Vision in flying insects
Martin Egelhaaf* and Roland Kern†

Vision guides flight behaviour in numerous insects. Despite their small brain, insects easily outperform current man-made autonomous vehicles in many respects. Examples are the virtuosic chasing manoeuvres male flies perform as part of their mating behaviour and the ability of bees to assess, on the basis of visual motion cues, the distance travelled in a novel environment. Analyses at both the behavioural and neuronal levels are beginning to unveil reasons for such extraordinary capabilities of insects. One recipe for their success is the adaptation of visual information processing to the specific requirements of the behavioural tasks and to the specific spatiotemporal properties of the natural input.

Addresses
Lehrstuhl für Neurobiologie, Fakultät für Biologie, Universität Bielefeld, Postfach 100131, D-33501 Bielefeld, Germany
*e-mail: martin.egelhaaf@uni-bielefeld.de
†e-mail: roland.kern@uni-bielefeld.de

Abbreviations
HSE   horizontal system, equatorial cell
LGMD lobula giant movement detector
TC   tangential cell

Introduction

As an observer moves through a natural environment, his or her photoreceptors typically receive a wildly fluctuating pattern of image flow. It is the task of the brain to interpret this complex spatiotemporal input and to make use of it in guiding behaviour. Existing artificial vision systems are outperformed by nervous systems in many respects in their ability to process retinal image flow. This is most remarkable for insect brains, with their small number of neurons and the extraordinary speed with which retinal images are processed. Because of the relative ease with which their nervous systems can be examined electrophysiologically and using imaging techniques, insects have served for many years as model systems for analysing the processing of retinal image flow [1–7]. During the review period, there have been important new developments that aid understanding of not only insect vision but, quite generally, how behaviourally relevant visual information is processed.

Behavioural tasks

To understand the mechanisms underlying visually guided behaviour, a causal relationship between visual input and behavioural output needs to be established. This has been possible for various behavioural contexts [4,8,9]. By artfully manipulating the environment, those spatiotemporal features of the visual input that are decisive for behavioural control

can be pinpointed. Only three particularly well analysed examples can be summarised here: visual course control; estimation of travelled distance; and pursuit of moving targets.

Visual course control: Optic flow is an important source of information used to control the course and velocity of locomotion. For example, regulating the angular velocity of the retinal image of the environment controls the flight speed of bees. Accordingly, bees decelerate when flying, for example, through a narrow gap [4]. When intending to move straight, it has been concluded that bees and flies equate the overall optic flow on their eyes [4,10]. If one eye is occluded, an optomotor equilibrium can be reached only on a slightly curved path [11,12]. Flies reach this equilibrium only on average, whereas individual paths of locomotion can deviate from it almost arbitrarily depending on the animals' momentary intentions. Optic flow not only helps mediate a straight course of locomotion but might also elicit turns, to prevent collision with an obstacle, for example. It was concluded that when a fly approaches a wall, the time at which a sharp saccade-like turn is elicited and the direction of the saccade depend on the characteristics of retinal image expansion [13•].

Estimation of travelled distance: It is essential for a worker bee to determine the distance between a food source and her hive. This information, in addition to flight direction, is communicated to her hive mates by the waggle dance and allows them to find the food source. Distance estimation is hard to accomplish during flight, because many distance cues that can be used while walking are not available. By contrast to walking ants [14,15•], flying bees gauge distance in terms of the optic flow experienced during flight to the food source (Figure 1; [4]). Since translational optic flow depends on the three-dimensional layout of the environment, distance information gathered in this way is ambiguous. Nevertheless, the ambiguities do not lead to problems, as long as the recruited bee tends to fly on the same route as the forager and if the environment does not change much between the flight of the forager and that of recruited bees. Whereas such changes of the environment were systematically made for experimental analysis [16,17••,18••], they occur only rarely in natural environments during a day or couple of days. Hence, visual estimation of flight distance is not reliable in all circumstances but is sufficient for specific needs under normal behavioural conditions.

Pursuit of moving targets: Some insects are able to chase moving targets, be it prey or a mate, in virtuosic aerial manoeuvres (Figure 2a; [19–23]). As the visual input is very complex during these manoeuvres, it has been hard to unravel the underlying control systems. By reducing the complexity of the visual input and using dummy targets

Figure 1
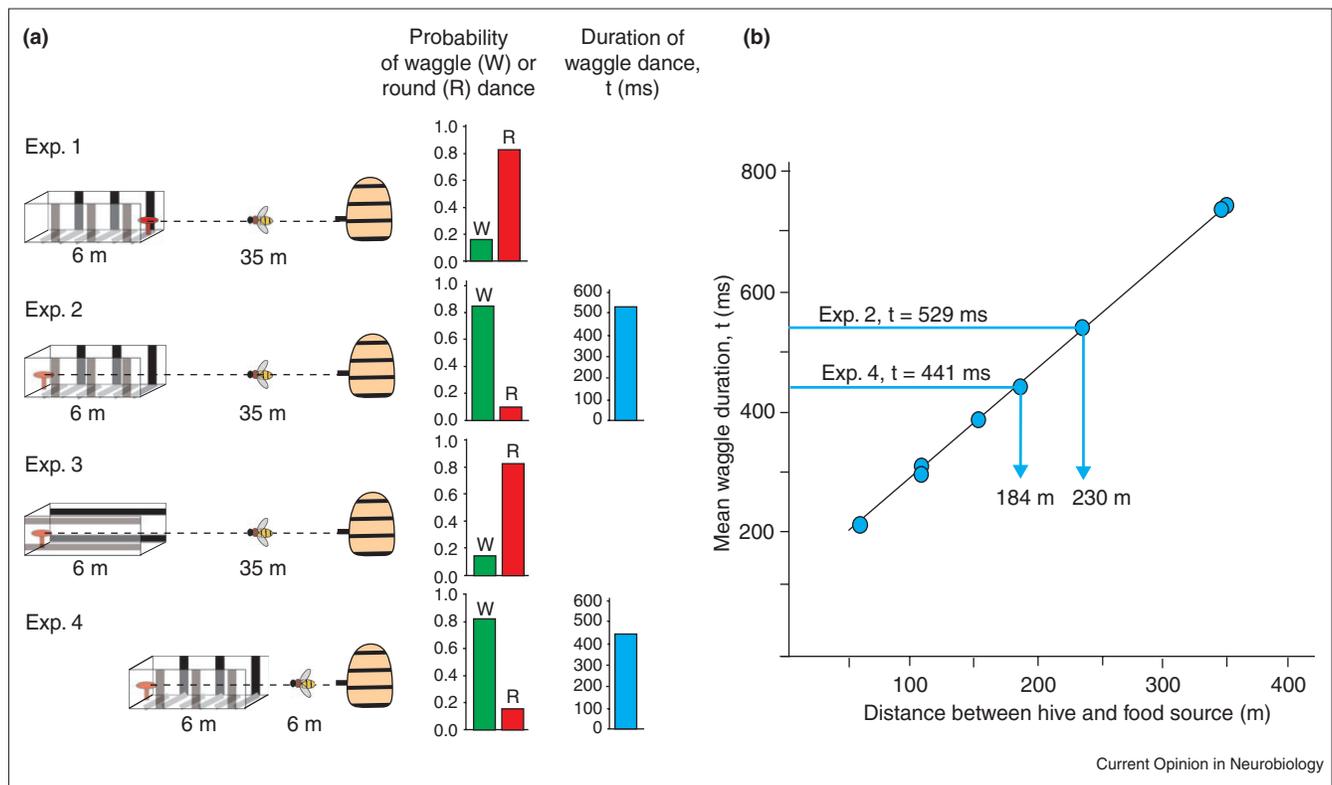
Honeybees measure distances in terms of optic flow and communicate this information to their hive mates by the waggle dance. Behavioural analysis of how honeybees estimate the distance travelled between their hive and a food source. **(a)** Layout for the experiments using tunnels and probabilities of waggle (W; green bars) and round dance (R; red bars) for the different experiments. A tunnel with a length of 6 m in and a width of 11 cm was positioned either at a distance to the hive of 35 m in (not drawn to scale) or at a distance of only 6 m in. The walls of the tunnel were either covered with a texture that contained vertically oriented elements (Exp.1, Exp.2, Exp.4) or horizontally aligned stripes (Exp.3). When the food source was placed at the entrance of the tunnel (Exp.1), the bees performed mainly round dances, signalling a short distance to the food source. When the food source was placed at the end of the tunnel containing vertically oriented texture (Exp.2), the returning bees performed mainly waggle dances, signalling much larger distances to the hive, although the actual travel distance was not much increased. A food source at the same distance, however, located in a tunnel with horizontally oriented stripes (Exp.3), again led mainly to round dances. The main difference between Exp.2 and Exp.3 is that in the former much optic flow is evoked on the eyes of the honeybee while flying along the tunnel, whereas in the latter case there is only little optic flow, because the contours are mainly oriented along the flight direction. When the tunnel covered with vertical contours and the food source close to its end is placed near to the hive (Exp.4), mainly waggle dances are performed, which are shorter than those performed in Exp.2 (compare blue bars). These experiments show that travelled distance is measured in terms of optic flow. **(b)** Calibration of the odometer of the honeybee. Mean duration of waggle dances elicited by outdoor feeders at various distances to the hive. Also shown are the mean durations of waggle dances measured in Exp.2 and Exp.4 and their equivalent outdoor flight distances, as read from the regression line. At a mean distance between the honeybees and the tunnel wall of 5.5 cm, 1 ms of waggle in the dance corresponded to 17.7° of image motion on the eyes. (Adapted from [17••]).

moving on well-defined paths, however, it has been possible to analyse the chasing behaviour of male blowflies. It was concluded that flies employ similar viewing strategies to those of primates: spontaneous changes in gaze are done rapidly by saccades [24], whereas moving targets are followed by smooth pursuit [25•]. The pursuit system of flies is relatively simple but rapid and efficient. The forward velocity of the chasing fly is controlled by the angular size of the target, whereas its turning velocity depends on the angle by which the target is seen. During pursuit, primate-like catch-up saccades are observed only when the target changes its trajectory too rapidly to allow the pursuer to follow smoothly. Model simulations revealed that even these catch-up saccades, which occur frequently during chases of real fly targets [22], can be explained as a by-product of

the smooth pursuit system if neuronal latencies and the inertia of the chasing fly are taken into account [25•].

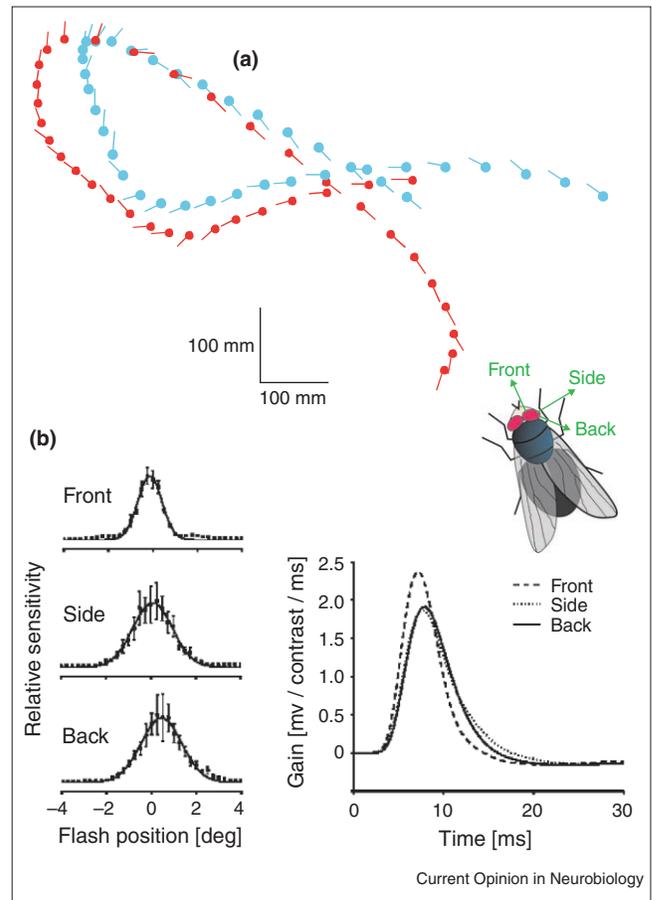## Neuronal circuits for visual information processing

Which computational strategies allow insects to perform so extraordinarily well in visually guided orientation? Although researchers are far from being able to understand the functioning of the neural circuits mediating the various components in the behavioural repertoires of insects, it is becoming increasingly clear that visual information processing is exquisitely adapted to the operating conditions in a normal behavioural context. Such adaptations are present already at the level of photoreceptors and may be followed up to the highest levels of visual information processing.

One example is the visual mechanisms involved in chasing behaviour. In many insects, the design of the male visual system is highly specialised. Apparently, this male-specific specialisation has evolved to match the need for higher accuracy in the frontal part of the visual field, where the target is held in a relatively fixed position during chases [26]. Moreover, the temporal resolution has been found recently to be enhanced in this part of the eye in male blowflies (Figure 2) as a consequence of specific ionic currents and biophysical properties of the photoreceptors [27•,28•]. These specialisations, together with a male-specific connection pattern between photoreceptors and second-order neurons [29], result in a more reliable performance of the frontal part of the eye [28•]. Although there is good anatomical evidence for sex-specific neuronal circuits at more central processing stages in male flies [30–32], it is not yet possible to assess the functional significance of these circuits for chasing behaviour.

An approaching object, such as a predator, is characterised by increasing retinal size. Neurons detecting looming stimuli have been characterised in moths [33] and in locusts [3,34,35•,36•]. In locusts, the lobula giant movement detector (LGMD) neurons respond best to objects on a collision course. By relating the neuronal activity to steering responses of tethered flying animals, it was concluded that this neuronal system plays a role in predator avoidance [36•]. Despite disagreement as to the details [3,34,35•,36•], it appears that the LGMD response to looming stimuli is mediated by three distinct processes: motion-sensitive excitation impinging retinotopically onto a dendritic subfield of LGMDs; an inhibitory network acting presynaptically onto the motion-sensitive pathway; and feedforward inhibition impinging on two additional dendritic subfields of LGMDs. Many properties of LGMDs can be captured by network models of their input organisation [3,35•].

Optic flow elicited by self-motion is specified by global, rather than merely local, features. This implies that mechanisms extracting optic-flow information from the retinal input need to combine local motion measurements from large areas of the visual field. Accordingly, local motion information has been shown to be spatially pooled on the extended dendrites of the tangential cells (TCs) in flies [2,6,7]. The preferred directions of the local motion detectors that synapse onto a given TC appear to coincide with the directions of the velocity vectors characterising the optic flow induced during particular types of self-motion [37]. This sophisticated pattern of local preferred directions is not affected by sensory experience but is the consequence of phylogenetic adaptations [38]. In the fly, specificity for certain types of optic flow has been shown to be much enhanced by synaptic interactions between TCs in the ipsilateral and/or contralateral half of the visual system. As a consequence, individual TCs are thought to be tuned to certain types of self-motion or to the relative motion between objects and their background [39–41,42•,43•,44••].
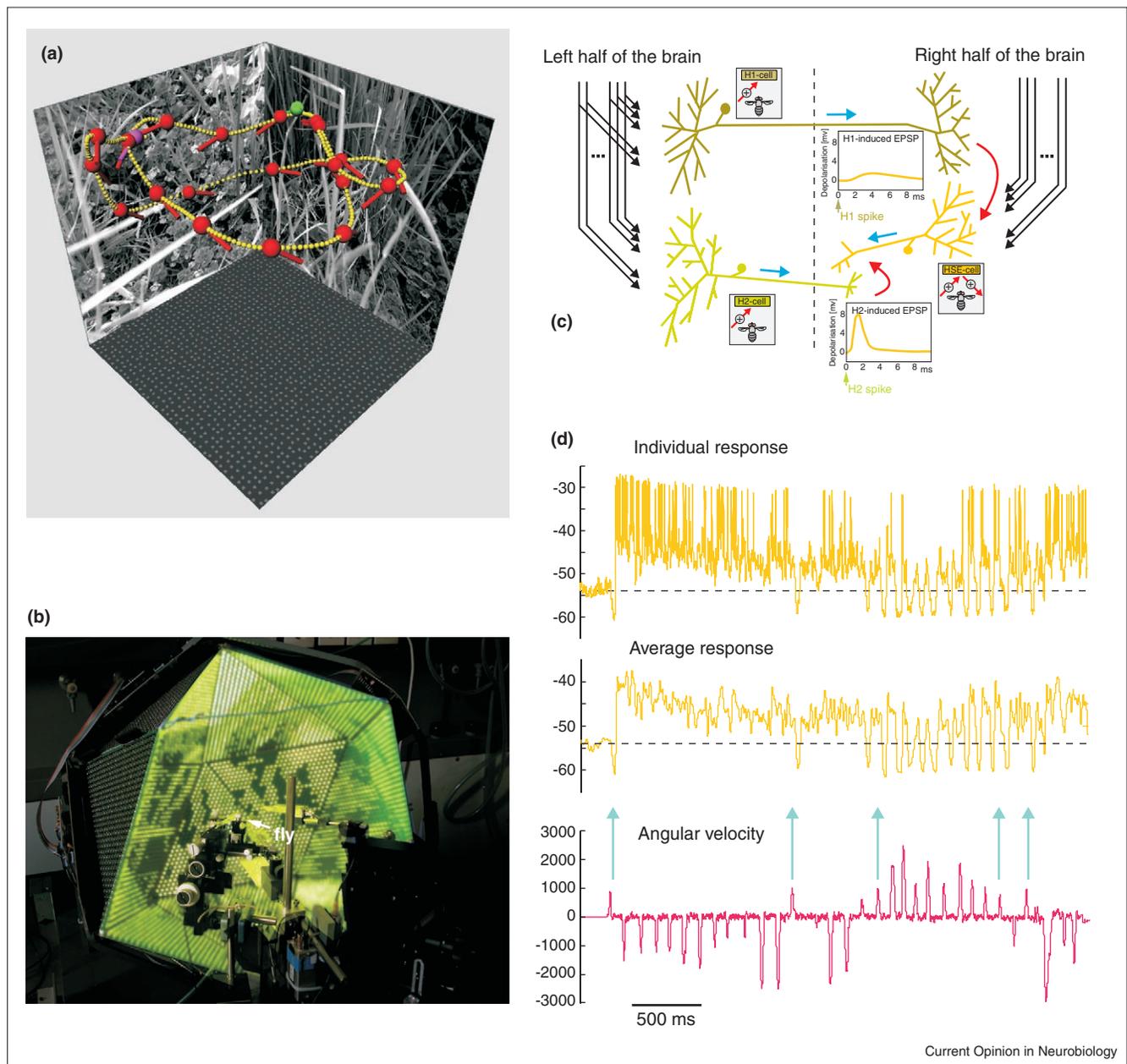
Figure 2

Current Opinion in Neurobiology

Retinal adaptations of male blowflies to pursuit of female targets. **(a)** Example of a chasing manoeuvre as seen from above. The position and the orientation of the body long-axis of the leading fly (blue) and of the chasing fly (red) are shown every 20 ms. The chasing fly closely follows the leading fly, thereby fixating it in the dorso-frontal part of its visual field. During chases, the pursuer may reach angular velocities of more than 3000°/s. (Data from Böddeker). **(b)** Spatial (left) and temporal sensitivities (right) of photoreceptors of the male fly subserving the frontal visual field are larger than those of photoreceptors looking to the side or backwards. The spatial sensitivity of photoreceptors was determined by light flashes directed at the eye from various angular positions in the cell's receptive field. Data are fitted by a Gaussian model. The temporal sensitivity of photoreceptors is given by their impulse response. It is shorter and faster for frontal photoreceptors than for sideways- and backwards-looking ones. (Adapted from [28•]).

In addition to extending knowledge on the wiring diagrams of the neuronal circuits underlying optic-flow processing, it has been possible to account for some of the underlying computations in terms of biophysical properties of nerve cells and their synaptic interactions. For example, a synapse that conveys visual motion information gathered by TCs in one half of the brain via another TC to the contralateral visual system was analysed. Synaptic signal transfer was found to operate linearly and very reliably within a certain dynamic range. In this range, motion information is signalled by the visual system with a large gain [45••,46•].

Figure 3

Response of a blowfly motion-sensitive neuron to optic flow as experienced during a free-flight manoeuvre. **(a)** Section of a flight trajectory monitored in a cubic cage (40 × 40 × 40 cm) covered on its side walls with a natural texture. The position of the fly is shown in yellow every 10 ms. The position and orientation of the body long-axis are shown in red every 130 ms; the starting position is indicated in mauve, the end position in green. **(b)** *OmniMaxX*, a high-speed panoramic visual stimulation device, consisting of 14 of the 20 triangles of an icosahedron, each of which forms a printed circuit board subserving 7168 light-emitting diodes in total. The device operates at 370 updates per second. In the foreground, the micromanipulators by which recording electrodes are inserted into the fly's brain can be seen. **(c)** Input organisation of the HSE-cell, the activity of which was recorded. The HSE-cell receives input from the eye ipsilateral to its main dendrite from many retinotopic motion-sensitive elements. Consequently, it is depolarised by front-to-back motion and hyperpolarised by back-to-front motion. The HSE-cell receives additional input on its main dendrite from the H1-cell or close to its axon terminal from the H2-cell. The spike activity of H1 and H2 is increased during back-to-front motion in the contralateral visual field and elicits EPSPs in HSE (see insets). As a consequence of its input organisation, the right HSE-cell can be expected to be depolarised during counterclockwise rotations of the fly and hyperpolarised during rotations in the opposite direction. **(d)** Responses to behaviourally generated stimuli. Upper trace: individual response; HSE responds to motion with graded depolarisations and hyperpolarisations; spikes superpose the graded potential changes; the resting potential is indicated by a dashed line. Middle trace: average response. Bottom trace: angular velocity. Sharp angular velocity peaks corresponding to saccade-like turns of the fly dominate the time-dependent angular velocity profile. By contrast to expectations based on the input organisation of the HSE-cell, there are no obvious depolarising response peaks during preferred direction motion evoked by counterclockwise saccades. However, there are brief pronounced hyperpolarisations going along with clockwise saccades; some of these hyperpolarizing peaks and the corresponding saccades are indicated by arrows (Data shown in **(a)**, **(b)** and **(d)** from [57••]; data shown in **(c)** from [41]).

Hence, synaptic signal transfer appears to be adapted to convey motion information reliably and without distortion in the behaviourally relevant operating range.

Representation of behaviourally generated optic flow

Knowing about the wiring of a neuronal circuit does not allow us to infer safely how efficiently and reliably information is processed and represented in natural behavioural situations. Two constraints are particularly relevant. The first pertains to the reliability of neural coding. Neurons are inherently noisy elements; accordingly, neuronal responses to identical stimuli may be highly variable. This variability limits the precision and timescale of representing motion information. This important and still-controversial topic has been reviewed recently [6,47,48]. The other constraint pertains to the peculiar dynamics of natural optic flow, which are largely determined by the dynamics of the animal's self-motion. The direction of self-motion may change rapidly, such as during saccadic turns during flight [24,49], or an order of magnitude more slowly, as during walking [50•]. Natural stimuli thus differ largely from those usually used for the analysis of visual information processing, be it constant velocity stimuli or white-noise velocity fluctuations. Therefore, the neuronal representation of natural optic flow is currently being analysed using different approaches.

Because it is not yet possible to record from neurons in freely moving insects, indirect approaches have been used in flies to assess the responses of TCs to behaviourally generated optic flow. Recordings have been made from the brain of flies that were rotated in a natural outdoor setting about their vertical body-axis [51•], partly with a dynamic mimicking the rotational self-motion component experienced in free flight [52•]. In another approach, the optic flow experienced by moving flies was reconstructed and subsequently replayed to animals during nerve-cell recordings. This approach has been employed for various behavioural situations during tethered flight in a flight simulator [53–55], during unrestrained walking [50•,56] and most recently during free flight in a three-dimensional environment [57••]. The simulation of free flight has been possible thanks to the development of sophisticated techniques (Figure 3a,b). First, free-flight behaviour can be monitored with unprecedented resolution by means of sensor-coils [24,49]. Second, a panoramic visual stimulator for presentation of optic flow that is sufficiently fast for visual stimuli as experienced by a fly during rapid saccade-like turns has been designed [57••]. Although it would be premature to draw general conclusions on the basis of the studies on processing of behaviourally generated optic flow, it might be safe to conclude that the neuronal responses to complex optic flow as experienced during unrestrained locomotion can be understood only partly in terms of the concepts that were established on the basis of experiments done with conventional motion stimuli.

One example is shown in Figure 3. As judged from its input organisation, the HSE-cell (horizontal system equatorial cell) , a major output element of the fly visual-motion pathway, is expected to respond best during rotations of the animal about its vertical body-axis (Figure 3c; [41]). The responses to optic flow experienced by free-flying flies only partly fit these expectations [57••]. The cell responds with graded depolarisations superimposed by spikes almost during the entire flight sequence. Saccades going along with optic flow in the cell's null direction lead to brief pronounced hyperpolarisations. By contrast, saccades eliciting preferred direction motion do not lead to corresponding depolarisations. This is not merely because of saturation of the response, because saccades fail to elicit depolarisations even during phases of the flight sequence in which the overall depolarisation of the cell is much smaller than the maximal depolarisation level that can be evoked by visual motion (Figure 3d). This example illustrates that it is difficult to predict the performance of the system during complex flight manoeuvres, even when wiring diagrams and responses to simplified optic-flow stimuli are well established.

Understanding these complex responses might be further complicated, because the properties of fly TCs were shown to change as a result of stimulus history [58–62,63•,64•]. Although the functional significance of these adaptive processes is still debated, they might play a role in adjusting the operating range of the mechanisms underlying optic-flow processing in different behavioural contexts.

Conclusions and perspectives

In spite of their tiny brains, insects are able to solve sophisticated visual orientation problems sufficiently fast and reliably to make them the most successful phylum in terms of number of species and biomass. This might have been accomplished because the insect brain appears to be no general-purpose information-processing device, but is kept as simple as possible by adapting the visual system to the specific needs encountered in normal life. During the review period, it became increasingly clear that, on its own, systems analysis of the processing of visual information with conventional stimuli is not sufficient to assess which aspects of the environment, as well as the animal's own behaviour, are encoded by neuronal circuits. Rather, the functional significance of neural computations might become evident only if visual information processing is viewed also from the perspective of sensory and behavioural ecology. To learn how nervous systems solve visual orientation problems in an efficient and parsimonious way, it is necessary to know about both the neuronal circuits and the conditions under which they operate.

Because of the efficiency of visually guided orientation in insects, there is great interest in applying principles of insect motion information processing to autonomous artificial systems. Although this has been successful for some behavioural components [65–70], many biomorphic

autonomous robots appear still to be dull compared with the original after which they are modelled. By contrast to man-made systems, however, natural vision systems have been tested and improved on a much longer timescale by many millions of years of evolution.

Update

In a recent paper [71••] a novel flight simulator is described that combines realistic, interactive visual environments with mechanosensory and olfactory stimuli in conjunction with multichannel neurophysiological recording. Initial experiments reveal that this system, used on tethered flying insects, is potentially very useful to examine activity from groups of neurons during realistic closed-loop behaviour in virtual environments. As the visual image flow is presented at a frame rate of only 60 frames/s, the system is suitable for insects with relatively slow photoreceptors. Moreover, image motion should not be too fast to avoid aliasing problems. All these conditions appear to be perfectly satisfied for the nocturnal moths for which the flight simulator has been developed.

Acknowledgements

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