Neurons involved in the processing of optic flow are usually analyzed using stimuli designed by the experimenter. However, in real life optic flow depends on locomotive behavior. We characterized the performance of motion-sensitive neurons in the visual system of the fly using optic flow as occurring in behavioral situations during object fixation. Optic flow generated by tethered flying flies in a flight simulator was subsequently replayed while recording the responses of two cell types in the fly’s motion pathway presumably involved in the detection of objects and of deviations from a straight flight course, respectively, FD1b cells, which are representatives of the so-called figure-detection cells, responded very specifically to object motion. Although object selectivity of these cells is attributable to inhibition during large-field motion, the influence of background motion during object fixation was almost negligible. In contrast, the cells of the so-called horizontal system (HS cells) are most sensitive to background motion, as elicited during deviations of the animal from its course. During object fixation, the responses of HS cells depended on both object and background motion. The simulated distance of the background to the fly did not have a strong influence on the responses of either cell type. The specificity for detecting deviations from a straight course is enhanced by subtraction of the signals of HS cells in both halves of the brain. In contrast, the FD1b cells in the two halves of the brain need to interact in a nonlinear way to ensure efficient detection of objects.

Key words: behaviorally relevant stimuli; figure-ground discrimination; insect; object fixation; optic flow; visual system

**MATERIALS AND METHODS**

**Animal preparation.** Blowflies of the genus *Lucilia* were obtained from laboratory stocks. All experiments were done on female flies. For intracellular recordings flies were used that had hatched not more than 2 d before the experiment. The flies taken for extracellular recordings were usually older than 2 d. Animals were prepared as reported previously (Kimmerle and Egelhaaf, 2000). In short, the rear surface of the head capsule was opened to get access to the right optic lobe from posterior. The head capsule was supplied with Ringer’s solution. To avoid movements, the proboscis was cut, and the gut was pulled out from behind. The antennae were removed, and the antennal muscles were cut. 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’s solution. The wounds were sealed with wax. The animals were adjusted in the setup by aligning the eye equator in a horizontal plane. Electrophysiological recordings were always performed in the right optic lobe.

**Recording techniques.** All FD1b cells were recorded extracellularly with glass electrodes (Hägenberg or Clark; outer/inner diameter: 1.5/1.17 mm). Pulled on a vertical puller (Getra, Munich, Germany) and filled with 1 M KCl solution, the electrodes had resistances of 4–8 MΩ. A wide tip electrode filled with Ringer’s solution and connected to a syringe was used as an indifferent electrode and to control solution supply to the head capsule. The recorded signal was bandpass-filtered and amplified with standard electrophysiological equipment (built by the electronic workshop of the Max-Planck-Institut (MPI) für biologische Kybernetik, Tübingen, Germany). Spikes were transformed into pulses of fixed height and duration and fed into a personal computer (PC) via the digital or the analog-to-digital (A/D) port of an I/O card (DT2801 A; Data Translation, Germany).
Marlboro, MA) at a sampling rate of 1 kHz. Most of the recordings were additionally stored on DAT (recorder: DTC-670; Sony, Tokyo, Japan). In these cases spike discrimination was performed off-line. All HS cells were recorded iontophoretically with glass electrodes filled with 0.1 M KCl (Sutter Instruments, San Rafael, CA) and with 1 M KCl solution, the electrodes had resistances of 40–90 MΩ. Different electrodes were the same in the extracellular recordings. To confine the current spread to the particular functional criteria (see below), in some experiments the cells were stained iontophoretically (current, approximately −1 nA). In these cases the electrodes were filled with a solution of Lucifer yellow (Sigma, Deisenhofen, Germany) and stained cells were examined in the living animal without further dissection under a fluorescence microscope (Optonplan; Leitz, Wetzlar, Germany). The recorded signal was amplified 10-fold with standard electrophysiological equipment (built by the electronic workshop of the MPI für biologische Kybernetik, Tübingen, Germany). The recorded signal was amplified 10-fold with standard electrophysiological equipment (built by the electronic workshop of the MPI für biologische Kybernetik, Tübingen, Germany). The recorded signal was amplified 10-fold with standard electrophysiological equipment (built by the electronic workshop of the MPI für biologische Kybernetik, Tübingen, Germany). The recorded signal was amplified 10-fold with standard electrophysiological equipment (built by the electronic workshop of the MPI für biologische Kybernetik, Tübingen, Germany). The recorded signal was amplified 10-fold with standard electrophysiological equipment (built by the electronic workshop of the MPI für biologische Kybernetik, Tübingen, Germany). 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RESULTS

Spatial integration properties of the FD1b cell

FD1b cells are excited by front-to-back motion of small objects in the ipsilateral visual field and are inhibited by motion in the opposite direction. The excitatory receptive fields of the FD1b cells as recorded in the present study were centered around an azimuthal position of +15°. Their frontal margins were determined to lie between −15° and −45° and their lateral margins to lie between +60° and +90° (Fig. 1a). The distinguishing feature of all FD cells is that they respond stronger to motion of small objects than to large-field motion (Egelhaaf, 1985b). This was also the case for FD1b cells (Fig. 1b). Inhibition of the FD1b cell was strongest, for rotational large-field motion around the fly’s vertical body axis was presented binocularly and weaker when large-field motion was restricted to the ipsilateral side of the visual field. Based on their preferred direction of motion (front-to-back) and the location of their excitatory receptive field (centered at +15°) the FD1b cells could be classified as FD1 according to the original classification system for FD cells (Egelhaaf, 1985b). However, unlike FD1 cells, they were inhibited by contralateral motion not only in one but in both directions and were therefore named FD1b (Fig. 1b; Kimmerle and Egelhaaf, 2000). Inhibition was stronger during contralateral back-to-front motion than during front-to-back motion (Fig. 1b). Contralateral front-to-back motion reduced the activity of the FD1b cell to simultaneous motion of an object at +15° virtually independent of the stimulus position in the contralateral visual field (Fig. 1c). In contrast, inhibition by contralateral back-to-front motion was stronger in the frontal part of the visual field.

Cellular responses to behaviorally generated optic flow

The results shown in Figure 1 indicate that the selectivity of FD1b cells for moving objects is attributable to an inhibitory input reducing their firing rate during background motion. The question thus arises how well these cells signal object motion in behavioral situations in which the optic flow is continuously changed by the animal’s flight behavior and in which the eyes are confronted with simultaneous object and background motion. Moreover, how do the responses of FD1b cells compare with responses of cells that are not inhibited by large-field motion, such as the HS cells?
Optic flow stimuli generated by the fly in a flight simulator during object fixation (Kimmerle et al., 2000) were replayed while recording the activity of FD1b and HS cells (Fig. 2). In the flight simulator (Fig. 2a) the yaw torque of the fly was continuously measured (Fig. 2b) and directly coupled to the velocity of object and background. As in free flight, a clockwise torque resulted in counterclockwise pattern rotation around the vertical axis of the fly and vice versa. To simulate a situation in which the fly passes a close object in front of an infinitely distant background, a constant front-to-back velocity (“translational motion”) was added to the object motion but not to the background motion. During an initial period of background motion alone the fly tried to stabilize the retinal image, as indicated by torque fluctuations around the zero level (Fig. 2b, white area; Heisenberg and Wolf, 1988; Warzecha and Egelhaaf, 1996). Then the object appeared in front of the fly, and the fly tried to turn toward it as can be inferred from the shift of the average turning strength to positive values (Fig. 2b, shaded area). As a consequence of this response the object could be fixated by the fly in the frontolateral part of the visual field (Fig. 2c). The continuous torque fluctuations produced by the fly led to pronounced velocity fluctuations of object and background (Fig. 2d).

The motion traces generated in this way were replayed (Fig. 2e) while recording the responses of FD1b and of HS cells. Before the object appeared in the visual field, the FD1b cells fired only weakly (Fig. 2f). However, after appearance of an object strong responses were elicited during object motion in the preferred direction of the FD1b cell. The response modulated with the velocity of the object. In contrast, the HS cells strongly responded to background rotation before the object appeared (Fig. 2g). The changes in the membrane potential mainly followed the time course of the background ve-
After appearance of the object the membrane potential fluctuations continued to follow the rotational velocity of object and background without obvious changes.

Further fixation trials were chosen for replay (Fig. 3). The motion stimuli used in the second replay condition originated from a behavioral situation in which the background was simulated to be distant and the object to be close (Fig. 3a). After the object was introduced, it was fixated in the frontal part of the right visual field (Fig. 3a, top panel). As a consequence, the velocity of the object was fluctuating around zero, whereas the background in both parts of the visual field was drifting in the direction opposite to the turning direction (Fig. 3a, second panel from top). As in the first replay condition, the FD1b cell fired only weakly during background motion alone. Stronger modulations of the firing rate were measured during object motion (Fig. 3a, third panel from top). The membrane potential of the HS cells was strongly modulated by background motion before the object appeared (Fig. 3a, bottom panel). Because the background was translating from front to back, corresponding to the preferred direction of the HS cells, an average depolarization of the HS cells was observed. During object fixation, the HS cells were, on average, hyperpolarized because of the background drifting in the opposite of the preferred direction of the cells.

The motion traces used in the third replay condition were generated in a behavioral experiment in which the object was simulated to be very close and the background to be distant (Fig. 3b). The fly could not fixate the object over an extended period of time (Fig. 3b, top panel). However, several strong turns shortly after the start of object motion compensated the object’s translational velocity to some extent for a brief period of time (Fig. 3b, second panel from top). The FD1b cell responded to the appearance of the fast object with a strong activity increase (Fig. 3b, third panel from top). Because the object moved out of the receptive field of the FD1b cell very quickly, the response was only short. The HS cells were on average depolarized before the object appeared because of the translating background (Fig. 3b, bottom panel). During the attempt of the fly to fixate the object, the concurrent counterrotation of the background led to a hyperpolarization of the HS cells.

In summary, FD1b cells fired weakly as long as no object was present, whereas the membrane potential of HS cells strongly modulated with the background velocity. FD1b cells started responding strongly after the object appeared in their receptive field. In contrast, the response of HS cells during object fixation seemed to be less strongly influenced by object motion and more strongly influenced by background motion.

Responses of cells contralateral to the object

In all experiments described so far, the object was moving in the visual field ipsilateral to the recorded cells. Because visually guided behavior is mediated by neurons in both halves of the brain, one also has to take into account the responses of the respective cells contralateral to object motion. In the present experiments, the responses of FD1b and HS cells contralateral to object motion were inferred from the responses of the recorded cells to the mirror symmetric versions of the stimuli. To interpret the responses of neurons in both halves of the brain with respect to their potential significance in visually guided orientation behavior, one needs an assumption about how their signals interact on the way to the motor output. As a working hypothesis, the signals originating from the ipsilateral and the contralateral neurons were supposed to be subtracted (for an explanation, see Materials and Methods).

As expected, unlike ipsilateral FD1b cells contralateral FD1b cells did not respond with a strong increase in firing rate modulation after object appearance in the second replay condition (Fig. 4a). However, a slight increase of the average firing rate as compared to the period before object appearance was observed (Fig. 4a, bottom curve). This increase can be explained by the fact that object fixation was accompanied by background rotation in the preferred direction of the contralateral FD1b cells.

Subtraction of the ipsilateral and contralateral FD1b responses led to an attenuation of the response increase as was recorded in ipsilateral FD1b cells after object appearance (Fig. 4b). The firing rate modulations followed the changes in object velocity rather closely. However, fast negative velocity transients of the object are only partly reflected in the response trace. This can be explained by the limited dynamical response range of the ipsilateral FD1b cell.
during motion in the anti-preferred direction, which is attributable to the relatively low resting activity of the cell. The responses of ipsilateral and contralateral HS cells to the same replay appeared to be almost mirror-symmetrical, both before and after object appearance (Fig. 4c). As a consequence, after subtraction the signal had a very similar time course as the HS responses of each optic lobe when regarded separately (Fig. 4d). The HS response followed the changes in background velocity very closely. In the following quantitative analyses the responses obtained after subtracting the cellular signals of both halves of the brain will be considered in addition to the responses of the cells ipsilateral to the object.

**Specificity of the FD1b cell and HS cells for object and background motion**

How strong are the responses of both cell types to an object moving in front of its background during fixation as compared to background motion alone? The ipsilateral FD1b cells responded more strongly to object than to background motion in the preferred direction, irrespective of the replay condition (Fig. 5a). When the responses of the FD1b cells of both optic lobes were subtracted, the differences between the firing rates during object and background motion became smaller (Fig. 5b). The difference signal of the two heterolateral FD1b cells was thus less specific for preferred direction object motion than the response of the ipsilateral FD1b cell alone.

The HS cells became more depolarized during background motion than during object motion in the preferred direction (Fig. 5c). In two replay conditions the HS cells were hyperpolarized during object motion in the preferred direction, which can be explained by the concurrent motion of the background in the opposite direction. The differences between the responses to background motion and object motion became more pronounced when the signals of the ipsilateral and contralateral HS cells were subtracted (Fig. 5d). The HS cells thus can be concluded to respond rather specifically to background motion when confronted with optic flow as generated in a behavioral situation. Subtraction of the signals from both optic lobes is suited to increase the specificity of the HS cells for rotational background motion around the fly’s vertical body axis.

**Influence of object and background motion during object fixation**

Each of the motion sequences used for replay was modified in two ways to compare the influence of object and of background motion on the responses of FD1b and the HS cells during object fixation. This approach is illustrated in Figure 6 for the second replay condition (close object, distant background). In an “only object” version background motion was stopped when the object appeared (Fig. 6a, top panel). The object moved as in the original motion trace. In an “only background” version (Fig. 6a, bottom panel) no object was displayed, whereas background motion continued in the same way as in the original motion trace. In the present example, the modulations of the firing rate of FD1b cells in response to object motion did not seem to be affected in a conspicuous way by the absence of background motion (Fig. 6b, compare top and middle response traces). This notion is supported by the high correlation of both responses (Fig. 6b, peak at time 0 in upper CCG). If no object was displayed, the FD1b cells almost ceased firing because of background rotation in the opposite of the preferred direction of the cells (Fig. 6b, bottom response trace). Accordingly, the correlation between the responses to original and only background replay was weak (Fig. 6b, lower CCG). The HS cells were, on average, less hyperpolarized during presentation of the only object version than during presentation of the original motion trace (Fig. 6c, compare top and middle response traces). In contrast to the effect of this modification on the average potential, the time course of the membrane potential modifications was similar during presentation of the original and modified motion traces, as indicated by the strong correlation (Fig. 6c, upper CCG). When presenting the only background version, the membrane potential modifications of the HS cells were weaker than during presentation of the original motion traces (Fig. 6c, compare bottom and middle response traces) and accordingly the correlation was comparatively weak (Fig. 6c, lower CCG).

Thus, whereas the responses of FD1b cells were only weakly influenced by background motion but strongly influenced by object motion, the responses of the HS cells depended in a more complex way on object and background motion: removing background motion mainly affected the average membrane potential, whereas removing the object had a stronger influence on the modulations of the membrane potential.

The influence of either modification on the cellular responses to the different replay conditions was quantified in terms of the peak of the respective CCG and in terms of the changes in the average response rate (Fig. 7). The average responses of ipsilateral FD1b cells hardly changed when the only object versions of the first two replay conditions were presented (Fig. 7a, filled symbols). In contrast, they decreased during presentation of the only background version (Fig. 7a, open symbols). Hence, the activity of FD1b cells in these situations was almost exclusively determined by object motion and independent of background motion. The only object
version of the third replay condition increased the FD1b activity, whereas the activity in the corresponding only background version led to an activity decrease compared to the response to the original replay. After subtraction of the ipsilateral and the contralateral responses the influence of background motion, i.e., the increases in the mean firing rate caused by presentation of the only object version, became significantly more pronounced in the second replay condition \((p < 0.01, \text{paired } t \text{ test}; \text{compare filled triangles in Fig. 7a,b}).\)

The temporal modulations of the firing activity of the ipsilateral FD1b cell were not much changed during presentation of the only object versions of the tested replay conditions as is indicated by the strong correlation of the respective responses as well as by direct comparison of the response traces (Fig. 7c). Thus, background motion had only very little influence on the modulation of the firing rate of the FD1b cell. The opposite was true for object motion. Almost no correlation remained between the only background and the original versions. Subtraction of the responses of the ipsilateral and contralateral FD1b cells led to the same conclusion (Fig. 7d).

The average response of the ipsilateral HS cells was influenced by both object and background motion (Fig. 7e). During presentation of the only object versions the membrane potential was raised above the level measured during presentation of the original motion traces. Presentation of the only background version resulted in a more negative average membrane potential. Subtraction of the HS signals of both optic lobes further increased the influence of background motion considerably \((p < 0.05 \text{ for each of the replay conditions, paired } t \text{ test}; \text{compare filled triangles in Fig. 7e,f}).\)

The membrane potential modulations of the ipsilateral HS cells were slightly altered during presentation of the “only object” versions (Fig. 7g). More pronounced changes were obtained when object motion was removed. The influence of object motion on the membrane potential modulations of the HS cells was thus stronger than the influence of background motion. However, the differences between the modifications were not as strong as in FD1b cells. An inversion of the relative contribution of object and background motion was observed after subtraction of the responses of the HS cells in both optic lobes (Fig. 7h). In this case stopping background motion had a stronger impact on the response modulation than removing the object.

In summary, replaying optic flow experienced by a fly in three different behavioral situations of object fixation revealed that in each situation object motion was the key determinant for the activity of FD1b cells. Background motion had only little influence on the FD1b cell responses, although this cell is assumed to owe its selectivity for object motion to inhibitory input from cells sensitive for large-field motion. The responses of the HS cells depended on both object and background motion. Subtraction of the response of both optic lobes led to an increase of the influence of background motion in both cell types.

**Influence of simulated background distance**

Does the distance between object and background have any influence on the responses of FD1b and HS cells to object motion? To answer this question, three fixation trials were chosen from the behavioral experiments in which the simulated distances between object, background, and fly were the same (object close, background distant). The translational component of background motion of each of the three motion traces was subsequently modified (1) by stopping background motion completely, (2) by eliminating...
the translational component of background motion, thus mimicking an infinitely distant background, or (3) by increasing the translational velocity to simulate a closer background. These changes refer to the entire trial, i.e., before and after object appearance. The average firing activity of ipsilateral FD1b cells neither changed significantly when background motion was stopped nor after increasing or decreasing the translational velocity of background motion and thus the simulated distance of the background to the fly (Fig. 8a, paired t test). However, an influence of background translation was observed when the signals of the FD1b cells of both optic lobes were subtracted (Fig. 8b). In this case, the firing rate decreased with increasing velocity of background translation, i.e., with increasing background proximity. The modulation of the firing activity of FD1b cells was neither much affected by stopping background motion nor by changing its translational velocity. This was true for both the responses of the ipsilateral cells (Fig. 8c) as well as for the subtracted signal from both optic lobes (Fig. 8d).

The average membrane potential of ipsilateral HS cells was more positive when background motion was stopped (Fig. 8e; p < 0.05 for the first and second motion trace, not significant for the third motion trace; paired t test). No changes were observed after eliminating the translational component of background motion or after increasing the translational velocity. The same conclusion could be drawn when the signals of the cells of both optic lobes were subtracted (Fig. 8f). The membrane potential modulations of the HS cells were somewhat attenuated by stopping background motion (Fig. 8g). This effect was increased when the signals of both optic lobes were subtracted (Fig. 8h). Changing the velocity of background translation did not much affect the membrane potential modulations of the HS cells.

In summary, stopping background motion increased the average responses and attenuated the membrane potential modulations of HS cells. Changing the simulated distance of the background did not change the responses of any of the two cell types. Only if the signals of the FD1b cells of both optic lobes were subtracted the response decreased with increasing background proximity.
**DISCUSSION**

Motion-sensitive cells presumably involved in object detection (FD1b cells) and cells of the compensatory optomotor system (HS cells) were confronted with optic flow as experienced by a behaving fly engaged in object fixation. FD1b cells responded very specifically to object motion. The responses were to a large extent independent of concurrent background motion. This finding was surprising, given the fact that FD1b cells are most likely inhibited by neurons most sensitive to large-field motion. In contrast, the responses of HS cells depended on both object and background motion. Whereas object motion had a stronger influence on the temporal modulation of the HS response than background motion, background motion had a stronger influence on the average response level than object motion. Subtraction of the signals of both optic lobes led to a decrease in the specificity of FD1b cells for object motion and to an increase of the specificity of the HS cells for background motion.

**Classification of FD1b cells**

FD cells were first described by Egelhaaf (1985b). Introducing a new classification system, Gauck and Borst (1999) subdivided FD-like cells according to whether and how strong they are inhibited during ipsilateral large-field motion. Ipsilateral inhibition, however, might be masked by the ipsilateral excitatory input if the horizontal extent of the motion stimulus is not sufficiently large (Kimmerle and Egelhaaf, 2000). This notion is corroborated by the finding that ipsilateral inhibition was much stronger in the present as compared to a previous study on the FD1b cell, in which we used stimuli with a smaller horizontal extent (Kimmerle and Egelhaaf, 2000, their Fig. 1, compare b, second box with a, second box; the shift of the median of the $R_{LF}/R_{SF}$ distributions amounts to 0.53). Because all FD1b cells recorded in the present study received inhibitory input from both the ipsilateral and the contralateral visual field and because the strength of binocular and of ipsilateral inhibition was unimodally distributed, we suggest that FD1b cells form a homogeneous class of cells that cannot be further subdivided on the basis of their presently known properties. FD1b cells are likely to belong to the so-called rCI-Ha cells of the Gauck and Borst (1999) classification scheme.

**Replay of behaviorally generated optic flow**

In the present study behavioral and cellular responses were not recorded simultaneously. Electrophysiological recordings in behaving animals are possible in some behavioral paradigms, for instance, in monkeys (Newsome et al., 1989; Gallant et al., 1998;
Vinje and Gallant, 2000) (for review, see Newsome, 1997) but can hardly be achieved in flying flies (but see Heide, 1983). Can the cellular responses recorded in the present replay experiments be regarded as equivalent to the responses in behavioral situations? Replaying behaviorally generated optic flow in a behavioral situation in the flight simulator under open-loop conditions induces weaker responses of the flies than in the preceding closed-loop situation (Heisenberg and Wolf, 1988). However, there is evidence that the latter effect is attributable to signal processing at a stage subsequent to the motion-sensitive TCs: (1) the responses of another fly TC (the H1 cell) are the same in a tethered flying fly and in a fixed fly (Heide, 1983). (2) The response variability of TCs is much smaller than behavioral variability. Bimodal response distributions as found in object fixation behavior (Kimmerle et al., 2000) could not be found in any TC so far. In model simulations a considerable amount of noise had to be added to the output of a single pair of TCs to simulate realistic optomotor behavior in the fly (Warzecha and Egelhaaf, 1996). (3) So far, there is no evidence that the responses of TCs are influenced by other sensory pathways than the visual pathway or by nonvisual signals from the central parts of the fly brain. Therefore, the responses of the FD1b and HS cells recorded in replay experiments are considered to be indicative of the responses of these cells in a behavioral situation.

Object and background specificity
HS cells responded rather specifically to background motion, i.e., they were more strongly activated before the object appeared than during object fixation (Fig. 5c). This can be explained by the fact that, when the fly tried to turn toward the object, the background rotated in the opposite (the HS cells’ anti-preferred) direction. This counter-rotation also explains why stopping background motion during the period of object fixation led to an increase in the average membrane potential of the HS cells (Fig. 7e). The HS cells were also influenced by object motion because the object was moving within their receptive field. Consequently, not displaying the object led to a stronger hyperpolarization. During the period of object fixation the average responses of the HS cells did not depend on background translation, at least for the tested translational velocities (Fig. 8e). This finding cannot be explained on the basis of the response properties of HS cells which were, so far, determined with constant velocity motion (Hausen, 1982b; Horstmann et al., 2000).

In contrast to HS cells, FD1b cells responded specifically to object motion and only weakly during background motion alone (Fig. 5a). This finding is most likely the consequence of inhibitory input FD1b cells receive from TCs sensitive to large-field motion. During object fixation the responses of FD1b cells were mainly determined by object motion, whereas background motion had little influence on the cellular response (Figs. 7a,c, 8a,c). This property is by no means trivial, because object selectivity of the FD1b cell is based on inhibition during background motion (Fig. 1). The inhibitory elements might themselves be inhibited during object fixation and concurrent background counterrotation. Moreover, the FD1b cells were not only affected by background motion via inhibitory large-field elements but also directly by their retinotopic input. The relative independence of the responses of FD1b cells from background motion during object fixation is probably a consequence of a balance between excitation and inhibition mediated by the retinotopic input as well as between inhibition and disinhibition mediated by large-field elements. Thus, although object selectivity is attributable to inhibitory input from elements tuned to large-field motion, the neuronal circuitry seems to be organized such that the influence of background motion on FD1b cell firing is reduced to a minimum in behaviorally relevant situations.

Processing of the signals of both optic lobes
Optomotor course stabilization in flies has been suggested to result from a subtraction of signals mediated by motion-sensitive cells in the right and the left optic lobe (Götz, 1975). As a working hypothesis, we initially assumed that further processing of both the HS and FD1b responses might involve subtraction (see Materials and Methods). For both cell types the difference signals were more strongly influenced by background motion than the responses of the respective ipsilateral cell alone. Course stabilization is accomplished by a reduction of global rotational movements. Assuming that HS cells play a central role in this behavioral context, their increasing specificity for background motion resulting from signal subtraction appears advantageous and supports the hypothesis of Götz (1975). Subtraction of the heterolateral neuronal signals could be realized by linear transmission and a simple symmetrical connection to the flight motor without lateral interactions. For object fixation, a stronger influence of background motion cannot be considered supportive. Therefore, subtraction does not appear a suitable way to integrate the signals of the FD1b cells of both optic lobes. We suggest that transmission of the FD1b signals to the motor system may involve lateral inhibitory interactions and/or nonlinearities such as a threshold. Such mechanisms could avoid the high selectivity for object motion of the FD1b cell being compromised by the respective contralateral cell that is not subjected to object motion.

General implications
Cells sensitive to relative motion between an object and its background have been found in different species (see introductory remarks). In primates, the responses of such cells located in cortical area MT are further integrated on a higher processing level in area MST. Cells in different regions of area MST are sensitive to optic flow as might occur during self-motion as well as to object motion (Tanaka et al., 1993; Duffy and Wurtz, 1995; Britten and Wezel, 1998). Accordingly, area MST has been suggested to play a central role in navigation and figure-ground segregation. So far MST cells have been characterized mainly with artificially designed optic flow stimuli. The present study underlines the significance of behaviorally generated stimuli when assessing the characteristics of visual interneurons. FD cells are likely to be key elements in figure-ground discrimination during flight and appear thus suited to guide the fly’s approach toward objects of potential interest (e.g., landing sites). When confronted with stimuli as occur in a behavioral situation during object fixation, the FD1b cells of the fly show a high degree of object specificity and relative invariance to background motion. We conclude that the use of more naturalistic stimuli in electrophysiological experiments promises a deeper insight into the functional role and performance of nerve cells in real life.

REFERENCES
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