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Responses of blowfly motion-sensitive neurons to reconstructed optic flow along outdoor flight paths

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Abstract The retinal image flow a blowfly experiences in its daily life on the wing is determined by both the structure of the environment and the animal's own movements. To understand the design of visual processing mechanisms, there is thus a need to analyse the performance of neurons under natural operating conditions. To this end, we recorded flight paths of flies outdoors and reconstructed what they had seen, by moving a panoramic camera along exactly the same paths. The reconstructed image sequences were later replayed on a fast, panoramic flight simulator to identified, motion sensitive neurons of the so-called horizontal system (HS) in the lobula plate of the blowfly, which are assumed to extract self-motion parameters from optic flow. We show that under real life conditions HS-cells not only encode information about self-rotation, but are also sensitive to translational optic flow and, thus, indirectly signal information about the depth structure of the environment. These properties do not require an elaboration of the known model of these neurons, because the natural optic flow sequences generate—at least qualitatively—the same depth-related response properties when used as input to a computational HS-cell model and to real neurons.

Keywords Optic flow · Natural stimuli · Motion detection · Active vision · Behaviour

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Introduction

As animals move through the world, they experience a distinct pattern of continuous change in the retinal image. This so-called optic flow is a rich source of information for the control of orientation, the direction of heading, and for guiding navigation (e.g. Gibson 1950; Lappe 2000; Zanker and Zeil 2001). Whereas rotation-induced optic flow is independent of the distance of objects, translation-induced optic flow contains distance information on the structure of the environment, albeit in relative terms: optic flow generated by a slow movement through dense vegetation may be the same as that generated by fast flight through open country with scattered trees. Computing relevant information from optic flow is most demanding when translational and rotational movements are superimposed for instance when animals change their direction of heading or their gaze during locomotion (e.g. Dahmen et al. 1997, 2001; Koenderink 1986; Koenderink and Doorn 1987; Prazdny 1980). The pattern of movement thus plays an important role in structuring optic flow, to the extent that some insects move in specific ways to produce a particular type of image motion (locusts and mantids: reviewed by Kral and Poteser 1997; bees: Lehrer and Srinivasan 1994; wasps: Voss and Zeil 1998; Zeil et al. 1996).

Flight behaviour thus structures optic flow. For instance cruising flies fly straight for most of the time and change their heading direction by rapid, saccadic body turns (*Calliphora vicina*: Schilstra and van Hateren 1999; van Hateren and Schilstra 1999; *Drosophila melanogaster*: Heisenberg and Wolf 1979, 1993; Tammero and Dickinson 2002; *Fannia canicularis*: Zeil 1986; *Musca domestica*: Wagner 1986; *Syritta pipiens*: Collett and Land 1975). Head movements stabilize gaze direction even better than expected on the basis of saccadic changes of flight direction (Hengstenberg 1991; Land 1973; van Hateren et al. 1999). During a yaw body saccade the head turns at a higher angular speed than

the body, thus further minimizing the time over which prominent rotational optic flow is generated (Schilstra and van Hateren 1998). The saccadic viewing strategy largely segregates image flow resulting from rotational movements from image flow resulting from translational movements of the animal helping to detect disturbances to its intended flight path (Collett 1980), and the relative distance of objects, which create discontinuities in the translational optic flow field (Blaj and van Hateren 2004; Eckert and Zeil 2001; Land and Collett 1997; Schilstra et al. 1998; Srinivasan 1993; van Hateren et al. 1999). During translation a nearby object appears to move faster than its background thereby generating visual motion parallax cues that can provide the perceived world with a third dimension (blowflies: Kimmerle et al. 1996; bees: Lehrer et al. 1988; Srinivasan et al. 1989).

Recent electrophysiological experiments have lent support to the hypothesis that the specific organization of flight behaviour of blowflies may serve to extract depth information from optic flow. Optic flow processing in the fly is carried out by about 40–60 so-called tangential cells (TCs) in the third visual neuropil, the lobula plate, which all have relatively large receptive fields and are assumed to be tuned to different types of optic flow (reviews by: Borst and Haag 2002; Egelhaaf et al. 2002; Hausen and Egelhaaf 1989; Krapp 2000; Laughlin 1994). Three identified TCs of the horizontal system (HS) in each hemisphere of the blowfly brain respond in a directionally selective manner to horizontal visual motion, as it occurs for instance during rotations about the vertical (yaw) axis (Hausen 1982a, b). When optic flow as experienced in free flight is replayed to HS-cells the neuronal signals provide information on translational self-motion between saccades and thus, implicitly, on the spatial relation of the animal to its environment (Kern et al. 2005b; Lindemann et al. 2005; van Hateren et al. 2005). This evidence indicates that, in contrast to previous conclusions (e.g. Haag and Borst 2001; Hausen 1982a, b; Horstmann et al. 2000; Kern et al. 2001b; Krapp et al. 2001), the responses of HS-cells to translational optic flow may play an important role in orientation behaviour.

These response properties were only discovered, after it became possible to replay optic flow to neurons that was generated by the flies themselves in free flight. However, the reconstruction of natural optic flow has so far been restricted to space-confined indoor flight cages (Kern et al. 2001b, 2005b; Lindemann et al. 2003b; van Hateren et al. 2005) which, on the one hand, make it possible to reconstruct flight paths and head orientation with high precision, but on the other hand lack a number of properties of outdoors scenes: (1) natural scenes can contain objects at all distances, from close-by to infinity, which results in a patchy and sparse distribution of translational optic flow (Zanker and Zeil 2005); (2) objects, textures and contrast can be distributed very unequally in different viewing directions; (3) natural scenes can contain significant environmental background motion, generated for instance by wind-driven vegetation.

To understand the design principles of visual motion sensitive interneurons it is thus important to check whether conclusions drawn from experiments in space-confined flight arenas are also valid under outdoor conditions. In this study we therefore reconstructed natural optic flow outdoors by recording the 3-D flight paths of flies together with their longitudinal body axis orientation, and by subsequently moving a panoramic imaging device along the same, and along systematically displaced, paths. We later replayed these image sequences to motion-sensitive neurons in the fly visual system and to a computational model of the fly motion pathway, to determine the influence of rotational and translational optic flow components on the neuronal responses.

Methods

Our analysis is based on the sequential steps of reconstructing flight paths, reconstructing and replaying optic flow and of modelling (sketched in Fig. 1a).

Recording flight paths

Blowflies of the genus *Calliphora* were attracted to a location at the edge of open bushland on the campus of the Australian National University (Fig. 1b, c) by olfactory bait (rotten bovine liver). Blowflies landing on nearby leaves and branches were filmed with a pair of Redlake MotionPro 500 high-speed digital video cameras at 500 frames/s with a spatial resolution of 1,024×1,024 pixels. The space we monitored had a size of approximately 70 cm × 70 cm × 70 cm. To reconstruct the views seen by the flies (see below) we used a 3-D positioning platform mounted on a trolley (robotic gantry, for details see Zeil et al. 2003). One camera viewed the area from above and was fixed to the robotic gantry. The other camera was mounted on a tripod and viewed the scene from the side. The optical axes of the cameras were carefully aligned orthogonally to each other with the aid of a set of markers on a levelled Perspex cube. The reference cube was positioned above one of two nails (separated by 20 cm) that were driven into the soil as a geocentric reference for both camera system and robotic gantry allowing us to accurately align the camera and the gantry coordinate systems (see below). Video sequences were stored as uncompressed 8-Bit AVI-files on computer hard disk for off-line processing. The 2-D position and longitudinal body axis orientation of flies were determined frame by frame with the aid of custom-built software, using standard image-processing algorithms (Lindemann et al. 2003a). Knowing the relative position of the two cameras, it was then possible to transform 2-D image coordinates into an orthographic 3-D coordinate system (e.g. Boeddeker et al. 2003; Zeil 1983). Extracting 3-D flight paths in this way takes time and switching from recording flight paths

Fig. 1 **a** Outline of methods. Flight paths of blowflies were recorded outdoors with two orthogonally oriented digital high-speed cameras at 500 frames/s. We used custom-made software (FlyTrace) to reconstruct the 3-D flight paths and the horizontal body axis orientation of flies. To reconstruct what the animals had seen during their flight manoeuvres, we used a robotic gantry to move a panoramic imaging device exactly along previously recorded flight paths. The panoramic image sequences were transformed to Cartesian coordinates and further processed by 3-D rendering software to generate the data format required by a flight simulator, used for electrophysiological experiments, and by a computational model of the fly's visual system. The natural image sequences were then replayed in a panoramic flight simulator to major output neurons (HS-cells) of the blowfly's visual motion pathway and to model HS-cells. **b** Panoramic view of the experimental set-up as seen by a blowfly. The semi-natural open bushland on the Australian National University campus is a natural habitat of blowflies. The *numbers* correspond to numbers on the site plan in **c**. The symbols mark the start (*) and the end (+) of the blowfly's flight path that is shown in Fig. 3. **c** Site plan of the location. The contour interval is 2 m. *Grey areas* indicate vegetation. The recording site is indicated by an *arrow*

to recording optic flow required rearrangement of the camera-gantry system. To have similar light conditions we therefore reconstructed the visual input experienced by the recorded flies at exactly the same location 1 day later around the same time of day.

Reconstructing natural optic flow

We moved a panoramic imaging device (Chahl and Srinivasan 1997) along the previously recorded flight paths with the aid of the robotic gantry (Zeil et al. 2003). The robotic gantry was levelled and positioned at the same place on different days by using the embedded nails as fixed external markers. The repositioning accuracy was better than 0.5 cm and approximately 1° in orientation. The gantry can service an area of 1 m^3 with a positioning accuracy of 1 μm. Panoramic images were recorded with a CCD camera (JVC TK860E), the gain control of which was switched off. The camera viewed a reflective cone with a 140° vertical and 360° horizontal field of view. For technical reasons it was not possible to move the imaging device at the speed of flies. Instead we moved the camera to successive positions along the flight path to record images, which resulted in a sampling rate of 1 frame/s. Note that we therefore cannot reconstruct the effects of environmental motion. Images were digitized to 768×576 pixels at 8-bit resolution by a frame

grabber and stored directly on the hard disk of a computer. These sequences were transformed (''unwarped'') offline from polar to Cartesian coordinates (Chahl et al. 1997) and processed by 3-D rendering software (Open Inventor, Silicon Graphics) to interface with the data format required by the replay screen (see below). Since the panoramic imaging device cannot be rotated, the resulting image sequences contained only the translational optic flow component. The rotational optic flow component resulting from yaw rotations of the fly was simulated by rotating the panoramic images appropriately. We did not simulate other rotational degrees of freedom, because rotations of the head about the pitch and roll axes are generally small during flight (Schilstra and Van Hateren 1998).

To determine the influence of rotational and translational optic flow components on neuronal responses we used three modifications of the original optic flow in our electrophysiological experiments:

- *No Translation A*: We removed the translational components by taking the panoramic image at an arbitrary position along the flight paths (we selected 80 ms after takeoff, see Fig. 3a) and by rotating it with the angular velocity profile of the original body yaw rotations throughout the flight sequence.
- *No Translation B*: To test for potential effects of textural differences of the environment on the neuronal responses, we repeated this procedure with a different image and rotated the panoramic image the fly had seen 80 ms before landing (see Fig. 3a, 640 ms), through the same rotational sequence as in *No Translation A*.
- *Displacement*: To investigate whether the response properties of HS-cells depend on the spatial layout of the environment, we displaced the imaging device 40 cm laterally relative to the original flight path, away from close vegetation, and reconstructed the optic flow as if the fly had flown along its path at that location.

To assess the density and spatial distribution of motion signals available to the visual system during these outdoor manoeuvres, we used the recorded image sequences as input to a 2-D motion detector model (2DMD, Zeil and Zanker 1997). The 2DMD is formed by 460×170 equally spaced pairs of elementary motion detectors (EMDs), oriented orthogonally with horizontal or vertical preferred directions, respectively; one pair centred on each image pixel location. The EMDs are simple correlation-type motion detectors (reviews: Borst and Egelhaaf 1989; Reichardt 1987) composed of a first-order linear low-pass filter and an arithmetic multiplication of the low-pass filtered signal originating from one photoreceptor and the unfiltered signal originating from a neighbouring photoreceptor. The spatial sampling distance was set to 4° and the time constant of the temporal low-pass filter was 4 ms. The output of 2DMD shows the 2-D distribution of the local motion directions and the local image motion amplitudes as signalled by individual elementary correlation-type detectors (for details see Zanker and Zeil 2005; Zeil and Zanker 1997). We do not use the 2DMD to simulate HS responses, but to visualize the distribution and properties of motion signals as the fly in natural environments encounters them.

Replay electrophysiology

The image sequences we recorded outdoors were played back to visual interneurons on a panoramic screen (FliMax). FliMax approximates a sphere with an inradius of 0.224 m by 14 of the 20 triangles of an icosahedron and holds 7,168 light-emitting diodes (LEDs), the intensity of which can be varied individually in 8 intensity steps (3 bits) at a refresh rate of 370 Hz (for details see Lindemann et al. 2003b). The 500 Hz movies were sub-sampled by linear interpolation of the luminance values on a pixel-by-pixel basis between successive frames, in order to replay them at 370 Hz. We prevented spatiotemporal aliasing during fast saccadic turns by appropriate spatial pre-filtering (Lindemann et al. 2003b).

We used the symmetry of the frontal deep pseudopupils to align the flies' visual field with the stimulus device (see Franceschini 1975). Intracellular recordings were made with standard electrophysiological equipment using electrodes pulled on a Brown-Flaming Puller (P-97, Sutter Instruments) from borosilicate glass (GC100TF10, Clark Electromedical). Filled with 1M KCl they had resistances between 20 and 38 MOhm. Voltage signals were low-pass filtered (corner frequency 2.4 kHz) and sampled at a rate of 4 kHz (I/O-card DT3001, Data Translation) using the VEE Pro 5.0 (Agilent Technologies) in conjunction with DT VPI (Data Translation) software. We recorded responses from three major output neurons of the motion vision system, the so-called HS-cells, in the right optic lobe of 1- to 2-day-old female blowflies (*Calliphora vicina*) from laboratory stocks, following standard procedures (see Warzecha et al. 1993). HS-cells respond best to visual stimuli containing mainly horizontal motion components. There are three HS-cells in the left and three HS-cells in the right lobula plate of the blowfly brain. The receptive fields of the HSN-, HSE-, and HSS-cell cover the dorsal, equatorial, and ventral part of the ipsilateral visual field, respectively (Hausen 1982a, b). HS-cells were identified by their characteristic response mode, their preferred direction of motion and the location of their receptive fields (Hausen 1982a, b). During the experiments temperatures ranged between 28 and 36°C as measured close to the position of the fly in the centre of FliMax. Instead of rearranging the recording electrodes to measure the response properties of the three contralateral HS-cells we assessed their responses by presenting a mirror-version of the panoramic image series and continued measuring the cells in the right

optic lobe of the fly brain. The stimulation protocol, repeated as often as possible, was as follows: 1 s with all LEDs lit at half the maximum brightness, 0.5 s fading of LEDs brightness to the values corresponding to the first frame of the subsequently replayed image sequence, replay of a pseudo randomly chosen image sequence (original optic flow, three targeted modifications and mirror-versions), 7 s inter-stimulus interval with all LEDs lit at the mean brightness calculated from the image sequence. The inter-stimulus interval ensured that subsequent stimulus presentations did not influence each other. Results are based on recordings from the three HS-cells in one fly and two HSN-cells from two further flies. For each stimulus condition 14–145 responses to the complete protocol were recorded per cell. Data are presented as mean responses unless stated otherwise.

Modelling motion sensitive neurons

We simulated HS-cell responses with a computational model of the fly's visual motion pathway, that was originally developed to explain the responses to simple experimenter-designed stimuli (Borst et al. 1995, 2003; Egelhaaf and Borst 1989; Egelhaaf et al. 1989; Kern et al. 2001a) and that was recently also shown to explain responses to optic flow generated under free-flight conditions in the laboratory (Lindemann et al. 2005). The model is organized as follows (Fig. 2, adapted from Lindemann et al. (2005)):

Input images are sampled by Gaussian low-pass filters ($\sigma = 2°$) and fed into the model's photoreceptors, spaced equally at 2° along elevation and azimuth. The array of photoreceptors forms a rectangular grid with 51 rows and 86 columns. The temporal response properties of the photoreceptors and the second-order neurons, the so-called Large Monopolar Cells (LMCs), are jointly modelled by a linear filter kernel derived from a white-noise analysis of the LMCs in the fly (James 1992). The next processing layer is composed of retinotopically arranged correlation-type motion detectors (EMDs), that incorporate a first-order low-pass filter (time constant: 10 ms) and a first-order high-pass filter (time constant 60 ms). A simple equivalent circuit of a one-compartment passive membrane patch spatially pools the outputs of EMDs, where the positive and negative outputs of the EMDs control excitatory and inhibitory conductances, respectively. This processing layer is thought to correspond to the dendritic tree of the HSE-Cell (for details and parameters see Lindemann et al. 2005). The model visual field covers $-50° \le \phi \le 120°$ in azimuth and $-50° \le \theta \le 50°$ in elevation for the right HSE. For the left HSE the mirrored input field covers $-120° \le \phi \le 50°$ in azimuth 0° corresponds to the frontal equatorial direction. The weights of the different movement detectors throughout the visual field are tuned according to the known spatial sensitivity distribution of the HSE-Cell (after Hausen 1982a, b; Krapp et al. 2001). A first-order low-pass filter (time constant 8 ms) applied to the integrated signal approximates the temporal filtering properties of the neuron.

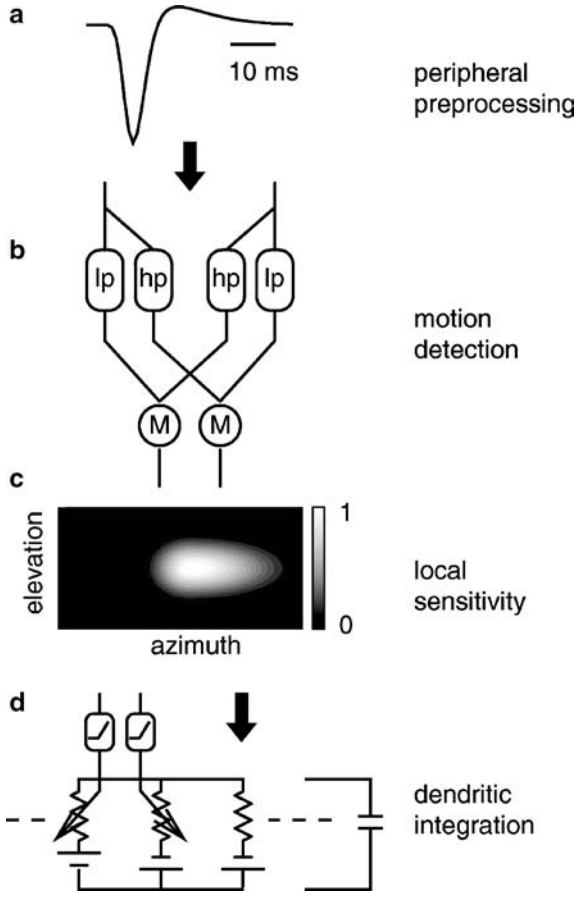

Fig. 2 Schematic diagram of the model of the blowfly visual motion pathway. **a** Impulse response of linear filter representing the photoreceptor/lamina monopolar cell response. **b** Elaborated correlation type motion detector (*hp* first-order high-pass filter, *lp* first-order linear low-pass filter, *M* algebraic multiplication. **c** The weighted local sensitivity distribution for the model of the right HSE-Cell (contour plot in Mercator projection; *brighter areas* indicate greater sensitivities); the left HSE-Cell is modelled in a mirror-symmetric manner. **d** Circuit representation of the passive membrane model

Results

We recorded 11 outdoor flight paths of blowflies, including the orientation of their longitudinal body axis. Five of these sequences include departures from resting sites and landings on nearby leaves (Fig. 3). In other sequences flies are simply passing through the recording area (Fig. 4). One aspect is particularly noteworthy in these flight paths: all flights show the same organization with straight sections of flight being connected by saccadic changes in body orientation. Blowflies thus employ this flight strategy, independent of the space available to them, whether it is confined (Schilstra et al. 1999; Wagner 1986) or unconfined, as in our case.

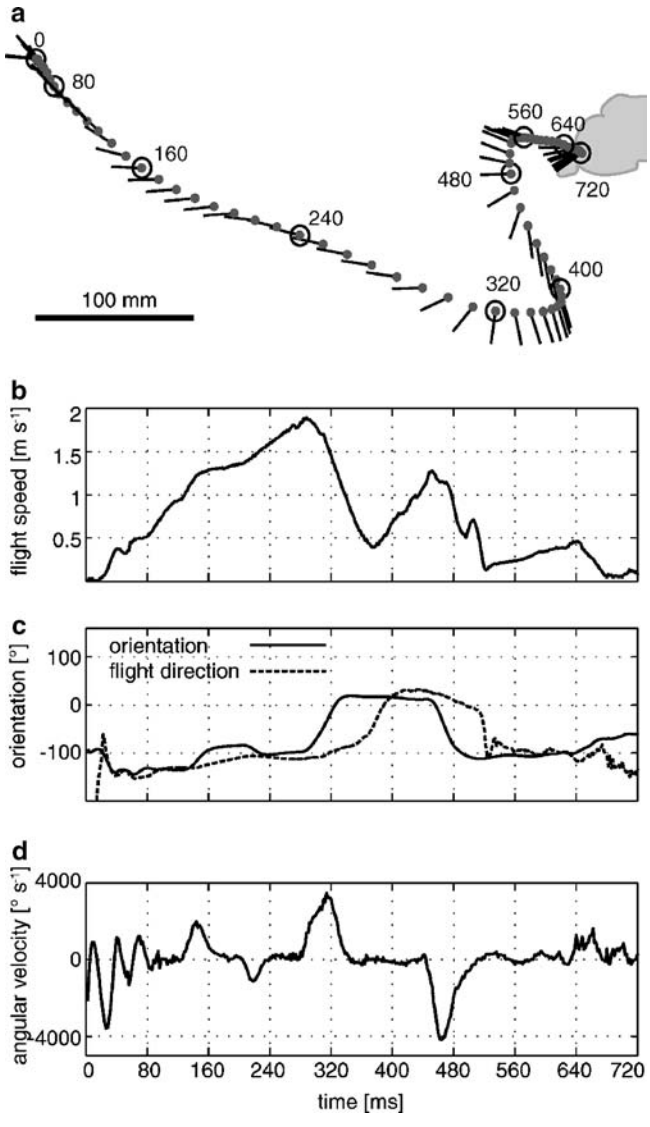

Fig. 3 Flight behaviour I. **a** Flight path of a female blowfly as seen from above. The position of the fly and the orientation of her longitudinal body axis were recorded at 500 frames/s but are shown every 10 ms. The fly took off from a vertical stick that provided a perch (indicated by an asterisk in Fig. 1b and landed on a leaf of a nearby shrub (indicated by plus sign in Fig. 1b. **b** Translational flight speed. **c** Orientation of the fly's longitudinal body axis (*solid line*) and flight direction (*dashed line*) in the external coordinate system. During this flight, the fly changed its gaze and heading direction through a series of short and fast body turns. Within less than 40 ms body orientation direction might change by 90°, corresponding to angular velocities of up to 4,000°/s (shown in **d**). As a consequence of her saccadic flight style flight direction and body axis orientation frequently deviate; the body axis already points in the new flight direction, while the fly is continuing to move on its previous course

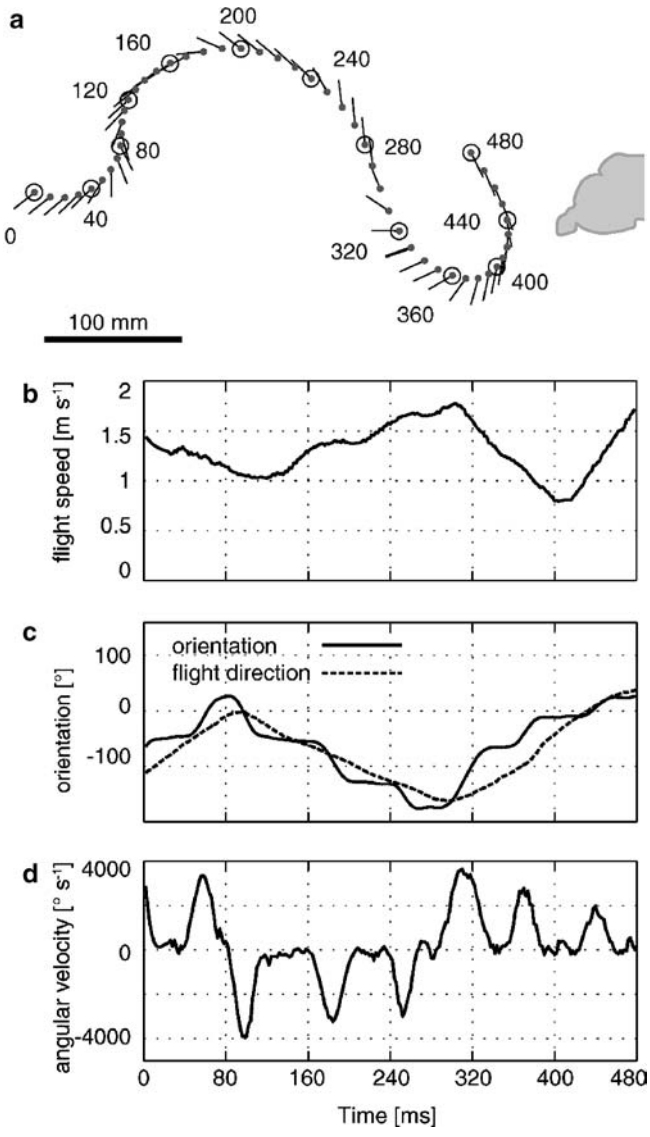

Fig. 4 Flight behaviour II. Flight path of another female blowfly as seen from above. The fly is cruising through the field of view of the cameras without landing. In less than 500 ms the fly changes body orientation by a series of 7 saccadic body turns. Conventions as in Fig. 3

For our replay experiments we selected the flight path of a female fly, which flew in such a way that artificial structures, like the holding bracket of the panoramic mirror were mapped during reconstruction to her lateral and posterior visual field. In this sequence, the fly took off from a vertical stick that we had put into the ground to provide a perch for the flies (indicated by a star in Fig. 1b). The fly then accelerated to almost 2 m/s within the first 300 ms (Fig. 3a, b) and after 720 ms of flight landed on a leaf of a nearby shrub (indicated by a plus sign in Fig. 1b). During this flight sequence, the fly changed its gaze and heading direction through a series of saccadic body turns that coincide with peaks in the yaw rotational velocity (Fig. 3d) in a similar way as has been previously described for blowflies flying in an indoor arena (Schilstra and van Hateren 1999). Between saccades the fly kept its body axis orientation more or less constant (Fig. 3c), so that as a consequence rotational optic flow was kept to a minimum. After a saccade the fly tends to drift sidewards for some ten milliseconds (Fig. 3a) with the longitudinal body axis orientation deviating considerably from the flight

direction (compare solid and dashed line in Fig. 3c). The second example shows a similar organization of flight behaviour, with the difference that it does not include takeoff and landing (Fig. 4). The fly also generates twice as many saccades during the same period of time as the one shown in Fig. 3, indicating some variability in the timing of these manoeuvres.

We recorded responses of HS-cells to the optic flow generated during the flight sequence shown in Fig. 3 and to modified versions of this sequence (see Methods). The neuronal responses are characterized by an irregular sequence of pronounced depolarizations that evoke bursts of action potentials of variable amplitude (Fig. 5b). There is no obvious relationship between body saccades and membrane potential changes in HS-cells, neither in original response traces (example in Fig. 5b) nor in the corresponding average over several stimulus presentations (Figs. 5c, d). De- and hyperpolarzsations in the right and the left HS-cells alternate for most of the flight, indicating that the cells respond in a directionally selective manner to image motion (compare Figs. 5c, d). When the responses to the original image sequence are compared to those from which translational components had been removed (''no translation'', see Methods), it becomes clear that the responses are similar throughout the sequence (compare grey and dashed lines in Fig. 5c, d). The rotational velocity thus dominates the HS-cell responses for large segments of the flight, regardless of whether or not rotational and translational components are mixed. In both conditions, the response amplitude is a monotonic function of angular velocity only for a narrow range of velocities. It rises for velocities up to about 500°/s, stays on a plateau until around 2,000°/s and decreases again at velocities higher than 2,000°/s (Fig. 5e, f). The response of the neuron thus reflects the animal's rotational velocity in a highly non-linear fashion (Egelhaaf and Reichardt 1987; Haag and Borst 1997; Kern et al. 2001b; van Hateren et al. 2005).

In some instances, however, HS responses to the original optic flow and to its pure rotational components (*No Translation A*) differ. These instances (grey area in Fig. 5c, d) are magnified in Fig. 6 for the three types of HS-cells. The response differences indicate that certain aspects that have a strong effect on the response of all three types of HS-cells are present in the original stimuli and are missing in the modified versions. Is it a difference in the ''texture'' of the scene at the particular location in space chosen for the *No Translation* condition as compared to the texture of the original scene? To check whether the specific appearance of the scene at this

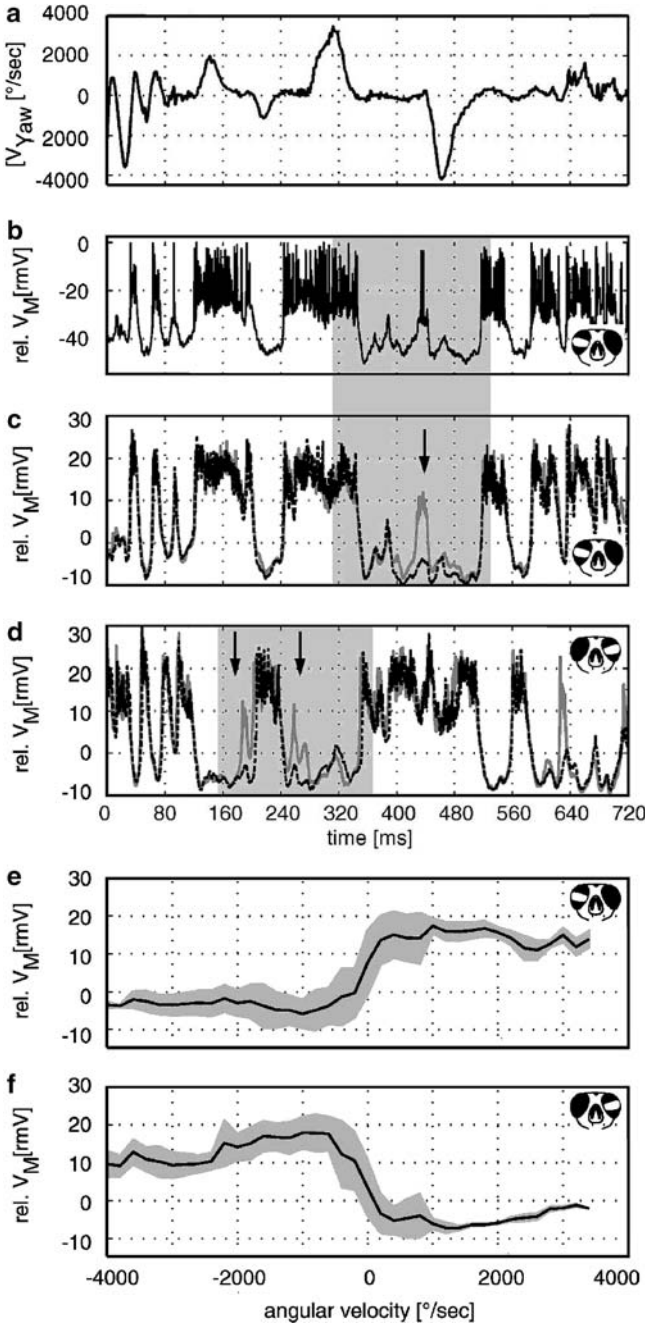

Fig. 5 Responses of motion sensitive neurons to natural optic flow. **a** Yaw rotational velocity during the sequence shown in Fig. 3. Yaw velocity peaks correspond to saccade-like turns of the fly. **b** Response of the right HSE-cell to the reconstructed image sequence for the flight shown in Fig. 3. The cell responds to motion with graded depolarizations and hyperpolarisations, with superposed action potentials. **c** Average HSE response in the right lobula plate. **d** Average HSE response in the left lobula plate. *Grey lines* in **c** and **d** indicate the response of HS-cells to the optic flow generated during the original flight sequence, *dashed lines* the response to optic flow from which the translational components had been removed (*No Translation*). The resting potential was obtained during a 250-ms period prior to motion onset and has been subtracted. *Arrows* indicate the instances when the responses to the original and to the modified version of optic flow differ. The *grey areas* in **c** and **d** indicate the parts of the responses that are shown in a greater magnification in Fig. 6. **e** The response of the right HSE-cell to the original optic flow (*grey line* in **c**) as a function of turning velocity (taken from **a**). Angular velocity has been binned at 200°/s intervals. The *grey area* indicates the standard deviation of the membrane potential in each bin. **f** Conventions as in **e** but for the left HSE-cell. The time course of angular velocity and the average response trace were shifted relative to each other by 23 ms before plotting in **b**–**f**, the time shift at which the cross-correlation function has its maximum

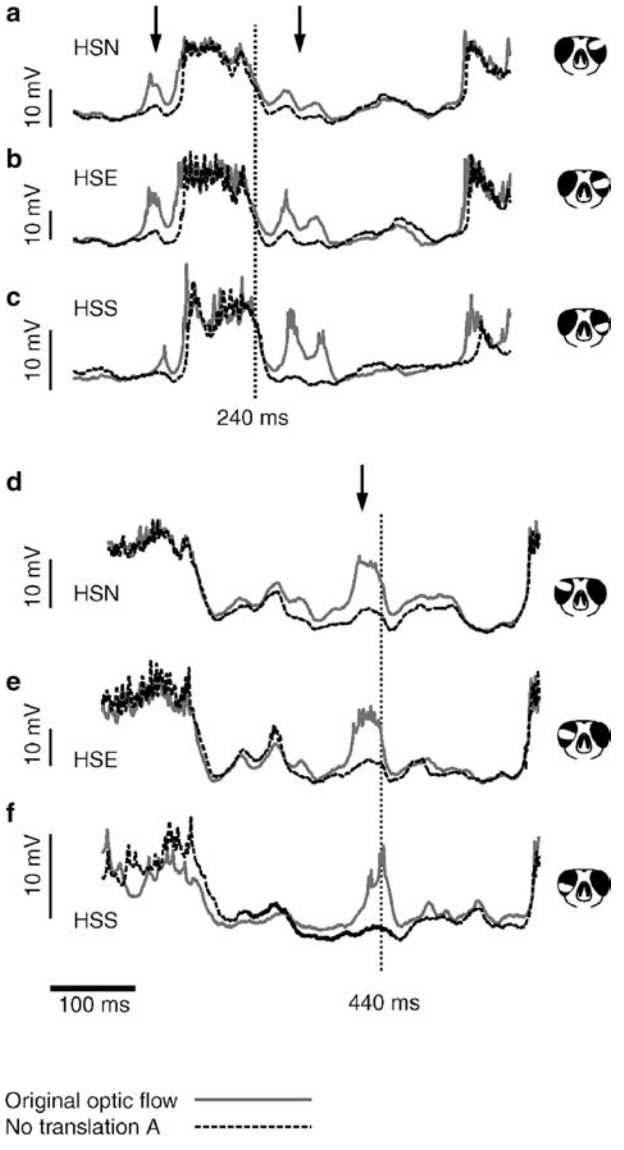

Fig. 6 Instances when HS responses to original optic flow differ from those to rotational optic flow. The *vertical lines* indicate the time after take-off and allow a comparison of the neuronal responses with the flight behaviour (Fig. 3). Average responses of **a** left HSN-cell, **b** left HSE-cell, **c** left HSS-cell; **d** right HSN-cell, **e** right HSE-cell, **f** right HSS-cell. *Grey lines* indicate the response of HS-cells to the optic flow generated during the original flight sequence. *Dashed black lines* modified optic flow without translational components (*No translation A*)

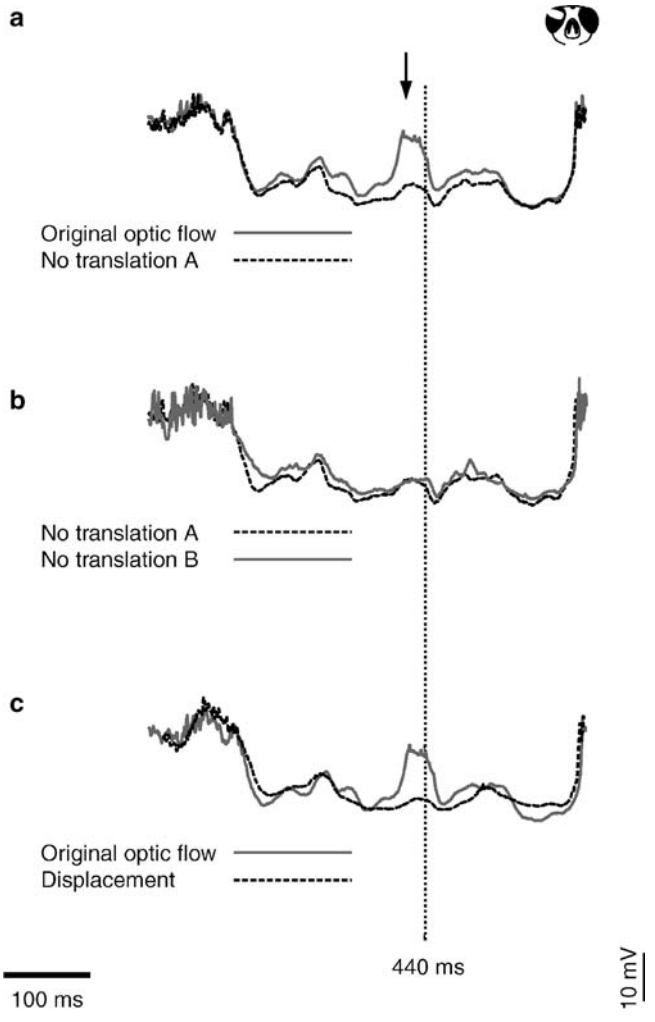

Fig. 7 Comparison of HS responses to original optic flow with responses to optic flow generated on modified trajectories. Conventions as in Fig. 6. **a** Average response of the right HSN-cell (taken from Fig. 6d for comparison). **b** HSN-responses to rotations at two different locations. **c** Comparison of HSN-responses to original optic flow and to the optic flow generated on a trajectory displaced by 40 cm away from the shrub

location has an impact on the neuronal responses, we determined responses to rotations at another location (*No translation B*, for location see Fig. 3a, 640 ms) with exactly the same angular velocity profile and compared the resulting neuronal responses. The neuronal responses to both conditions are very similar (Fig. 7b) and show similar deviations from responses to the original optic flow stimulus. These response differences can thus not primarily be attributed to differences in the "texture" of the scene at these two locations, but rather to translational optic flow components related to the depth structure of the environment. A closer look at instances where deviations occur between the neuronal responses to the original and the *No Translation* conditions reveals that they coincide with instances at which leaves and branches of a nearby shrub move in the receptive field of the HS-cells as a result of the fly's movement (see Fig. 8a). HS responses thus seem to be strongly influenced by the relative motion of nearby objects through the cell's receptive field during translational movements which are only present in the original stimulus, but not in the *No Translation* modifications.

To determine the impact of particular spatial features of the environment, i.e. its depth structure, on HS-cell responses we compare their responses to optic flow reconstructed on the original and on displaced paths. The optic flow generated by the original trajectory being displaced 40 cm away from the shrub leads to an HSN-response, which is very similar to the response under the *No Translation* condition (Fig. 7c). The leaves and

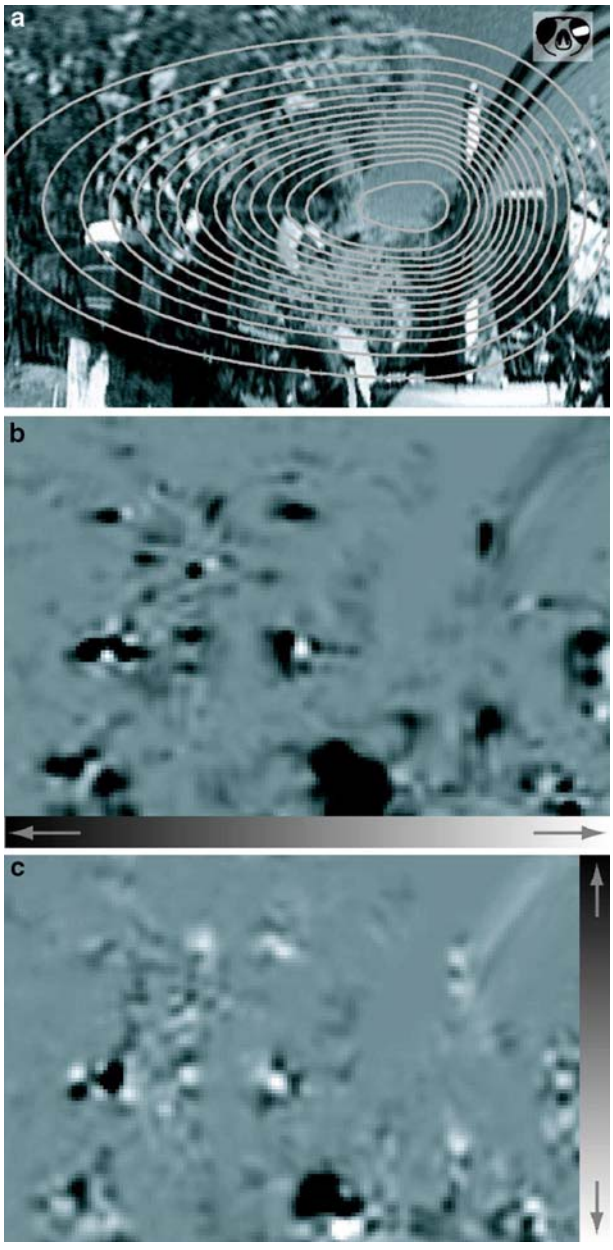

Fig. 8 **a** View of the environment as seen by the blowfly. A contour plot of the spatial sensitivity distribution of the left HSE-Cell is superimposed on the view 240 ms into the flight shown in Fig. 3. The sensitivity distribution is adapted from Krapp et al. (2001) and used in the HSE-cell model. The receptive field centre lies at the eye's equator at elevation 0° and azimuth −15°. The field of view is 170° wide in the horizontal and 115° high in the vertical dimension. **b** Horizontal response component of the 2-D motion detector model at time 240 ms. *Medium grey level* indicates weak motion signals, *dark grey levels* indicate strong right-to-left motion, and *light grey* indicates left-to-right motion (see *horizontal grey scale*). At this point in time the translational movement of the fly leads to right-to-left motion of branches and leaves in the visual field, which is also the preferred motion direction of the left HS-cells. **c**Vertical response component of the 2-D motion detector model at flight time 240 ms. *Medium grey level* indicates weak motion signals, *dark grey levels* indicate strong bottom-up motion, and *light grey* indicates top–down motion (see *vertical grey scale*)

branches of the shrub after the displacement are projected to parts of the visual field, where the sensitivity of HS-cells is lower and the translational optic flow components are weaker as compared to the original situation, because the shrub is now further away. The resulting optical flow is thus similar to the *No translation* condition. This finding corroborates our conclusion based on the *No translation* conditions that HS-responses are only weakly influenced by the specific texture of the environment, but strongly so by the spatial layout of objects therein.

We assessed the spatial distribution of motion signals available to the visual system during outdoor flight manoeuvres, by using the recorded image sequences as input to a 2-D motion detector model ("2DMD"). The local motion analysis confirms that strong local signals are generated in those instances of flight, when deviations in the neuronal responses to the original optic flow stimuli and the modified versions are most prominent. The translational movement of the fly leads to horizontal right-to-left motion of the leaves at time 240 ms (Fig. 8b), which is the preferred motion direction of HS-cells (compare to the response of the HS-cells shown in Fig. 6a, b). The depolarizations in the HS-cell membrane potential that are absent when the cell is confronted with pure rotational stimuli are thus likely to be caused by the relative movement of nearby objects.

We went on to check whether these complex responses of HS-cells to natural optic flow can be explained by what we know about information processing in the fly visual motion pathway. We find that the HSE model responds to our natural image sequences in qualitatively the same way as the real neurons we recorded from (Fig. 9). Both the HSE-cell (Fig. 9b, d) and the model responses (Fig. 9a, c) are dominated for most of the time by rotational velocity and they de- and hyperpolarize during basically the same sections of the flight. Although the time courses of neuron and model responses differ in details, they clearly respond to optic flow from which we had removed the translational components, in much the same way (arrows). Real HS-cells and their model also respond to the passage of nearby objects, for instance, when—in our reconstructed optic flow sequence—leaves of a nearby shrub appear in the receptive field.

Discussion

We recorded flight paths of blowflies under natural outdoor conditions and replayed the optic flow they had experienced to motion sensitive neurons in their motion processing pathway. We confirm that blowflies employ a saccadic flight strategy not only when flying in space-confined flight arenas (Kern et al. 2005a; Schilstra et al. 1999), but also under outdoor conditions. Although the membrane potential changes of HS-cells are dominated

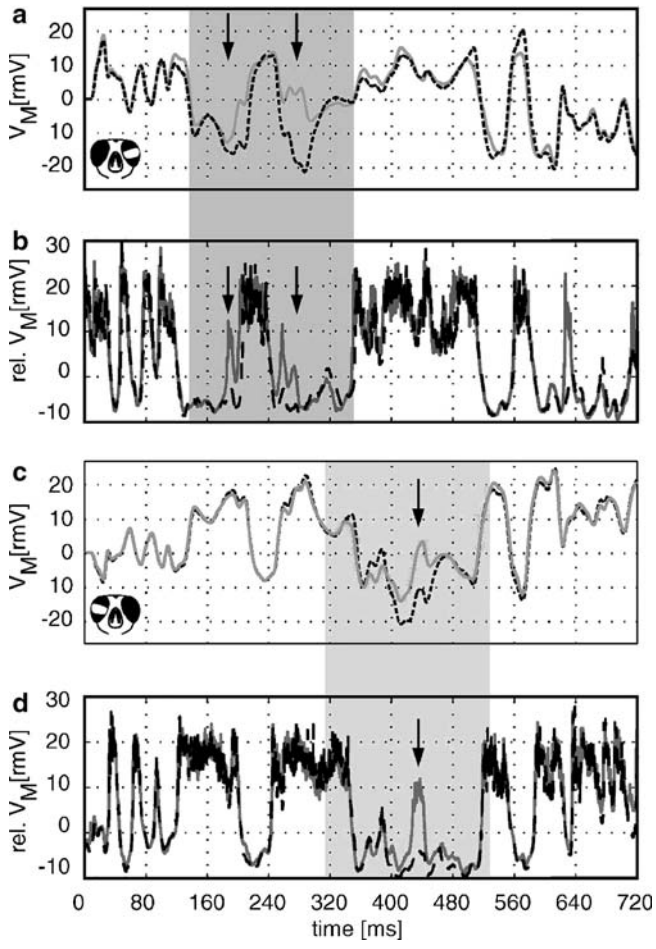

Fig. 9 Comparison of HS-cell responses and model responses. **a** Response of the left HSE-model to the original optic flow (*grey lines*) and to the *No translation* flow (*black lines*). **b** Average HSE response in the left lobula plate for comparison (taken from Fig. 5d). **c** Response of the right HSE-model to the original optic flow (*grey lines*) in comparison to the responses to the *No translation* flow (*black lines*). **d)** Average HSE response in the right lobula plate for comparison taken from (Fig. 5c)

by the responses to the rotational components of optic flow and represent them in a highly non-linear way, HS-cells are also sensitive to translational flow components. This was especially obvious when close objects appeared in the receptive field of neurons. HS-cell responses thus contain information on the spatial layout of the environment and might play a role in object detection and obstacle avoidance. We show that these response properties do not require a revision of the known mechanisms underlying HS-cell responses because the same image sequences generate qualitatively similar responses in a computational HS-cell model.

Neuronal coding of natural optic flow: a critical assessment

The ideal way to obtain a complete description of the natural operating conditions for motion vision and to analyse the corresponding neural response would be to record the visual input of a freely behaving animal and to simultaneously monitor the neural activity, as Passaglia et al. (1997) have done in horseshoe crabs. However, it is currently not possible to do this in freely moving flies, so that we have to use an indirect approach to characterize the responses of their motion sensitive TCs to natural optic flow. One advantage of this way of reconstructing motion signals is that it allows us to modify them in systematic ways, which helped us, in the present study, to identify the features in the natural environment that determine neuronal activity. However, a number of limitations remain as we will discuss in the following.

One problem with current replay approaches is that the brightness range of a sunny day cannot be reproduced in electrophysiological experiments. To date, there have been only two electrophysiological studies on blowfly motion sensitive neurons that were conducted outdoors. The conclusions these studies reached are contradictory. Lewen et al. (2001) concluded that the coding properties of a visual motion-sensitive neuron in the blowfly (the so-called H1-neuron) are highly dependent on the brightness of a scene. In contrast, Egelhaaf et al. (2001) concluded that H1-responses at constant temperature are largely independent of brightness changes over several orders of magnitude as they occur during the day, but are affected by temperature changes (Egelhaaf et al. 2001; see also Warzecha et al. 1999). The controversy can be resolved in future, when high-luminance displays become available.

A number of further technical improvements are needed. For instance, without obstruction-free panoramic mirrors, we inadvertently introduce new visual features into the scene, such as the mirror holding brackets, as we ''replace'' the fly by our panoramic imaging device. In addition, because of the low sampling rate needed for reconstruction, we were unable to investigate the extent to which motion generated by wind-driven vegetation degrades optic flow (see Zanker and Zeil 2005). We presumably overestimate the impact of environmental noise, because the low sampling rate and the low speed of the gantry artificially increases the amplitude of vegetational movements between successive frames. Hence, the coding performance as we measure it in neurons may improve, when it will be possible to reconstruct the environmental motion noise actually experienced by the fly during rapid flight manoeuvres.

Most importantly, we were unable to measure the head movements of flies and we thus had to neglect their consequences for the optic flow actually experienced by the flies. The optic flow we reconstructed, therefore, does not accurately represent what the flies had seen. During a body saccade, the head initially rotates against the direction of body rotation to keep gaze direction constant. The head then executes a fast saccadic gaze shift into the direction of body rotation and subsequently stabilizes gaze again for the remainder of the body sac-

cade. Gaze is thus stabilized for approximately 60% of the time it takes to execute a body saccade (Schilstra et al. 1998; van Hateren et al. 1999). As a consequence, the separation of translational and rotational optic flow is expected to be much better, when head orientation is taken into account, so that our conclusions are likely to remain valid, once head movements can be measured in insects flying outdoors.

Natural optic flow and our understanding of visual information processing

Simple, artificial stimuli have been crucial tools for identifying the neural computations in the visual motion pathway in insects, but for a number of reasons, they do not easily allow us to predict the performance of motion processing modules in a natural context. Natural environments are characterized by large variation in contrast, a patchy distribution of objects and a pronounced depth structure. Nervous systems have evolved to compute behaviourally relevant information under such complex natural conditions in an efficient and robust way and their design is likely to reflect the statistical and dynamical properties of these conditions (Betsch et al. 2004; Burton and Laughlin 2003; Eckert and Zeil 2001; Kayser et al. 2004; Olshausen and Field 1996; Reinagel 2001; Simoncelli 2003; Simoncelli and Olshausen 2001; van Hateren 1997). Since the structure of the environment and the animal's own movements both determine the image motion pattern animals experience, the processing of natural optic flow can only be investigated from the viewpoint of the behaving animal (e.g. Eckert and Zeil 2001; Kayser et al. 2004).

Several attempts have been made recently to tackle these issues in flies. Dror et al. (2001) for instance have analysed the responses of a computational model of fly motion sensitive neurons to natural scenes moving at a constant rotational velocity. The main result was that the model is a good steady-state image velocity estimator relatively independent of the textural details of natural scenes, in contrast to stimuli consisting of sinusoidal grating patterns. This conclusion has now been confirmed in electrophysiological experiments in which natural scenes were moved at a constant velocity across the receptive field of HS-cells (A. Straw et al., submitted). Our results corroborate the point that differences in the appearance of natural scenes have little effect on the responses of fly motion sensitive neurons, but they also show that the dynamical properties of the behaviourally generated optic flow strongly influence the neuronal responses. This aspect has been stressed by several recent studies, which analysed the performance of identified neurons in the visual system of the fly by confronting them with image sequences as they are experienced during walking and flight in indoor environments with a 3-D structure (Egelhaaf et al. 2001; Kern et al. 2000, 2001b, 2005b; Kimmerle and Egelhaaf 2000a, b; Lindemann et al. 2003b, 2005; van Hateren et al. 2005; Warzecha and Egelhaaf 1996, 1997). During walking, the response of the HSE-Cell does reflect the animal's turning direction nearly independently of the texture and spatial layout of the environment, but is also affected by translational flow when the animal walks close to objects (Kern et al. 2001a, b). In the present study these responses to translational optic flow are more pronounced, presumably because the speed of flying flies is much higher than that of walking flies. When HSE-Cells are confronted with the optic flow reconstructed from free flight manoeuvres the time course of the response is not proportional to the time course of the fly's rotational velocity, which casts doubt on the common view that the HSE-cell acts primarily as a rotation detector (Kern et al. 2005b; Lindemann et al. 2003b, 2005; van Hateren et al. 2005). These studies also show that HSE responses can provide information about translation and thus, implicitly, about the spatial relation of the animal to its surroundings during the intervals between saccades. A coherence analysis between stimulus and response revealed that information about object distances is confined to low frequencies in the time course of the HSE responses and that the visual effects of the remaining small head rotations are encoded at higher frequencies. Recent evidence, including the one we presented here, thus suggests that the fly's saccadic vision strategy facilitates the processing of information on the spatial structure of the environment (Kern et al. 2005a, b; van Hateren et al. 2005; Lindemann et al. 2005): between saccades, HS-cells respond to image flow generated by near-by objects.

It remains to be seen whether and how down-stream neuronal circuits decode the rotational and the translational response components of HS-cells. One possibility is that the responses of the left and right HSE-cells are combined to enhance the specificity of the intersaccadic responses to the translational optic flow components. Separation of translational and residual rotational intersaccadic response components may be achieved by frequency filtering (Kern et al. 2005a, b). In addition down-stream neurones (e.g. Gronenberg and Strausfeld 1990; Strausfeld and Gronenberg 1990) could receive information from the blowfly's motor system or from the halteres about when a saccade is made and when rotational optic flow is expected to occur (Webb 2004)

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