Neural Processing of Naturalistic Optic Flow

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Stimuli traditionally used for analyzing visual information processing are much simpler than what an animal sees in normal life. When characterized with traditional stimuli, neuronal responses were found to depend on various parameters such as contrast, texture, or velocity of motion, and thus were highly ambiguous. In behavioral situations, all of these parameters change simultaneously and differently in different parts of the visual field. Thus it is hardly possible to predict from traditional analyses what information is encoded by neurons in behavioral situations. Therefore, we characterized an identified neuron in the optomotor system of the blowfly with image sequences as they were seen by animals walking in a structured environment. We conclude that during walking, the response of the neuron reflects the animal's turning direction nearly independently of the texture and spatial layout of the environment. Our findings stress the significance of analyzing the performance of neuronal circuits under their natural operating conditions.

Key words: motion vision; optic flow; fly; self-motion; naturalistic stimuli; neuronal representation

Global retinal image shifts elicited when animals and humans move through an environment ("optic flow") are exploited efficiently to guide their locomotion. Accordingly, neurons have been found in various animal groups that are sensitive to optic flow (for review, see Lappe, 2000). Optic flow is independent of the three-dimensional (3D) layout of the environment when rotating on the spot, but depends on the distance between an object and the eyes during movements with a translatory component. Theoretical solutions to disambiguate self-motion and 3D information exist (Koenderink, 1986), and animals may compute unambiguous velocity information to guide their behavior (for review, see Srinivasan et al., 1999). Nonetheless, responses of motion-sensitive neurons are ambiguous, because they depend on various stimulus parameters such as contrast, texture, or velocity of motion (Eckert, 1980; Baker, 1990; Wolf-Oberhollenzer and Kirschfeld, 1990; Cassanello et al., 2000). These findings are based on stimuli that were designed for analytical purposes and are much simpler than the optic flow an animal encounters in behavioral situations.

Therefore, we characterized a motion-sensitive neuron, the HSE-cell, in the visual system of the blowfly with optic flow experienced by freely walking animals. For technical reasons, the analysis could not be done with optic flow elicited during flight. Because flies spend much time walking around in their environment, walking may be as important for flies as flying (Dethier, 1976). The HSE-cell is a key element in optomotor course control (for review, see Hausen and Egelhaaf, 1989; Egelhaaf and Borst, 1993). The responses of the HSE-cell, recorded in an electrophysiological replay situation, can be assumed to be essentially the same as the responses in the corresponding behavioral situation (Heide, 1983) [for detailed discussion, see Kimmerle and Egelhaaf (2000)]. The HSE-cell pools the outputs of many retinotopically organized motion-sensitive elements. Their preferred directions are adapted to make the HSE-cell sensitive to rotations about the vertical body axis. The specificity of the HSE-cell for rotational optic flow is further enhanced by synaptic input from the contralateral eye (Horstmann et al., 2000; Krapp et al., 2001). Nonetheless, the specificity for the rotational flow component is low when stimulated with simple approximations to optic flow. The HSE-cell also responds strongly to translational optic flow (Hausen, 1982a,b; Horstmann et al., 2000; Kern et al., 2000), and its response amplitude depends on parameters such as velocity, contrast, and the size and spatial frequency content of the stimulus (Hausen, 1981, 1982b). Given these findings, we expected the responses of the HSE-cell to naturalistic optic flow to provide only ambiguous information about the animal's self-motion. Surprisingly, the actual responses appear to encode the turning direction of the animal largely independently of the spatial layout of the environment and, thus, of the translatory component of the optic flow.

MATERIALS AND METHODS

Flies walking in an arena (diameter 0.5 or 0.31 m, height 0.3 m) were recorded on videotape (50 Hz). The walls of the arena were covered with random textures (see Figs. 1, 2*G–M*, 3*E*), and the floor was homogeneously white. The arena was illuminated indirectly from above (lumi-

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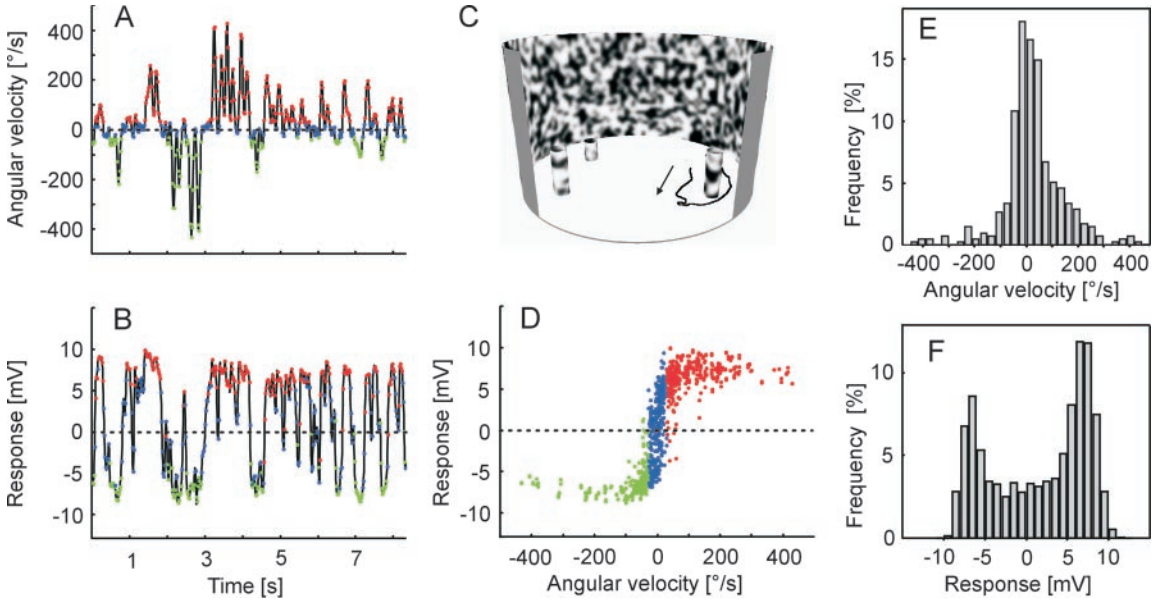

Figure 1. Responses of the HSE-cell when stimulated with behaviorally generated optic flow. *A*, Turning velocity of the walking fly. *Red* and *green dots* denote angular velocities of leftward and rightward turns, respectively, larger than ±30°/sec; *blue dots* mark angular velocities in between. Only every other velocity value is colored (temporal resolution: 20 msec). *Dotted horizontal line* indicates 0°/sec. *B*, Time-dependent average response of eight HSE-cells to the image sequence corresponding to the track indicated in *inset*. The average response was smoothed by a running average (width: 30 msec). *Red* and *green markers* denote responses elicited by leftward and rightward turns, respectively, of the fly with angular velocities larger than ±30°/sec. *Blue markers* indicate responses to angular velocities in between. Response values are colored at half the frame rate of the stimulus, although they were sampled at 2 kHz. *Dotted horizontal line* indicates the resting potential. *C*, Textured arena (diameter 0.5 m; height 0.3 m) with three objects and walking path of fly (*black curve*). Starting point of track and walking direction indicated by *arrow*. For clarity, the orientation of the animal is not shown; only its subsequent positions were drawn and connected. *D*, Response amplitude as a function of turning velocity. Color code is the same as *A* and *B*; temporal resolution was 10 msec. *Dotted horizontal line* indicates the resting potential. Response latencies were compensated in *B* and *D* by the shift of the peak of the cross-correlogram of the time-dependent angular velocity and the average response trace (30 msec). *E*, Distribution of angular velocities of the fly on the walking track (width of velocity classes: 30°/sec). *F*, Corresponding distribution of response levels of the HSE-cell (width of response classes: 1 mV).

nance: 210 cd/m^2 at center of the floor). Textured objects were introduced into the arena. The video sequences were digitized. The position of the head and the orientation of the flies were automatically detected in each frame by specifically designed software. From the parameters of locomotion, the retinal projection of the arena was computed using a virtual reality software (REALAX; RealAx Software, Karlsruhe, Germany). Computations were done after linear interpolation between subsequent positions of the fly along its walking track. The corresponding orientations were interpolated linearly on the basis of their sine and cosine components. In this way, 100 images per second were calculated, which was required because of the high temporal resolution of the fly's eye. The time-dependent position traces were filtered by a triangular filter (width: 50 msec). Because of the small size of the position jitter, there were hardly any consequences for the retinal images. The time-dependent orientation of the fly's body axis was filtered by a triangular filter with a width of 130 msec. The choice of the time constant was motivated by the specific walking mode of flies. Flies were shown to oscillate with every step cycle at ~10 Hz around their direction of propagation. Because these oscillations of the body axis are largely compensated by head movements, they induce only negligible image displacements (Strauss and Heisenberg, 1990). Hence our filtering of the time-dependent orientation traces led to the best approximation of the optic flow on the eyes of walking flies that we can obtain by the currently available techniques.

The reconstructed motion sequences were used in electrophysiological experiments. The stimulus sequences were replayed either in their original or in a manipulated form (specified in Figure legends). The motion sequences were presented on a computer monitor with a special video player that allowed us to present 100 images per second (luminance: darkest pixel 0.1 cd/m^2, brightest pixel 61.4 cd/m^2; 64 brightness steps). At this rate, no spatial aliasing occurred even at the highest angular velocities of the walking animal. The small difference in luminance of the visual input in the behavioral and electrophysiological experiments is likely to be insignificant (Hausen, 1981). Image size was ±60° in both azimuth and elevation, with 0°/0° corresponding to the frontal midline of the animal. The image thus covered most of the receptive field of the HSE-cell (Hausen, 1982b).

The dissection of the animals and the details of the recording procedure follow our standard laboratory routine (Kern et al., 2000). Intracellular recordings were made from the HSE-cell in the right optic lobe of ~1-d-old female flies of the genus *Lucilia*. The HSE-cell was identified by its response mode, its preferred direction of motion, and the location of its receptive field. Experiments were performed at temperatures between 22° and 27°C. Image sequences were presented in pseudorandom order with a 10 sec interstimulus interval. The first image of a sequence was presented for 1 sec before motion started. The average membrane potential in the last 250 msec of this period was taken as the resting potential. All responses are given with respect to this level, which varied between cells from −40 to −48 mV. Data were sampled at 2 kHz. Because different numbers of stimulus presentations were obtained for different cells, average responses to a given stimulus sequence were determined by first averaging over all individual response traces of each cell and subsequent averaging over these mean responses.

Differences between responses elicited by the original and by a manipulated stimulus may be attributable to the different stimuli as well as to neuronal variability. To disambiguate these two factors, the similarity of responses to different stimuli was related to the similarity of responses to identical stimulation. The similarity is determined by the ratio of the peak of the normalized cross-correlation of individual responses between stimulus classes and the peak of the normalized cross-correlation of responses within a class. The peaks in the cross-correlograms were occasionally shifted in time backward or forward by 20 msec, at most. On average, however, the time shift was 0 msec. The similarity index was first determined for each cell and then averaged over cells.

A similarity index of 1 may be obtained if the responses elicited by the original and the manipulated stimulus have an identical time course but differ in their amplitude. Therefore, it was determined that the responses to the two different stimuli fluctuate over time with approximately the same amplitude. This was done by first averaging and filtering (rectangular filter; width: 30 msec) the individual responses to a given stimulus.

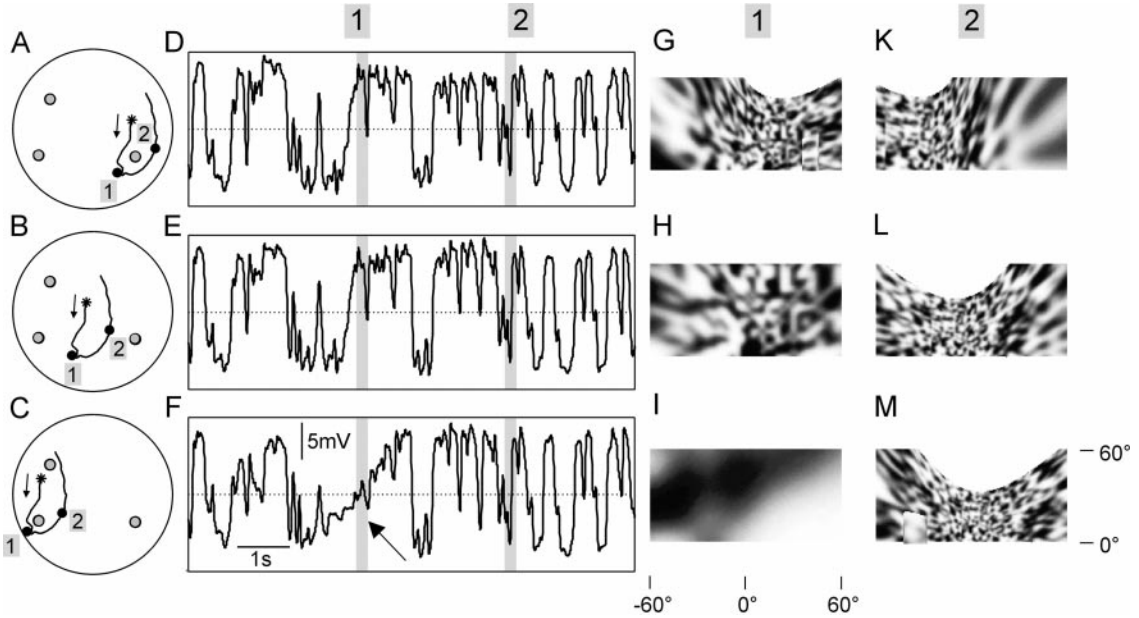

Figure 2. Influence of the spatial layout of the environment on the neuronal responses. Average responses (*D–F*) to image sequences experienced by a fly walking on the original track (*A*), on the same track displaced to the center of the arena (*B*), and to the opposite wall of the arena (*C*). *Asterisks* in *A–C* mark the starting point of the tracks; *arrowheads* point to initial walking direction. *Large circles* denote object positions. The tracks display only the position of the fly but not the orientation of its body axis. *Numbered filled circles* along the tracks correspond to the images seen by the fly (*G–M*) at the respective positions. *D–F*, Responses of eight HSE-cells (temporal resolution: 5 msec) were averaged and smoothed by a running average (width: 30 msec). *Numbered shaded sections* of the neuronal responses correspond to the images seen by the fly (*G–M*) at the respective instances of time (*A–C*, *numbered circles)*. The *arrow* in *F* indicates the section of the response traces where it differs from those shown in *D* and *E*. *Dotted horizontal line* indicates the resting potential. The *bottom white part* of the images corresponding to the white floor of the arena is not shown in *G–M*. The original track (*A*) and the corresponding response (*D*) are the same as shown in Figure 1, *C* and *B*, respectively.

Then the SD over time was calculated for each average response. Finally, the ratio between the SDs of the responses to the manipulated and the original version of the stimulus was calculated. The values averaged over cells ranged between 0.9 and 1.1, indicating very similar amplitudes of the responses to manipulated and original stimuli.

RESULTS

The response of the HSE-cell to optic flow seen by a walking fly is shown in Fig. 1. The HSE-cell responds to motion with pronounced graded depolarizations and hyperpolarizations even when recorded close to the output terminal (Hausen, 1982a). The fly's distance from the arena wall and from the objects changed while it walked around a textured object (Fig. 1*C*). Even while it walked on a relatively straight section of the track, the fly continually changed the direction of its longitudinal axis. These changes go along with modulations of the fly's angular velocity (Fig. 1*A*). As a consequence, the membrane potential of the HSE-cell fluctuates around the resting level (Fig. 1*B*), following to some extent the modulations of the angular velocity. For small angular velocities the response amplitude increases much with increasing velocity (Fig. 1*D*). In this range, the angular velocity can be estimated from the time-dependent cellular responses [however, see Egelhaaf and Reichardt (1987); Bialek et al. (1991); Haag and Borst (1997)]. Strikingly, most of the range of angular velocities generated by walking flies is represented by only a small part of the operating range of the HSE-cell. Although the angular velocity distribution has a single peak (Fig. 1*E*), the distribution of the corresponding responses shows two distinct peaks (Fig. 1*F*). Hence, while the fly is walking, the HSE-cell tends to switch between two activity levels. This finding suggests that the HSE-cell encodes the direction of the rotational optic flow component largely independently of the fly's distance from the arena wall or from objects.

This hypothesis is challenged by displacing the original walking track (Fig. 2*A*) within the arena. We replayed the optic flow that would have been experienced by the fly on the displaced tracks (Fig. 2*B*,*C*). In this way we determined neuronal responses to image sequences, which differ largely because of the different layout of the environment as viewed from the different walking tracks (Fig. 2*G–M*) but contain the same rotational component. The response traces obtained on the first displaced walking track are very similar to the responses obtained on the original track (Figs. 2*D*,*E*, 3*A*, *left*). On the basis of individual response traces, it is hardly possible for a human observer to determine whether responses correspond to a given original stimulus or to its manipulated version. However, the neuronal response to the optic flow generated on the second displaced track (Fig. 2*C*,*F*) differed substantially from the two others in one section (Fig. 2*F*, *arrow*). In the corresponding section of the walking track, the fly is extremely close to the arena wall. As a consequence, there are only few edges in the fly's field of view (Fig. 2*I*), and the HSE-cell responds weakly. Nonetheless, for most of the walking track the responses obtained for the second displaced walking track are hardly distinguishable from the other responses (Figs. 2*D–F*, 3*A*, *right*).

In accordance with the above results, the HSE-cell was found to encode robustly the fly's turning direction for various walking tracks and manipulations of the visual environment. The responses did not change much when the objects, which were present in the arena during the behavioral experiment, were removed before the image sequences were reconstructed (Fig.

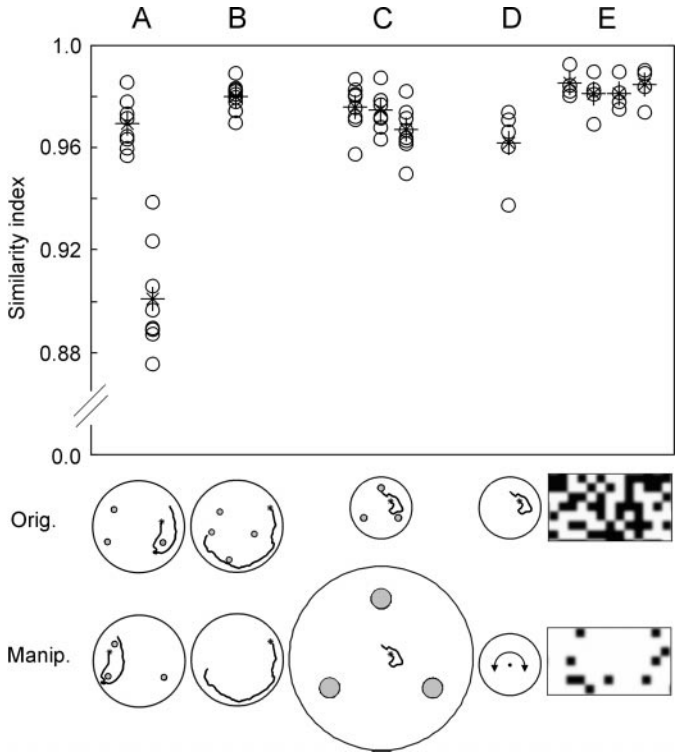

Figure 3. Similarity of responses to the original and manipulated optic flow. A similarity index of 1 indicates that the time courses of individual responses obtained under the two different stimulus conditions are as similar as the time courses of individual responses obtained under the same stimulus condition. *Open circles*, Results for individual cells; *asterisks*, mean results. Part of the manipulations are illustrated in the *insets*. *Circles* in *insets* denote the position and diameter of objects in the arena. *A*, Similarity of responses to the track in its original position versus the track displaced to the center of the arena (*left*) and versus the track displaced to the opposite side of the arena (*right*). The arena (diameter 0.5 m, height 0.3 m) and the tracks are the same as in Figure 2. *B*, Four objects present during the original walk were removed (arena size and pattern same as in *A*). *C*, An arena (diameter 0.31 m, height 0.3 m) was enlarged by a factor of 1.5, 2.0, and 3.0 (corresponding data from *left* to *right*). The enlargement includes the objects as well as the pattern on the arena wall and on the objects (for pattern, see *E*, *top inset*). The position of the track with respect to the arena center was kept the same. *D*, The translational component of the original walking track was eliminated and only the rotational component remained. This modification corresponds to a fly rotating around the arena center. No objects were present in the arena (diameter 0.31 m, height 0.3 m; pattern as in *C*). *E*, The original 50% black-and-white texture was exchanged by a texture with 12% black elements. This was done for the originally sized arena (diameter 0.31 m, height 0.3 m) and for the arena enlarged by a factor of 1.5, 2.0, and 3.0 (corresponding data shown from *left* to *right*). The texture density of the patterns covering the objects were kept as in the originally sized arena. The enlargement of the arena includes the pattern on the arena wall and on the objects. The track was the same as in *C*. The duration of the motion sequences was 8.3 sec (*A*), 11 sec (*B*), 6 sec (*C–E*). Number of cells: 8 (*A*), 10 (*B*), 8 (*C*), 5 (*D*), and 4 (*E*); total number of response traces: 237 (*A*), 132 (*B*), 177 (*C*), 120 (*D*), and 148 (*E*).

3*B*). Similarly, increasing the size of the arena, thereby reducing the translational optic flow component, only marginally influenced the responses of the HSE-cell (Fig. 3*C*). Hence, the HSE-cell seems to encode the turning direction quite independently of the distance of the fly from the arena wall. This conclusion is corroborated by the finding that eliminating the translational optic flow component entirely, by rotating the fly in the center of the arena at the original turning velocities, still leads to responses that are similar to those obtained on the original walking track

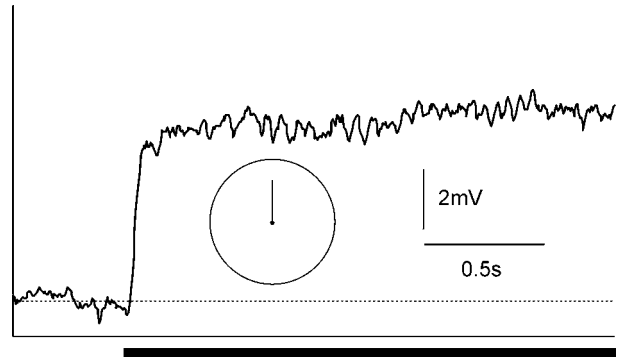

Figure 4. Average response of the HSE-cell to optic flow as seen on an artificial, straight path of locomotion (*inset*) starting in the center of a randomly textured arena (diameter 0.5 m; height 0.3 m; for texture see Fig. 1*C*). The translational velocity was 0.08 m/sec. The stimulus sequence was calculated in the same way as described for the behaviorally generated stimuli. *Dotted horizontal line* indicates the resting potential as obtained during the 250 msec period before motion onset. The average response was smoothed by a running average (width: 30 msec). The *thick horizontal bar* indicates the time of simulated walking. Number of cells: 4; total number of response traces: 18.

(Fig. 3*D*). To appreciate the significance of this finding, it should be noted that the HSE-cell strongly responds to translatory optic flow experienced on an artificial straight walking track (Fig. 4).

The responses of the HSE-cell to changes in the density of texture elements on the wall of the arena (Fig. 3*E*) are rather robust. The latter finding suggests that the HSE-cell might also encode robustly the animal's turning direction in a more natural environment.

DISCUSSION

Our experimental results reveal that, apart from extreme situations, the fly HSE-cell extracts the direction of turns from complex behaviorally generated optic flow largely independently of the three-dimensional layout and the textural properties of the environment. This finding is remarkable, given the highly ambiguous responses of the HSE-cell when stimulated with simple approximations to optic flow (Hausen, 1982a,b; Horstmann et al., 2000; Kern et al., 2000) and its pronounced responses to purely translational optic flow (Fig. 4). To what extent our conclusions obtained for walking flies generalize to free flight could not be analyzed so far. This important point will be approached with a much faster stimulation setup that is being developed currently.

Our approach to the stimulation of visual interneurons with behaviorally generated optic flow differs from other recent approaches in which visual interneurons were stimulated by image sequences that an animal might have seen on artificial tracks of locomotion (Pekel et al., 1996; Kim et al., 1997; Mulligan et al., 1997; Kern et al., 2000). To our knowledge, behaviorally generated retinal image sequences have been used so far only to study the performance of models of visual systems (Passaglia et al., 1997; Kording et al., 2000).

The peculiar dynamic properties of behaviorally generated visual input might be the most decisive reason why the HSE-cell extracts the direction of self-motion more specifically than was expected from the responses to simple stimuli. This interpretation is suggested by the poor specificity of the HSE-cell for the rotational flow component when the velocity changes only slowly or is even constant (Fig. 4) (Kern et al., 2000). Model simulations indicate that this peculiar feature is attributable mainly to the

nonlinearities inherent in the mechanism of motion detection (Egelhaaf and Reichardt, 1987; M. Egelhaaf, unpublished observations). It should be noted that no dynamic stimuli lead to the near invariance of the HSE-cell responses with respect to the layout of the environment. Rather the motion detection system has to operate in a range in which it does not transmit linearly the time course of pattern velocity (Egelhaaf and Reichardt, 1987; Egelhaaf, unpublished observations). Moreover, it is suggested by electrophysiological results (R. Kern, unpublished observations) and by model simulations that the retinal input must contain a broad range of spatial frequencies for the neuronal responses to become nearly independent of its textural properties. Finally, the nonlinear spatial integration properties of the HSE-cell (Borst et al., 1995; Single et al., 1997) are likely to be the main reason for the virtual independence of the HSE-cell responses from texture density. So far, there is no evidence that adaptational processes that were found to affect fly neurons such as the HSE-cell (Maddess and Laughlin, 1985; Ruyter van Steveninck et al., 1986; Harris et al., 1999, 2000; Kurtz et al., 2000) play an important role in shaping the responses of the HSE-cell to optic flow elicited during walking (Kern, unpublished observations).

Our experimental results indicate that the characteristics of the computations underlying optic flow processing in the fly might have evolved on a phylogenetic time scale to extract behaviorally relevant features of self-motion from natural optic flow. Further experiments as well as model simulations are currently being performed to investigate in which way these computations are adapted to the complex spatiotemporal properties of optic flow as generated by the behaving fly in different behavioral contexts. The outcome of the present experiments stresses the importance of analyzing the performance of neuronal circuits under conditions that resemble those of behaving animals.

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