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Visual afferences to flight steering muscles controlling optomotor responses of the fly

Martin Egelhaaf
Max-Planck-Institut für biologische Kybernetik, Spemannstrasse 38, D-7400 Tübingen, Federal Republic of Germany

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Summary. In tethered flying house-flies (*Musca domestica*) visually induced turning reactions were monitored under open-loop conditions simultaneously with the spike activity of four types of steering muscles (M.b1, M.b2, M.I1, M.III1). Specific behavioral response components are attributed to the activity of particular muscles. Compensatory optomotor turning reactions to large-field image displacements mainly occur when the stimulus pattern oscillates at low frequencies. In contrast, turning responses towards objects are preferentially induced by motion of relatively small stimuli at high oscillation frequencies. The different steering muscles seem to be functionally specialized in that they contribute to the control of these behavioral responses in different ways. The muscles I1, III1 and b2 are preferentially active during small-field motion at high oscillation frequencies. They are much less active during small-field motion at low oscillation frequencies and large-field motion at all oscillation frequencies which were tested. M.b2 is most extreme in this respect. These steering muscles thus mediate mainly turns towards objects. In contrast, M.b1 responds best during large-field motion at low oscillation frequencies and, thus, is appropriate to control compensatory optomotor responses. However, the activity of this muscle is also strongly modulated during small-field motion at high oscillation frequencies and, therefore, may be involved also in the control of turns towards objects. These functional specializations of the different steering muscles in mediating different behavioral response components are related to the properties of two parallel visual pathways that are selectively tuned to large-field and small-field motion, respectively.

Abbreviations: FD (cell) figure detection (cell); *HS* (cell) horizontal (cell)

Introduction

Visual orientation behavior is a complex problem: The information conveyed by the retinal input signals has to be processed by the brain and to be transformed into activity patterns of particular muscular systems which finally mediate the motor actions. Various aspects of sensory-motor transformation have been analyzed in different insect species. For three reasons insects are advantageous in this respect. (i) Many species rely heavily on visual information in controlling their orientation behavior. (ii) Although the underlying motor patterns may be complex, to mention only the virtuosic flight maneuvers of many insects, they are often sufficiently stereotyped to allow an experimental analysis under laboratory conditions. (iii) The nervous systems are relatively accessible to an investigation. Moreover, nerve cells involved in sensory information processing and motor control can be identified individually in different animals due to their structural constancy and highly invariant functional properties.

These advantages have been systematically exploited in the fly, analyzing at different levels the mechanisms underlying certain aspects of motion-dependent visual orientation. Behavioral response components as expressed in free (Land and Collett 1974; Collett 1980a, b; Wehrhahn et al. 1982; Wagner 1986a, b) and tethered flight (Reichardt and Poggio 1976; Reichardt et al. 1983; Reichardt 1986; Heisenberg and Wolf 1984; Wehrhahn 1985; Egelhaaf et al. 1988) were studied, as well as the response properties of visual interneurons (Hausen 1984; Egelhaaf et al. 1988; Hausen and Egelhaaf 1989). Moreover, there are various studies concentrating on motor and mechanical aspects of flight control in flies (for review see Nachtigall 1983). The mechanisms underlying the optomotor control

of two types of turning responses have been analyzed in particular detail, (i) the *compensatory optomotor turning reaction* which transforms visually perceived rotatory large-field motion into flight torque and stabilizes the flight course against internal and external disturbances and (ii) *orientation responses towards objects* which are induced by retinal image displacements of relatively small objects and can serve fixation of objects in the frontal part of the retina.

There is now good evidence that these behavioral responses are mediated by two parallel control systems with different sensitivities to the size and the dynamical characteristics of the moving pattern (Geiger and Nässel 1982; Götz 1983b; Heisenberg and Wolf 1984; Egelhaaf 1985a–c, 1987; Bausenwein et al. 1986; Egelhaaf et al. 1988; Hausen and Wehrhahn, in press). In the housefly (*Musca*) and the blowfly (*Calliphora*) one of them ('large-field system') is most sensitive to the motion of extended patterns and controls the yaw torque mainly at low oscillation frequencies (below about 0.1 Hz) of the stimulus. In contrast, the other control system ('small-field system') is tuned to relatively small moving objects and shows its strongest responses at high oscillation frequencies (between about 1 Hz and 4 Hz) i.e. in a frequency range where the large-field system contributes to the turning responses with only a relatively small gain (Egelhaaf 1987). By correlating behavioral response characteristics and physiological properties of visual interneurons two different functional classes of output cells of the third visual ganglion, the Horizontal Cells (HS-cells) and the Figure Detection cells (FD-cells), were concluded to be an integral part of these control systems. Both cell types pool the output of large retinotopic arrays of local movement detectors and are assumed to acquire their different sensitivities to different global retinal motion patterns by specific interactions with other motion-sensitive large-field neurons (Reichardt et al. 1983; Hausen 1984; Egelhaaf 1985c; Hausen and Egelhaaf 1989). The HS-cells are specialized to evaluate large-field image displacements as are induced during rotatory self-motion of the animal about its vertical axis. The outputs of these cells, therefore, signal course deviations and are used to control corrective flight torques (Hausen 1981, 1982a, b; Reichardt et al. 1983; Hausen and Wehrhahn 1983, in press; for review see Egelhaaf et al. 1988; Hausen and Egelhaaf 1989). The FD-cells, on the other hand, signal retinal image displacements of relatively small objects against the background. Their functional significance could, therefore, involve orientation towards objects (Egelhaaf 1985a, b; Egelhaaf et al. 1988).

How are these representations of different global retinal motion patterns transformed into the different behavioral orientation responses? So far, there is not much known in this respect at the cellular level. A comparison of the dynamic properties of the HS- and FD-cells with the behavioral responses, however, suggests that high frequency modulations in the output signals of the HS-cells must be greatly attenuated somewhere between the lobula plate and the final motor output. In contrast, the FD-cells remain effective in controlling yaw torque at high oscillation frequencies (Egelhaaf 1987; Egelhaaf, unpubl.). This suggests that the relative contributions of each cell class to the final motor response varies according to the dynamic properties of stimulus motion.

At the output side of the system there is quite detailed knowledge on the organization of the muscular systems involved in the control of turning responses in flight. There are two groups of flight muscles, (i) the large indirect power muscles which are assumed to flap the wings up and down, and (ii) the small steering muscles which control the different flight maneuvers by adjusting the wing kinematics (for review see Heide 1983). Owing to the electrophysiological and behavioral studies of Heide and co-workers on the blowfly (*Calliphora erythrocephala*) and housefly (*Musca domestica*) (Heide 1971a, b, 1975, 1983; Spüler and Heide 1978; Spüler 1980; Hirth 1981) and of Götz and Heide on *Drosophila* (Götz 1983a, b; Götz and Heide, unpubl.) we know much about the functional properties of some of the steering muscles involved in yaw torque control. The muscles b1, b2, I1 and III1 (nomenclature according to Heide 1971a) have been studied particularly carefully with respect to the turning directions they mediate and their visual afferences. In all these muscles the visual input was shown to be directionally selective for motion with one of the two eyes being dominant in controlling their activity.

The characteristics of the visual input to these muscles was mainly analyzed with grating patterns of a given angular size moving with a constant velocity. These experiments, thus, do not allow an assessment of the role of the large-field and small-field system in controlling their activity. For this reason, it turned out to be necessary to re-examine the functional properties of the steering muscles in this respect. This is the main objective of the present study. Since the large-field and the small-field system were found to differ mainly in their

dynamical and spatial integration properties (see above), the analysis was done with stimuli of varying angular horizontal extent and dynamic properties. In order to allow a direct comparison of steering muscle activity and the different behavioral response components, both were monitored simultaneously. On this basis it has been possible to conclude that the different steering muscles involved in yaw torque control are functionally specialized with respect to their visual afferences and the response components they mediate.

Material and methods

The experiments were performed with female house-flies, *Musca domestica* (L.) obtained from laboratory stocks. The head of the animal was fixed to the thorax with a mixture of wax and colophonium. A triangular piece of cardboard was glued to the wax just above the frontal part of the thorax. The ocelli were covered with the same mixture of colophonium and wax. The legs were removed under light carbon dioxide anesthesia. In preliminary experiments all three pairs of legs were removed. In most of the experiments, however, only the legs on one side of the body were cut off. This seemed to improve the readiness of the animals to fly in the subsequent experiments.

Pieces of tungsten wire (diameter: 0.025 mm; length 10–20 mm) were used as electrodes to record from the different steering muscles. The tips of the electrodes were electrolytically sharpened in a solution of 71 g $NaNO_2$ and 34 g KOH in 100 ml distilled water. Using cuticular marks for appropriate positioning, the electrodes were pushed through the cuticle and inserted directly into the muscle, with the long axis of the electrode roughly parallel to the muscle fibres (M.b2, M.I1, M.III1) or perpendicular to them (M.b1). The muscles are termed according to an anatomical study on *Calliphora* (Heide 1971a). The reference electrode was inserted into the ventral part of the thorax. The electrode wires were fixed to the cuticle at their entrance site with a small drop of wax. The wires were bent downwards to prevent interference with the moving wings. In some experiments two muscles were recorded from simultaneously. In most experiments, however, electrodes were inserted into only one muscle.

With the cardboard triangle at their back, the flies were suspended from a torque compensator which prevented both rotatory and translatory movements of the animal. This allowed the direct measurement of the instantaneous yaw torque (Fermi and Reichardt 1963; Götz 1964). In the flying fly, the electrode wires were grasped by forceps which were mounted on a specifically designed micromanipulator and could be controlled by it. Via the forceps the electrodes were connected to the amplifiers. To improve the signal-to-noise ratio, the signals were fed into a low-pass filter with a cut-off frequency between 1 kHz and 3 kHz. In some experiments the movements of the fly's scutellum were monitored. This was done with a contact free inductive displacement transducer (multi-NCDT, Serie 300; Micro-Epsilon Meßtechnik). Therefore, a small piece of an iron grid was waxed to the scutellum. In the flying fly, the scutellum oscillates roughly sinusoidally with the frequency of the wings. The minimum and maximum values of the signal correspond to the extreme upstroke and downstroke positions of the beating wings. Therefore, this signal could be used as a reference for determining the phase of a muscle spike within the wing beat cycle (Hirth 1981; Heide 1983). The simultaneously recorded yaw torque, muscle spike and wing beat signals were directly inspected on the oscilloscope screen, stored on magnetic tape (3968 A Intrumentation Tape Recorder, Hewlett Packard), further processed by a signal averager (4202 Princeton Applied) and fed into a computer (IBM-AT).

The animals were positioned in the centre of two concentric pattern cylinders with diameters of 105 mm and 100 mm, respectively. The outer cylinder ('ground') was opened in its rear to allow access to the steering muscles with the recording forceps. Its horizontal angular extent amounted to 240°. The inner stimulus pattern consisted of a cylinder segment ('figure') of 10° width. The height of both cylinders was 76 mm which corresponds, in its vertical direction, to an angular extent of the stimulus of about ±21° as seen by the fly. Both the background and the segment of the inner cylinder were covered with a vertical square-wave grating. The spatial wavelength of its fundamental frequency component was 10°. The average luminance of the vertical stripe was about 190 $cd \cdot m^{-2}$ and that of the background cylinder amounted to about 405 $cd \cdot m^{-2}$. The contrast was about 0.45 and 0.6 for the stripe and the background, respectively.

The fly was alternately stimulated by synchronous sinusoidal oscillation of the figure and the background ('large-field motion') and by the figure oscillating alone while the background was kept stationary ('small-field motion'). There was no interval between small-field and large-field motion. The large-field stimulus covered both eyes symmetrically, whereas the vertical stripe mimicking small-field motion was oscillated only in front of one eye at a time. In the experiments shown here the oscillation amplitude was ±10°, the oscillation frequency either 0.1 Hz or 1 Hz. The experiments were carried out under open-loop conditions, i.e. the responses of the fly did not affect the visual stimulus. The data shown here were obtained from a total of 54 flies.

Results

The location of the steering muscles b1, b2, I1 and III1 is shown schematically in Fig. 1 in a lateral view of the thorax. The activity patterns of most of the steering muscles studied here were reported to be controlled by motion in front of both eyes, with one eye, however, clearly being dominant (Heide 1983). In the present study, the fly was alternately stimulated by oscillatory coherent large-field motion in front of both eyes and by small-field motion in front of one eye only. The moving stripe was usually placed in front of the dominant eye. As in other studies, the final motor output mediated by the different steering muscles was simply correlated with their spike activity. The complicated transformation of muscle activity into the different wing beat parameters and eventually the flight torques (Götz et al. 1979; Zanker 1987) was not taken into account.

In most experiments the spike activity of one of the steering muscles and the yaw torque were recorded simultaneously as a function of time. This

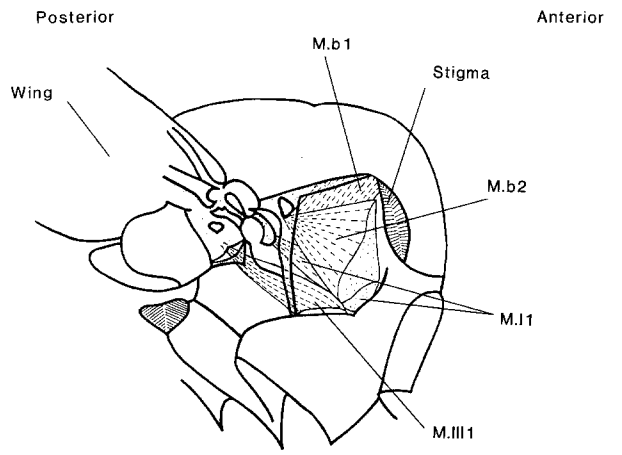

Fig. 1. Lateral view of the right side of the thorax. The steering muscles lying immediately below the cuticle are indicated by dashed lines. Only those muscles which were recorded from are named according to the nomenclature of Heide (1971a). M.b1 and M.b2 insert at the basalar sclerite, M.I1 inserts at the first axillary sclerite, and M.III1 inserts at the third axillary sclerite. Redrawn from Heide (1971a)

was done in each fly for several presentations of the stimulation program which allowed averaging of the resulting responses (Figs. 2a–5a). In all examples shown here, the muscles were recorded on the right side of the animal, while the figure was placed in front of the respective dominant eye at a mean angular position of either +30° or −30° as seen from the frontal midline of the animal (see insets in Figs. 2a–5a). Usually spike frequency histograms were derived from the muscular data. In some flies where M.b1 was recorded, also the phase of occurrence of the spike in the wing beat cycle was monitored in addition (Fig. 5). From the time-dependent responses as measured in different flies the mean amplitudes of the response modulations were determined separately for large-field and small-field motion at both oscillation frequencies (Figs. 2b–5b).

Let us first consider the behavioral responses. In Figs. 2a–5a, positive and negative yaw torques

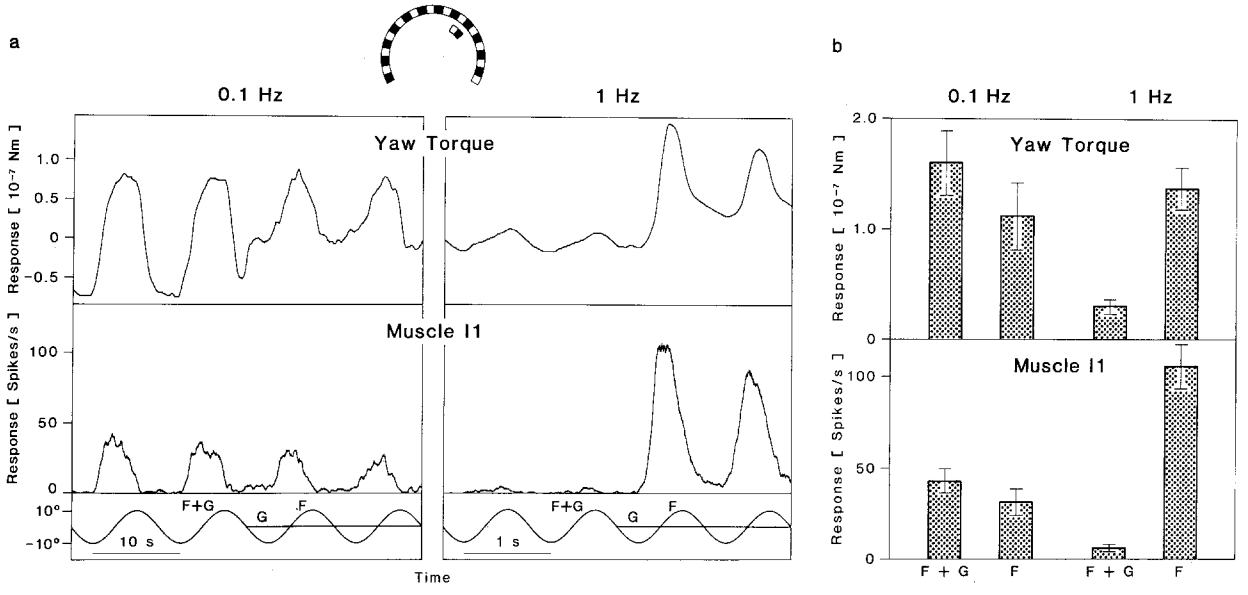

Fig. 2a, b. Simultaneously recorded yaw torque responses and spike activity of the right steering muscle I1. **a** Time-dependent responses; **b** mean amplitude of response modulations. The fly was stimulated by oscillatory motion of a cylindrical stripe pattern (the 'ground' G) and a vertical cylinder segment (the 'figure' F). F was placed in front of the right eye, the dominant eye of the right M.I1, at a mean angular position of 30° as seen from the frontal midline of the animal (see inset). The oscillation frequency amounted to either 0.1 Hz or 1 Hz, as indicated in the figure. Initially F and G were oscillated synchronously for two cycles ('large-field' motion). Then G stopped moving and F continued oscillating for another two cycles ('small-field' motion). In **a** the stimuli are indicated in the bottom diagrams which represent deviations of F and G from their respective mean positions. Upward and downward deflections indicate clockwise and counter-clockwise motion, respectively. The oscillation amplitude amounted to 10°. In the yaw torque traces in **a** positive and negative responses indicate intended turns to the right and left, respectively. The mean response modulations in **b** were derived for 11 flies and a total of 93 (at 0.1 Hz) and 545 (at 1 Hz) stimulus presentations from time-dependent diagrams such as the sample record shown in **a** under the 4 different stimulus conditions used here. Bars: standard error of the mean. The different time-dependent response profiles used for calculating the mean response modulations were average responses each obtained from a single fly and 2–20 (at 0.1 Hz) or 10–80 (at 1 Hz) consecutive stimulus presentations. During oscillatory large-field motion the yaw torque oscillates about the zero line. During small-field motion and, particularly, at high oscillation frequencies positive torques are generated indicating intended turns of the fly towards the figure. The largest yaw torque amplitudes are generated during large-field motion at low oscillation frequencies and small-field motion at high oscillation frequencies. In contrast, the largest response amplitudes are induced in M.I1 during small-field motion at high oscillation frequencies. Its activity is considerably smaller under all other stimulus conditions tested here

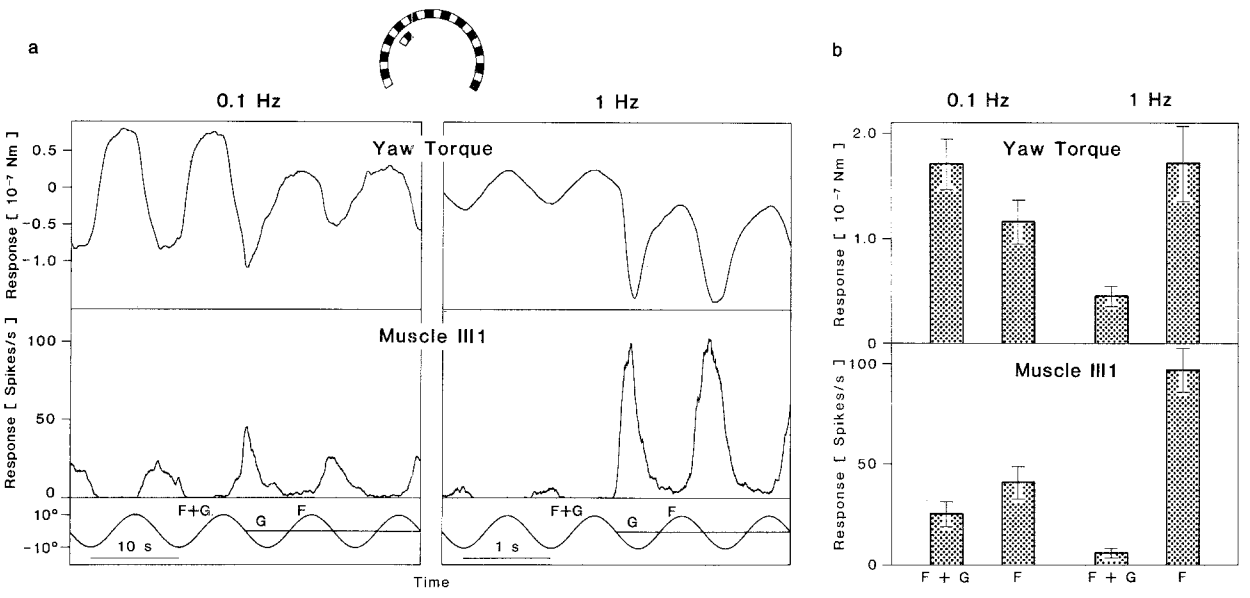

Fig. 3a, b. Simultaneously recorded yaw torque response and spike activity of the right M.III1 as induced by oscillatory large-field and small-field motion at 0.1 Hz and 1 Hz. Data evaluation and stimulus conditions as described for Fig. 2. Only F was placed in front of the left eye at a mean position of −30° as seen from the fly's frontal midline, since M.III1 is activated most prominently by motion in front of this eye. Mean response amplitudes displayed in **b** were derived from 11 flies and a total of 146 (at 0.1 Hz) and 796 (at 1 Hz) stimulus presentations. The behavioral responses are qualitatively same as in Fig. 2. Only during small-field motion negative torques are generated, indicating turns towards the left side, since the figure was placed in front of the left eye. As M.I1, M.III1 shows its most pronounced activity during small-field motion at high oscillation frequencies. It is much less active during all other stimulus conditions tested here

indicate turning tendencies to the right and left, respectively. During rotatory large-field motion the fly tries to follow the pattern motion with the yaw torque being symmetrical around zero. This optomotor response would, in free flight, reduce the relative angular velocity between the stimulus and the eyes. During small-field motion the yaw torque signal no longer oscillates around zero. Instead, it is in the direction which would, under closed-loop conditions, bring the target to the front of the eyes. This means that the average torque responses are positive when the figure stimulates the right eye and negative when it stimulates the left eye. However, the response amplitudes differ under the different conditions. At low oscillation frequencies the response to large-field motion is much larger than to small-field motion. In contrast, at high oscillation frequencies, the response to small-field motion has a much larger amplitude than to large-field motion. These conclusions are supported by the corresponding mean amplitudes of the yaw torque modulations as shown in Figs. 2b–5b. The behavioral data are important as a control, apart from being a reference for the simultaneously recorded muscle activity. Since they are essentially indistinguishable from earlier data obtained in behavioral experiments with intact flies (Egelhaaf 1987), they provide strong evidence, that the dissection procedure used to implant electrodes in the fly's muscles does not impair the yaw torque responses in any obvious way.

The spike frequency of all steering muscles is modulated periodically with the oscillation frequeny of the stimulus and thus correlated in some way with the torque responses. However, the activity patterns of the particular muscles differ in several respects. Most important, they differ in (i) the turning directions during which they are activated, (ii) their spontaneous activity during unstimulated flight, (iii) their preferential activation by the ipsi- or contralateral eye, (iv) their sensitivity to small-field and large-field motion, and (v) their dependence on the oscillation frequency of the stimulus pattern.

M.I1 is most active during intended turns to the ipsilateral side (Fig. 2a), whereas M.III1 and M.b2 fire synergistically during turning reactions to the contralateral side (Figs. 3a and 4a). These muscles are almost inactive during turning reactions in the respective opposite directions as well as during straight flight. Although all three muscles are affected by motion in front of both eyes (Spüler 1980; Heide 1983), they all have a pronounced dominant eye. While M.I1 is activated mainly by front-to-back motion in front of the ipsilateral eye, both M.III1 and M.b2 are excited by front-to-back

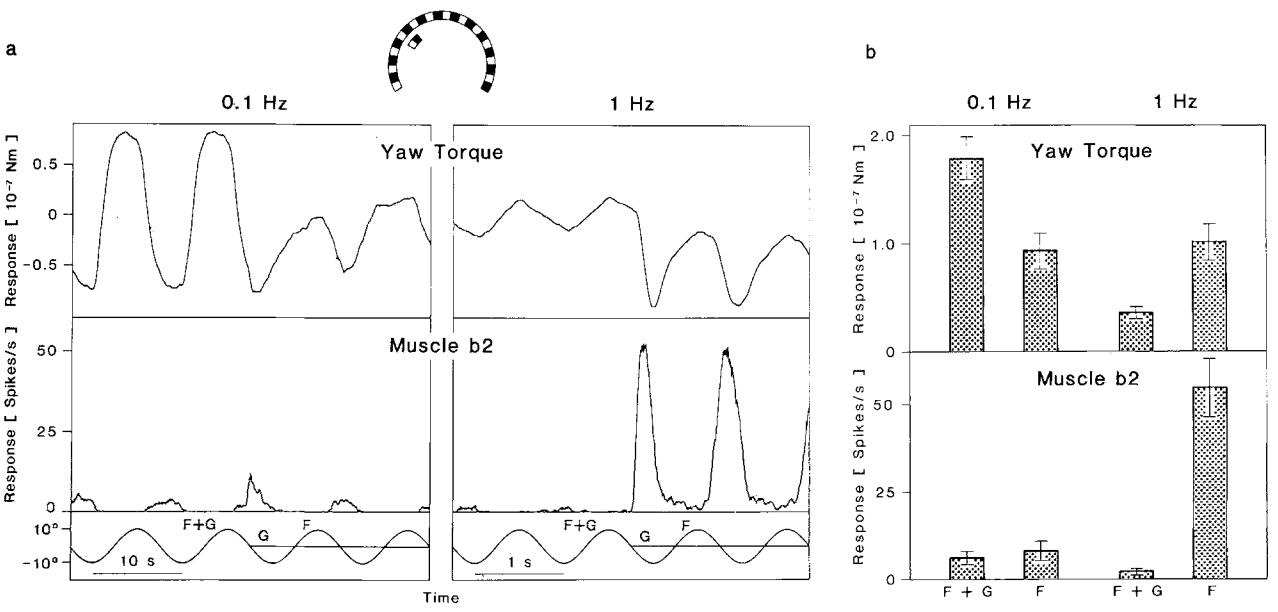

Fig. 4a, b. Simultaneously monitored yaw torque response and spike activity of the right M.b2 as induced by large-field and small-field motion at 0.1 Hz and 1 Hz. Data evaluation and stimulus conditions same as explained in legend of Fig. 2. Only F was placed in front of the left eye at a mean angular position of 30° (see inset). Left eye is the dominant eye for the right M.b2. Behavioral responses were essentially same as the ones shown in Figs. 2 and 3. During small-field motion negative response peaks are induced which indicates intended turns towards the figure in front of the left eye. M.b2 shows only large responses during small-field motion at high oscillation frequencies. Only weak responses can be observed under the other stimulus conditions tested here. In this respect, M.b2 is more extreme than M.I1 and M.III1. Mean data shown in **b** derived from 12 flies and a total of 129 (at 0.1 Hz) and 489 (at 1 Hz) stimulus presentations

motion in front of the contralateral eye. These findings are fully in accordance with previous studies (Heide 1971b, 1975, 1983; Spüler and Heide 1978; Spüler 1980; Götz 1983a). However, two important features of M.I1, M.III1 and M.b2 have not been reported before. (i) Their activity patterns depend on the dynamic properties of the visual stimuli. (ii) They are activated in a different way during coherent large-field motion in front of both eyes and small-field motion in the visual field of their dominant eye. As is obvious from both the time-dependent diagrams and the mean response amplitudes (Figs. 2–4), these muscles show by far their largest activity at high oscillation frequencies during small-field motion in front of their dominant eye. Under all other stimulus conditions their activity is, although to a different degree, considerably smaller. M.b2 is most extreme in this respect, in that it responds only very weakly during binocular rotatory large-field motion at both oscillation frequencies as well as during small-field motion at low oscillation frequencies. Under these stimulus conditions, the responses of M.I1 and M.III1 are somewhat larger. In any case, these three steering muscles appear to mediate yaw torque mainly during small-field motion at high oscillation frequencies. They seem to be much less involved in yaw torque control during the other stimulus conditions tested here.

M.b1 differs in various respects from the other steering muscles analyzed here. It fires during all phases of the stimulus cycle and its activity is only modulated about a mean response level. This property is also reflected in a high spontaneous activity during straight flight. With a mean spike rate of 75.8 Hz ($\pm$10.2 S.E.M., $n=10$ flies), the spontaneous activity of M.b1 was found in the present study to be smaller than reported before. This value is significantly smaller than the wing beat frequency which was in the range of 120 and 150. In contrast, other authors (Heide 1971b, 1975, 1983; Götz 1983a) found the spontaneous activity of M.b1 to equal approximately the wing beat frequency. This quantitative difference cannot be resolved so far. It should be noted, however, that it does not seem to be due to a poor state of the animals in the present experiments, because (i) the wing beat frequencies lay in the same range as reported before (Heide 1975), (ii) the corresponding yaw torque responses were as in intact animals (see above), and (iii) the phase of occurrence of the M.b1 spikes within the wing beat cycle was as found in previous

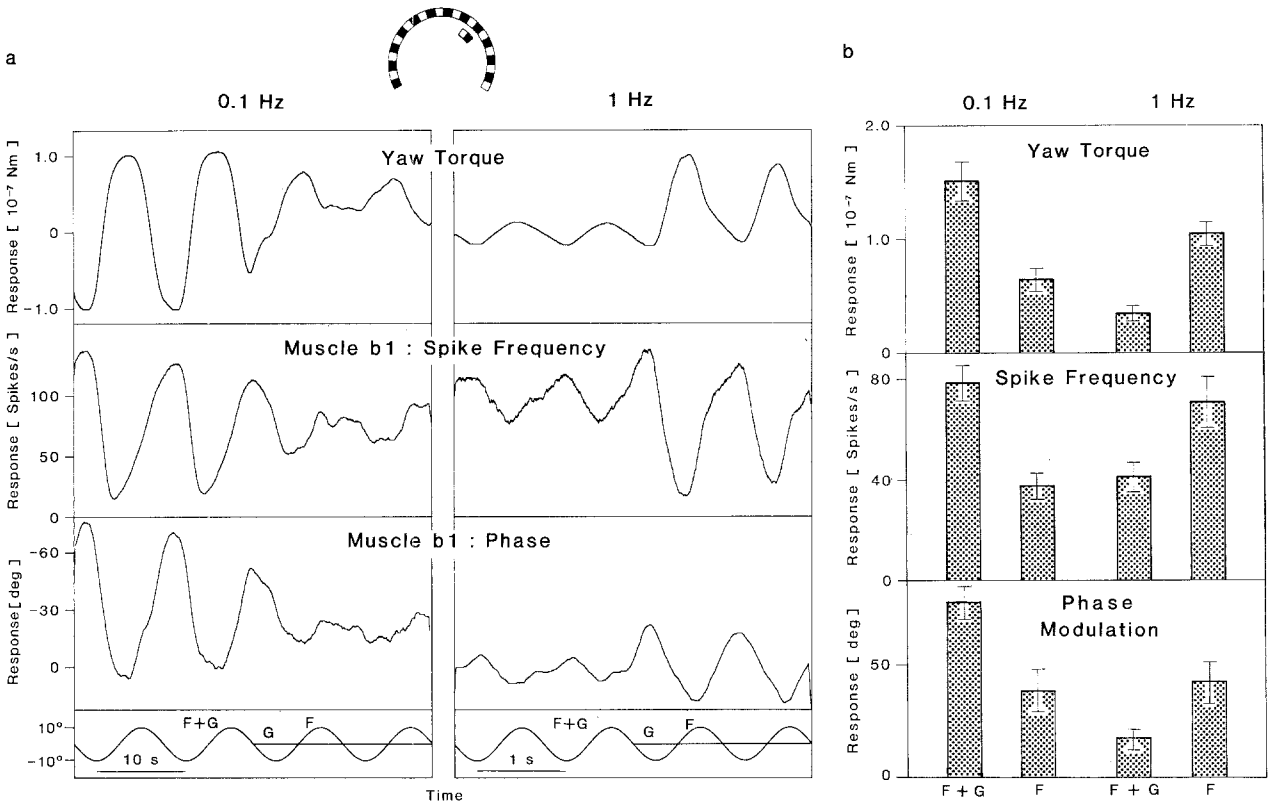

Fig. 5a, b. Simultaneously monitored yaw torque response, spike activity of the right M.b1 and phase of the M.b1 spike within the wing beat cycle as induced by large-field and small-field motion at 0.1 Hz and 1 Hz. Yaw torque and spike frequency evaluated in the same way as described in legend of Fig. 2. To determine the phase of the M.b1 spike, the extreme upstroke position of the wing is used as reference point and was set to 0°. The ratio of the latency between the spike and the nearest reference point to the time interval between the preceding and following reference point was used as phase of the spike in the wing beat cycle. Negative phases thus indicate that the spike occurs before the wing reaches its maximum upstroke position. F was placed in front of the right eye at a mean angular position of 30° (see inset). **b** The mean modulation of the yaw torque, the spike frequency and the phase angle. Behavioral and spike frequency data simultaneously obtained in 17 flies and a total of 215 (at 0.1 Hz) and 794 (at 1 Hz) stimulus presentations. The phase of the M.b1 spike in the wing beat cycle was monitored in addition in only 3 animals and a total of 36 (at 0.1 Hz) and 119 (at 1 Hz) stimulus presentations. The spike frequency of M.b1 during stimulus motion is modulated about a spontaneous activity level. In contrast to the other steering muscles studied here, the response modulations are most pronounced during binocular rotatory large-field motion at 0.1 Hz and small-field motion at 1 Hz. The phase of occurrence of the M.b1 spike is modulated with the oscillation frequency of stimulus motion. The phase is delayed when the spike frequency increases and the fly tries to turn to the contralateral side. Note the quantitative differences in the pattern of mean spike frequencies and phase angles under the conditions tested here

studies (see below). The M.b1 spike rate decreases during induced turning responses to the ipsilateral eye much below the level of spontaneous activity. This is mainly due to an inhibitory effect elicited by ipsilateral motion (see also Heide 1975). At least during large-field motion at low oscillation frequencies the spike rate may also increase above this level. The mean spike frequency modulations of M.b1 depend in a way different from the other steering muscles studied here on both the oscillation frequency and the angular horizontal extent of the stimulus pattern (Fig. 5a, b, middle diagrams). Here the largest response modulations are found during coherent binocular large-field motion at low oscillation frequencies. Almost equally large mean response modulations are induced during small-field motion at high oscillation frequencies. The mean spike frequency modulations during the two other stimulus conditions tested here are considerably smaller. Altogether, the activity pattern of the torque responses is reflected much better by the activity pattern of M.b1 than by any other of the steering muscles tested here.

There is an additional feature of M.b1 which might be important to its role in controlling yaw torque generation. It has been reported that the phase within the wing beat cycle at which the M.b1

spike occurs is well controlled by mechanosensory input from the wings and strongly depends on the stimulus conditions (Hirth 1981; Götz 1983a, b; Heide 1983). The M.b1 spike usually occurs before the wing reaches its extreme upstroke position. When the spike frequency is decreased in some way the phase of the spikes in the wing beat cycle is slightly delayed. The spike may then occur even slightly after the wing has reached its upstroke maximum. Since even at spike frequencies as high as the wing beat frequency M.b1 does not operate under conditions of complete tetanus (Heide 1971b), the remaining small changes in tension during the wing beat cycle were proposed to be important for the fine control of the wing movements (Hirth 1981; Götz 1983a, b; Heide 1983). Although it is hard to assess the relative importance for torque generation of changes in the spike frequency and the phase at which a spike occurs, the changes in the phase relationship of the M.b1 spike was tested in 3 flies. The results are displayed in the bottom diagrams of Fig. 5. The extreme upstroke position of the wing is used as reference point and was set to 0°. The ratio of the latency between the spike and the nearest reference point to the time interval between the preceding and the next reference point was used as phase of the spike within the wing beat cycle (Fig. 5a, bottom diagram). It is obvious from the time-dependent diagrams that the phase of the M.b1 spike is not constant but varies during the stimulation cycle. This variation is synchronous with the modulations in spike frequency. During turns to the contralateral side the phase is advanced, while the spike frequency increases. The mean modulation in phase angle thus parallels the modulation in spike frequency. Nevertheless, there are some quantitative differences. Although both the spike frequency modulations and the phase modulations are most pronounced during large-field motion at low oscillation frequencies, the phase modulation is much smaller during small-field motion at high oscillation frequencies. Here the spike frequency modulations are almost as large as during large-field motion at low oscillation frequencies, whereas the phase modulations have little more than half the amplitude. Whether this difference indicates somewhat different determinants of the spike frequency of M.b1 and the phase within the wing beat cycle at which the spike occurs cannot be decided on the basis of the relatively small number of flies tested in this situation. In any case, both the phase relationship and the spike frequency show a strong dependence on the stimulus during large-field motion at low oscillation frequencies. In this respect they differ considerably from M.I1, M.III1 and M.b2.

Discussion

The different steering muscles mediating turning responses in flying flies are functionally specialized. Depending on the behavioral context, a given yaw torque amplitude may be generated by different combinations of steering muscles. Part of the steering muscles (M.b2, M.III1, MI1) are predominantly active during orientation responses towards objects, whereas another muscle (M.b1) appears to be also involved in optomotor course stabilization. In tethered flying flies, these response components are induced by different types of retinal motion patterns. Turning responses towards objects, and consequently the muscles b2, III1 and I1, are activated mainly during small-field motion at high oscillation frequencies. In contrast, compensatory optomotor turning reactions to rotatory large-field motion are strongest at low oscillation frequencies. Under these stimulus conditions M.b1 shows particularly large modulations in its spike frequency as well as in the phase in the wing beat cycle where the spikes are generated.

Visual afferences representing different types of retinal motion patterns are a decisive determinant of the steering muscles' functional specializations. The properties of these afferences are the result of a sequence of information processing steps, part of which have been characterized at the neuronal level. Some aspects of this pathway are summarized schematically in Fig. 6. The retinal motion patterns are initially evaluated by a two-dimensional retinotopic array of local movement detectors (Reichardt 1987; Egelhaaf et al. 1988). This local motion information segregates at the level of the third visual ganglion into two pathways that are specifically tuned to large-field and small-field motion and, therefore, have been referred to as large-field and small-field system, respectively (Egelhaaf 1987). By correlating the different behavioral response components with the functional properties of visual interneurons the two pathways were concluded to be represented by the HS- and FD-cells which spatially integrate the local movement detectors in a different manner (see Introduction). Not much is known about the cellular mechanisms underlying the further processing of these signals. However, at least two additional information processing stages had to be inferred indirectly by comparing the functional properties of the HS- and FD-cells with the behavioral responses. (i) A kind of frequency filter was proposed in the path-

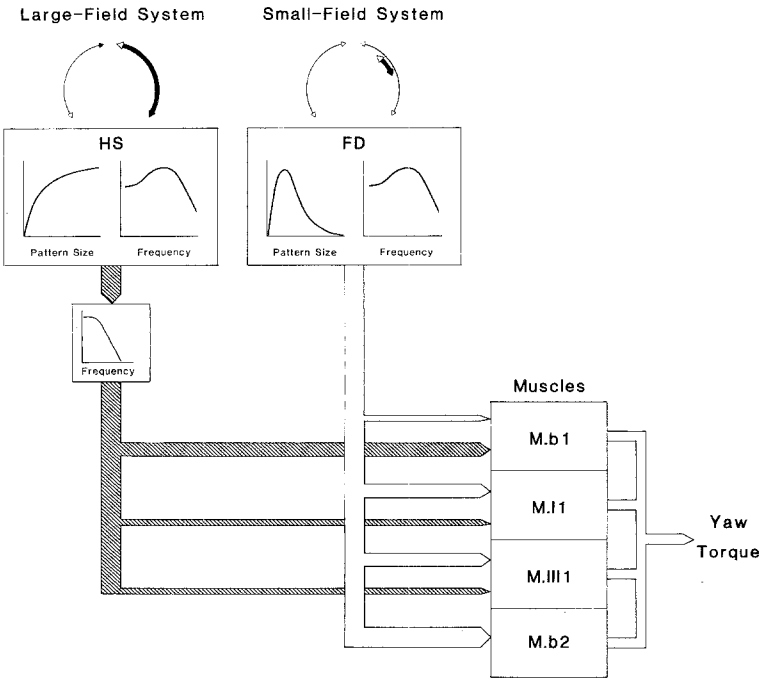

Fig. 6. A tentative wiring scheme illustrating the simplest possible distribution of the large-field and small-field system to the steering muscles b1, III1, I1, and b2. Only the 2 control systems on the right are represented. They are assumed to mediate the only direct input to those steering muscles that receive their dominant input during visually induced turns in clockwise direction. Only these muscles are indicated irrespective of whether they are located on the ipsilateral or contralateral side. At the level of the third visual ganglion the large-field and small-field system are represented by the HS- and FD-cells, respectively. Their dependence on the oscillation frequency and the size of the moving stimulus is indicated by insets. The visual input organization of the 2 cell classes indicated by arrows. Filled and open arrow-heads indicate excitatory and inhibitory influences, respectively, the diameter of the arrows the strength of the input. Note that only two of the 3 HS-cells are represented by this input organization, since the 3rd one does not receive input from the contralateral side (Hausen 1982a). As a representative of the FD-cells, the input organization of the FD4-cell is shown; other FD-cells differ with respect to their receptive fields and the inhibitory influence exerted by movement in the contralateral visual field (Egelhaaf 1985b). These differences, however, are not important in the present context. A kind of low-pass filter (indicated by an inset) has to be assumed in the large-field system which attenuates fast response transients in the HS-cell output signals (Egelhaaf 1987). The outputs of the large-field and small-field system are distributed to the different steering muscles and modulate their activity with a different gain as is indicated by thickness of the corresponding arrows. Of course, additional visual input to the steering muscles cannot be excluded

way of the large-field system which attenuates the high frequency components in the HS-cell signals (see Fig. 6). This processing stage was interpreted as a special adaptation to match the dynamical properties of the large-field system and the retinal image displacements the fly experiences in free flight in such a way that active turns are not much hindered by optomotor responses (Egelhaaf 1987). Of course, this does not exclude the existence of additional mechanisms which may cope with the visual consequences of active turns (see Heisenberg and Wolf 1984, 1988). (ii) The fly does not always respond to small-field motion with a turning reaction. Often single response peaks are omitted in an all-or-none fashion. Thus the signals carried by the small-field system seem to be gated by some other determinants (not shown in Fig. 6). Wind input may play an important role since, at least in some flies, the responses to visual small-field motion occur much more reliably during simultaneous wind stimulation of the tethered flying fly (Egelhaaf, unpubl.).

Based on these conclusions, it is suggested by the present results that the large-field and small-field systems eventually converge with a different gain on different muscles (see Fig. 6). M.b2, M.III1 and M.I1 are likely to receive their most conspicuous input from the small-field system, whereas M.b1 receives a prominent input from the large-field system. The influences of the respective other control systems are, although to a different extent, much weaker.

Can the visual input of the different steering muscles solely be explained by input from the large-field and small-field system as is suggested in Fig. 6 or are additional elements required? To answer this question, not only the visual input originating from the dominant eyes of the different steering muscles should be taken into account. Characteristic, although weaker, response modulations are expected to be induced also by motion in the respective contralateral visual field. This is because the HS- and FD-cells are affected in a specific way by motion in front of both eyes. In addition to their main sensitivity to ipsilateral front-to-back motion, part of the HS-cells respond to motion from back to front in the contralateral visual field due to synaptic connections with another large-field cell of the contralateral lobula plate (see Fig. 6) (Hausen 1982a, b). This suggests

that those steering muscles which receive input originating from the HS-cells can be expected to respond, without assuming any further direct input, not only to motion in front of their dominant eye but also, at least to some degree, to motion in front of the other eye. In contrast, all FD-cells known so far are excited by small-field motion in front of only one eye. They are inhibited by large-field motion in front of both eyes (Fig. 6) most likely due to interactions with elements sensitive to large-field motion (Egelhaaf 1985b, c). This suggests that the response modulations of steering muscles which are driven by follower elements of the FD-cells should be reduced when, in addition to small-field motion in front of their dominant eye, another stimulus pattern is moved simultaneously in front of the respective contralateral eye. When a muscle is driven by *both* the large-field and the small-field system, motion in front of the non-dominant eye is expected to induce opposing effects, an excitatory influence from one of the control systems and an inhibitory one from the other. Of course, both effects may cancel each other depending on the relative contribution of the two control systems and the exact stimulus conditions. Indeed, a corresponding antagonism has been found in the steering muscles III1 and I1 (Spüler 1980; Heide 1983).

In the present study this topic has not been addressed explicitly. In some experiments, however, the figure was also placed in front of the non-dominant eye. In the muscles III1, I1 and b2 only potential excitatory effects can be analyzed in this way, since they virtually do not show any spontaneous activity. No significant activity could be induced in M.b2 at either oscillation frequency by motion in front of the non-dominant eye. This is consistent with the finding that M.b2 only shows very weak responses to large-field motion (see Fig. 4) and supports the conclusion that it is virtually driven by the small-field system only (Fig. 6). In contrast, in both M.III1 and M.I1 there are weak excitatory effects to back-to-front motion in front of the non-dominant eye with their amplitudes being slightly smaller than to large-field motion with the same frequency. Together with the inhibitory effect also induced by motion in front of the non-dominant eye (Spüler 1980), this suggests the conclusion that both steering muscles are driven by input originating from the FD-cells and to a lesser extent from the HS-cells (Fig. 6). It should be noted that on the basis of the present experiments which used only binocular patterns as large-field stimuli it cannot be decided whether the reduced spike frequency found during binocular rotatory large-field motion is due to inhibitory influences from the non-dominant eye only (see above) or also from the dominant eye. The latter influence is expected if these steering muscles receive their main input, as is proposed here, from the FD-cells. Despite this qualification, the present data clearly show that M.I1, M.III1 and M.b2 are activated strongly during turning reactions towards small moving patterns in front of their respective dominant eyes. In contrast, they are much less active during compensatory optomotor responses as are induced by binocular rotatory large-field motion.

The interpretation of the properties of M.b1 are more complicated. Out of all steering muscles investigated so far, this muscle receives the most pronounced contribution from the large-field system. In accordance with the interpretation that this is represented at the output of the optic lobes by the HS-cells, M.b1 also shows the appropriate response modulations to oscillatory motion in front of its non-dominant eye. Being spontaneously active, M.b1 is inhibited by rotatory motion towards its ipsilateral side. Moreover, the spike frequency was found to increase slightly above the spontaneous activity level during large-field motion towards the contralateral side. If both the increase and decrease in spike frequency were mediated by a single type of input cell corresponding to a follower neuron of the HS-cells (see Fig. 6), M.b1 is expected to be tonically inhibited, at least slightly, by this element during straight flight, which induces front-to back motion on both eyes.

On the basis of the present experimental evidence it can, thus, be concluded hat the characteristic features of the large-field and small-field system are sufficient to account for the specific visual input organization of the different steering muscles. It should be noted, however, that it is only the simplest possible scheme to attribute the response modulations of the steering muscles induced by motion in front of their non-dominant eye exclusively to the binocular input organization of the HS- and FD-cells. Moreover, this interpretation is based on the implicit assumption that the functional properties of both cell classes are not considerably altered in flying animals. For methodological reasons, however, this assumption cannot be tested so far. Of course, additional direct visual afferences to the steering muscles cannot be excluded and may emerge in future more refined experiments. Moreover, only 4 of the 17 pairs of steering muscles which were described anatomically (Heide 1971a) have been systematically analyzed so far with respect to their functional proper-

ties. However, there are indications (Heide 1971b, 1975) that additional steering muscles might be involved in mediating turning responses.

Interestingly, other functional specializations have been described in part of the steering muscles of the fruitfly *Drosophila* (Götz 1983b) which cannot be accounted for on the basis of the scheme outlined here. The muscle I1 was shown to adapt flexibly to artificial closed-loop conditions where the retinal image displacements of a stimulus pattern that result from the animal's own actions are oppositely directed as would be expected under natural conditions; other steering muscles do not show this high degree of flexibility (Götz 1983b). These findings, together with the aforementioned gating of the pathway mediating small-field motion (see above), demonstrate that there must be factors others than the visual afferences, as characterized in the present and in previous studies (e.g. Reichardt et al. 1983; Egelhaaf et al. 1988), which control the steering muscles and the turning responses of the fly.

Nevertheless, the visual afferences to the steering muscles may be the most prominent determinants of their activity patterns. An understanding of how the large-field and small-field system converge on the different steering muscles and are used to mediate compensatory optomotor responses and object-induced turns represents another step towards unravelling the mechanisms underlying two of the most basic orientation responses flying animals have to have in their behavioral repertoire.

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