ertebrate eyes range widely in form and level of function, from simple assemblies of photoreceptors to advanced compund and camera eyes capable of sophisticated visual processing. *Invertebrate Vision* is a complete synthesis of our current knowledge concerning how invertebrates see, the principles used to process visual information and how vision is used in the daily struggle for survival. Topics include photoreceptor optics, phototransduction in photoreceptors, sensitivity to light, endogenous control of visual adaptation, the collection and coding of information, eye design and function, vision in water, colour and polarization vision, the neural computation of visual motion, visual orientation and the processing of pattern. With contribututions from an international panel of experts in invertebrate vision, this book will appeal to graduates and researchers interested in the visual and sensory sciences as well as in biology, neuroscience, computer science and robotics.

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Invertebrate Vision

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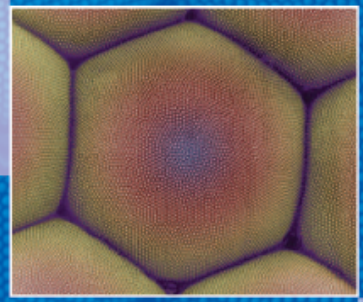
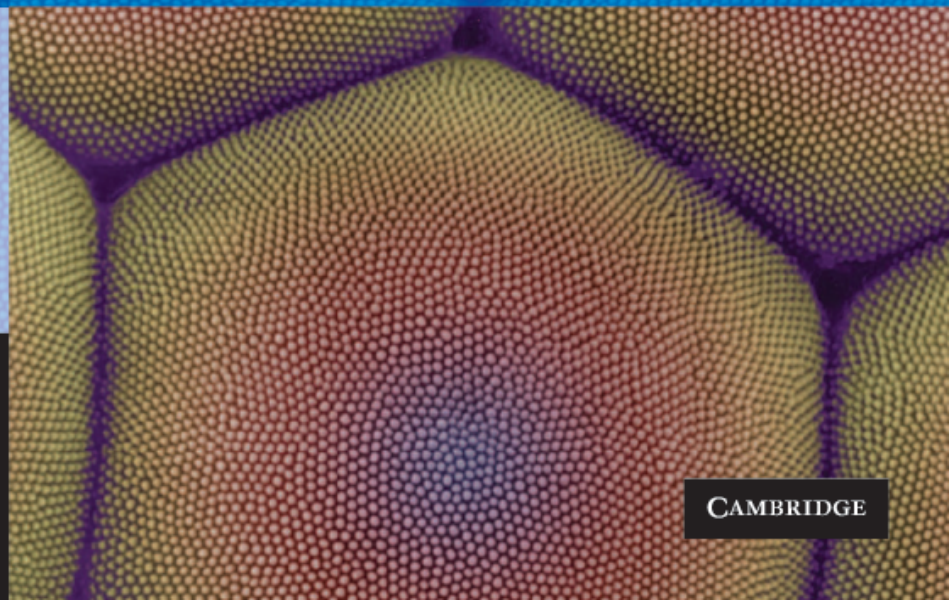


Invertebrate Vision

Edited by **Eric Warrant and Dan-Eric Nilsson**



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10

The neural computation of visual motion information

MARTIN EGELHAAF

10.1 SIGNIFICANCE OF VISUAL MOTION INFORMATION

Retinal image motion is elicited when a moving object crosses the visual field ('object motion'). However, even if the outside world is stationary there is continuous image flow on the retina when the animal moves about in the environment. This so-called optic flow is a rich source of information about the three-dimensional layout of the environment as well as the path and speed of locomotion (Dahmen *et al*., 1997; Lappe, 2000; Eckert and Zeil, 2001). For instance, during forward translation the optic flow across both eyes is directed backwards with the apparent velocity of closer objects being larger than that of more distant ones. In contrast, during a pure rotation about the vertical body axis optic flow is directed backward across one eye, but forward across the other. In this situation, the retinal velocities are independent of the distance of objects to the animal. Given that animals may often rotate and translate simultaneously, the optic flow is likely to be much more complex in natural situations. Moreover, flying animals have six degrees of freedom, three of rotation, and three of translation, a feature that further increases the complexity of the optic flow as compared to that of animals moving on the ground.

Amongst invertebrates, optic flow has been shown, primarily in insects and crustaceans, to be an important source of visual information. Because of the relative ease with which their nervous systems can be approached electrophysiologically and by imaging techniques, selected insect and crustacean species serve as model systems for analysing the mechanisms underlying the processing of visual motion.

10.2 VISUAL MOTION AND THE CONTROL OF BEHAVIOUR

Visual motion has been shown to play an important role in behavioural control in a wide range of arthropod species (reviews: Collett *et al*., 1993; Srinivasan and Zhang, 2000; Egelhaaf and Kern, 2002). This section summarises a selection of behavioural components that are guided by visual motion.

10.2.1 Optomotor following

The historically first analysed motion-driven behavioural response is optomotor following which appears to occur not only in arthropods, but in all mobile animals. An animal viewing a moving wide-field pattern tries to follow the pattern by movements of its eyes (if they are mobile as in crabs), its head, or its entire body. Wide-field pattern motion is believed to mimic deviations from an intended course as may be induced by an external disturbance or by internal asymmetries in the motor system. The resulting retinal movement forms the input of a velocity servo, which reduces the retinal slip by compensatory eye, head, or body rotations. As a consequence, the course of locomotion or the gaze of the animal is stabilised.

Optomotor following has been investigated during unrestrained locomotion (e.g. Hertz, 1935; Collett, 1980; Kern and Varjú, 1998), but also by means of sophisticated instruments which permitted measurements of the yaw torque of tethered, walking, or flying animals or of compensatory movements of the head and/or eyes. In these experiments, the retinal input was either exclusively controlled by the experimenter ('open-loop'), or the torque signal generated by the animal was used to control pattern movements in a similar way as during unrestrained locomotion (e.g. Thorson, 1964; Götz, 1975; Reichardt and Poggio, 1976; Heisenberg and Wolf, 1984; Hensler and Robert, 1990; Barnes and Nalbach, 1993; Kern *et al*., 1993; Blanke *et al*., 1997; Tammero *et al*., 2004).

How well optomotor following reduces the retinal image slip can be quantified by the response gain, i.e. the ratio of the animal's own velocity to that of the moving pattern. The gain was found to range between 0.4 and 0.9 in different species (Collett, 1980; Zanker and Collett, 1985; Lönnendonker and Scharstein, 1991; Warzecha and Egelhaaf, 1996) and to depend on the dynamics of pattern motion. In flies, the optomotor system is tuned to compensate mainly for slow drifts generated, for instance, by internal asymmetries

of the locomotory system (Collett, 1980; Heisenberg and Wolf, 1984; Egelhaaf, 1987). Optomotor following of hawkmoths has a moderate gain at small oscillation frequencies; in contrast to flies, however, the gain has a sharp peak at relatively high frequencies around 4 Hz. This characteristic might be an adaptation to the feeding habits of this moth, which is able to hover in front of flowers wiggling considerably in the air (Farina *et al*., 1994; Kern and Varjú, 1998). In crabs with mobile eyes, optomotor following is very effective up to oscillation frequencies of 1 Hz (Nalbach, 1989).

Optomotor responses are not only evoked by rotational optic flow. Many flying insects follow translational movements by increasing or decreasing their forward velocity. Translational optic flow may help to stabilise the distance of hovering hawkmoths to a flower on which they are feeding (Farina *et al*., 1995; Kern and Varjú, 1998). Moreover, translational optic flow is exploited by flies and locusts to control speed and/or height relative to the ground (Götz, 1968; David, 1982a, b; Preiss, 1993). In addition, bees control their flight speed by regulating retinal velocity: they decelerate when the translational optic flow increases, for instance, when passing a narrow gap (Srinivasan *et al*., 1996; Chapter 11).

10.2.2 Visual course control

Optic flow may be used to control the course of locomotion. For instance, bees tend to fly through the centre of a narrow gap or a tunnel, balancing the retinal velocities and, thus, the distances to the left and the right boundaries of the opening (Kirchner and Srinivasan, 1989; Chapter 11). Whereas ants appear to balance the vertical angle subtended by landmarks on either side (Heusser and Wehner, 2002), bees and flies were concluded to balance the overall optic flow on their eyes (Götz, 1975; Srinivasan *et al*., 1991). This strategy may have consequences if one eye is occluded. In this situation, walking blowflies reach a state of balanced optic flow only on a slightly curved path (Kern and Egelhaaf, 2000; Kern *et al*., 2000). All these conclusions are based on the average performance of the animals and do not take into account the actual optic flow patterns on the eyes, which may be quite complex over time. For instance, when flying through a straight tunnel flies execute sequences of saccades and, thus, actively generate a succession of mainly rotational and translational optic flow (see Section 10.2.7).

Optic flow does not only help to mediate a straight course of locomotion, but may also elicit turns, for instance, to prevent collisions

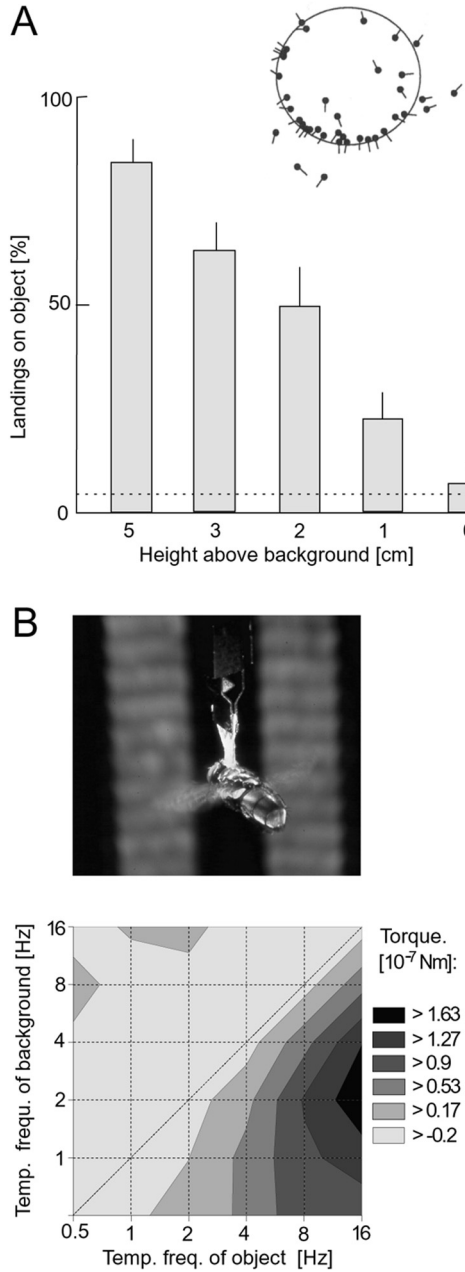

Fig. 10.1 Object detection. A. Bees are able to use motion parallax cues to distinguish an object from a similarly textured background. The apparatus presents a textured disc positioned under a sheet of clear perspex at variable height above a similarly textured background.

with obstacles. When a fly approaches an obstacle, such as a textured wall, the resulting image expansion evokes a sharp saccade-like turn to prevent the fly from crashing into the obstacle (Tammero and Dickinson, 2002a, b).

10.2.3 Object detection and range perception

Motion cues may provide the world with a third dimension. When an animal passes or approaches a nearby object, the object appears to move faster than its background. Several insects have been shown to use relative motion efficiently to detect objects and to infer their distance. Walking *Drosophila*, for instance, are well able to discriminate the distance of different objects on the basis of slight differences in their retinal velocities (Schuster *et al*., 2002). Bees (Lehrer *et al*., 1988; Srinivasan *et al*., 1989) and blowflies (Kimmerle *et al*., 1996) can use motion cues to discriminate between the heights of objects. Thereby they mainly use relative motion information at the edges of objects (Fig. 10.1A) (Srinivasan *et al*., 1990; Kimmerle *et al*., 1996; Kern *et al*., 1997). Hawkmoths hovering in front of flowers also use motion cues to control their distance to them (Pfaff and Varjú, 1991; Farina *et al*., 1994).

The control system underlying object detection has been characterised in tethered flies flying in a flight simulator (Virsik and

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Caption for Fig. 10.1 (cont.)
Bars show percentages of landings occurring on the disc, for various heights of the disc above the background. The detectability of a disc decreases with decreasing height, reaching a random level (*dashed line*) when the height is 0. The bees tend to land at the edge of the disc (*inset*) (Srinivasan *et al*., 1990). B. Object detection by tethered blowflies flying in a flight simulator in front of a grating pattern used as visual stimulus. Forward motion of the fly was simulated by backward motion of gratings in front of both eyes. In a section of the pattern the velocity was intermittently increased or decreased, simulating a nearby or a distant object. The object and background velocities are given as temporal frequencies. *Contour plot* gives the amplitude of the torque response elicited by object motion. The detectability of the object and thus the strength of torque depend on both object and background velocities. The object is only detected if it moves faster than the background, as is the case in natural situations. The detectability of fast objects is enhanced by low background velocities (data taken from Kimmerle and Egelhaaf, 2000a).

Reichardt, 1976; Reichardt and Poggio, 1979; Reichardt *et al*., 1983; Egelhaaf, 1985a; Kimmerle and Egelhaaf, 2000a; Kimmerle *et al*., 2000). Only two features of this control system will be mentioned here. First, object detection is facilitated if moderate background motion is present, such as during translation in an environment where the background is relatively close to the animal (Fig. 10.1B) (Kimmerle and Egelhaaf, 2000a). Second, since for a given stimulus condition the object-induced fixation response is elicited in an all-or-none fashion, motion-induced object fixation is suggested to be gated in the visuomotor pathway (Kimmerle *et al*., 2000).

10.2.4 Landing

Flying animals cannot always stay aloft, but have to come to the ground regularly. They tend to select pronounced objects and, in particular, their edges as landing sites (Srinivasan *et al*., 1990; Kimmerle *et al*., 1996; Kern *et al*., 1997). An approach directed perpendicularly to a potential landing site generates looming cues, i.e. the retinal image expands. Flies have been shown to use this information to initiate deceleration at a critical level of image expansion (Wagner, 1982) and to extend their legs in preparation for landing (Goodman, 1960; Taddei-Ferretti *et al*., 1980; Borst and Bahde, 1988; Borst, 1990; Waldvogel and Fischbach, 1991; Tammero and Dickinson, 2002a).

However, insects do not always approach their landing sites perpendicularly. Looming cues are weak when the insect lands on a flat surface. In this situation, bees continually decelerate when approaching the surface. Their speed is roughly proportional to the height above the ground. Since the apparent retinal velocity depends on the distance to the ground, the animals hold the image velocity approximately constant while approaching the surface. This strategy guarantees smooth landing without requiring knowledge about the height above the landing site (Srinivasan *et al*., 2001; Chapter 11).

10.2.5 Estimation of travelled distance

Bees and some ant species need to acquire distance information on foraging excursions to be able to return to their hive or nest. Whereas walking animals may use mechanosensory input from their own movements, distance estimation is much harder to accomplish during flight. Bees could be shown to gauge distance in terms of the optic flow experienced during the flight to a food source (review: Srinivasan and

Zhang, 2000). Since the optic flow generated during translational movements 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 bees tend 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 exploited for experimental analysis of the mechanisms of odometry (Fig. 10.2) (Esch and Burns, 1996; Srinivasan *et al*., 2000a; Esch *et al*., 2001; Hrncir *et al*., 2003; Tautz *et al*., 2004), they may 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 sufficient for the specific needs under normal behavioural conditions.

10.2.6 Pursuit of moving targets

Many arthropods follow moving objects and may eventually catch them. Targets can be potential prey or mates. Dragonflies or tiger beetles pursue other insects to catch and eventually eat (Gilbert, 1997; Olberg *et al*., 2000). In the context of mating behaviour, male flies chase females in acrobatic visually controlled flight manoeuvres. They thereby fixate the target in the frontal part of their visual field by saccadic turns with angular velocities of up to 5 000°/s (Land and Collett, 1974; Collett and Land, 1975; Wagner, 1986a; Zeil, 1983; Land, 1993).

Although it is generally agreed that the retinal position and velocity of the target serves as input variables of the pursuit control system, the way the retinal position error is transformed into torque is still controversial. On the one hand, smooth pursuit has been proposed (Collett, 1980). On the other hand, a saccadic tracking strategy has been put forward (Wagner, 1986a). For chasing behaviour of blowflies, it has recently been possible to clarify this problem by using dummy targets moving on experimenter-controlled paths. The forward velocity of the chasing fly is controlled by the angular size of the target. The turning velocity depends on the angle from which the target is seen (Boeddeker and Egelhaaf, 2003; Boeddeker *et al*., 2003). During pursuit, catch-up saccades are observed only when the target changes its trajectory too rapidly to allow the pursuer to follow smoothly (Fig. 10.3A). Model simulations revealed that even these catch-up saccades can be explained as a by-product of the

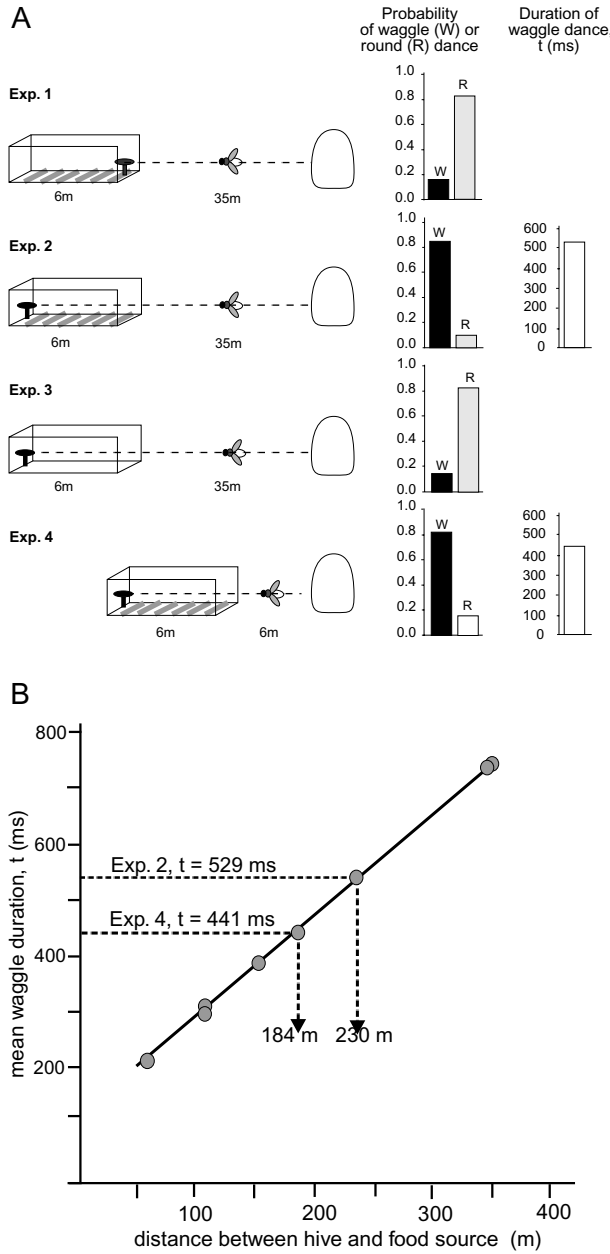

Fig. 10.2 Distance estimation and the behavioural analysis of how honey bees estimate the distance travelled between their hive and a food source. Honey bees measure distances in terms of optic flow and communicate this information to their hive mates by the waggle dance. A. Layout for the experiments using tunnels and probabilities of waggle (*W*; *black bars*) and round dance (*R*; *grey bars*) for the different experiments. A tunnel of 6 m length and a width of 11 cm was positioned

smooth pursuit system if neuronal latencies and the inertia of the chasing fly are taken into account (Boeddeker and Egelhaaf, 2005).

The praying mantis fixates targets by saccadic head and body movements (Rossel, 1980). After being fixated, moving targets are held in the fovea either by smooth or saccadic eye movements. The degree to which either tracking strategy is employed depends not only on the features of the background, but also on target velocity (Fig. 10.3B).

10.2.7 Orientation by active vision

Retinal image displacements are determined to a large extent by the animal's own behaviour. By active movements, various insect species

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Caption for Fig. 10.2 (cont.)
either at a distance to the hive of 35 m (not drawn to scale) or at a distance of only 6 m. The walls of the tunnel were either covered with a texture of vertically oriented elements (Exp. 1, Exp. 2, Exp. 4) or of 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) led again 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 honey bee while flying along the tunnel, whereas in the latter case there is only little optic flow, since 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 the hive (Exp. 4), waggle dances are mainly performed, which are shorter than those performed in Exp. 2. These experiments show that travelled distance is measured in terms of optic flow. B. Calibration of the odometer of the honey bee.
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-off from the regression line. At a mean distance of the honey bees to the tunnel wall of 5.5 cm, 1 ms of waggle in the dance corresponded to 17.7° of image motion on the eyes (data redrawn from Srinivasan *et al*., 2000a).

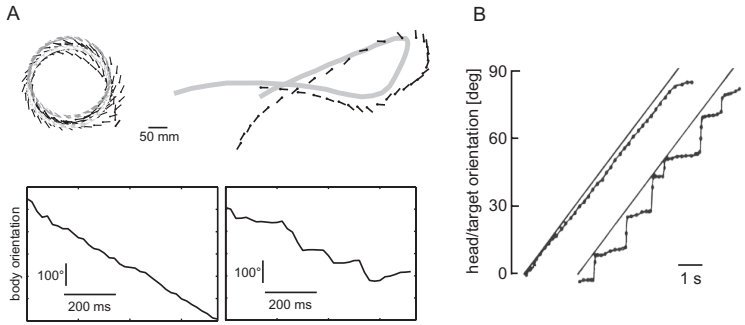

Fig. 10.3 Pursuit of moving targets. A. Smooth and saccadic tracking during chasing flights of male blowflies. *Left*: top view of a flight trajectory of a fly (*black markers*) chasing a black sphere that moves on a circular track in a horizontal plane (*grey line*). The fly is indicated by the position of its centre (*circle*) and the orientation of its body axis (*line*). The fly follows the target for 4 s. The fly is shown every 20 ms. *Right*: example of a flight trajectory of a fly chasing another fly in top view. Below the trajectories the orientation of the chasing fly is shown as a function of time. Only a section of the chases is displayed. Whereas the fly turns smoothly for most of the time when chasing a smoothly moving target, pronounced body saccades occur when chasing another fly (Boeddeker and Egelhaaf, 2003a). B. Object tracking in a mantid with and without textured background. A stationary mantid tracks an object (diameter 10°) that may represent a potential prey and moves with a constant velocity (*continuous lines*). The head orientation is given by the *dots connected by lines*. Also, 0° corresponds to the head orientation that, at the beginning of the experiments, coincides with the target position. When the background is homogeneous, tracking is smooth (*left trace*). When the background is textured, tracking becomes saccadic (*right trace*) (Rossel, 1980).

acquire information about the spatial structure of their environment (Land and Collett, 1997; Kral, 2003). Locusts, for instance, perform periodic sidewise body movements (or 'peering'), thereby viewing the world from a sequence of vantage points. They use the resulting motion parallax to assess the distance to a target before they accurately leap upon it (Sobel, 1990; Collett and Paterson, 1991; Kral, 1998). Mantids sitting in ambush execute similar peering movements before striking at a prey (Rossel, 1979; Poteser and Kral, 1995).

Bees and wasps perform distinct flight manoeuvres ('orientation flights') when leaving their nest or a newly discovered food place. They do not depart on a straight course, but 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; Voss and Zeil, 1998). Thus, rather than performing sidewise movements as locusts do, bees and wasps tend to pivot around the goal. The optic flow pattern generated in this way contains information on the distance between the goal and environmental objects. In contrast, the optic flow pattern generated by sidewise movements contains information about distances between objects and the animal (Collett and Zeil, 1996).

Flying and walking flies shift their gaze during free flight by saccadic turns of body and head, keeping gaze basically fixed between saccades (Land, 1973; Schilstra and van Hateren, 1999; van Hateren and Schilstra, 1999; Tammero and Dickinson, 2002b; Blaj and van Hateren, 2004). This active viewing strategy largely separates the image flow resulting from rotational and translational movements of the animal. Since the rotational optic flow component does not depend on the distance between the eyes and environmental objects, whereas the translational flow component does, the saccadic flight strategy may help the nervous system to extract information about the spatial layout of the environment (see also Section 10.7).

10.2.8 Interactions between behavioural components

Behavioural components and the underlying control systems are usually investigated in isolation for analytical reasons. However, in natural situations the various systems may operate in parallel and are often required to interact. Three examples will illustrate potentially ensuing problems.

Different, even mutually exclusive, behavioural components may be evoked by similar motion stimuli. For instance, landing responses may be triggered by image expansion when the animal is approaching a potential landing site. On the other hand, image expansion may signal an approaching predator or an impending collision with an obstacle. The latter situations would require escape responses such as an abrupt turn. Landing and collision avoidance were shown in *Drosophila* to be elicited by image expansion in different areas of the visual field and at different expansion velocities (Tammero and Dickinson, 2002a).

Optomotor following, believed to have the function of stabilising the course of locomotion, may under certain circumstances prevent the animal from flying straight through a narrow tunnel. Due to some asymmetry in the flight trajectory, the image velocities on one eye

might be larger than those on the other. The optomotor system will then lead to a turn towards this site. If no precautions are taken, this may lead to a collision with the wall. The optomotor equilibrium concept (Götz, 1975) has been proposed to represent one solution. Since the response of any biological movement detection system only increases with velocity within a limited velocity range and then decreases again (Borst and Egelhaaf, 1989), the turning tendency mediated by the optomotor system reverses its direction if the velocity in front of one eye is becoming too large. The animal is then expected to turn in the opposite direction reducing the risk of a collision (Götz, 1975). Recent model simulations raise doubts that the optomotor equilibrium concept may work under closed-loop conditions and a separate control system has been proposed to mediate a saccadic turn away from the wall, if a critical expansion velocity is reached (Tammero and Dickinson, 2002b; Reiser and Dickinson, 2003).

The ability to pursue moving targets or to fixate stationary objects may be hindered by optomotor responses. Any turn towards a selected target leads to a displacement of the background in the opposite direction. Optomotor responses may oppose such goal-directed turns. There are several possibilities to solve this apparent conflict. First, the set point of the optomotor control system may be adjusted during pursuit or object fixation to match the visual consequences of the animal's expected turning velocity (Virsik and Reichardt, 1976; Collett, 1980). Second, the reafferent visual input during an intended turning response towards an object may be suppressed by an efference copy signal (Heisenberg and Wolf, 1988). Third, if object-induced turns are executed sufficiently rapidly, they may be finished before they are impeded by optomotor responses if these are sensitive only to low-frequency velocity changes (Section 10.2.1; Egelhaaf, 1987).

10.3 STEPS OF VISUAL MOTION COMPUTATION

The behavioural significance of motion vision in arthropods is reflected in an abundance of motion-sensitive neurons in their nervous systems (reviews on insects: Hausen, 1981; Hausen and Egelhaaf, 1989; Rind and Simmons, 1999; crustacea: Wiersma and Yanagisawa, 1971; Wiersma *et al*., 1982). Neurons responding specifically to visual motion have been found at all stages of the arthropod nervous system, ranging from the second visual neuropile to descending neurons connecting the brain with the motor control centres in the thoracic ganglia.

The properties of motion-sensitive visual interneurons are elaborated along the visual motion pathway. Whereas motion-sensitive neurons in the peripheral visual system respond to motion only in a small area of the visual field, neurons at subsequent processing stages tend to have large receptive fields that may even subserve both eyes. Part of these higher order neurons were concluded to respond preferably to the complex optic flow patterns that are evoked in different behavioural situations. For instance, some neurons respond best during coherent wide-field motion as may occur while an animal turns around a particular body axis (reviews: Hausen, 1981; Hausen and Egelhaaf, 1989; Egelhaaf and Warzecha, 1999; Krapp, 2000; Borst and Haag, 2002; Egelhaaf *et al*., 2002, 2005). Others respond best to object motion as may occur while the animal pursues a moving target or passes a stationary object in its environment (Collett, 1971; Collett and King, 1975; Olberg, 1981; Egelhaaf, 1985b, c; Olberg, 1986; Olberg and Pinter, 1990; Gilbert and Strausfeld, 1991; Gauck and Borst, 1999; Kimmerle and Egelhaaf, 2000a, b).

All these neurons are directionally selective to some degree. Other thoroughly studied wide-field neurons, the so-called 'descending contralateral movement detector' (DCMD) and 'lobula giant movement detector' (LGMD) of locusts are not directionally selective, but respond equally well to local motion in different directions and to changes in brightness (Rowell and O'Shea, 1976a, b; Rowell *et al*., 1977). This is also true for several classes of so-called 'movement fibres' in crustaceans (Wiersma *et al*., 1982). Although the LGMD/DCMD system is not directionally selective for local motion, it has recently been assigned a role in optic flow processing and is concluded to encode an impending collision by the characteristic time course of its response to an approaching object (Rind and Simmons, 1992, 1997, 1999; Rind, 1996; Simmons and Rind, 1996; Judge and Rind, 1997; Gabbiani *et al*., 1999, 2001, 2002, 2004). By comparing neuronal activity and steering responses during tethered flight this neuronal system has been concluded to play a role in predator avoidance (Gray *et al*., 2001). Apart from locusts, neurons detecting looming stimuli have been characterised in the cervical connective of flies (Borst, 1991) and in the lobula plate of moths (Wicklein and Strausfeld, 2000). However, in contrast to the LGMD/DCMD system the latter neurons respond directionally selective to local motion stimuli.

Motion information is not explicitly given by the retinal input, but has to be computed by the nervous system from the pattern of brightness changes as sensed by the array of photoreceptors.

Motion computation is possible, because the retinal image is correlated in space and time as a consequence of both the structure of natural environments and the way animals move in the world.

10.3.1 Computation of local motion information

The first explicit representation of visual motion is computed in parallel by arrays of motion detectors that cover the entire visual field (Fig. 10.4). Motion detection is a local process that compares changes in light intensity at neighbouring points in the visual field. It is assumed that local motion detection is accomplished in the second visual neuropile, the medulla. As is suggested by deoxyglucose activity labelling in flies, specific representations of visual motion information are found in the two most proximal layers of the medulla (Bülthoff and Buchner, 1985; Bausenwein and Fischbach, 1992). Moreover, electrophysiological studies revealed motion-sensitive neurons in both crustaceans and insects (crustacea: Glantz *et al*., 1995; insects: locusts, Osorio, 1986, 1987; flies, DeVoe and Ockleford, 1976; DeVoe, 1980; Gilbert *et al*., 1991; Douglass and Strausfeld, 1995, 1996, 2003). Most medulla neurons have small receptive fields as is expected from neurons involved in local motion detection. As a consequence of the small size of medulla neurons and the difficulty of recording their activity, conclusions concerning the cellular mechanisms underlying motion detection are still tentative, although much progress has been made during the last years (review: Douglass and Strausfeld, 2001; see Chapter 9).

Many features of motion detection can be accounted for by a computational model, the so-called correlation-type movement detector (Fig. 10.4) (reviews: Reichardt, 1961; Borst and Egelhaaf, 1989, 1993; Egelhaaf and Borst, 1993b; Clifford and Ibbotson, 2003). In its simplest form, a local movement detector is composed of two mirror-symmetrical subunits. The inputs of each subunit interact in a non-linear way after one of them has been delayed. The final detector response is obtained by subtracting the two subunit outputs. This mechanism leads to a useful motion estimate, because during pattern motion the two detector inputs receive, with a temporal delay, the same input. Various elaborations of this basic movement detection scheme have been proposed to account for the responses of fly motion-sensitive neurons under a wide range of stimulus conditions (Zaagman *et al*., 1978; Mastebroek and Zaagman, 1988; Egelhaaf and Borst, 1989; Egelhaaf *et al*., 1989; Borst *et al*., 1995, 2003; Single *et al*., 1997;

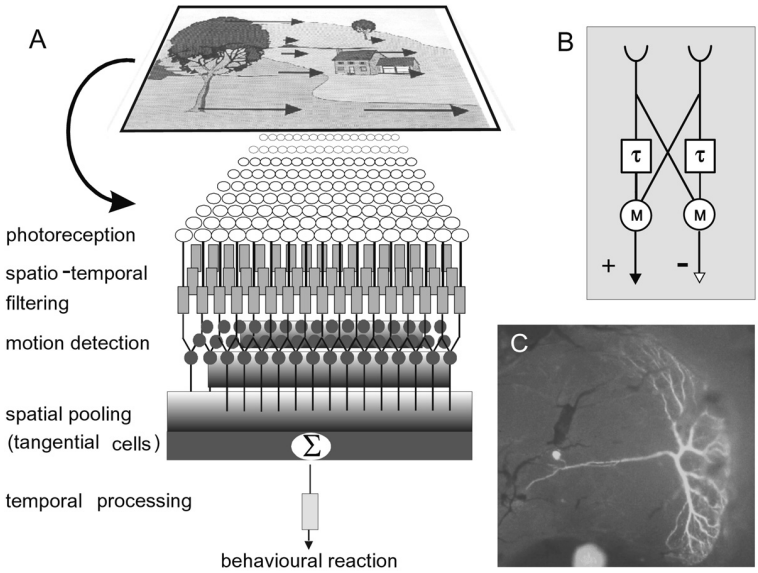

Fig. 10.4 Major processing steps of visual motion computation in arthropods. A. Schematic of the visual motion pathway. Images of the moving environment are projected on the array of photoreceptors. The input is spatially and temporally filtered before signals originating from neighbouring points in the visual space interact with each other. These interactions lead to local motion measurements. The outputs of many retinotopically organised local movement detectors are spatially pooled by so-called tangential cells (TCs). B. Organisation of a local movement detector in its simplest form. The movement detector receives spatially and temporally filtered signals from neighbouring points in space. The detector consists of two mirror-symmetrical subunits. In each subunit one of the inputs is temporally delayed (τ), before it interacts non-linearly with the undelayed signal of the other detector input. A multiplication-like interaction (*M*) is the lowest order nonlinearity that is sufficient to account for many aspects of the responses of the visual motion pathway. The subunit outputs contribute to the response of the (TCs) with opposite polarity, i.e., the two signals are subtracted. C. One of the (TCs), a so-called FD1 cell, in the third visual neuropile of the blowfly. The cell was filled with the fluorescent dye Lucifer yellow, before it was visualised in a whole-mount preparation under a fluorescence microscope.

Kern *et al*., 2001a) including natural optic flow as experienced under free-flight conditions (Lindemann *et al*., 2005).

There is good evidence that a multiplicative interaction between neighbouring retinal input channels complies with the overall

performance of insect movement detectors. First, the responses to grating patterns with sinusoidal brightness distribution moving at a constant velocity contain mainly the fundamental and second harmonic frequency components of the temporal frequency of the stimulus pattern (Egelhaaf *et al*., 1989; Ibbotson *et al*., 1991). This feature represents a fingerprint of a multiplicative interaction. Second, application of white-noise stimulation techniques suggested that the movement detector non-linearity can be approximated by a multiplication (Marmarelis and McCann, 1973; Kondoh *et al*., 1995). Third, apparent motion stimuli, i.e. subsequent stimulation of neighbouring points in the visual field by two stationary light sources, elicit directionally selective neuronal responses, if appropriate time delays between the stimuli are chosen (Marmarelis and McCann, 1973; Riehle and Franceschini, 1984; Franceschini *et al*., 1989; Schuling *et al*., 1989; Egelhaaf and Borst, 1992). When apparent motion is based on a sequence of stimuli with the same polarity, i.e. either brightness increments or decrements, the direction of motion is signalled correctly. In accordance with a multiplicative interaction, the opposite direction is indicated if stimuli with opposite polarity are used, a situation that hardly ever occurs naturally (Marmarelis and McCann, 1973; Egelhaaf and Borst, 1992).

The subtraction stage of the two subunit outputs of fly movement detectors was concluded to be realised by a combination of cholinergic and GABAergic synapses (Brotz and Borst, 1996). Direction selectivity of the movement detection circuit is considerably enhanced by this subtraction-like processing step (Egelhaaf *et al*., 1990; Kondoh *et al*., 1995). Whereas the above-mentioned movement detection schemes characterise the basic computations in formal terms, there are attempts to account for these computations in terms of neuronal wiring schemes (Higgins *et al*., 2004). However, the functioning of these schemes has not yet been tested for a wide range of stimuli and their internal structure is still tentative.

Motion detection in crayfish is based on a somewhat different mechanism that is reminiscent of the mechanism originally proposed to explain direction selectivity in the rabbit retina (Barlow and Levick, 1965). In crayfish, the interaction between neighbouring retinal inputs is accomplished on the dendrite of motion-sensitive cells by excitatory inputs and delayed inhibitory inputs that subserve neighbouring points in visual space. The excitatory and inhibitory signals are mediated by cholinergic and GABAergic synapses, respectively (Bartels and Glantz, 1999). During motion in the preferred direction,

the excitatory input signals activated first arrive earlier than the delayed inhibitory signals and thus lead to a neuronal response. In contrast, during motion in the null direction the delayed inhibitory input, now activated first, suppresses the excitatory input that now arrives in the cell roughly simultaneously.

The movement detection mechanism does not operate on an immediate representation of the retinal brightness values but on a spatio-temporally filtered version of them (Fig. 10.4). This filtering takes place in the retina and the first visual neuropile, the lamina and leads to an enhancement of changes in brightness at the expense of the background brightness (Srinivasan *et al*., 1982; van Hateren, 1993; Laughlin, 1994; Juusola *et al*., 1996). This neural filtering is thought to maximise the transfer of information concerning time-dependent retinal images (van Hateren, 1997). Not all lamina output neurons show the same visual filter properties. There are also neurons that do not eliminate the mean brightness from their responses and are proposed to be involved in visual motion detection (Arnett, 1972; Jansonius and van Hateren, 1993a, b).

The spacing of the retinal inputs of a local movement detector limits its spatial resolution, i.e. the highest spatial frequency that leads to appropriate motion responses. Spatial frequencies that exceed this limit lead to spatial aliasing. The movement detectors then signal motion in a direction opposite to the actual direction of motion (Buchner, 1976). Whereas in the light-adapted eye motion, responses of flies are dominated by nearest neighbour interactions between pairs of input channels (Buchner, 1976; Riehle and Franceschini, 1984; Schuling *et al*., 1989), at low light levels input channels at larger angular distances become additionally involved (Pick and Buchner, 1979; Schuling *et al*., 1989). These adaptational changes can be interpreted as a trade-off between spatial resolution and the sensitivity of the movement detection system (Section 10.6.1).

10.3.2 Spatial pooling of local motion information

Since the optic flow as induced during locomotion has a global structure, it cannot be evaluated by local mechanisms alone. Rather, local motion measurements from large parts of the visual field need to be combined (Fig. 10.4). This is accomplished in the third visual neuropile by the so-called tangential cells (TCs). They spatially pool the outputs of many retinotopically arranged local motion-sensitive neurons and, accordingly, have large receptive fields. Most TCs are

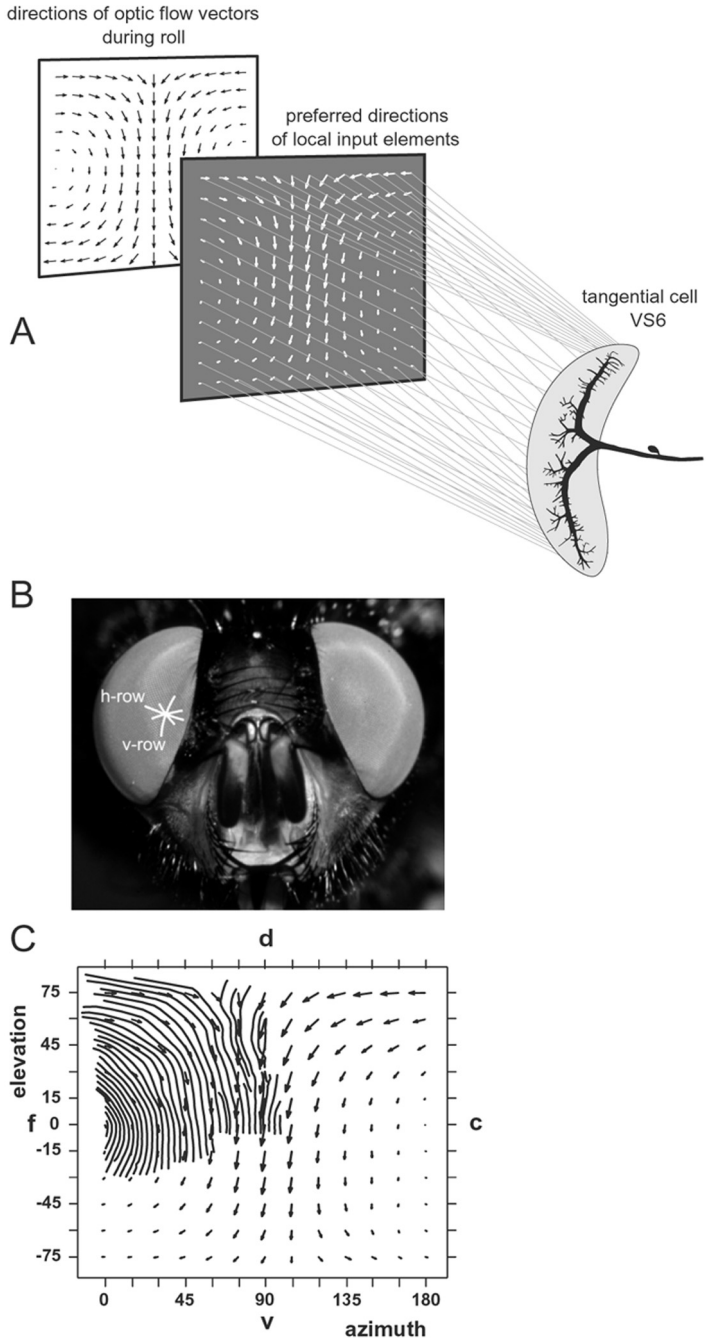

Fig. 10.5 Retinotopic input organisation of tangential cells (TCs).
A. Self-motion generates panoramic optic flow over the eyes. The black arrows represent the local motion vectors on the eye when the animal rolls around its longitudinal body axis. The local response properties

excited by motion in their preferred direction and are inhibited by motion in the opposite direction (Fig. 10.6A). Such neurons have been found in crustaceans (Wiersma *et al*., 1982; Glantz, 1998; Berón de Astrada and Tomsic, 2002; Sztarker and Tomsic, 2004), but have been analysed most extensively in insects (bee: DeVoe *et al*., 1982; Ibbotson, 1991b; locust: Rind, 1990b; lepidoptera: Ibbotson *et al*., 1991; Maddess *et al*., 1991; Wicklein and Varju, 1999) and in most detail in blowflies. In blowflies a set of approximately 50 TCs have been identified. All of them respond to different types of optic flow as induced by different types of self-motion (Fig. 10.4) (Hausen, 1981; Hausen and Egelhaaf, 1989; Egelhaaf and Warzecha, 1999; Krapp, 2000; Borst and Haag, 2002; Egelhaaf *et al*., 2002, 2005).

The local motion-sensitive elements that synapse onto a given TC do not all have the same preferred direction. Rather, in the case of flies, the preferred directions change gradually over the TC's receptive field and coincide with the directions of the velocity vectors in particular optic flow fields (Fig. 10.5A) (Krapp *et al*., 1998, 2001;

Caption for Fig. 10.5 (cont.)
of a TC, the VS6 cell, are adapted to detect this particular self-rotation. The cell, with its large dendrite, is assumed to mainly integrate signals from those local input elements whose preferred directions (*white arrows*) correspond to the direction of local motion vectors in roll-induced optic flow. B. Head of a female blowfly. *White lines* over the right eye indicate the course of ommatidial rows in the hexagonal eye lattice (Photograph: courtesy R. Hengstenberg). C. Receptive field organisation of the VS6 cell. Orientation and length of *arrows* at different angular positions indicate the neuron's local preferred direction and motion sensitivity in the right visual hemisphere. Also, 0° azimuth and 0° elevation corresponds to the point directly in front of the animal; small letters *f*, *c*, *d*, and *v* refer to the frontal, caudal, dorsal, and ventral aspects of the visual field. *Black thin lines* in the upper left quadrant indicate the course of ommatidial rows that are oriented about vertically in the equatorial region of the eye (cf. v row in B). The direction of visual motion is thought to be mainly analysed by interactions between ommatidia along the rows in the hexagonal eye lattice (cf. orientation of *rows* and *arrows* in C). In the dorso-frontal eye region the course of the v rows shifts towards a horizontal orientation. This change in orientation is reflected by the change in local preferred directions of VS6 in corresponding regions of its receptive field (experimental data taken from Krapp *et al*., 1998; Petrowitz *et al*., 2000).

Krapp, 2000). Hence, the spatial input organisation of TCs forms a basis of their specific sensitivity to optic flow induced by particular self-motions. Similar results could recently be obtained for a motion-sensitive neuron in the crab (Barnes *et al*., 2002). The sophisticated global patterns of preferred directions of fly TCs do not depend on visual experience and thus represent a phylogenetic adaptation to neuronal optic flow processing (Karmeier *et al*., 2001).

The characteristic pattern of local preferred directions of fly TCs is partly a consequence of the geometry of the compound eye lattice. The orientations of ommatidial rows coincide with the local preferred directions of particular fly TCs and with the directions of local velocity vectors occurring during locomotion (Fig. 10.5B) (Hausen, 1981; Petrowitz *et al*., 2000). The input organisation of some TCs can thus be established by interactions along the anatomical rows of the compound eye. Hence, the geometry of the fly compound eye appears to be a phylogenetic adaptation to parsimonious processing of optic flow.

Dendritic integration of local motion signals has various functional consequences for the neuronal representation of optic flow:

- Owing to their small receptive fields, the responses of the input elements of TCs are temporally modulated even when the stimulus pattern moves with a constant velocity. Since the signals of neighbouring input elements are phase-shifted with respect to each other, their pooling by the dendrites of TCs eliminates the temporal response modulations (Fig. 10.6B) (Egelhaaf *et al*., 1989; Single *et al*., 1997; Single and Borst, 1998; Haag *et al*., 2004). As a consequence, the responses of TCs reflect to some extent the time course of visual motion.
- TCs do not operate like odometers: their responses increase with increasing velocity, reach a maximum, and then decrease again. The location of the velocity maximum depends on the textural properties of the moving stimulus pattern. If the spatial frequency of a sine-wave grating is shifted to lower values, the velocity optimum shifts to higher values in such a way, that the ratio between the optimal pattern velocity and the spatial period of the stimulus pattern, i.e. the temporal frequency, is constant (Eckert, 1980; Buchner, 1984; Ibbotson, 1991a; Ibbotson *et al*., 1991). For the initial transient phase of responses to constant velocity motion, the temporal frequency optimum is at higher

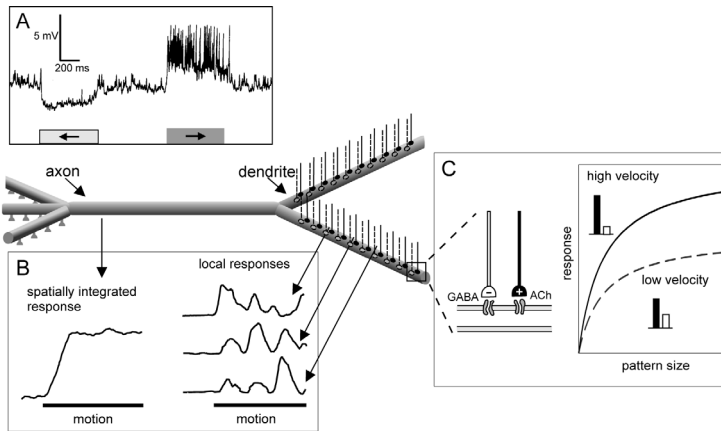

Fig. 10.6 Consequences of dendritic integration on the representation of visual motion: schematic depiction of a fly TC with two branches of the dendrite in the third visual neuropile, the axon and the axon terminal. The TC receives retinotopically organised input from local motion-sensitive elements (*vertical lines* terminating with 'synapses' — *black dots* (excitatory synapses) and *white dots* (inhibitory synapses) — on dendrite). A. As a consequence of this input the cell is excited by motion in its preferred direction and inhibited by motion in the null direction. B. Even when the velocity of motion is constant, the activity of the local input elements of the TCs is modulated depending on the texture of the surround in the receptive fields of the local elements. *Traces on the right* indicate the time-dependent signals of three local input elements of the TC. By dendritic pooling of many local elements this pattern dependence in the timecourse of the responses is eliminated to a large extent (*left trace*). C. Gain control in the TC makes its responses relatively independent of the number of activated input elements and, thus, of pattern size, while the response amplitude still depends on pattern velocity. *Left*: the enlargement illustrates that each point in visual space is subserved by a pair of input elements of the TCs, one of them being cholinergic and excitatory, the other GABAergic and inhibitory. *Right*: even during motion in the preferred direction both types of local input elements are activated, though to a different extent depending on the velocity of motion (*black and white columns*). As a consequence, the membrane potential approaches different saturation levels for different velocities when the number of activated local input elements increases.

frequencies than the steady-state optimum (Hausen, 1982b; Maddess and Laughlin, 1985; Warzecha *et al*., 1999). If the stimulus pattern does not consist of a mixture of spatial frequencies, as is characteristic of natural scenes, the responses of TCs are relatively independent of the textural details of the stimulus pattern (Dror *et al*., 2001; Kern *et al*., 2001a, b; Lindemann *et al*., 2005).

- The time course of TC responses is approximately proportional to the time-varying pattern velocity as long as the velocity changes are small (Egelhaaf and Reichardt, 1987; Bialek *et al*., 1991; Maddess *et al*., 1991; Haag and Borst, 1997). Due to the computational structure of local movement detectors, their spatially integrated responses do not only depend on pattern velocity, but also on higher order temporal derivatives (Egelhaaf and Reichardt, 1987). As a result, TC responses are no longer proportional to pattern velocity, if the velocity changes too rapidly (Egelhaaf and Reichardt, 1987; Haag and Borst, 1997). Nonetheless, velocity changes of up to 10–20 Hz are mainly represented in the neural responses, whereas higher frequencies are increasingly attenuated (Fig. 10.8C) (Haag and Borst, 1997; Warzecha *et al*., 1998).

10.3.3 Network interactions within the visual field of one eye and integration of motion information from both eyes

Dendritic pooling of motion input is not sufficient to obtain specific responses during particular types of self-motion. Both network interactions between TCs within one brain hemisphere and between both halves of the visual system have been characterised in some detail in the blowfly motion vision system.

Two types of network interactions between TCs within the ipsilateral optic lobe could recently be established:

- *Input organisation of CH cells*: The two centrifugal horizontal (CH) cells have wide profuse branching patterns in the lobula plate that represent both input and output arborisations (Hausen, 1976; Eckert and Dvorak, 1983; Egelhaaf *et al*., 1993). CH cells receive their ipsilateral input not from an array of retinotopic motion-sensitive neurons, but rather via electrical synapses from another class of TCs, the horizontal system (HS) cells.

Whereas HS cells receive direct motion input from local motion-sensitive elements, CH cells are driven by HS cells (Haag and Borst, 2002; Farrow *et al*., 2003). This connection scheme is concluded to lead to a spatial blur of the motion image on the CH cell dendrite and to be functionally relevant in the context of object detection (see below) (Cuntz *et al*., 2003).

- *Network interactions between VS cells*: Each of the ten vertical system (VS) cells possesses distinctive local preferred directions in different parts of their receptive field (Krapp *et al*., 1998). Dual recordings from pairs of VS cells show that they are electrically coupled. This coupling is responsible for the elongated horizontal extent of their receptive fields. Also, VS cells with a lateral receptive field have additional connections to a VS cell with a frontal receptive field and to the HS, tuning these cells to rotational flow fields. Hence, the receptive fields of VS cells consist of two components: one that they receive from local motion-sensitive cells on their dendrite, and one that they import from other large-field neurons (Haag *et al*., 2004).

To enhance the specificity of TCs for particular optic flow patterns, heterolateral interactions are particularly relevant. For instance, during forward translation the optic flow across both eyes is directed backward. In contrast, during a pure rotation about the animal's vertical axis, optic flow is directed backward across one eye, but forward across the other eye. Both types of optic flow can be distinguished if motion from both eyes is taken into account. Such a strategy appears to be adopted quite generally by arthropods. For instance, crabs use interactions between movement detectors that 'look' in opposite directions of the visual field (Kern *et al*., 1993; Sztarker and Tomsic, 2004). Moreover, motion-sensitive neurons with binocular receptive fields have been characterised in various insect groups (bee: DeVoe *et al*., 1982; Ibbotson and Goodman, 1990; Ibbotson, 1991b, moth: Collett, 1972; Rind, 1983; Kern, 1998, fly: Hausen, 1976; Hausen, 1982a, b; Horstmann *et al*., 2000; Haag and Borst, 2001; Krapp *et al*., 2001, locust: Rind, 1990a). Although such heterolateral interactions may increase neuronal specificity for particular types of optic flow, this specificity is far from being perfect and the neurons still respond to a wide range of 'non-optimal' optic flow stimuli (Hausen, 1982b; Horstmann *et al*., 2000; Kern *et al*., 2000; Karmeier *et al*., 2003).

For some binocular TCs of flies the underlying wiring scheme could be characterised. Two such wiring schemes are summarised here (Fig. 10.7):

- *Circuit for coherent wide-field motion* (Fig. 10.7A): The main output elements of this circuit are three so-called HS neurons. Owing to their retinotopic input they respond to ipsilateral front-to-back motion by graded depolarisations that are superimposed by spikelets of variable amplitude (Hausen, 1982b). The ipsilateral receptive fields of HS neurons cover the dorsal (HSN), the equatorial (HSE), and the ventral (HSS) part of the visual field (Hausen, 1982b; Haag and Borst, 1998). The HSE and HSN cells receive input from two spiking TCs, the H1 and the H2 cells that are sensitive to back-to-front motion in the visual field contralateral to the retinotopic input (Haag *et al*., 1999; Horstmann *et al*., 2000; Haag and Borst, 2001). As a consequence, the HSE and HSN cells have been proposed to respond best during turns of the animal about its vertical body axis, although both cells also respond to simultaneous front-to-back motion in the visual field of both eyes as occurs during translation (Hausen, 1982b; Horstmann *et al*., 2000; Kern *et al*., 2000; Krapp *et al*., 2001). Recent experiments with behaviourally generated optic flow suggest that the view that HS cells act as rotation detectors needs to be modified (see Section 10.7)
- *Circuit for object motion* (Fig. 10.7B): The FD1 neuron belongs to a group of neurons which respond best to the motion of relatively small objects, as an animal may encounter when it passes a nearby object (Egelhaaf, 1985b, c; Kimmerle *et al*., 1996; Gauck and Borst, 1999). Like other TCs the FD1 cell receives retinotopic input from the ipsilateral eye. To prevent the FD1 cell from also responding strongly to coherent wide-field motion, it is inhibited via GABAergic synapses by the so-called VCH cell, one of the two CH cells (Warzecha *et al*., 1993). The VCH cell is excited during ipsilateral front-to-back motion and contralateral back-to-front motion and is inhibited during contralateral front-to-back motion (Hausen, 1976; Eckert and Dvorak, 1983; Egelhaaf *et al*., 1993; Gauck *et al*., 1997; Haag and Borst, 2002; van Hateren *et al*., 2005). The VCH cell receives its ipsilateral input from the HS cells via dendro-dendritic synapses (see above) and its contralateral input from both the H1 and the H2 cells. As a consequence of this input organisation, the VCH cell

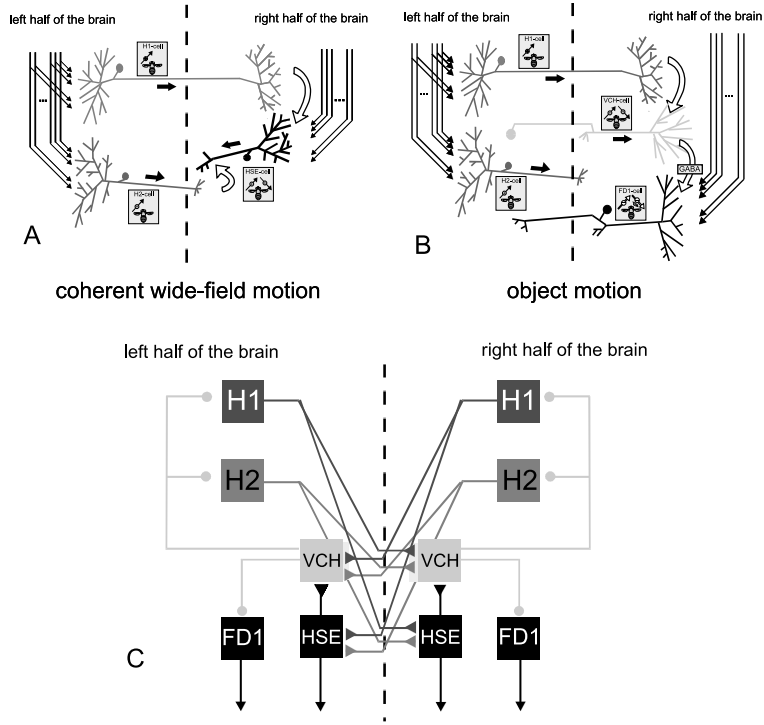

Fig. 10.7 Wiring diagram of neuronal circuits extracting different aspects of optic flow information. A. Circuit for coherent wide-field motion. Input organisation of the HSE cell of the blowfly. The HSE cell receives input from the eye ipsilateral to its main dendrite from many retinotopic motion-sensitive elements. As a consequence of this input, the HSE cell 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. As a consequence of its input organisation the right HSE cell can be expected to be depolarised during counter-clockwise rotations of the fly and hyperpolarised during rotations in the opposite direction. The cells are sketched only schematically. B. Circuit for object motion. The FD1 cell is one output element of this circuit. It receives retinotopic input from the ipsilateral eye to its main dendrite. To prevent it from firing during wide-field motion, it is inhibited by the VCH cell via GABAergic synapses. The VCH cell responds best to wide-field motion as indicated by the *inset*. It receives input from the contralateral eye from both the H1 and the H2 cells. C. Relationship of the two neuronal circuits sketched in A and B. The cells are indicated by *boxes*. Excitatory and inhibitory synapses are indicated by *triangles* and *circles*, respectively. Note the reciprocal recurrent inhibitory connections between neurons in both halves of the visual system.

prevents the FD1 cell from responding strongly to self-motion around the animal's vertical axis. Since the VCH cell does not respond much during forward translation (Egelhaaf *et al*., 1993), the FD1 cell is inhibited only weakly during this type of locomotion.

The circuits for coherent wide-field motion and for object detection do not operate independently, but are mutually interconnected in a complex way (Fig. 10.7C).

10.3.4 Convergence of visual motion information with other sources of information

Up to the level of TCs, the visual motion pathway is mainly devoted to the extraction of different aspects of optic flow information. Before visual motion information is used for behavioural control, it is often combined with information from other sensory modalities, with learnt representations about the environment and with factors related to the internal state of the animal, for instance, whether it is hungry, thirsty, or prepared to mate. Although there is good evidence that bees or wasps use optic flow to gain representations about their environment that are stored in their brain (reviews: Collett and Zeil, 1996; Land and Collett, 1997; Srinivasan *et al*., 1999; Collett and Collett, 2002; Chapter 11), not much is known about the underlying neuronal mechanisms. In contrast, there is some knowledge, mainly for locusts and flies, about the way other sensory modalities interact with visual motion input in guiding behaviour.

The flight speed of locusts is not only affected by optic flow but also by wind information mediated by mechanoreceptors on the antennae (Gewecke and Philippen, 1978). Moreover, course deviations are not only detected visually, but also by other sensors. In locusts and dragonflies, descending neurons connecting the brain with motor control centres in the thoracic ganglia co-process visual motion input, wind information, as well as proprioceptive input, signalling head movements and head position. All these inputs are combined such that the different descending neurons signal different types of course deviations as well as head movements of the animal (Olberg, 1981b; Rowell, 1989; Hensler, 1992a, b).

In flies, the halteres, small pendulum-like organs phylogenetically originating from hind wings, act as gyroscopes to detect angular body rotation during flight (Nalbach, 1993; Nalbach and Hengstenberg, 1994; Nalbach, 1998; Dickinson, 1999). The halteres mediate

compensatory head movements (review: Hengstenberg, 1993) and steering movements of the entire animal (Dickinson, 1999). Halteres provide information about body rotations at higher turning velocities than does the visual system (Hengstenberg, 1993; Sherman and Dickinson, 2003). Thus, the behaviourally relevant dynamic range of turning velocities is subdivided between the two sensory systems (Sherman and Dickinson, 2004). Visual motion information and signals originating from the halteres were found to converge on motor neurons in the circuit mediating compensatory head movements (Strausfeld *et al*., 1987). Moreover, activity of flight-steering muscles is affected by visual input (Heide, 1983; Egelhaaf, 1989; Tu and Dickinson, 1996), by input from the halteres (Fayyazuddin and Dickinson, 1996), and by input from mechanosensory afferents of the wings (Heide, 1983).

10.3.5 Neuronal control of behaviour

In locusts, there is much knowledge on the control of motor circuits in the thoracic ganglia by descending neurons. A population of these descending neurons transmits information about deviations from straight flight to the motor circuits for course control (Rowell, 1989). Some of these deviation detectors receive input from the visual motion pathway, from wind sensors on the antennae and from neck proprioceptors (Section 10.3.4). Although all components of steering, such as modifications of the wing stroke, rudder-like movements of the abdomen and of the hind legs as well as compensatory head movements, can be initiated by single descending neurons, steering in flight involves the concerted action of at least ten pairs of descending neurons synapsing onto motor neurons and premotor interneurons (Rowell, 1989; Hensler, 1992a, b). This whole system thus forms a kind of autopilot that controls corrective steering of the locust.

In flies much is known about the anatomy and, to a lesser extent, on the physiology of the control system mediating compensatory head movements (Milde *et al*., 1987; Strausfeld *et al*., 1987; Gilbert *et al*., 1995; Gronenberg *et al*., 1995). Some head motor neurons were shown to have directionally selective responses to visual motion. Their response properties are similar to those of individual TCs or combinations of them (Milde and Strausfeld, 1986; Milde *et al*., 1987). Some head motor neurons elicit head movements opposite to their preferred direction of visual motion suggesting a potential role in mediating compensatory head movements (Gilbert *et al*., 1995).

In contrast to locusts, only relatively little is known in flies about the neuronal organisation of motor control circuits in the thoracic ganglia. However, there is some indirect knowledge about the organisation of visually induced flight control from recordings of steering muscles during tethered flight. The circuits for coherent wide-field motion and for object motion (Section 10.3.3) converge with varying weight on the different steering muscles that control the fly's turning responses. Muscles involved in yaw torque control (Heide, 1983) receive differential input from both circuits: one of the steering muscles appears to receive input from both control circuits, whereas another steering muscle is only active when the turning response of the fly is elicited by object motion (Egelhaaf, 1989). Hence, the different steering muscles are functionally specialised to mediate different response components in visual orientation.

10.4 LINEARITIES AND NON-LINEARITIES IN NEURONAL COMPUTATION

Establishing neuronal wiring diagrams alone is not sufficient to understand how visual motion information is processed. One reason for this is that neurons are highly non-linear computing devices. There are only few examples where the computational consequences of these non-linearities have been analysed in the context of neuronal encoding of visual motion.

10.4.1 Gain control by dendritic integration of antagonistic motion input

Dendritic integration of signals from local motion-sensitive elements by blowfly and butterfly TCs was shown to be highly non-linear. When the signals of an increasing number of input elements are pooled, saturation non-linearities make the response largely independent of pattern size. As a consequence of the opponent local motion inputs (Section 10.3.1), the response saturates at different levels for different velocities. This gain control leads to responses that are almost invariant against changes in pattern size, while they still encode velocity (Fig. 10.6C) (Hausen, 1982b; Hengstenberg, 1982; Egelhaaf, 1985a; Maddess *et al*., 1991; Haag *et al*., 1992; Single *et al*., 1997). Moreover, recent model simulations suggest that gain control is decisive for explaining the responses of TCs to complex behaviourally generated optic flow (Lindemann *et al*., 2005) (see Section 10.7).

Gain control can be explained on the basis of the passive properties of TCs and the antagonistic nature of their motion input. Even during motion in the preferred direction both types of local input elements, i.e. the two mirror-symmetrical subunits of the movement detector (see Section 10.3.1), are suggested to be activated, though to a different extent, depending on the velocity of motion. As a consequence, with increasing numbers of activated input elements the membrane potential approaches different saturation levels at different velocities (Borst *et al*., 1995). The exact properties of gain control of TCs could be shown to depend on the geometry of the dendritic tree (Egelhaaf *et al*., 1994).

10.4.2 Voltage-dependent mechanisms

The computational consequences of dendritic pooling of local motion inputs (see Section 10.3.2) can be explained on the basis of the passive properties of the TC dendrite. This view is likely to be too simplistic as a wealth of active processes have been identified in the dendritic membranes of TCs (review: Borst and Haag, 2002). Amongst the voltage-dependent ion currents, fast sodium currents underlie spike activity in some TCs. In addition, delayed rectifying potassium currents and fast sodium-dependent potassium currents were identified. Different cell types differ with respect to the expression of these currents and thus in their electrical signals (Egelhaaf and Borst, 1995; Haag *et al*., 1997, 1999; Haag and Borst, 1998, 2000; Single and Borst, 1998; Dürr and Egelhaaf, 1999; Oertner *et al*., 2001). So far, the significance of active processes for the encoding of visual motion is still not well understood. One exception is the voltage-sensitive sodium currents that were shown to boost high-frequency fluctuations of the membrane potential (Haag and Borst, 1996). This feature may well increase the sensitivity of TCs to rapid velocity displacements that would otherwise be attenuated due to time constants involved in motion detection (Haag and Borst, 1997; Warzecha *et al*., 1998).

In addition to the above-mentioned sodium and potassium currents, voltage-sensitive calcium currents were also found in the dendrite and the presynaptic terminal of several blowfly TCs (Borst and Egelhaaf, 1992; Egelhaaf and Borst, 1995; Haag and Borst, 2000; Kurtz *et al*., 2001). These conductances show only little or no inactivation. Again different types of TCs differ with respect to the dynamics of the calcium channels (Haag and Borst, 2000; Dürr *et al*., 2001). Calcium accumulates in the cytosol during visual motion

stimulation. Whereas in the presynaptic region the most likely function of calcium is to trigger transmitter release, the function of dendritic calcium accumulation is less clear. It has been proposed that calcium plays a role as a second messenger in mediating adaptation to maintained visual motion stimulation (Kurtz *et al*., 2000; Section 10.6.2).

10.4.3 Synaptic signal transfer

Meaningful representations of optic flow are often achieved by interactions between TCs (see Section 10.3.3). To be beneficial, these synaptic interactions need to be carefully adjusted to the natural operating range of the system. Otherwise, synaptic transmission may severely distort the information being transmitted. This hazard is particularly daunting as the biophysical processes underlying synaptic transmission have been found in many systems to be intrinsically non-linear. Moreover, the transformation of the postsynaptic potential into spike activity may also be non-linear. Combined electrophysiological and optical imaging experiments were performed in the blowfly to analyse the relationship between the activity of a presynaptic TC and the spike rate of its postsynaptic target. The entire range of presynaptic depolarisation levels that can be elicited by motion in the 'preferred direction' was found to be transformed approximately linearly into the postsynaptic spike rate (Kurtz *et al*., 2001). This is surprising in the face of the potential non-linearities mentioned before. Linearity characterises transmission of membrane potential fluctuations up to frequencies of 10 Hz (Warzecha *et al*., 2003). Thus, the linear synaptic regime covers most of the dynamic range within which visual motion information is transmitted with a high gain (Section 10.3.2; Haag and Borst, 1997; Warzecha *et al*., 1998). Nonetheless, in addition to slow graded membrane potential changes, rapid presynaptic depolarisations such as spikes, are also transmitted reliably at this synapse (Warzecha *et al*., 2003). The function of this is unclear, since most spikes are not time-locked very reliably to motion stimuli (Section 10.5.2). As a consequence of the computational properties of the analysed synapse, visual motion information is transmitted largely undistorted to the contralateral visual system. This ensures that the characteristic dependence of neural responses on stimulus parameters such as velocity or contrast is not affected by the intervening synapse.

10.4.4 Transformation of postsynaptic potentials into spike trains

Spike generation is an inherently non-linear process, since spikes are generated only if the cell is sufficiently depolarised. Above the threshold the spike rate increases with depolarisation of the cell and eventually approaches a saturation level that is mainly set by the refractory properties of the neuron. Whether these non-linearities become relevant in the context of neuronal computation depends on the operating range of the neuron during sensory stimulation. Divergent conclusions have been drawn in this regard for different types of neurons involved in optic flow computation. First, in blowfly TCs the relationship between the postsynaptic potential and the corresponding spike rate was concluded to be linear for the entire range of depolarisations that can be evoked by preferred direction motion (Warzecha *et al*., 2000; Kretzberg *et al*., 2001a). Second, the DCMD/LGMD system of locusts was concluded to perform a multiplication of two inputs, one representing the size and the other the angular velocity of the edges of an approaching object, by a non-linear transformation of the postsynaptic potential into spike activity (Gabbiani *et al*., 2001).

10.5 ENCODING OF VISUAL MOTION IN REAL TIME

The timescale and reliability with which motion information is represented by nervous systems is constrained by the biophysical properties of nerve cells. Sensory information may be encoded either by graded changes in membrane potential or by sequences of action potentials.

In fly TCs, the postsynaptic signals originating from the retinotopic input elements superimpose and, depending on the direction of motion, the cell either depolarises or hyperpolarises in a graded fashion (Fig. 10.6A). In some TCs, graded membrane potential changes in the cell's output terminal could be shown to lead to transmitter release (Kurtz *et al*., 2001; Warzecha *et al*., 2003). In other TCs, most notably in those that project to the other side of the brain, the input and output regions are too distant for this mode of signal conduction, and the graded postsynaptic membrane potential changes are transformed into spike trains. The graded and the spiking mode of transmission are not mutually exclusive, since in many cells in which graded membrane potentials reach the output terminal,

the graded signals are superimposed and modified by voltage-dependent signals (Fig. 10.6A) (Hengstenberg, 1977; Hausen, 1982a; Haag and Borst, 1997, 1998; Haag *et al*., 1997, 1999; Kurtz *et al*., 2001). Recently, these different response modes have been investigated with respect to their consequences for the encoding of visual motion information.

10.5.1 Performance of spiking and graded potential neurons

Since blowfly TCs differ in their response mode, they are well suited for comparing the performance of spiking and graded potential neurons. The reliability with which constant velocity motion can be detected has been found to be basically the same for both response modes; the neuron with graded potentials performs better than the spiking one only at a timescale below 10 ms (Warzecha and Egelhaaf, 2001). A similar performance of both response types was found for the time that is required to detect the onset of motion as well as for the number of stimuli that can be discriminated reliably (Warzecha and Egelhaaf, 2001). Moreover, it was found that the velocity of a randomly fluctuating motion stimulus is represented by spiking and graded potential TCs similarly well – as long as the pattern moves in the cell's preferred direction. Velocity fluctuations above 10–20 Hz are encoded poorly by TCs of either response mode (Haag and Borst, 1997; Warzecha *et al*., 2003). This is because the time course of motion-induced responses of TCs not only depends on pattern velocity but also on its higher temporal derivatives (see Section 10.3.2; Egelhaaf and Reichardt, 1987; Haag and Borst, 1997).

In neurons that respond with graded membrane potential changes, information about a stimulus might be signalled at any instant of time. In contrast, in spiking neurons information resides only in the number of spikes per time interval, the timing of individual spikes relative to a stimulus, or in the temporal pattern of spikes (e.g. Rieke *et al*., 1997). Hence, it might be surprising that in the case of motion-sensitive TCs no principal difference in coding performance could be found between either response mode. There may be even situations where different time-varying stimuli can be better discriminated on the basis of spike responses than on the basis of graded responses, namely if spikes sharpen the temporal structure of the neuronal signal by amplifying fast membrane potential transients (Kretzberg *et al*., 2001b). If these membrane potential transients

are time-locked to the sensory stimulus, spikes may increase the temporal precision with which stimuli can be signalled (Haag and Borst, 1996).

10.5.2 The accuracy of encoding of visual motion

Even during constant velocity motion the activity of cells with either response mode fluctuates continuously. Moreover, when the same stimulus is presented repeatedly to a neuron, the responses may vary considerably (Fig. 10.8A). The spike count variance across trials of fly TCs is smaller than in motion-sensitive neurons in the primate cortex (see e.g. Warzecha and Egelhaaf, 1999; Barberini *et al*., 2000; Warzecha *et al*., 2000; Borst, 2003). Still, on the basis of individual spike trains it is not easily possible to discern stimulus-driven activity changes from those that are due to sources not associated with the stimulus ('noise'). The situation is further complicated because the variability of neuronal responses (Warzecha *et al*., 2000) and thus the transmitted information (Borst, 2003), depends on some stimulus properties, such as pattern contrast, but not on others, such as the dynamical range of motion velocities. In any case, neuronal response variability constrains the timescale on which time-varying motion can be represented.

Spike generation per se is generally thought not to limit the temporal precision of motion information processing, because spikes time-lock to rapid membrane potential fluctuations with a millisecond precision (Haag and Borst, 1996). As a consequence, spikes are only time-locked precisely to the stimulus, if the stimulus evokes membrane potential changes that are sufficiently fast and large relative to the membrane potential noise. In contrast, slow stimulus-induced membrane potential fluctuations mainly affect the spike rate and do not cause precise time-locking of spikes; the exact timing of spikes is then determined by the high-frequency components of the membrane potential noise (Fig. 10.8B) (Kretzberg *et al*., 2001a). Since the computations underlying direction selectivity require time constants of some tens of milliseconds (Sections 10.3.1. and 10.3.2), they attenuate the responses to high-frequency velocity fluctuations (Fig. 10.8C) (Haag and Borst, 1997; Warzecha *et al*., 1998). Hence, only very pronounced high-frequency velocity changes, such as the abrupt onset of motion, lead to rapid depolarisations that elicit spikes at a millisecond precision (Ruyter van Steveninck and Bialek, 1995; Ruyter van Steveninck *et al*., 2001; Warzecha and Egelhaaf, 2001). Otherwise the exact timing

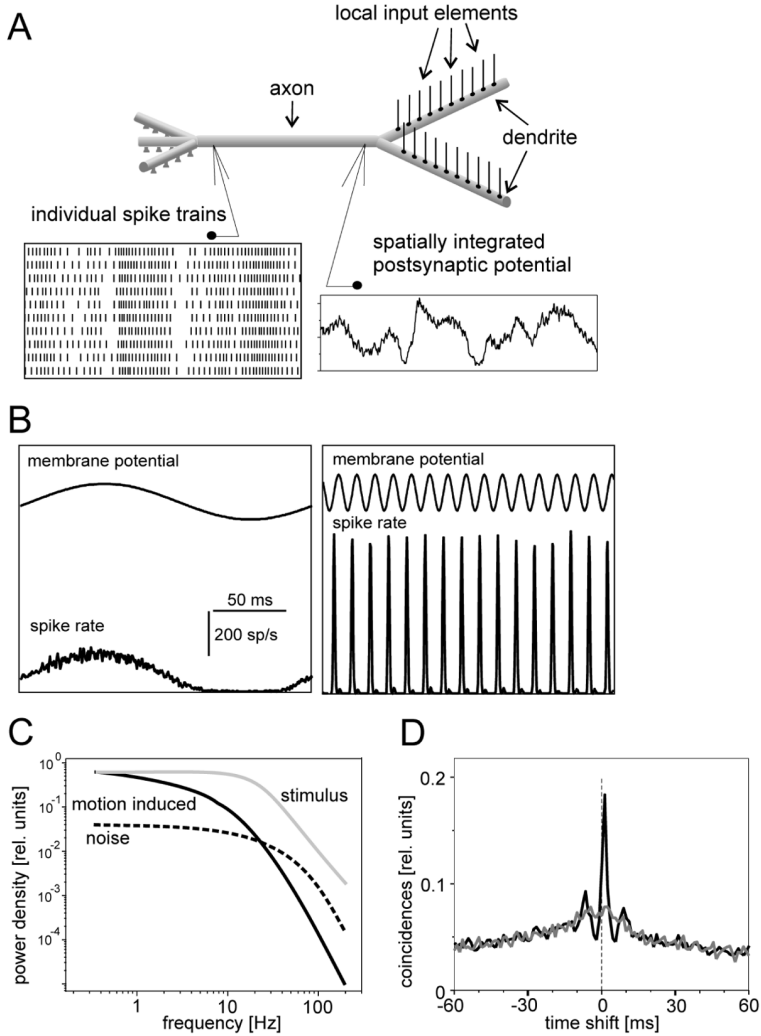

Fig. 10.8 Variability of neural responses and timescale at which optic flow information is signalled. A. Variability of responses of a spiking TC schematically indicated by two dendritic branches and axon. The cell transforms the summated postsynaptic potentials evoked by its retinotopic input elements into spike trains. Subsequent sample traces of individual spike trains evoked by repeated presentation of the same motion trace (random velocity fluctuations). *Vertical lines* denote spike occurrence. Although the overall pattern of neuronal activity is similar from trial to trial, there is variability in the temporal fine structure across trials (details in Warzecha *et al*., 1998, 2000). B. Time-locking of spikes to sinusoidal stimulus-induced membrane potential fluctuations

of most spikes is determined by membrane potential noise and visual motion is mainly represented by changes in spike rate.

Key evidence for these conclusions was the finding that spikes tend to be synchronised on a millisecond timescale in a pair of TCs with largely overlapping retinotopic input (Fig. 10.8D), suggesting that both TCs share high-frequency signals originating from their common input. Since, on average, the spikes of these TCs are mainly time-locked to velocity fluctuations on a coarse timescale (Fig. 10.8D), it is concluded that the synchronising signal components are attributable to noise in the common input of the TCs and not to the stimulus itself (Warzecha *et al*., 1998). This conclusion does not contradict the finding that the transmitted information rate increases with increasing temporal resolution at which the spike trains are scrutinised (Ruyter van Steveninck and Bialek, 1995; Ruyter van Steveninck *et al*., 1997;

Caption for Fig. 10.8 (cont.)
(5 or 80 Hz, *top traces*) in a model cell. The model is adjusted to fit the responses of a fly TC to motion stimuli. The stimulus-induced component of the membrane potential is superimposed by stochastic fluctuations that differ from presentation to presentation (not shown). PSTHs (*bottom traces*) illustrate that fast stimulus-induced membrane potential fluctuations are needed to trigger spikes with a high temporal precision. Slow stimulus-induced fluctuations lead to spike activity with a rate about proportional to the membrane potential (details in Kretzberg *et al*., 2001a). C. Dynamical properties of membrane potential fluctuations of a fly TC (the HSE cell) elicited by band-limited white-noise velocity fluctuations power spectra are shown for the motion stimulus, the motion-induced response component and the stochastic membrane potential fluctuations (noise). The motion-induced response component was determined by averaging many individual response traces. It contains most power below 20 Hz, although the stimulus contained higher frequencies. In the low-frequency range, the motion-induced response component is larger than the stochastic response component. Towards higher frequencies this relationship reverses (details in Warzecha *et al*., 1998). D. Cross-correlogram of responses to band-limited white-noise velocity fluctuations of two TCs (H1 and H2) with common synaptic input. Either synchronously recorded responses were used (*black trace*) or responses that were not recorded synchronously but obtained from repetitive presentation with the same motion stimulus (*grey trace*). Although TCs can generate spikes very precisely, most spikes time-lock to dynamical motion stimulation on a much coarser timescale (details in Warzecha *et al*., 1998).

Strong *et al*., 1998). Random velocity fluctuations that were frequently used in experimental analyses occasionally contain rapid velocity changes that are sufficiently pronounced to trigger at least some spikes with high temporal precision.

Although it is still debated to what extent rapid and slow velocity changes, and thus the exact timing of spikes, are functionally significant (Ruyter van Steveninck *et al*., 2001; Warzecha and Egelhaaf, 2001), it is generally agreed that this issue can only be resolved if we take into account the dynamics of retinal image displacements in different behavioural contexts (see Section 10.7).

Independent of the dynamics of natural image displacements, the speed with which visual motion can be detected is likely to be an important issue at least for fast flying insects. Given that neuronal responses are noisy, it will take some time to infer reliably relevant motion parameters from neuronal activity (Warzecha and Egelhaaf, 2001). Recent experiments on an ensemble of TCs, the so-called VS cells, analysed how the accuracy of a population code depends on integration time, on noise correlation between the participating neurons, and on the population size (Karmeier *et al*., 2005). The 10 VS cells are assumed to encode the animal's rotations around horizontally aligned body axes by means of graded potential changes (Krapp *et al*., 1998). Three major conclusions have been drawn with respect to real-time encoding of self-motion (Karmeier *et al*., 2005). First, for noise levels found in VS cells integration of neuronal activities over only 5 ms after response onset are sufficient to decode the rotation axis with high accuracy from the population response. Second, noise correlation between neurons (Haag and Borst, 2004) only has little impact on the population's performance. And third, although a population of only two VS cells would in principle be sufficient to encode any horizontal rotation axis, a population of 10 neurons is advantageous if the available integration time is short. In the case of the fly, short integration times are important to decode neuronal responses when controlling rapid flight manoeuvres (see Section 10.7).

10.5.3 Noise sources limiting the reliability of motion vision

The reliability of neuronal responses is constrained by various noise sources within the nervous system, such as phototransduction, the stochastic nature of ion channels that underlie all electrical activities of neurons, as well as synaptic transmission. In addition, the incoming

visual signal is inherently noisy because of the quantum nature of light. In fly motion-sensitive neurons, single-photon effects could be detected in the spike patterns of the motion-sensitive H1 neuron that is several synapses away from the photoreceptors (Lillywhite and Dvorak, 1981) and even in optomotor behaviour (Reichardt, 1965). Thus, at the sensitivity threshold of visual systems, the reliability of motion vision is limited by the physical limits of the visual input signal, i.e. by photon noise.

Although individual photons contribute much less to the overall photoreceptor response at higher light levels, the stochastic nature of light was recently concluded to limit the reliability with which visual motion information is represented by the fly visual system. All internal noise sources within the nervous system were supposed to be of minor relevance (Ruyter van Steveninck and Bialek, 1995; Borst and Haag, 2001; Lewen *et al*., 2001). However, at least for the light-adapted eye, noise sources inherent in synaptic transmission between photoreceptors and second-order neurons significantly affect the reliability with which visual information is signalled to higher order processing stages (e.g. Laughlin *et al*., 1987; Ruyter van Steveninck and Laughlin, 1996). Moreover, varying the brightness of moving dots in a random way affects the temporal pattern of spike responses of a fly TC only at noise levels much larger than photon noise (Grewe *et al*., 2003). Since blowflies are usually active during the day, it can be concluded that for most behaviourally relevant conditions, the reliability of encoding of visual motion information is constrained by noise sources inside the nervous system rather than by photon noise (see Grewe *et al*., 2003 for discussion of conflicting conclusions of previous studies).

10.6 ADAPTATION OF THE VISUAL MOTION PATHWAY TO ENVIRONMENTAL CONDITIONS

Motion information needs to be computed under a wide variety of conditions and thus the operating ranges of motion-detecting neurons may need to adapt. Two types of environmental changes are particularly obvious: (1) the several orders of magnitude change in ambient brightness during the course of a day, and (2) animals may be confronted by a wide range of velocities.

10.6.1 Brightness adaptation and its consequences

The stochastic nature of light is particularly obvious at low light levels, since the signal-to-noise ratio of photoreceptor responses decreases

with a decreasing intensity of light (reviews: Laughlin, 1994; Juusola *et al*., 1996). At low light levels, the reliability can be enhanced by either spatial pooling of the outputs of several photoreceptors thereby sacrificing spatial resolution, or by smoothing out the membrane potential noise elicited by single photon absorptions, thereby reducing the temporal resolution of the visual system. Indeed, the visual motion pathway of the fly pools from an increasingly larger area of the eye when it gets darker (Pick and Buchner, 1979; Schuling *et al*., 1989). Moreover, the time constants of photoreceptor responses tend to increase with decreasing brightness allowing for temporal smoothing of the consequences of the stochastic nature of light (review: Laughlin, 1994). Nocturnal moth species were shown to use more pronounced temporal low-pass filtering in their visual motion pathway than their diurnal relatives, thereby sacrificing spatial and temporal acuity for increased sensitivity (Theobald and O'Carroll, 2000; Theobald *et al*., 2001).

10.6.2 Adaptation to different dynamic ranges of visual motion

Motion vision systems operate under a variety of dynamical conditions. For instance, during walking the retinal images may be displaced much more slowly than during flight. Even in flying animals the dynamics of image motion may differ depending on their specific method of locomotion, i.e. whether the animal is hovering in front of a flower or cruising through its habitat. In various studies, mainly on flies, adaptational mechanisms have been inferred to adjust the visual motion pathway to these different dynamical conditions (review: Clifford and Ibbotson, 2003). Although it is generally agreed that many features of TC responses depend on stimulus history and, thus, may be regarded as adaptive, neither the underlying mechanisms nor the functional significance of most of these phenomena have yet been clarified. This is because adaptive processes have been studied by different stimulus paradigms and conceptual approaches.

In the initial study on motion adaptation in fly TCs, brief velocity increments and decrements were superimposed on constant velocity motion. The resulting cellular responses then appear to reflect, within a certain range of background velocities, velocity contrast, i.e. the ratio of the velocity change and the background velocity (Maddess and Laughlin, 1985). Hence, the sensitivity of the system is adjusted to the prevailing motion conditions.

In another approach, the response to brief displacements of a pattern in the cell's preferred direction was used as an indicator of neuronal performance. The decay time constant of this 'step response' decreases with increasing velocity of pattern motion preceding the motion step. The time constant of decay has been interpreted to reflect the time constant of the local motion detectors (Maddess and Laughlin, 1985; Ruyter van Steveninck *et al*., 1986; Borst and Egelhaaf, 1987; Maddess *et al*., 1991; Clifford and Langley, 1996). If this interpretation were correct, the steady-state velocity tuning of the visual motion pathway should shift towards higher velocities when the retinal motion is fast. Motion adaptation would thus help to extend the operating range of the system.

This appealing conclusion was recently disputed (Harris *et al*., 1999). The predicted shift in velocity tuning could not be found when a test stimulus was preceded by adapting stimuli covering a wide range of velocities. However, this finding is not entirely conclusive, since the velocity tuning was determined during the initial response transient after stimulus onset, whereas the predicted shift in velocity tuning pertains to the steady-state conditions of the response. During the initial response transient, the velocity dependence of the response is different from the steady-state dependence (Hausen, 1982b; Maddess and Laughlin, 1985; Egelhaaf and Borst, 1989; Egelhaaf and Borst, 1990; Warzecha *et al*., 1999) and may not depend exclusively on the time constant of the local motion detectors but also on other time constants of the motion pathway.

The discrepancies between the interpretation of the adaptive changes of responses to motion steps and the missing shift in velocity tuning were partly solved in a combined experimental and model study (Borst *et al*., 2003; Reisenman *et al*., 2003). If the movement detectors are equipped not only with a low-pass filter, but in addition with a high-pass filter having an adaptive time constant, the above-mentioned characteristics of motion adaptation can be explained.

Adaptive changes in motion sensitivity are also suggested by experiments using time-varying velocity fluctuations. When the range of velocity fluctuations was increased, the sensitivity of a TC for motion as determined by the relationship between pattern velocity and instantaneous response amplitude changed along with it (Brenner *et al*., 2000). This so-called adaptive rescaling indicates that the inevitably limited operating range of motion-sensitive neurons is somehow adjusted to the prevailing conditions. It has been concluded

that adaptive rescaling may operate on a wide range of timescales from milliseconds up to minutes (Fairhall *et al*., 2001).

The stimulus history not only affects the velocity sensitivity of TCs, but also their sensitivity to brightness contrast (Harris *et al*., 2000). Following motion adaptation, a much larger pattern contrast is required than before to drive the neuron to its half-maximum response. This reduction in response amplitude is not only the consequence of a decrease in the response gain, but also of a subtractive shift of the relationship between stimulus strength and response amplitude. One functional consequence of this change in gain became apparent, when motion adaptation during natural optic flow stimuli was analysed (see Section 10.7). Coding performance of the analysed neuron did not change upon motion adaptation. Only the response amplitude, and thus the gain of the system, decreased considerably. Since the overall information conveyed by the neuronal responses did not decrease despite the decrease in the mean spike rate, the information per spike increases. Hence, motion adaptation may serve as a mechanism to ensure parsimonious coding without sacrificing the reliability with which behaviourally relevant information is encoded (Heitwerth *et al*., 2005).

What are the mechanisms underlying motion adaptation and where in the visual pathway does motion adaptation take place? Motion adaptation is, at least partly, a local process, because only those areas of the receptive field of a TC adapt that were exposed to motion (Maddess and Laughlin, 1985; Ruyter van Steveninck *et al*., 1986). This finding led to the initial conclusion that adaptation takes place peripherally to the spatially integrating TCs. This conclusion is consistent with the finding that adaptation is not entirely direction selective (Maddess and Laughlin, 1985; Ruyter van Steveninck *et al*., 1986; Borst and Egelhaaf, 1987; Harris *et al*., 2000). Since the adaptive strength, nonetheless, depends to some extent on the direction of motion, at least some adaptation may take place at a processing stage after direction selectivity is established. Hence, motion adaptation is likely to operate at various levels of the visual system. At least one directionally selective component of adaptation operates at the level of TCs. Maintained motion in the cell's preferred direction leads to dendritic calcium accumulation that is assumed to open calcium-dependent potassium channels. In this way the gain of the system and thus its sensitivity to motion is reduced (Kurtz *et al*., 2000). Since dendritic calcium stays local during local motion stimulation (Borst and Egelhaaf, 1992; Egelhaaf and Borst, 1995; Dürr and Egelhaaf, 1999),

even a postsynaptic mechanism located on the large dendrites of TCs may account for the local nature of motion adaptation (Kurtz *et al*., 2000).

Some caution is required when interpreting the dependence of neuronal properties on stimulus history as a consequence of adaptation. In contrast to the widespread belief, response transients after motion onset are not necessarily due to adaptive changes of the system (Egelhaaf and Borst, 1989, 1990). Rather, any system, even with fixed time constants, requires some time to reach its steady-state response level. Moreover, even the presentation of a stationary stimulus may modify the subsequent response to motion stimuli. As indicated by earlier studies (Egelhaaf and Borst, 1989, 1990) and elaborated by recent model simulations (Harris and O'Carroll, 2002), such effects may be attributed to the dynamical properties of passive linear filters that are constituents of the visual motion pathway. Interestingly, the decrease in the decay time constant of the response to a motion step that is induced by motion adaptation can also, at least to some extent, be explained when implementing a filter with a long time constant peripherally to the local movement detectors (Harris and O'Carroll, 2002). This finding is remarkable because it shows that seemingly adaptive phenomena may emerge, even if there are no adaptive changes of system parameters. This conclusion is consistent with recent model simulations. First, adaptive rescaling (see above) can be explained as an emergent property of correlation-type movement detectors (see Section 10.3.1) without assuming any adaptive change of systems parameters, such as the time constants of the movement detector (Borst *et al*., 2005). Second, although the explanation of neuronal responses to natural optic flow (Section 10.7) requires some reduction in the overall gain of the system, there are no obvious consistent changes in other systems parameters such as time constants.

In conclusion, although the responses of the motion vision system of insects depend in a variety of ways on stimulus history, there is still no coherent view concerning the functional significance of these adaptive changes and the underlying mechanisms.

10.7 PROCESSING OF BEHAVIOURALLY RELEVANT VISUAL MOTION INFORMATION

Knowing the wiring of a neuronal circuit does not allow us to infer how efficiently and reliably information is processed and represented in natural behavioural situations. This is because traditionally visual

information processing is analysed with stimuli that are much simpler with respect to their spatial and dynamical features than the input an animal encounters in normal behavioural situations. Because visual systems evolved in specific environments and behavioural contexts, the functional significance of the information being processed requires an analysis of neuronal performance under conditions that come close to natural situations.

One important aspect is the dynamical properties of optic flow that are largely determined by the dynamics of the animal's self-motion and the three-dimensional layout of the environment. The characteristics of optic flow may differ greatly in different species and in different behavioural situations. For instance, some insects, such as hoverflies, dragonflies, and hawkmoths, are able to hover almost stationary in midair or in front of a flower (Collett and Land, 1975; Farina *et al*., 1994; Kern and Varjú, 1998). Accordingly, hoverflies have TCs that are tuned to lower velocities than fly species that do not hover (O'Carroll *et al*., 1996, 1997). From their current position in space these insects may rapidly accelerate and dart off at high velocities. The optic flow pattern and its dynamics may differ tremendously in the respective situations. Blowflies usually change their body and gaze direction rapidly by saccadic turns during flight (Schilstra and van Hateren, 1999; van Hateren and Schilstra, 1999) or, one order of magnitude more slowly, while walking (Kern *et al*., 2001b; Blaj and van Hateren, 2004). Since the optic flow pattern and its dynamics are species- and context-specific (see also Section 10.2.7) it may be reasonable to assume that the mechanisms extracting motion information are adapted to the behaviourally relevant conditions.

Because it is hard to record from visual interneurons in freely moving invertebrates, more indirect approaches have recently been used in insects to determine the responses of motion-sensitive neurons to behaviourally generated optic flow. Recordings have been made from the brains of flies that are oscillated with dynamics that mimic the rotational self-motion component as experienced in free flight (Lewen *et al*., 2001) or from tethered moths flying in a kind of flight simulator where the animal can influence its input in a similar way as under free-flight conditions (Fig. 10.9A) (Gray *et al*., 2002). The latter approach, though very elegant, can so far only be used for animals that are relatively large and change their direction of flight relatively slowly. In another approach, the optic flow experienced by behaving flies was reconstructed and replayed to the animal during

nerve cell recordings. This approach has been employed for various behavioural situations during tethered flight in a flight simulator (Warzecha and Egelhaaf, 1996, 1997; Kimmerle and Egelhaaf, 2000b) during unrestrained walking in a three-dimensional environment (Kern *et al*., 2000, 2001a) and recently during rapid free-flight manoeuvres in a three-dimensional environment (Fig. 10.9B) (Kern *et al*., 2001b, 2005; Lindemann *et al*., 2003; Boeddeker *et al*., 2005; van Hateren *et al*., 2005). The simulation of free flight has become possible thanks to the development of sophisticated techniques. First, free-flight behaviour can be monitored with unprecedented accuracy by means of sensor coils mounted on the head and thorax of the animal (Schilstra and van Hateren, 1999; van Hateren and Schilstra, 1999) or by high-speed digital cameras (Boeddeker *et al*., 2005). Second, a panoramic visual stimulator for presentation of optic flow has been designed that is sufficiently fast for visual stimuli as experienced by insects even during rapid saccadic turns (Lindemann *et al*., 2003).

These studies already revealed that the neuronal responses to complex optic flow, as experienced under behavioural conditions, can be understood only partly in terms of the concepts that were established on the basis of experiments done with conventional motion stimuli. Two examples of processing of behaviourally generated optic flow will be briefly discussed in the following.

A study carried out on tethered flying flies under closed-loop conditions analysed how well an object can be detected and fixated in the presence of translatory optic flow (Kimmerle and Egelhaaf, 2000b; Kimmerle *et al*., 2000). When the retinal input during successful fixation was replayed in electrophysiological experiments to an FD cell (a neuron thought to detect objects on the basis of motion cues: Section 10.3.3), the cell responded much more specifically to a small moving target than had been expected from previous experiments with conventional motion stimuli (Kimmerle and Egelhaaf, 2000). Thus, the computations underlying optic flow processing appear to be well matched to object detection in behavioural situations.

The other example pertains to the HSE cell, one output element of the neuronal circuit for coherent wide-field motion in the fly brain (Fig. 10.7A, Section 10.3.3). As mentioned above, during spontaneous flight blowflies execute a series of saccadic turns where the head shows angular velocity peaks of up to several thousand degrees per second. Between saccades, the gaze is kept stable. Results obtained from the HSE neuron with this behaviourally generated optic flow

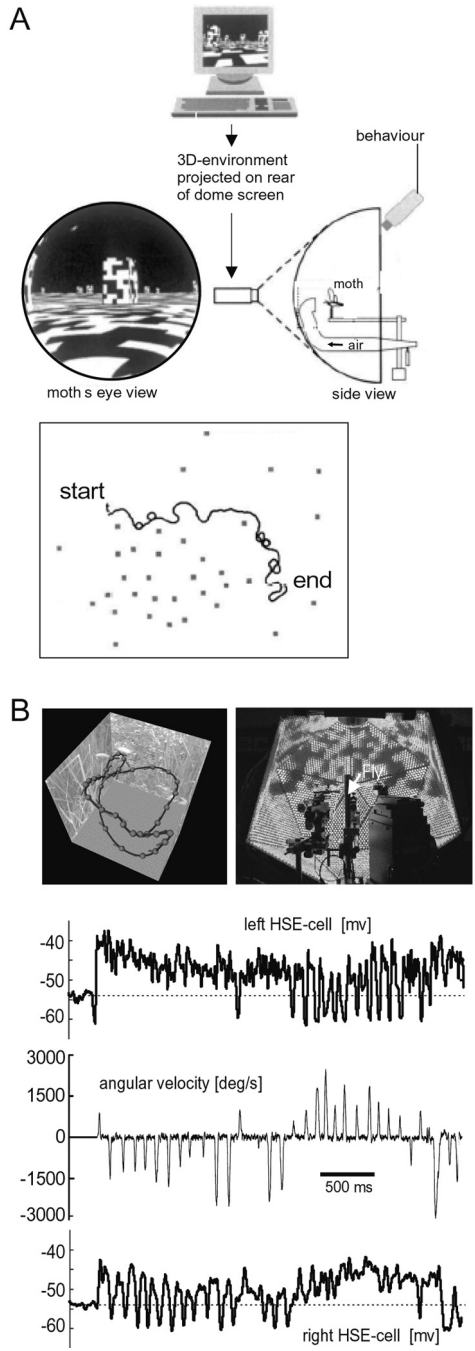

Fig. 10.9 Neuronal processing of natural optic flow. A. Setup of a virtual reality flight simulator to monitor neuronal responses of tethered flying moths under close-loop conditions. Visual environments were generated with rendering software. The image sequences are projected on a dome

do not match conclusions based on systems analysis of the neuron's properties with experimenter-designed stimuli (Kern *et al*., 2005):

- It was previously concluded that the HSE cell should mainly act as a detector of self-rotation of the animal around its vertical axis

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Caption for Fig. 10.9 (cont.)
screen. Abdominal steering movements of the tethered flying moth are monitored with an infrared camera. To simulate flight conditions, the moth was also supplied with wind that could be supplemented with odours. The behavioural responses are used to calculate the retinal image displacements that would have been generated by the moth's actions and reactions, if it were free to fly in its environment. The inset shows a virtual track of the moth as viewed from above during a closed-loop experiment. The small squares represent the position of vertical pillars within the sitmulated environment (Gray *et al*., 2002). B. Responses of the HSE cell of a blowfly to behaviourally generated optic flow as experienced during a free-flight manoeuvre. *Top left*: flight trajectory monitored in a cubic cage (0.4 m × 0.4 m × 0.4 m) covered on its side walls with images of herbage (the brightness of the walls is increased in the figure and the contrast of the textures reduced to enhance the visibility of the fly's trajectory). The trajectory is shown by the *black line*. The position and orientation of the head are shown every 100 ms. Time dependent traces: *Top trace*: average response of an HSE-cell in the left half of the visual system to behaviourally generated optic flow. The cell responds to motion with graded de- and hyperpolarisations. *Second trace*: angular velocity of the fly's head around its vertical axis. Sharp angular velocity peaks corresponding to saccade-like turns of the fly dominate the time-dependent angular velocity profile. Positive (negative) values denote counter-clockwise (clockwise) turns of the head in a head-centred coordinate system. *Third trace*: average response of an HSE cell in the left half of the visual system to behaviourally generated optic flow. In contrast to expectations based on the input organisation of the HSE cell (see Fig. 10.7A) there are no obvious response peaks during preferred direction motion (right HSE: counter-clockwise saccades; left HSE: clockwise saccades). However, there are pronounced hyperpolarisations accompanying null direction saccades (right HSE: clockwise saccades; left HSE: counter-clockwise saccades). The maintained depolarisation of the cell, especially between preferred direction saccades reflects the translational component of the optic flow and thus the distance to the arena walls (data from Lindemann *et al*., 2003).

(see Fig. 10.7A, Section 10.3.3). In contrast, our results with behaviourally generated optic flow show that the neuron fails to faithfully encode even the most prominent turns of the animal such as during saccades.

- Although the cell experiences the largest optic flow during saccades, it may actually encode behaviourally relevant information between saccades. Since blowflies keep their gaze stable between saccades (apart from small, broad-band yaw rotations), they may gather useful information about the outside world from the translational optic flow components that dominate at low frequencies in inter-saccadic intervals. Indeed, between saccades neuronal signals provide rich information about the spatial relation of the animal to its surroundings. It should be noted that distance is not signalled in this way in absolute terms but only relative to the fly's own velocity, because the retinal velocities evoked during translation are not only inversely proportional to distance, but also proportional to translation velocity. This implies that in walking flies the background should affect the responses of the HSE cell only when the fly is much closer to an object, just as has been found in electrophysiological experiments (Kern *et al*., 2001a, b).
- Motion-sensitive neurons are frequently expected to encode stimulus velocity. Indeed, stimulus velocity can be derived faithfully from the responses of blowfly motion-sensitive neurons, as long as the velocities and velocity changes are relatively small (see Section 10.3.2). However, under behaviourally relevant stimulus conditions the visual motion system of the blowfly operates, for a considerable portion of time, far beyond this linear range. These results suggest that the functional significance of neuronal mechanisms cannot be assessed unless the system is analysed under its natural operating conditions. It appears that, in contrast to previous views, the non-linearities of the visual motion system may be essential for HSE to encode information about the spatial relation of the animal to its environment. If the neuron encoded the entire velocity range that the system encounters in behaviour linearly, by far the largest responses would be generated during body saccades. This would leave only a very small response range for encoding optic flow in the inter-saccadic interval. Given the noisiness of neuronal signals (see above), it might then be difficult to extract meaningful information

about the spatial organisation of the surroundings from the neuronal responses. Hence, because the animal operates during saccades far beyond the linear range of the motion detection system, the HSE neuron is able to encode useful information about translation and thus about the spatial relation of the animal to the outside world. This finding emphasises that the significance of neuronal circuits can only be assessed if they are probed in the natural operating range.

So far only the role of individual neurons has been analysed in encoding of behaviourally relevant features from natural optic flow. With the available techniques for presenting behaviourally generated optic flow, it will now be the next step to understand how the specificity of individual neurons is increased by taking the entire population of TCs into account.

There are other factors that are not related to the visual stimuli but, nonetheless, are important for processing visual motion information under behaviourally relevant conditions. In poikilothermic animals, such as arthropods, body temperature and thus the temperature of the nervous system depends on the temperature of the environment as well as on the activity of the animal (Stavenga *et al*., 1993). Indeed, over the range of plausible operating temperatures the response latency of a fly TC decreases considerably and the signal-to-noise ratio of neuronal responses increases (Warzecha *et al*., 1999; Warzecha and Egelhaaf, 2000). Hence, optic flow processing does not only depend on the visual stimulus conditions but also on the animal's internal state.

So far, most studies on motion information processing of arthropods have been performed indoors. Recently, responses of a fly TC were concluded to cover a much larger dynamic range and to be more reliable in bright sunlight than under dimmer laboratory conditions (Lewen *et al*., 2001). Although these conclusions are not unanimously accepted and it is still under debate to what extent brightness affects the performance of TCs (Egelhaaf *et al*., 2001), it becomes increasingly clear that nervous systems seem to be shaped by evolution to solve efficiently and parsimoniously those computational tasks that are relevant for the survival of the animal. Therefore, one of the great issues for future research will be to understand how the biophysical properties underlying neuronal computation relate to the information that is to be processed under natural operating conditions.

10.8 CONCLUSIONS AND PERSPECTIVES

Despite their tiny brains, arthropods 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 may have been accomplished because arthropod brains appear to be no general purpose information processing devices, but are kept as simple as possible by adapting their visual systems to the specific needs encountered in normal life. In the context of visual motion information processing, it has become increasingly clear that conventional systems analysis on its own is not sufficient to assess what aspects of the environment and the animal's own behaviour are encoded by neuronal circuits. Rather, the functional significance of neural computations may only become evident if visual information processing is viewed from the perspective of sensory and behavioural ecology. To learn how nervous systems solve visual orientation tasks in an efficient and parsimonious way we need to know about both the neuronal circuits and the conditions under which they operate.

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