darker (Pick and Buchner, 1979; Schuling *et al.*, 1989). Moreover, the time constants of photoreceptors tend to get larger with decreasing brightness, allowing for temporally smoothing out the consequences of the stochastic nature of light (Dubs, 1981; Howard *et al.*, 1984; Kuster and French, 1985). These changes in the spatio-temporal properties of photoreceptors can be regarded as an adaptation to the prevailing conditions in a particular visual environment. Also in the above-discussed chasing system of male flies, pooling of the output of an increased number of photoreceptors is presumably employed as a strategy to increase the sensitivity of the system in the retinal region which is involved in chasing. Since, in contrast to the other eye regions where each ommatidium houses photoreceptors with different spectral sensitivity, all photoreceptors in the acute zone of male flies have the same spectral sensitivity. The adaptation of males to spot females efficiently has to be paid for: males sacrifice colour

vision in this part of the retina in order to concentrate all its photoreceptors on the biologically important task of chasing potential mates (Hardie, 1986).

- Light emanates from a light source as a wave. Waves show interference phenomena part of which are relevant with respect to eye design. This is particularly true for diffraction which occurs at apertures, such as the pupils of eyes or the boundaries of ommatidial lenses in the case of compound eyes. Light passing through one part of an aperture interferes with that passing through another part, resulting in an interference pattern which tends to degrade the quality of the retinal image. Diffraction is one reason why eyes cannot get arbitrarily small. Since the minimal diameter of photoreceptors is limited, a minimum area of retina is needed to resolve a given number of points in space or, in other words, a better spatial resolution requires a larger eye. The above mentioned acute zones of increased spatial resolution found in certain eye regions of animals living in a flat world or in male flies are only required because of these physical constraints. If there were no physical limitations with respect to the size of photoreceptors and aperture, there would be no reason, why spatial acuity should not be very high for the whole retina. However, because apertures and, thus, ommatidial lenses need to have a minimum size, an eye with a given surface can house only a limited number of ommatidia. If the area of the eye and the field of view is given, the spatial resolution can be only increased in parts of the eye by decreasing the interommatidial angle. However, this measure, inevitably leads to a decrease in spatial resolution in other eye regions. Consequently, any specialisation has to be paid for. Nonetheless, if the sensitivity distribution is adapted to the visual habitat of the animal, the overall performance of the system can be optimised in this way.

Limitations of the accuracy of neural coding

There is another constraint which limits the time scale on which information can be processed and transmitted in nervous systems. This constraint pertains to the way nervous systems encode information. They do this in either of two principally

different ways, either by graded changes in their membrane potential or by sequences of action potentials. Photoreceptors and their postsynaptic elements basically transmit information by graded membrane potential changes. In neurons that respond mainly with graded changes in their membrane potential, information about a stimulus might be signalled at any instant of time. In contrast, in spiking neurons no information is signalled between the spikes. Here the information resides only in the number of spikes per time interval, the timing of individual spikes relative to a stimulus or the temporal pattern of spikes (Perkel and Bullock, 1968; Rieke *et al.*, 1997). Since there is an upper limit for the rate at which spikes can be generated, the bandwidth of spiking neurons is principally limited. Thus, it might be expected that, for instance, it may take longer for a spiking neuron to signal changes in the stimulus conditions than for a neuron responding with graded changes in membrane potential. Interestingly, this expectation is not met by the experimental findings: A spiking neuron and a neuron conveying information with graded membrane potential changes at the same level of integration in the fly's motion pathway do perform quite similarly in coding the onset of a motion stimulus or in representing the time course of pattern velocity (Warzecha *et al.*, 1993; Warzecha, 1994; Haag and Borst, 1997). Only on a very short time scale below 10 ms does the neuron with graded potential changes perform better than the spiking one (Warzecha *et al.*, 1993; Warzecha, 1994).

The main difference why spiking neurons and neurons with graded membrane potentials do not perform as differently as one might expect, is likely to be neuronal noise. Both the membrane potential in cells with graded potentials as well as the interspike interval in spiking neurons fluctuate continually even during constant stimulation. Moreover, when the same stimulus is presented repeatedly to a neuron, the responses may vary quite a lot. It is quite common that the variance of neuronal responses is almost as large as the average response amplitude (Tolhurst *et al.*, 1981; Vogels *et al.*, 1989; Miller *et al.*, 1991; Britten *et al.*, 1993). Neuronal noise is, thus, a major constraint which limits the performance of neuronal computations.

The constraints imposed by the limited channel capacity of spiking neurons as well as by neuronal

noise are particularly obvious in the time domain: As a consequence of stochastic signal fluctuations, it is not clear when just looking at, for instance, a spike train, whether changes in the interspike interval are induced by some stimulus or are just due to a noise source. This raises the question for the time scale on which stimulus-related information can be conveyed by neurons. In the following we shall see that this time scale depends on three factors (i) the dynamics of the stimuli, (ii) the way the stimuli are processed, and (iii) the dynamical properties of stochastic signal fluctuations. Owing to a lack of consistent data, there is currently much controversy about the time scale on which neurons process and transmit information (Shadlen and Newsome, 1994; Shadlen and Newsome, 1995; Softky, 1995; Rieke *et al.*, 1997). The constraints limiting the reliability of neural coding are known particularly well for the motion pathway of the fly. Therefore, we concentrate here on this system.

Most spikes of motion-sensitive neurons in the fly visual system occur time-locked to visual motion with a precision in the range of only several tens of milliseconds, even when the direction of motion changes rapidly (Warzecha *et al.*, 1998). The relative imprecision in the timing of spikes is not the consequence of a particular imprecise spike generation mechanism in the motion sensitive neurons. If the membrane potential changes of a neuron induced by its synaptic input are sufficiently transient, spikes time-lock to these changes with a temporal precision in the millisecond range. However, since the computations leading to a directionally selective response to motion inevitably require time constants in the range of some tens to hundreds of milliseconds (for review, see Egelhaaf and Borst, 1993b), the stimulus-induced membrane potential fluctuations in motion sensitive neurons do not follow high-frequency velocity changes with a high gain. Consequently, in the motion vision system of the fly the exact timing of most action potentials is determined in the motion vision system by stochastic membrane potential fluctuations (Warzecha *et al.*, 1998). Hence, mainly changes in spike activity on a coarser time scale provide in this system reliable information about what is going on in the outside world. Different computational needs are imposed on neurons involved in other tasks. Accordingly, much more rapid stimulus-induced membrane potential

changes and, thus, a much more precise time-locking of spikes to stimuli are found, for instance, in neurons of the fish electrosensory system involved in object detection (Kawasaki, 1993), in the system mediating acoustic sound localisation of vertebrates (Carr, 1993) or the mechanosensory system of flies involved in coupling the activity of flight motor neurons to the temporal phase of wing beat (Fayyazuddin and Dickinson, 1996).

Though in the latter systems very precise timing of spikes to the sensory input is necessary for solving the computational tasks of the respective systems (i.e. detecting an object, localising a sound source or coupling the activity of flight motoneurons to the temporal phase of the wingbeat), there might be no computational requirements for such precise time-locking of spikes to visual motion stimuli. Biological motion vision systems are either required to sense self-motion of the animal or the motion of objects. Because of inertia and friction impeding rapid velocity changes of objects, virtually no behaviourally relevant motion stimuli change their direction at temporal frequencies which would demand for their resolution a temporal precision of spiking in the millisecond range. Whether this notion is true needs to be elucidated in experiments where the dynamics of the natural motion input of animals is analysed. There are almost no studies where this has been done so far. On exception is optomotor position stabilisation of the hummingbird hawk moth hovering in front of flowers (see above). It has been shown that flowers, on which the hawk moth is feeding, may wiggle in the wind at frequencies between about 1 and 2 Hz (Farina *et al.*, 1994). In the context of male chasing behaviour, up to ten turns per second have been observed in certain fly species (Wagner, 1986; Land, 1993). Hence, neuronal representations of even the fastest changes in the direction of self-motion that may occur in nature do not require a very precise timing of spikes. In the context of optomotor course stabilisation in flies, first attempts have been made to analyse the neuronal coding of motion stimuli that were generated in a flight simulator by the animal's own actions and reactions. The resulting velocity fluctuations occurring during course stabilisation had most power at frequencies below 5 Hz (Warzecha and Egelhaaf, 1996). Accordingly, on the basis of neuronal responses, these behaviourally generated

motion stimuli can be decoded most reliably at a time scale of some tens of milliseconds, i.e. at a time scale where the timing of individual spikes does not matter (Warzecha and Egelhaaf, 1997). Hence, it might be not disadvantageous for an animal, that its motion pathway does not represent stimuli with a precision in the millisecond range. Obviously, motion information processing is just one computational task of the visual system the underlying principles of which we understand to some extent. Other constraints are imposed on other tasks. In any case, if we want to understand specific adaptations of animals, invertebrates and vertebrates, to their particular ecological niches, it is very important to be aware of the constraints imposed not only by this niche but also of the neuronal machinery through which the task has to be solved.

Conclusion

In order to fully understand the organisational principles of sensory systems and the neuronal machinery that exploits the information provided by

them, we need to take at least the following three aspects into account:

- We need to know the natural operating conditions of the system.
- We need to know the computational task which the system has to solve.
- We need to know the limitations set by physics as well by the neuronal hardware that is available to solve a particular computational problem.

As we have seen, many of the structural and functional adaptations appear to be quite sophisticated, although they are simple in their basic principles. Nonetheless, animals, and even arthropods, often easily outperform any man-made devices in particular tasks, just to remind you of the chasing behaviour in flies. The fascinating thing about all this is, that they do it often with brains as tiny as the head of a pin. This might be only possible, because neuronal circuits are subject to much longer testing than is possible for any technical system. Shouldn't some tens to hundreds of million years be enough to lead to sophisticated and, at the same time, parsimonious solutions to even daunting tasks?

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