B. Kimmerle · M. Egelhaaf

Detection of object motion by a fly neuron during simulated flight

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Abstract Object detection on the basis of relative motion was investigated in the fly at the neuronal level. A representative of the figure detection cells (FD-cells), the FD1b-cell, was characterized with respect to its responses to optic flow which simulated the presence of an object during translatory flight. The figure detection cells reside in the fly's third visual neuropil and are believed to play a central role in mediating object-directed turning behaviour. The dynamical response properties as well as the mean response amplitudes of the FD1b-cell depend on the temporal frequency of object motion and on the presence or absence of background motion. The responses of the FD1b-cell to object motion during simulated translatory flight were compared to behavioural responses of the fly as obtained with identical stimuli in a previous study. The behavioural responses could only partly be explained on the basis of the FD1b-cell's responses. Further processing between the third visual neuropil and the final motor output has to be assumed which involves (1) facilitation of the object-induced responses during translatory background motion at moderate temporal frequencies, and (2) inhibition of the object-induced turning responses during translatory background motion at high temporal frequencies.

Key words Figure-ground discrimination · Optic flow · Visual system · Relative motion · Insect

B. Kimmerle (✉)[1] · M. Egelhaaf
Lehrstuhl für Neurobiologie, Fakultät für Biologie,
Universität Bielefeld, Postfach 10 01 31,
D-33501 Bielefeld, Germany

Present address:
[1]Institut für Neurobiologie, FB Biologie,
Freie Universität Berlin, Königin-Luise-Str. 28–30,
D-14195 Berlin, Germany,
e-mail: kimmerle@neurobiologie.fu-berlin.de
Fax: +49-30-8385455

Abbreviations *TC* tangential cell · *FD-cell* figure detection cell · *PSTH* peristimulus time histogram

Introduction

'Seeing' is not only concerned with analysing static images with respect to brightness, texture and colour. Rather, visual systems also have to deal with motion, which is a visual feature of outstanding importance. Objects well disguised or hidden in a richly textured surround, such as a bird sitting in the foliage of a tree, are easily perceived if they start moving. Sensing relative motion between an object and its background can thus help to detect the object. Relative motion between the retinal images of object and background is not only elicited if objects move in the visual field. Also during self-motion the retinal images are in continuous flow. This so-called 'optic flow' depends on the movement of the observer as well as on the 3D-structure of the surround. During translatory self-motion the retinal velocity of a stationary object is inversely related to its distance from the observer, i.e. close objects pass by faster than more distant objects. Object detection based on relative motion as the only available cue has been investigated e.g. in humans (Regan and Beverly 1984), in monkeys (Miles and Kawano 1987), in bees (Srinivasan et al. 1990) and in flies (e.g. Virsik and Reichardt 1976; Reichardt et al. 1983; Egelhaaf 1985a; Kimmerle et al. 1996). In several animal species neurons have been described that are suited to detect relative motion and were consequently suggested to be involved in object detection (e.g. monkeys: Allman et al. 1985; Tanaka et al. 1986; cats: Sterling and Wickelgren 1969; pigeons: Frost and Nakayama 1983; toads: Tsai 1990; dragonflies: Olberg 1981, 1986; hawkmoths: Collett 1971; flies: Egelhaaf 1985b).

The fly is an excellent system to study object detection on the basis of optic flow both on the behavioural and on the neuronal level. In a behavioural study with a flight simulator it has been shown that tethered flying

flies, under certain conditions, try to turn towards an object which was presented during simulated translatory flight (Kimmerle et al. 1997). Translatory motion was mimicked in these experiments by front-to-back motion of gratings displayed in front of the flies' eyes. Whether the flies responded and how strong the turning responses were depended on the simulated distances of object and background: (1) strong turning responses were only elicited when the object was simulated to be closer to the fly than the background, i.e. when object motion was faster than background motion. Hardly any responses were elicited when object motion was slower than background motion, simulating a flight situation in which the fly passes a hole, and (2) within a certain range of velocities the turning responses were facilitated by background motion.

Optic flow is processed in the fly's third visual neuropil, the lobula plate, by a set of motion sensitive cells. These so-called tangential cells (TCs) have extended dendrites on which they spatially integrate the outputs of local motion sensitive elements. As a result, the TCs respond to motion within large parts of the visual field (review: Hausen 1984). Motion in the preferred direction leads to an excitation of the TCs, whereas motion in the opposite direction causes an inhibition. Among the TCs, the figure-detection cells (FD-cells) (Egelhaaf 1985b) respond strongest to motion of objects which are smaller than the cells' excitatory receptive field as defined by the local input elements. This small-field tuning of the FD-cells is due to additional inhibitory inputs by other TCs which mediate information on large-field motion in the ipsi- and contralateral visual field. The spatial input organisation of FD-cells – excitatory central receptive field and inhibitory surround – thus makes the FD-cells suited to detect in the optic flow relative motion between an object and the background. FD-cells are output elements of the lobula plate and project into the lateral protocerebrum where they probably synapse on descending neurons. FD-cells have been suggested to play a crucial role in mediating object-directed turning responses (Egelhaaf 1985a,b,c; Egelhaaf et al. 1988; Reichardt et al. 1989; Hausen and Wehrhahn 1990). It has been suggested recently that, in addition to the FD-cells described by Egelhaaf (1985b), further types of fly TCs exist which also exhibit small-field-tuning (Gauck and Borst 1999).

The present study analyses to what degree FD-cells can account for the object-directed turning behaviour elicited during translatory flight (Kimmerle et al. 1997). The analysis is done on a representative of the FD-cells. Since the response characteristics of this cell type are similar but not equal to the previously described FD1-type (Egelhaaf 1985b), it will be referred to as FD1b-cell. The FD1b-cell is first characterised shortly. Its responses to relative motion are then compared to the behavioural responses which were previously elicited by the same stimuli (Kimmerle et al. 1997). On the basis of this comparison further processing steps in the sensory-motor pathway of the object detection system of the fly are discussed.

Material and methods

Animal preparation and electrophysiological recording

Most experiments were done on female blowflies of the genus *Lucilia*, a few on *Calliphora erythrocephala*. The age of the flies ranged from one to several days. All flies were bred in our laboratory stocks. The flies were briefly anaesthetised with CO_2 and glued with the back of their thorax and their abdomen onto a small preparation platform. The wings were immobilised with low-temperature melting wax. The legs were amputated and the head was pitched downwards and fixed ventrally to the thorax with wax. The rear surface of the head capsule was opened to get access to the right optic lobe from posterior. To avoid desiccation the head capsule was supplied with ringer solution (concentrations in $mmol \cdot l^{-1}$: NaCl 128.3; KCl 5.4; $CaCl_2$ 1.9; $NaHCO_3$ 4.8; Na_2HPO_4 3.3; KH_2PO_4 3.4; glucose 13.9; pH 7.1). Fat tissue, air sacs and part of the tracheae covering the optic lobe were removed. To avoid movements of the brain caused by contractions of the oesophagus and antennal muscles the proboscis was cut, the gut was pulled out from behind, the antennae and the muscles were removed. Some of the neck muscles were severed. In most preparations the abdomen was opened and the heart was removed. The abdomen was then filled with ringer. Apart from the hole in the back of the fly's head, the wounds were sealed with wax. The animals were adjusted in the setup using the symmetry of the deep pseudopupil (Franceschini and Kirschfeld 1971).

Experiments were performed at room temperature (approximately 20 °C). Glass electrodes (Hilgenberg or Clark; outer diameter: 1.5 mm; inner diameter: 1.17 mm) were used to record extracellularly the spike activity of the FD1b-cell (see below) in the right lobula plate. Pulled on a vertical puller (Getra, München) and filled with 1 $mol \cdot l^{-1}$ KCl-solution the electrodes had resistances of 4–8 MΩ. A glass capillary with a broken tip filled with ringer solution was used as an indifferent electrode. The indifferent electrode was connected to a ringer syringe allowing to control the ringer level in the head capsule. The recorded signal was bandpass filtered and amplified with standard electrophysiological equipment. Spikes were transformed into pulses of fixed height and duration and fed into a Pentium-PC via an I/O-card (DT2801 A, Data Translation) at a sampling rate of 1 kHz. The programs for stimulus control and data acquisition were written in ASYST (Keithley Instruments).

Visual stimuli

The same stimuli were used as in previous behavioural experiments (Kimmerle et al. 1997). The stimuli were presented on two CRT screens (Tektronix 608; see Fig. 1A in Kimmerle et al. 1997). The CRT screens were placed symmetrically in front of the fly subtending an angle of 90°. The fly was positioned at the point where the orthogonals through the screen centres intersect, its longitudinal body axis pointing towards the midline between the two screens (visual angle: 0° per definition). In this configuration the right (left) screen subtended a horizontal visual angle from $\pm 11°$ to $\pm 80°$ in front of the right (left) eye. In the vertical the screens extended from $+29°$ (dorsal visual field) to $-29°$ (ventral visual field). Periodic square-wave gratings were generated by two image synthesisers (Picasso, Innisfree) at a frame rate of 100 Hz. The luminance of the bright and dark stripes was in the range of 35–40 cd m^{-2} and 3.5–4 cd m^{-2}, respectively, yielding a contrast of approximately 0.8 on each screen. The spatial wavelength of the pattern amounted to 1.1 cm, corresponding to a visual angle of about 6.3° in the region where object motion was displayed. Within a narrow window on the right (left) screen, extending from $\pm 19.0°$ to $\pm 31.6°$ in the horizontal direction and across the whole screen in the vertical direction, the pattern could be moved independently from the pattern in the remaining parts of the screen. Pattern motion within the windows will be referred to as 'object motion', pattern motion in the remaining part of the screens will be referred to as 'background motion'.

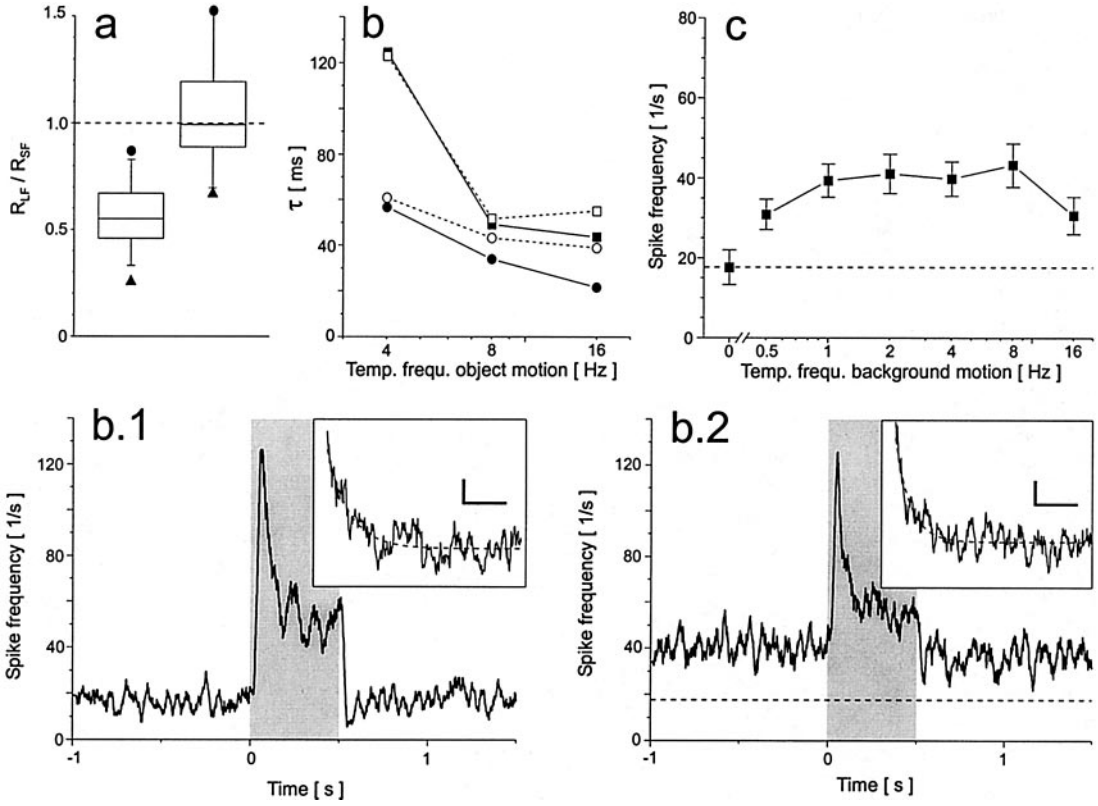

Fig. 1a–c General response properties of the figure-detection 1b-cell (FD1b-cell). **a** Strength of the bilateral (*left box*) and of the ipsilateral (*right box*) small-field tuning, defined as the ratio of the responses to the respective large-field stimulus (R_{LF}), i.e. to either uniform bilateral rotatory or ipsilateral motion, and the responses to small-field motion (R_{SF}). The *box charts* show the median, the quartiles and the 5- and 95-percentiles of the respective distribution. Extrema are indicated by the *circles* and *triangles*. *Dashed line* represents the level of equal responses to large-field motion and to small-field motion ($R_{LF}/R_{SF} = 1$). Values < 1 indicate small-field tuning. $n = 22$ (*left box*); $n = 17$ (*right box*). **b.1, b.2** Time-course of the response to ipsilateral object motion at a temporal frequency of 8 Hz presented during 0.5-s time intervals (*shaded columns*). The background was stationary (**b.1**) or translating at a temporal frequency of 2 Hz (**b.2**). *Dashed line* indicates activity recorded while the pattern was stationary. Time scale is given with respect to the onset of object motion. Peristimulus time histograms (PSTHs) were smoothed with a 31-ms rectangular filter. *Insets* show the respective PSTHs within a time window starting with the response peaks and ending with the end of object motion and the exponential fits (*dashed lines*). PSTHs in the insets were smoothed with an 11-ms rectangular filter. Vertical (*horizontal*) scale bars: 20 spikes s^{-1} (100 ms). **b** Activity decay after onset of object motion. *Solid lines and filled symbols* show the time constants obtained from first order exponential fits to PSTHs smoothed with an 11-ms rectangular filter. *Dashed lines and open symbols* show the respective data obtained from fits to PSTHs smoothed with a 31 ms rectangular filter. *Squares* indicate responses to object motion while the background was stationary, *circles* indicate responses to object motion during translatory background motion at a temporal frequency of 2 Hz. **c** Spike frequency during uniform translatory motion. *Dashed line* represents spontaneous activity $n = 9$ (**b.1**, **b.2**, **b**, **c**). Error bars denote SEMs (**c**)

The visual input of the fly during translatory flight was simulated by presenting front-to-back motion on both screens at a constant temporal frequency which was the same for object motion and for background motion ('uniform translatory motion'). After 5 s of uniform translatory motion, relative motion was introduced on the right screen for 0.5 s by abruptly increasing or decreasing the temporal frequency of object motion. In this way the presence of an object in front of or behind the background was simulated. With 2-s inter-stimulus intervals the presentation of relative motion was repeated three times alternately on the left and on the right screen. This stimulus sequence constituted one trial. The temporal frequencies of object motion during relative motion and of background motion varied between trials. Altogether 22 different combinations of temporal frequencies were used. They were chosen from a set of 7 temporal frequencies (0, 0.5, 1, 2, 4, 8 and 16 Hz). The successive presentation of these 22 combinations in a pseudorandom order made up one experimental run. The number of runs during which one FD1b-cell was recorded varied from 1 to 7. Only complete runs were evaluated.

All experiments were done on the FD1b-cell in the right half of the visual system. The responses of the contralateral FD1b-cell were inferred from the responses of the ipsilateral cell to stimuli which were mirrored with respect to the sagittal plane of the fly. This procedure can be considered legitimate because of the bilateral symmetry of the fly brain.

Identification of cells

When first described, FD-cells were categorised into four different response types and named accordingly FD1-FD4 (Egelhaaf 1985b). The FD-cell types were found to differ with respect to (1) their preferred direction of motion, (2) the location of their excitatory receptive field, and (3) the preferred direction of the contralateral inhibitory input. In the present study, the protocols for identification of the cells consisted of five different stimuli which lasted for 1 s each and were presented in immediate sequence. The stimuli were: (1) stationary pattern, (2) counterclockwise uniform rotatory motion (i.e. back-to-front on the right screen, front-to-back on the left screen), (3) clockwise uniform rotatory motion, (4) back-to-front object motion on the right (ipsilateral) screen, and (5) front-to-back object motion on the right (ipsilateral) screen. In each run of the test protocol this sequence of stimuli was repeated ten times. All cells analysed in the present study were excited by front-to-back object

motion and inhibited by back-to-front object motion. They responded stronger to front-to-back object motion than to clockwise uniform rotatory motion. Their excitatory receptive field was in the fronto-lateral visual field between ca. −15° and +60°. According to these properties they could be classified as FD1. In accordance with the properties of the FD1-cells as described by Egelhaaf (1985b) they were strongly inhibited by contralateral back-to-front motion. However, in contrast to Egelhaaf (1985b) they were also weakly inhibited by contralateral front-to-back motion. Because of this difference the cells recorded in the present study will be referred to as FD1b, the affix 'b' indicating bidirectional inhibition in front of the contralateral eye. The bidirectional contralateral inhibition of this cell type and a more detailed description of the spatial integration properties will be presented in another account (B. Kimmerle and M. Egelhaaf, unpublished observations). For most of the cells the identification protocol was also run with the left screen illuminated homogeneously so that large-field motion was restricted to the (right) ipsilateral part of the visual field. For many of the cells test protocols were run several times.

Data analysis

Peristimulus time histograms (PSTHs) were first calculated for each cell individually with a temporal resolution of 1 ms, then averaged over cells and finally smoothed with a rectangular filter. The width of the filter is given in the legends of the respective figures. Spike frequencies during uniform translatory motion as shown in Fig. 1c were calculated as average frequencies obtained in 1-s time intervals prior to the onset of the relative motion stimuli. Responses to the 22 different relative motion stimuli presented on the right, i.e. ipsilateral, screen were evaluated within two time intervals: (1) an 'early response' was calculated as the average spike frequency within a 100-ms-interval starting 15 ms after the onset of relative motion, and (2) a 'late response' was calculated as the average spike frequency obtained within a 400-ms interval immediately following the interval within which the early response was determined. Responses to the stimuli presented on the left (contralateral) screen were calculated as the average spike frequency within a 500-ms-interval starting 15 ms after relative motion onset. Time-averaged spike frequencies were first calculated for single cells and subsequently averaged over cells. One of nine cells in the data set was recorded in *Calliphora*.

Results

General response properties

A basic feature of FD-cells is that they respond stronger to small moving objects than to motion within large parts of the visual field ('small-field tuning').This property was found in all cells included in the analysis when tested with large-field motion within both the right and the left half of the visual field ('binocular small-field tuning', Fig. 1a). Most of these cells were also tested with respect to the strength of their small-field tuning as determined with unilateral large-field motion on the ipsilateral side ('ipsilateral small-field tuning'). Only about half of the cells (9 out of 17) exhibited ipsilateral small-field tuning. In the other 8 cells, uniform ipsilateral motion (i.e. object motion and background motion at the same temporal frequency) led to a somewhat larger spike frequency than object motion alone. The distributions of the bilateral and of the ipsilateral small-field tuning were unimodal; the variability in both was large. The decrease in the strength of the small-field tuning when stimulating only ipsilaterally indicates that a considerable amount of the underlying inhibition was due to motion in front of the contralateral eye. Note that the absence of ipsilateral small-field tuning in part of the cells does not necessarily imply an absence of inhibition, but can be due to the excitation mediated by the local input elements being *stronger* than the inhibition mediated by large-field motion. The FD-cells recorded in the present study were excited by front-to-back motion within restricted parts of the ipsilateral visual field. The sensitivity maximum of their excitatory receptive field was located at about +15° (not shown). On the basis of these criteria they could be classified as FD1 according to the categorisation by Egelhaaf (1985b). However, they are referred to as FD1b because inhibition from the contralateral visual field was not restricted to back-to-front motion as described by Egelhaaf (1985b), but was also found, although weaker, during front-to-back motion (B. Kimmerle and M. Egelhaaf, unpublished observations).

The time-course of the responses of the FD1b-cell to object motion in the absence (Fig. 1b.1) and in the presence (Fig. 1b.2) of background motion was characterised by a fast activity increase immediately after the onset of object motion, followed by a slower activity decrease. The time constant of the activity decay after onset of object motion was estimated by fitting first order exponential functions to the PSTHs. The responses became more transient for high than for low temporal frequencies of object motion (Fig. 1b). Moreover, background motion reduced the decay time of the responses to object motion. This conclusion is independent of the exact filtering procedure applied to the PSTHs (Fig. 1b).

As a reference for the responses to relative motion, the activity of the FD1b-cell during uniform translatory motion was analysed (Fig. 1c). Uniform translatory motion caused the FD1b-cell to slightly increase its spike frequency relative to its activity of ca. 17 spikes s^{-1} recorded when the pattern was stationary. The temporal frequency tuning curve shows a broad optimum at a rather low spike frequency (compare the spike frequency to the responses elicited by relative motion stimuli shown in the following figures). Note that the spike frequencies were obtained after spike activity had reached a steady state.

In the following, the responses of the FD1b-cell to relative motion are compared to behavioural responses that were obtained with the same stimuli as presented in a previous account (Kimmerle et al. 1997). Because of their transient nature the responses of the FD1b-cell to relative motion on the ipsilateral side were evaluated separately within a short initial 100-ms time window ('early response') and in a subsequent 400-ms time window ('late response').

Background simulated to be at an infinite distance

Object motion in front of a background which was simulated to be at infinite distance by leaving the

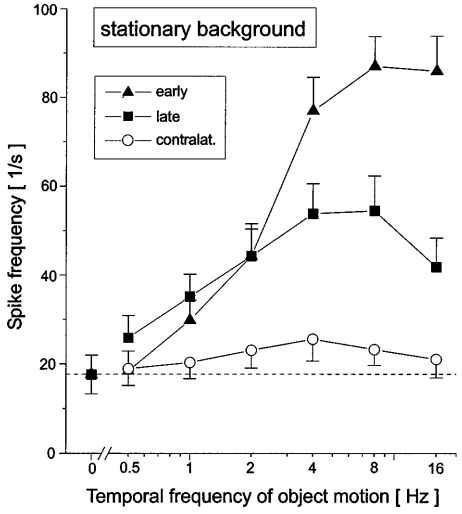

Fig. 2 Responses of the FD1b-cell to object motion in front of a stationary background. Dependence of the spike frequency on the temporal frequency of object motion presented on the ipsilateral (*filled symbols*) and on the contralateral (*open symbols*) side of the cell's excitatory receptive field. *Dashed line* represents activity while the pattern was stationary $n = 9$. Error bars denote SEMs

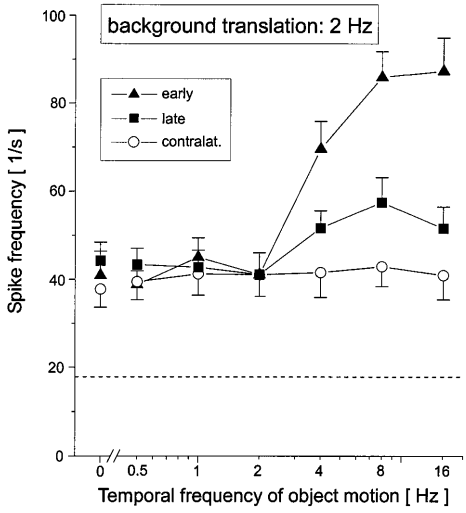

Fig. 3 Responses of the FD1b-cell to object motion at variable temporal frequencies during translatory background motion at a temporal frequency of 2 Hz. Explanations as for Fig. 2

background pattern stationary, increased the spike frequency of the FD1b-cell (Fig. 2). With increasing temporal frequency of object motion the responses became stronger. In the upper range of temporal frequencies the early response was much larger than the late response. Whereas the early response remained high up to the fastest temporal frequency tested, the late response dropped when object motion was displayed at a temporal frequency of 16 Hz. The temporal frequency tuning of the early response was thus shifted towards faster moving stimuli as compared to the late response. Object motion on the contralateral side led to only weak activity changes in the FD1b-cell. A slight activity increase was induced during object motion at temporal frequencies above 0.5 Hz. The responses of the FD1b-cell revealed no qualitative differences from the behavioural responses (compare with Fig. 3A in Kimmerle et al. 1997). The dependence of the early neuronal responses on the temporal frequency of object motion are in better accordance with the behavioural data than the dependence of the late neuronal responses because, as in the behavioural experiments, the response level did not decrease at the highest temporal frequency tested (16 Hz).

Background simulated to be distant

The responses to relative motion in front of a distant background, simulated by translatory background motion at 2 Hz, depended on whether the object moved faster or slower than the background (Fig. 3). When object motion was faster than background motion, simulating the presence of an object in front of the background, the spike frequency increased with respect to the firing during uniform translation. The early responses elicited by these stimuli were strong, whereas the late responses were only slightly elevated. When object motion was slower than background motion, simulating a hole in the background, the spike frequency of the FD1b-cell was not much affected. Relative motion presented on the contralateral side virtually did not change the spike frequency. These characteristics of the FD1b-cell responses are again in good agreement with the behavioural results (compare with Fig. 2b in Kimmerle et al. 1997). The flies did not show turning responses towards the object, if background motion was faster than object motion. However, they tried to turn towards the object, if object motion was faster than background motion. Similar to the condition when the background was stationary, the behavioural as well as the early neuronal responses increased up to the highest temporal frequency of object motion that was tested (16 Hz).

Background simulated to be close

The responses of the FD1b-cell to relative motion in front of a close background, simulated by translatory background motion at 16 Hz, were quite large (Fig. 4a). The early and the late responses depended in different ways on the temporal frequency of object motion: with increasing temporal frequency of object motion the responses of the FD1b-cell became more and more sustained. During contralateral object motion a weak decrease in the spike frequency with increasing temporal frequencies of object motion could be observed. These findings are corroborated by inspecting the time course of the responses. The PSTHs show that transient responses were not only elicited after switching object

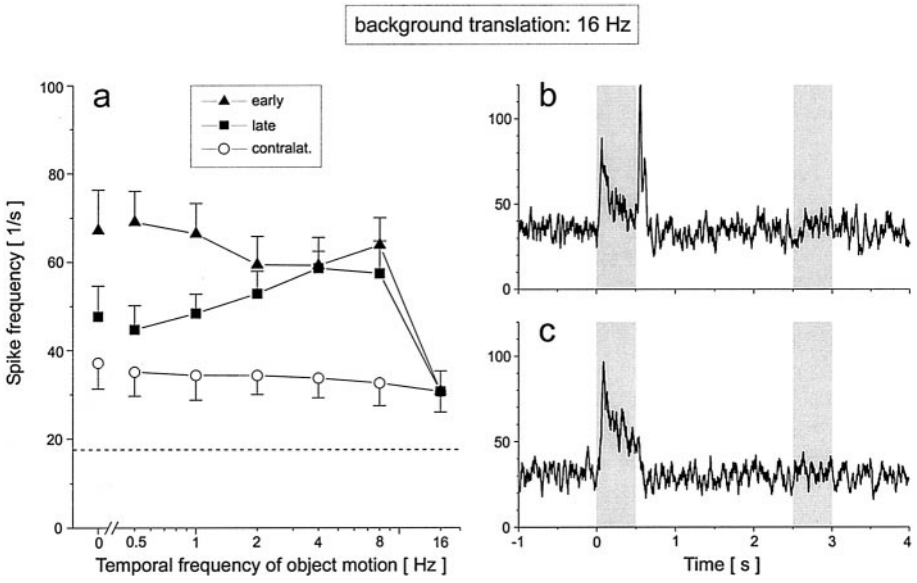

Fig. 4a–c Responses of the FD1b-cell to object motion during translatory background motion at a temporal frequency of 16 Hz. **a** Dependency of the spike frequency on the temporal frequency of object motion. Explanations as for Fig. 2. **b, c** PSTHs obtained from presentation of a stationary object (**b**) and of object motion at a temporal frequency of 8 Hz (**c**). During the time interval highlighted by the left (*right*) grey boxes the relative motion stimulus was presented on the ipsilateral (contralateral) screen. Time scales are given with respect to the onset of object motion on the ipsilateral screen. PSTHs were smoothed with a 31-ms filter

motion to 8 Hz (Fig. 4c), but also when the object stopped moving at all (Fig. 4b). Note that the stationary object presented in front of a fast translating background elicited a response that had a time-course comparable to responses elicited by moving objects. Another interesting feature of the PSTH shown in Fig. 4b is the short and strong activity increase after the end of the relative motion stimulus and the return to uniform translatory motion. A similar response peak was also found after object motion at temporal frequencies of 0.5 Hz, 1 Hz, 2 Hz and 4 Hz (not shown). The neuronal responses to object motion with a simulated close background differed substantially from the corresponding behavioural responses. Whereas in the FD1b-cells considerable responses were elicited, no strong responses could be found in the behavioural turning reactions (Kimmerle et al. 1997). It is noteworthy that for some stimulus conditions, weak turning reactions were observed after the beginning *and after the end* of the relative motion stimuli, reminiscent of the increase in the spike frequency of the FD1b-cell as described above (Fig. 4b) within the same time intervals. However, these turning reactions were by far not as strong as those obtained when the object moved faster than the background, whereas the FD1b-responses were just as strong.

A close object in front of backgrounds simulated at variable distances

The responses to a close object, simulated by fast object motion (16 Hz), were influenced by the temporal frequency of background motion (Fig. 5). The early response of the FD1b-cell to fast object motion was strong when the background was stationary and remained about equally strong during background translation at temporal frequencies of up to 2 Hz. Faster translation reduced the early response. The late response remained almost constant over a large range of temporal frequencies of background motion. Only if the background was stationary or translating at a temporal frequency of 0.5 Hz or 16 Hz it was weaker. For background motion at all temporal frequencies up to 4 Hz the early responses were much larger than the late responses, underlining the transient nature of the FD1b-cell's responses to fast object motion. The firing activity during object motion on the contralateral side was slightly raised above the level obtained when the object and background were stationary. The dependence of the FD1b responses on the temporal frequency of background motion during contralateral object motion was

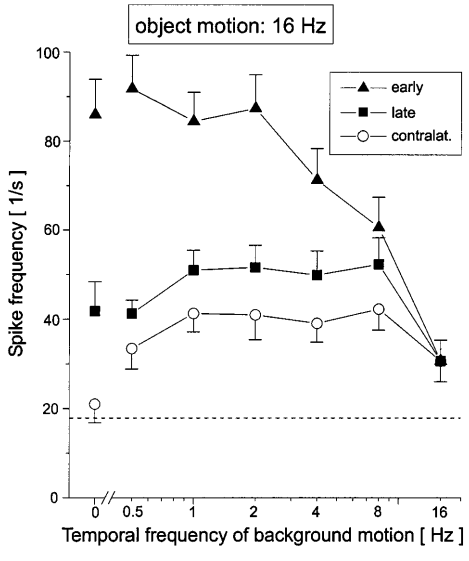

Fig. 5 Influence of background motion on the responses of the FD1b-cell to object motion at a temporal frequency of 16 Hz. Object motion was presented on the ipsilateral (*filled symbols*) or on the contralateral (*open symbols*) side of the cell's excitatory receptive field. Further explanations as for Fig. 2

similar to that during uniform translation (compare open symbols in Fig. 5 to Fig. 1c). Thus, object motion on the contralateral side affected the FD1b-cell only weakly. The influence of background motion on the responses of the FD1b-cell is clearly different from its influence on the corresponding turning responses of the fly: Background motion was found to facilitate the turning responses to fast object motion and led to responses up to twice as strong as when the background was stationary (see Fig. 4 in Kimmerle et al. 1997). In contrast, the early responses of the FD1b-cell to fast moving objects were very strong when the background was stationary and did not increase further during background translation.

Comparison of the time-course of the behavioural and neuronal responses

When the object moved fast, the turning response was sustained until the end of the relative motion stimulus, irrespective of whether the background was stationary (Fig. 6a) or translating at a temporal frequency of 2 Hz (Fig. 6c) (Kimmerle et al. 1997). In contrast, as has already been pointed out, the responses of the FD1b-cell were highly transient (Fig. 6b, d). In the case of a stationary background the behavioural response could, in principle, be explained to result from the neuronal response after lowpass filtering the latter. Such a transformation could be achieved by integrating the spike activity over large time windows. However, during background motion the spike activity quickly decreased after the initial peak and reached a level comparable to the activity prior to and after relative motion. Therefore, the information about the end of relative motion was not represented in the neuronal signal. The behavioural response thus cannot be explained on the basis of the response of the FD1b-cell alone.

Discussion

It was investigated to which extent the sensitivity of flies to relative motion in object-directed turning behaviour (Kimmerle et al. 1997) can be explained on the basis of the response properties of a representative of the FD-cells, a class of visual interneurons presumed to mediate object-directed turning behaviour in the fly (Egelhaaf 1985b, c). The specificity of the FD1b-cell for small moving objects versus large-field motion was shown to depend on whether large-field motion is presented bilaterally or only in the ipsilateral half of the visual field. The FD1b-cell responded transiently to object motion alone and the responses became even more transient during bilateral background motion from front-to-back, as is elicited on the eyes during translatory flight. The responses of the FD1b-cell to object motion during simulated translatory flight can explain part, but not all, of the features observed in the behavioural experiments. First, the strength of the turning responses could be explained on the basis of the responses of the FD1b-cell as long as the background was either stationary or moving from front to back in both visual fields at a moderate temporal frequency (2 Hz); this visual input corresponds to translatory flight in front of an infinite or distant background. Second, during fast translatory background motion, object motion at low temporal frequencies elicited strong responses in the FD1b-cell. In contrast, no strong turning reactions were observed under these conditions. Third, translatory background motion at temporal frequencies around 2 Hz strongly increased the behavioural responses to fast object motion, but not the responses of the FD1b-cell. Finally, although the turning responses started to decrease after the end of relative motion, the information about the end of a relative motion stimulus was not represented in the FD1b-cell's responses under all conditions.

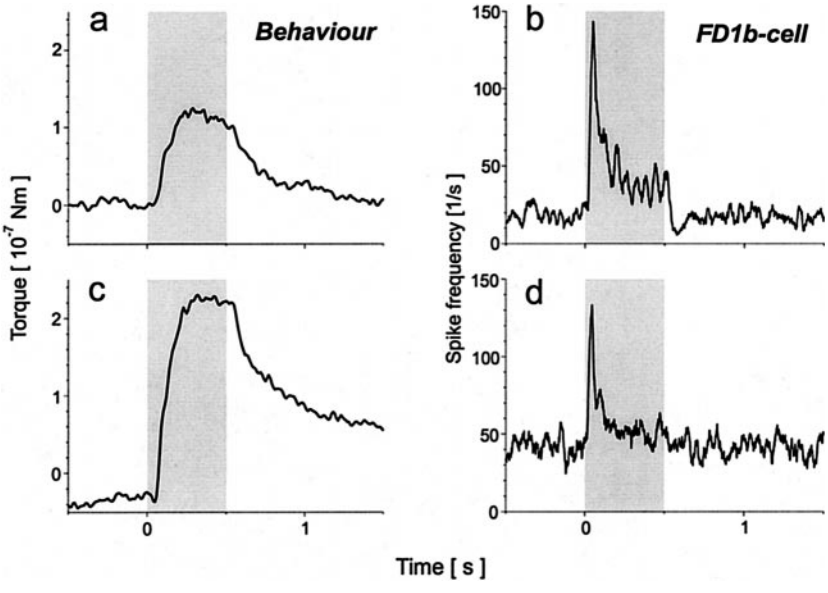

Fig. 6a–d Comparison of the time-course of the behavioural and neuronal responses. Plots show the time-course of the behavioural turning responses (**a, c**) and the firing activity of the FD1b-cell (**b, d**) before, during (*shaded areas*) and after object motion at a temporal frequency of 16 Hz. The background was either stationary (**a, b**) or translating at a temporal frequency of 2 Hz (**c, d**). Time scales are given with respect to the onset of object motion. Behavioural responses: for experimental details and data evaluation see Kimmerle et al. (1997). Neuronal responses: PSTHs were smoothed with a 31-ms rectangular filter. $n = 9$ cells

Identification of cells

The cells recorded in the present study were classified according to the classification system of Egelhaaf (1985b) and were named FD1b. A new classification system for TCs inhibited by motion in front of the contralateral side of the visual field was recently suggested (Gauck and Borst 1999). This classification system is based on differences in the strength of ipsilateral inhibition as the main classification criterion. According to Gauck and Borst (1999) the distribution of the strength of ipsilateral small-field tuning indicates the existence of two classes among the FD1-like cells. Gauck and Borst (1999) found a small proportion of cells which had a very strong ipsilateral small-field tuning, whereas the majority of cells were either weakly or not ipsilaterally small-field tuned. The latter class of cells was further subdivided into two cell types, according to whether or not their activity induced by ipsilateral large-field motion is smaller than their responses to object motion. The distribution of the strength of the ipsilateral small-field tuning was unimodal in both the second class of cells described by Gauck and Borst (1999) as well as in our data. We suggest that ipsilateral inhibition of the FD1b-cell may be masked by the excitatory input, if the spatial extent of the large-field stimulus is too small. This conclusion is supported by the finding that using stimuli with a larger horizontal extent led to a shift of the distribution towards stronger ipsilateral small-field tuning (B. Kimmerle and M. Egelhaaf, unpublished observations). Thus there is no reason to subdivide the cells recorded in the present study into different subtypes. Likewise, it may be possible that the weakly and the not ipsilaterally small-field tuned TCs described by Gauck and Borst (1999) also do not represent different types of cells. A more detailed account of the spatial integration properties of the FD1b-cells will be given elsewhere (B. Kimmerle and M. Egelhaaf, unpublished observations).

Dynamic response properties of the FD1b-cell

After the initial response peak to motion onset the spike activity of the FD1b-cell was found to decrease rapidly, depending on the temporal frequency of object motion and on the presence or absence of background motion. The influence of the temporal frequency on the activity decay of another TC, the H1-cell, after motion onset has been investigated by Maddess and Laughlin (1985). The time constants obtained in the H1-cell are roughly one order of magnitude larger for a given temporal frequency than those obtained in the present study in the FD1b-cell (compare Fig. 1b in the present study with Fig. 9b in Maddess and Laughlin 1985). This difference might be due to differences in the stimuli, such as spatial extent of the pattern or luminance. An alternative explanation is that the response dynamics of the FD1b-cell are different from those of the H1-cell due to the specific input organisation of the FD-cells. In contrast to the H1-cell, FD-cells are inhibited by other TCs. The activity decay of the FD1b-cell responses may be accelerated by the inhibitory interaction with one or several TCs.

The responses of the FD1b-cell were furthermore shown to be more transient during relative motion than during object motion in front of a stationary background. A possible explanation is that background translation might increase the activity of the inhibitory input of the FD1b-cells. Indeed, a major inhibitory element of the FD1-cell (Warzecha et al. 1993) has been shown to be activated above its resting-level during translatory motion (Egelhaaf et al. 1993) and to exhibit transient response properties (Dürr 1998). Alternatively, the influence of background motion on the temporal response properties of the FD1b-cell might also be explained by the fact that the FD1b-cell is in a different adaptational state (Maddess and Laughlin 1985; de Ruyter van Steveninck et al. 1986; Borst and Egelhaaf 1987; Harris et al. 1999) during background motion than in situations without background motion. Irrespective of the different possible explanations, the responses of the FD1b-cell to object motion become more transient during translatory background motion compared with object motion in front of a stationary background.

Why compare the behavioural responses with the responses of FD1b-cell?

Turning responses of the fly around its vertical body axis are thought to be controlled by two systems in parallel which have different dynamical properties (Egelhaaf 1987, 1989). Fast object-directed turning behaviour is mediated by the object detection system. The optomotor system for course control compensates for global rotatory motion of the retinal image as occurs during changes in the direction of locomotion. The behavioural responses elicited by the motion stimuli used in the present study have been shown not to be influenced to a large extent by the optomotor system due to the dynamical response properties of the latter which prevent it from responding strongly to short stimuli (see Kimmerle et al. 1997 for a more detailed discussion of this issue). Consequently, the turning responses were concluded to be mediated mainly by the object detection system. On the level of the lobula plate the object detection system is supposed to be represented by the FD-cells (Egelhaaf 1985a, b, c; Egelhaaf et al. 1988; Reichardt et al. 1989). In the behavioural experiments of Kimmerle et al. (1997), the object was positioned in the most sensitive part of the FD1b-cell's receptive field. Hence, this cell can be supposed to respond strongest to these relative motion stimuli among the class of FD-cells. The FD1b-cell is therefore considered to represent a major element in the sensory-motor pathway mediating

turning responses as described previously (Kimmerle et al. 1997).

Responses of the FD1b-cells in both brain hemispheres

When comparing the neuronal responses to relative motion with the corresponding turning responses of the fly one has to take into account that there is a counterpart of the recorded cell in the contralateral half of the brain. The responses of the FD1b-cell contralateral to the recorded FD1b-cell have been inferred by presenting to the recorded cell stimuli which were mirrored with respect to the sagittal plane of the fly. However, it is not yet clear how the signals of the FD-cells in both halves of the brain interact. It has been suggested that in the fly optomotor system for course stabilisation the signals originating from both brain hemispheres are subtracted, whereas in the system controlling the thrust of the animal the signals are added (Götz 1975).

If a subtraction of the responses of corresponding neurons in both brain hemispheres is assumed in the system mediating object-directed turning behaviour, the transient phase of the responses of the FD1b-cell to object motion in front of a stationary background (Fig. 2) or during slow background translation (Fig. 3) matches the corresponding behavioural turning responses very well: the subtracted FD1b responses increase up to the fastest object motion tested. Very weak or no responses result in the situations in which the object moved slower than the background, corresponding to situations in which the object was simulated to be located behind the background, i.e. to be a hole in the background.

The clear differences between behavioural and neuronal responses during fast background motion remain if a subtraction of the responses of the FD1b-cells of both brain hemispheres is assumed, because object motion did not influence the activity of the contralateral FD1b-cell (Fig. 4). Thus, in contrast to the behavioural responses, the neuronal responses were strong also after subtraction of the responses of the right and left FD1b-cell.

The differences between the behavioural and the neuronal responses with respect to the influence of translatory background motion (Fig. 5) become even more pronounced, if a subtraction of the neuronal signals is assumed. After subtraction, the strongest neuronal responses to fast object motion are obtained for a stationary background. Background motion at increasing temporal frequencies monotonically reduces the responses. In contrast, the strongest turning responses were elicited during background translation.

Taken together, subtracting the responses of the ipsilateral and the contralateral FD1b-cell does not lead to a better match between behavioural and neuronal responses. Moreover, under certain conditions, subtraction of the ipsi- and contralateral neuronal responses was shown to reduce the specificity of the FD1b-cell for object motion (B. Kimmerle and M. Egelhaaf, unpublished observations).

Implications for further processing in the object detection system

The following characteristics of object-directed turning behaviour of the fly cannot be explained on the basis of the responses of the FD1b-cell: (1) background translation may facilitate the object-directed turning responses, (2) strong turning responses are only elicited if the object is simulated to be located *in front of* the background, and (3) during relative motion between object and background, the fly remained 'on object-course' and returned to straight flight only after cessation of relative motion.

If the FD-cells play a decisive role in mediating the object-directed turning, the discrepancies between the FD1b-cell response and the behavioural response need to be accounted for. There are various possibilities to explain the differences: The FD-cells not characterised in the present study may differ in their properties from the FD1b-cell and can account for the above-mentioned behavioural response characteristics. Although the stimuli were chosen such that the FD1b-cell can be supposed to respond optimally, it cannot be ruled out that the responses of other FD-cells are suited to account for the observed behavioural responses. If this is not the case, further processing of the FD1b signals at subsequent stages of the nervous system would require an enhancement of the responses during background translation at temporal frequencies in the range 0.5–4 Hz and an inhibition of the responses during fast background translation in the region of 16 Hz.

An enhancement of the responses during background translation at a moderate velocity could, in principle, be achieved by an interaction with other TCs sensitive to front-to-back motion. The response of the TCs of the 'horizontal system' (HS-cells, Hausen 1982a) to sustained motion depends roughly in the same way on the temporal frequency as the facilitatory influence of background translation on the object-directed turning responses (temporal frequency tuning of the HS-cells: Hausen 1982b). It might thus be conceivable that the activity of an HS-cell (or the activity of another cell sensitive to front-to-back motion with a similar temporal frequency tuning) acts in a facilitatory way on the signal of the FD1b-cell.

Since objects simulated at a greater distance than the background are not attractive to the behaving fly, the strong responses of the FD1b-cell to these relative motion stimuli have to be inhibited at some stage. Cells mediating this inhibition should be tuned to high temporal frequencies as occurring when the background is close and respond weakly to slow background translation. However, there are no TCs known so far that have a temporal frequency tuning which would allow to explain a strong inhibition of the FD1b-responses during background translation at 16 Hz and a weak or no inhibition during background translation at 2 Hz.

Although a lot is known about the sensory processing of optic flow in the visual system of the fly, this study has

shown that there are still great gaps when it comes to link the neuronal responses at the level of the output elements of the lobula plate with visual orientation behaviour. Processing stages in the sensory-motor pathway subsequent to the lobula plate which have to be investigated in order to fill these gaps include (1) the descending neurons that arborize in the protocerebrum and receive input from different visual pathways as well as mechanosensory input originating from the antennae (Gronenberg and Strausfeld 1990; Strausfeld and Gronenberg 1990), (2) the motor neurons in the thoracic ganglia innervating the flight motor, and (3) the flight motor itself consisting of a number of steering muscles with different functions in flight control (Heide 1983). The present study provided some indications about which processing steps have to be expected on these integration levels in the context of object-directed turning behaviour.

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References

Allman J, Miezin F, McGuinness E (1985) Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). Perception 14: 105–126

Borst A, Egelhaaf M (1987) Temporal modulation of luminance adapts time constant of fly movement detectors. Biol Cybern 56: 209–215

Collett TS (1971) Visual neurones for tracking moving targets. Nature (Lond) 232: 127–130

Dürr V (1998) Dendritic calcium accumulation in visual interneurons of the blowfly. Doctoral dissertation, Universität Bielefeld

Egelhaaf M (1985a) On the neuronal basis of figure-ground discrimination by relative motion in the visual system of the fly. I. Behavioural constraints imposed on the neuronal network and the role of the optomotor system. Biol Cybern 52: 123–140

Egelhaaf M (1985b) On the neuronal basis of figure-ground discrimination by relative motion in the visual system of the fly. II. Figure-detection cells, a new class of visual interneurons. Biol Cybern 52: 195–209

Egelhaaf M (1985c) On the neuronal basis of figure-ground discrimination by relative motion in the visual system of the fly. III. Possible input circuitries and behavioural significance of the FD-cells. Biol Cybern 52: 267–280

Egelhaaf M (1987) Dynamic properties of two control systems underlying visually guided turning in house-flies. J Comp Physiol A 161: 777–783

Egelhaaf M (1989) Visual afferences to flight steering muscles controlling optomotor responses of the fly. J Comp Physiol A 165: 719–730

Egelhaaf M, Hausen K, Reichardt W, Wehrhahn C (1988) Visual course control in flies relies on neuronal computation of object and background motion. Trends Neurosci 11: 351–358

Egelhaaf M, Borst A, Warzecha A-K, Flecks S, Wildemann A (1993) Neural circuit tuning fly to motion of small objects. II. Input organization of inhibitory circuit elements revealed by electrophysiological and optical recording techniques. J Neurophysiol 69: 340–351

Franceschini N, Kirschfeld K (1971) Les phenomènes de pseudopupille dans l'oeil composé de *Drosophila*. Kybernetik 9: 159–182

Frost BJ, Nakayama K (1983) Single visual neurons code opposing motion independent of direction. Science 220: 744–745

Gauck V, Borst A (1999) Spatial response properties of contralateral inhibited lobula plate tangential cells in the fly visual system. J Comp Neurol 406: 51–71

Götz KG (1975) The optomotor equilibrium of the *Drosophila* navigation system. J Comp Physiol 99: 187–210

Gronenberg W, Strausfeld NJ (1990) Descending neurons supplying the neck and flight motor of Diptera: physiological and anatomical characteristics. J Comp Neurol 302: 973–991

Harris R, O'Carroll D, Laughlin S (1999) Direction-independent component in fly motion adaptation. In: Göttingen neurobiology report 1999. Thieme, Stuttgart, p 434

Hausen K (1982a) Motion-sensitive interneurons in the optomotor system of the fly. I. The horizontal cells: structure and signals. Biol Cybern 45: 143–156

Hausen K (1982b) Motion sensitive interneurons in the optomotor system of the fly. II. The horizontal cells: receptive field organization and response characteristics. Biol Cybern 46: 67–79

Hausen K (1984) The lobula complex of the fly: structure, function and significance in visual behaviour. In: Ali M (ed) Photoreception and vision in invertebrates. Plenum, New York, pp 523–559

Hausen K, Wehrhahn C (1990) Neural circuits mediating visual flight control in flies. II. Separation of two control systems by microsurgical brain lesions. J Neurosci 10: 351–360

Heide G (1983) Neural mechanisms of flight control in Diptera. In: Nachtigall W (ed) Biona report 2. Akad Wiss Mainz. Fischer, Stuttgart, pp 35–52

Kimmerle B, Egelhaaf M, Srinivasan MV (1996) Object detection by relative motion in freely flying flies. Naturwissenschaften 83: 380–381

Kimmerle B, Warzecha A-K, Egelhaaf M (1997) Object detection in the fly during simulated translatory flight. J Comp Physiol A 181: 247–255

Maddess T, Laughlin SB (1985) Adaptation of the motion-sensitive neuron H1 is generated locally and governed by contrast frequency. Proc R Soc Lond Ser B 225: 251–275

Miles F, Kawano (1987) Visual stabilization of the eyes. Trends Neurosci 10: 153–158

Olberg RM (1981) Object- and self-movement detectors in the ventral nerve cord of the dragonfly. J Comp Physiol A 141: 327–334

Olberg RM (1986) Identified target-selective visual interneurons descending from the dragonfly brain. J Comp Physiol A 159: 827–840

Regan D, Beverly KI (1984) Figure-ground segregation by motion contrast and by luminance contrast. J Opt Soc Am A 1: 433–442

Reichardt W, Egelhaaf M, Guo A (1989) Processing of figure and background motion in the visual system of the fly. Biol Cybern 61: 327–345

Reichardt W, Poggio T, Hausen K (1983) Figure-ground discrimination by relative movement in the visual system of the fly. Part II: towards the neural circuitry. Biol Cybern 46 [Suppl]: 1–30

Ruyter van Steveninck RR de, Zaagman WH, Mastebroek HAK (1986) Adaptation of transient responses of a movement-sensitive neuron in the visual system of the blowfly *Calliphora erythrocephala*. Biol Cybern 54: 223–236

Srinivasan MV, Lehrer M, Horridge GA (1990) Visual figure-ground discrimination in the honeybee: the role of motion parallax at boundaries. Proc R Soc Lond Ser B 238: 331–350

Sterling P, Wickelgren BG (1969) Visual receptive fields in the superior colliculus of the cat. J Neurophysiol 32: 1–15

Strausfeld NJ, Gronenberg W (1990) Descending neurons supplying the neck and flight motor of Diptera: organization and neuroanatomical relationships with visual pathways. J Comp Neurol 302: 954–972

Tanaka K, Hikosaka K, Saito H, Yukie M, Fukada Y, Iwai E (1986) Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. J Neurosci 6: 134–144

Tsai HJ (1990) Responses of toad's tectal neurons to in-phase movements of object and textured background. J Comp Physiol A 167: 857–863

Virsik R, Reichardt W (1976) Detection and tracking of moving objects by the fly *Musca domestica*. Biol Cybern 23: 83–98

Warzecha A-K, Egelhaaf M, Borst A (1993) Neural circuit tuning fly visual interneurons to motion of small objects. I. Dissection of the circuit by pharmacological and photoinactivation techniques. J Neurophysiol 69: 329–339