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How Do Flies Use Visual Motion Information to Control their Course?

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With 3 Figures

Abstract

In the fly compensatory optomotor turning reactions and orientation turns towards objects are induced by coherent rotatory displacements of the entire retinal image of both eyes and by small moving objects, respectively. These motion patterns are evaluated by two parallel pathways, the large-field and small-field system. These pathways eventually converge in a complex way on those flight steering muscles which mediate turning responses of the animal. This visuo-motor transformation of the retinal motion patterns is accomplished in both pathways by three processing steps: (i) Detection of motion in the different parts of the visual field by retinotopic arrays of movement detectors. (ii) Extraction of the different motion patterns by spatial integration over appropriately aligned movement detectors and interactions between different integrating elements. (iii) Temporal tuning of the spatially integrated motion information.

Two different behavioral responses contribute to visual orientation of flies. (i) *Compensatory optomotor turning reactions* are activated by coherent rotatory displacements of the entire visual scene; they stabilize the flight course against internal and external disturbances. (ii) *Orientation responses towards objects* are induced by local retinal image motion; they displace the images of objects into the frontal part of the visual field. These different motion-dependent response components have been shown by behavioral and electrophysiological experiments to be mediated by two pathways, the large-field and the small-field system. Both extract different types of retinal motion patterns and act in parallel on those flight steering muscles which control turning responses (for review, see EGELHAAF et al. 1988). In each control system this visuo-motor transformation is accomplished by three subsequent processing step (for review, see EGELHAAF and BORST 1990b): (i) Detection of local motion in the different parts of the visual field by retinotopic arrays of movement detectors. (ii) Evaluation of separate representations of coherent rotatory large-field motion and small-field motion of objects by appropriate spatial integration of local motion information as well as by intra- and interocular interactions between different spatially integrating elements. (iii) Matching of the dynamical properties of these representations of large-field and small-field motion to the needs faced by the fly in free flight. Finally, the pathways representing large-field and small-field motion converge again on the muscular system which mediates turning responses of the animal.

Local motion detection

The direction and velocity of motion are not represented explicitly at the level of the retinal input. Instead, the time-dependent brightness values as sensed by the two-dimensional array of photoreceptors are the only information available to the visual system. The initial explicit representation of motion information in the nervous system is computed by local movement detectors. There is good experimental evidence that in insects (REICHARDT 1961, 1987; BUCHNER 1984; BORST and EGELHAAF 1989) but also in other animals including man (e. g. SANTEN and SPERLING 1984; for review, see BORST and EGELHAAF 1989) this processing step can be accounted for by the formal model circuit shown in Fig. 1 B. The movement detectors have two input elements which feed two mirror-symmetrical subunits. The input signal of one branch of each subunit is delayed and then multiplied with the instantaneous signal of the neighboring input channel. The final output of the detector is given by the difference between the two subunit outputs. On average, each detector subunit calculates a kind of spatio-temporal cross-correlation of the

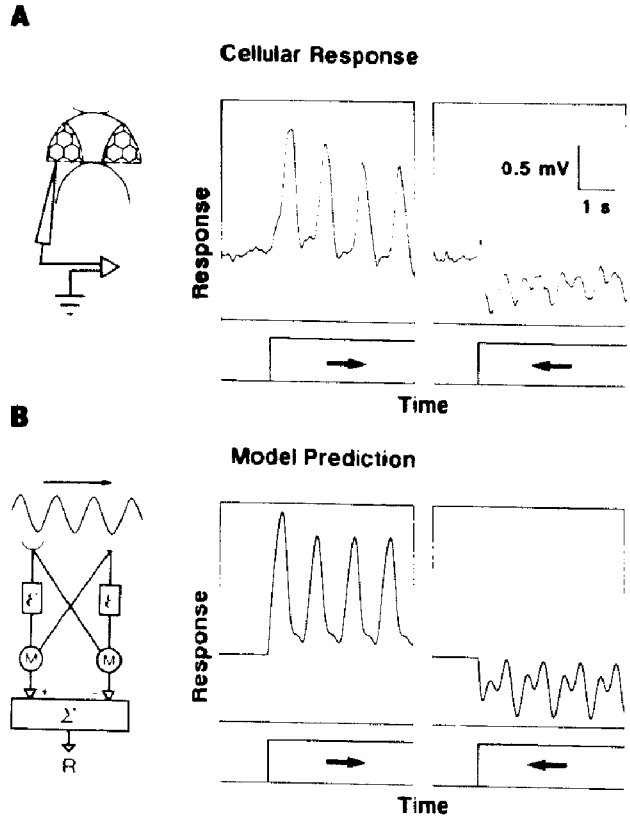

Fig. 1. Responses of (A) local movement detectors in the visual system system of the fly and of (B) the movement detector model of the correlation type to sinusoidally modulated gratings moving with a constant velocity in the preferred (left diagrams) and null direction (right diagrams). (A) Intracellularly recorded graded membrane potential changes of a HS-cell in the lobula plate of the blowfly. The time course of the response of individual detectors is derived by moving a sinewave grating behind a small vertical slit. The responses are temporally modulated over time in a characteristic way, although the stimulus moved with a constant velocity. (B) The responses of the HS-cell can be explained by the motion detection model shown in the inset (M: multiplication stage; ε: delay unit). Experimental data and model simulation taken from (EGELHAAF et al. 1989).

local light intensity fluctuations at neighboring points in the retinal image. The two subunits of a detector are already directionally selective to some extent and have an opposite polarity. However, they may also respond to some extent to correlated input signals which are not caused by motion, such as fluctuations of the mean light intensity. Since these response components are identical in both subunits, they become eliminated by the subtraction stage which, therefore, enhances the direction selectivity of the movement detector (EGELHAAF et al. 1989; BORST and EGELHAAF 1990).

By combined pharmacological and electrophysiological experiments the cellular basis of the subtraction stage of the fly's motion detection system could be unraveled. There is evidence that this important processing step is located on the dendrites of the spatially integrating elements in the third visual ganglion (see below) (BORST and EGELHAFF 1990). The subtraction stage uses GABA as its inhibitory transmitter (EGELHAAF et al. 1990). Although various cellular mechanisms have been proposed for the multiplicative interaction between the movement detector input channels (SRINIVASAN and BERNARD 1976; TORRE and POGGIO, 1978; GRZYWACZ and KOCH 1987), there is no convincing evidence so far in favor of any of these mechanisms (compare e.g. SCHMID and BÜLTHOFF 1988 and EGELHAAF et al. 1990).

From a functional point of view it is most important to understand what information about the moving visual scene is represented explicitly by the local movement detectors. Movement detectors as realized in the visual system of the fly do not represent pure velocity sensors which indicate correctly the direction and speed in which the different segments of the retinal image are moving. Instead, their responses are strongly influenced by the textural properties of the moving patterns such as its spatial frequency content and contrast (REICHARDT 1961, 1987; GÖTZ 1964; BUCHNER 1984). Moreover, the response of a local movement detector is not constant but modulated over time, even if the stimulus pattern moves at constant velocity (Fig. 1 A). The time course of the response modulations depends in a characteristic way on both the velocity and the texture of the pattern (EGELHAAF et al. 1989). This behavior of the fly's movement detection system can be accounted for almost perfectly by the formal movement detector model as outlined above (Fig. 1 B).

In conclusion, a local movement detector on its own does not yield reliable information on the direction and speed in which the different pattern segments are moving. This suggests that additional processing steps are required to extract less ambiguous motion estimates from the activity patterns of the retinotopic arrays of movement detectors.

Extraction of retinal motion patterns

Spatial integration over the array of local movements detectors and interactions between different integrating elements are used by the fly as a simple strategy to obtain explicit neuronal representations of both rotatory displacements of the entire retinal image and motion of small objects. There are mainly two reasons for the

significance of some sort of spatial integration. (i) Since a large number of movement detectors control only a few motor output variables some sort of spatial convergence has to be expected. (ii) Spatial integration is the simplest means to get rid of the time-dependent modulations of the local detector response (see above; EGELHAAF et al. 1989).

This kind of spatial integration is accomplished by a set of about 50 large

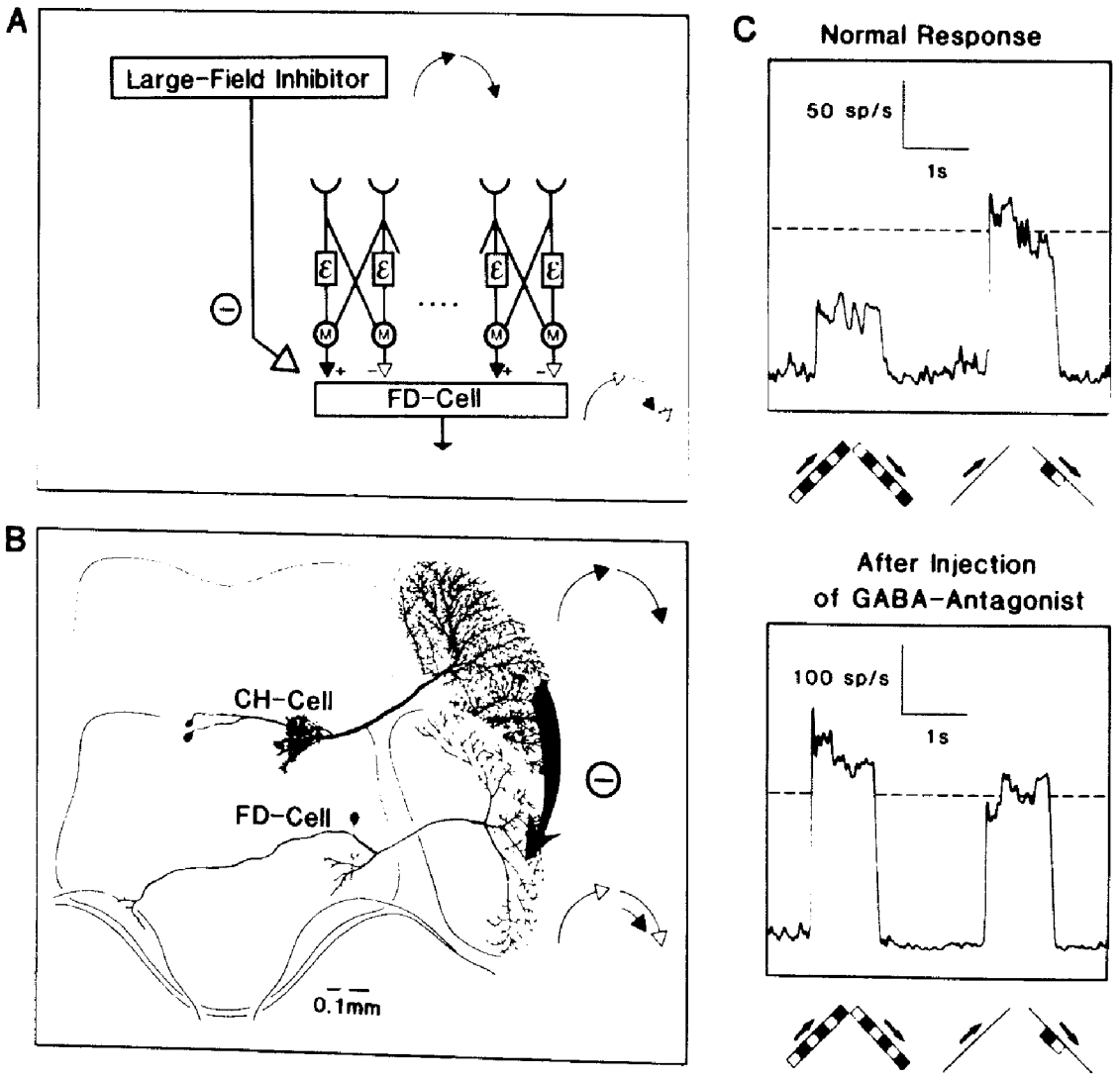

Fig. 2. Mechanism underlying the tuning of the FD1-cell to small-field and relate motion. (**A**) Schematic model of the mechanism: The FD1-cell is assumed to integrate spatially over an array of local movement detectors and to be inhibited in some way by an element sensitive to coherent rotatory large-field motion in front of either eye. Model modified from (EGELHAAF 1985b). (**B**) Anatomy of the FD1-cell and its likely large-field inhibitor, the CH-cells (FD1-cell taken from (EGELHAAF 1985a; CH-cells taken from (HAUSEN 1976a). (**C**) Spike frequency histogram of the response of a FD1-cell before and after injection of the GABA-antagonist picrotoxinin. Stimuli were presented on two monitor screens mounted symmetrically in front of the eyes (see inset); a grating was used as stimulus pattern; the small-field stimulus was located in the excitatory receptive field of the FD1-cell in the visual field of the right eye. Before injection of the GABA-antagonist, the cell responds with a larger amplitude to small-field than to large-field motion. After injection of the GABA-antagonist the spike frequency in response to motion increases dramatically; the response amplitudes are now somewhat larger during large-field than during small-field motion. Data taken from (EGELHAAF 1990).

interneurons in the lobula plate, the posterior part of the third visual ganglion in the fly's brain. These neurons can be identified individually owing to their highly invariant physiological and anatomical properties (for review, see HAUSEN and EGELHAAF 1989). Two functional classes of output cells of the lobula plate play a decisive role in yaw torque control and represent the cellular analogues of the large-field and small-field system at this processing stage. (i) The HS-cells are most sensitive to coherent rotatory large-field motion about the vertical axis of the animal as is induced during deviations from the flight course (HAUSEN 1982a, b). (ii) The FD-cells respond best to small-field motion and relative motion of an object with respect to its background (EGELHAAF 1985a, b). The HS- and FD-cells are assumed to receive their direct retinotopic input from the subunits of the local movement detectors (see above; for the FD-cells this is illustrated in Fig. 2A). However, the specific sensitivy of both cell types to large-field and small-field motion, respectively, is the consequence of appropriate interactions with other types of neurons. Part of the HS-cells receive additional input from the contralateral eye owing to synaptic input from another identified large-field neuron. This input makes the HS-cells selective for rotatory large-field motion about the vertical axis of the animal (HAUSEN 1982a, b). The input organization of the FD-cells is more complex. To guarantee that they are mainly activated by small moving objects, they have to be prevented from responding also to large-field stimuli moving in their preferred direction. This is accomplished by inhibiting the FD-cells by large-field elements with the appropriate preferred directions (EGELHAAF 1985a, b).

There is a likely candidate for such a large field inhibitor. The pair of CH-cells may play this role at least for one type of FD-cell, the FD1-cell (Fig. 2B). The CH-cells are excited by rotatory binocular large-field motion (HAUSEN 1976a, b) just as was proposed for the large-field inhibitor of the FD1-cell (EGELHAAF 1985b). Moreover, it is suggested by immunohistochemical labelling that the CH-cells are GABAergic and, thus, inhibitory elements (MEYER et al. 1986). In recent experiments, the large-field inhibition of the FD1-cell and consequently, its selectivity for small-field motion could be eliminated reversibly by application of an antagonist of GABA (Fig. 2C) (EGELHAAF 1990). This speaks in favor of the interpretation that the CH-cells represent the large-field inhibitor of the FD1-cell. In any case, a representation of small-field and relative motion is computed in the fly's brain by an inhibitory GABAergic interaction between elements which spatially integrate to a different extent over the two-dimensional array of local movement detectors.

In conclusion, at the level of the spatial integration stage the two-dimensional representation of motion as provided by the movement detectors segregates into different pathways that convey specific information on large-field and small-field motion, respectively.

Temporal tuning of the spatially integrated representations of motion information

The different retinal motion patterns as induced during various types of flight maneuvers are not only characterized by the spatial distribution of motion vectors

but also by characteristic dynamical features. Hence, it may be not surprising that what response mode the animal adopts at the behavioral level does not only depend on whether it is confronted with either large-field or small-field motion. Instead, the dynamics of the retinal image motion plays an important role in determining to what extent the fly compensates for deviations from its flight course or tries to orient towards an object. This could be demonstrated in behavioral experiments on tethered flying flies where the visually induced torque was measured during stimulation with large-field and small-field stimuli oscillating at various frequencies about the vertical body axis of the fly. It was found that rotatory large-field motion is compensated best when it reverses its direction only slowly. In contrast, small moving targets induce orientation turns mainly when they alternate their direction at a much higher rate (EGELHAAF 1987; REICHARDT et al. 1989). This different dynamical tuning of the large-field and small-field system, respectively, is achieved after the spatial integration stage. The dynamical properties of the spatially integrating units in the lobula plate seem to be determined by their local movement detector input (EGELHAAF and BORST 1989, 1990a). By comparing the responses of the HS-cells with the corresponding behavioral compensatory turning responses, some kind of low-pass filter has to be postulated somewhere between the third visual ganglion and the final motor control centers in the thoracic ganglia (EGELHAAF 1987; EGELHAAF et al. 1988). As a consequence of this temporal filter, active turns of the animal which are usually brief and fast (WAGNER 1986) and, consequently, result in transient changes in the direction of rotatory large-field displacements of the retinal image are not impeded by compensatory optomotor turning reactions. This leads to a partial dynamical segregation of the visual consequences of active and unintended turns. In contrast, there is no such elimination of fast response transients in the pathway tuned to small-field and relative motion (EGELHAAF 1987; EGELHAAF et al. 1988). Hence, this system remains operational during active turns of the animal.

Convergence of the different visual control systems mediating turning responses

The large-field and small-field system, respectively, converge in a complex way on the different steering muscles which control the fly's turning responses. This has been concluded from simultaneous recordings of the visually induced spike frequency modulations of the different steering muscles and the corresponding yaw torque responses. The different muscles involved in yaw torque control (HEIDE 1983) receive differential input from both control systems (Fig. 3) (EGELHAAF 1989). For instance, the activity pattern of the so-called b1-muscle is rather similar to the behavioral responses showing its most pronounced spike frequency modulations during large-field motion at low oscillation frequencies and small-field motion at high frequencies (compare Fig. 3A and 3C). In contrast the so called b2-muscle only shows pronounced responses to small-field motion at high oscillation frequencies (Fig. 3B). The b1-muscle, thus, receives input from both the pathway representing large-field and small-field motion, while the muscle b2 essentially gets its input from the small-field system alone (EGELHAAF 1989). Hence,

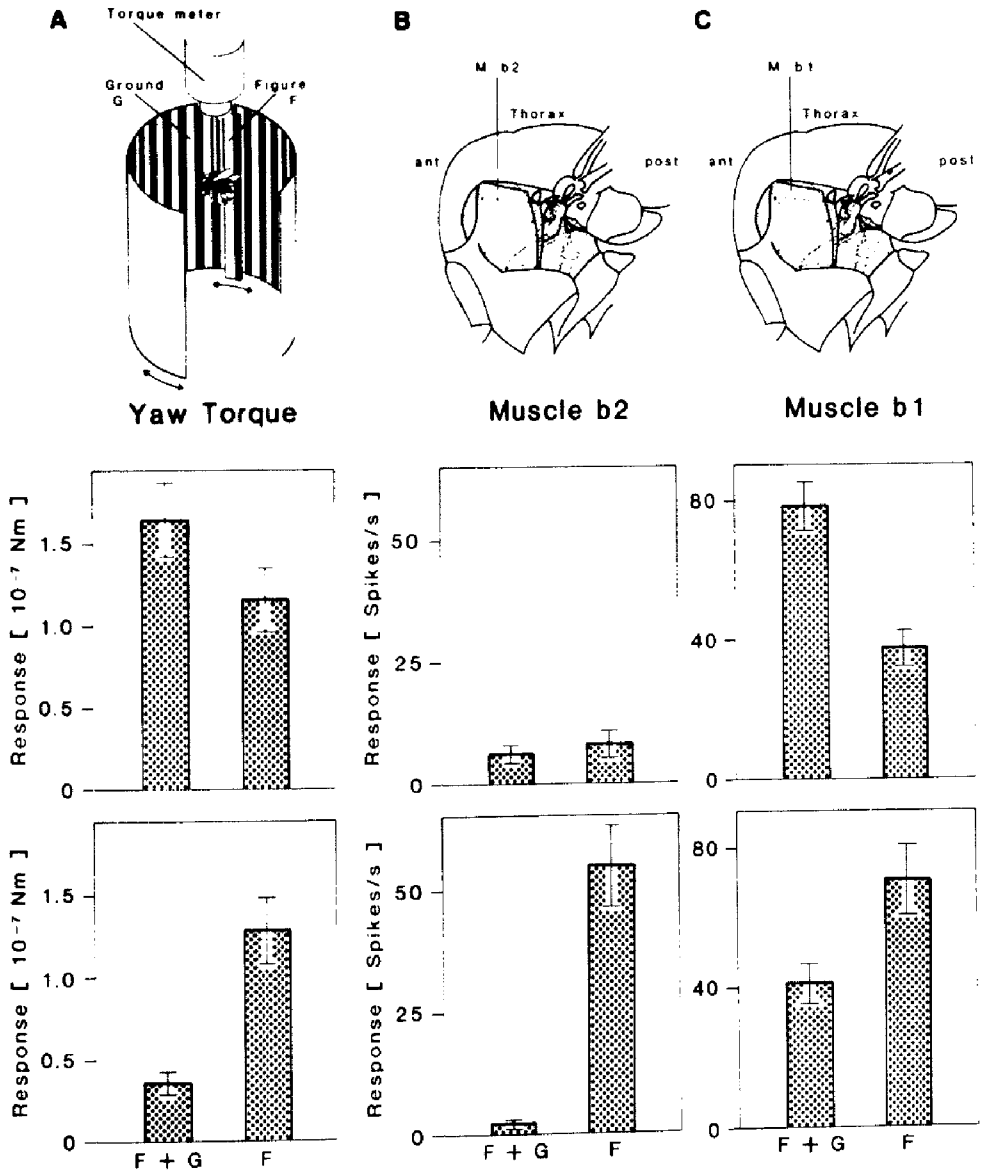

Fig. 3. Yaw torque responses and spike activity of two types of flight steering muscles. The fly was stimulated by oscillatory motion of a cylindrical stripe pattern ('ground' G) and a vertical cylinder segment ('figure' F). The oscillation frequency was either 0.1 Hz or 1 Hz. F and G were oscillated synchronously (F + G; large-field motion) or F alone while G was stationary (F; small-field motion). (**A**) Yaw torque responses: The responses to large-field and small-field motion represent the mean amplitudes of compensatory optomotor turning reactions and orientation turns towards objects, respectively. At low oscillation frequencies the compensatory optomotor responses are larger than the orientation turns towards objects; at high oscillation frequencies the orientation turns have a larger amplitude than the optomotor following responses. (**B**) Spike frequency of the b2 muscle. M.b2 shows only large responses during orientation turns towards objects at high oscillation frequencies. (**C**) Spike frequency modulations of the b1 muscle. The activity pattern of the M.b1 shows its most pronounced spike frequency modulations during large-field motion at low oscillations frequencies and small-field motion at high oscillation frequencies. The error bars indicate the S.E.M. data taken from (EGELHAAF 1989).

the different steering muscles represent to a different degree information on large-field and small-field motion and are, thus, functionally specialized to mediate different response component in visual orientation.

Conclusions

The main topic of this article was to summarize our current knowledge about the main processing steps in the nervous system of the fly underlying the transformation of large-field and small-field motion into compensatory optomotor turning reactions and orientation turns towards objects, respectively. In the first step of analysis the different computations have been established on the basis of stimulus-response relationships obtained at the behavioral level. This allowed to define what had to be explained at the underlying neuronal level and to design the appropriate visual stimuli which allowed to identify in electrophysiological experiments the neuronal elements participating in the computations of motion information. The cellular analogues of part of these processing steps could be established in this way; for instance, the HS- and FD-cells were concluded to represent, as output elements of the visual system, an important part of the large-field and small-field system, respectively. The neuronal equivalents of other processing steps in the motion pathway have not been discovered, so far. Despite these gaps in our knowledge, it is now possible to go one step further and to try to explain at least certain of the computations of the motion pathways in terms of biophysical mechanisms and synaptic interactions. At this level of analysis the cellular nature of the subtraction stage of the local movement detectors as well as the small-field tuning of the FD-cells could already be explained. Other important processing steps, such as the multiplicative interactions between the detector input channels or the temporal low-pass filter in the large-field system, have, so far, been elusive to an understanding in cellular terms. Hence, it will be an important goal for the next years to unravel the cellular mechanisms also of these computations of the motion pathway in the fly. This seems to be of widespread relevance, because computations such us a multiplication-like interaction between two incoming signals or the temporal filtering of signals are essential not only in motion information processing but also in other information processing tasks and in other animals. An example for a multiplication-like interaction is the coincidence detection of signals from the two ears in the acoustic pathway of owls which is used to locate an object, such as a prey, acoustically (KONISHI, 1986). Examples for neuronal pathways where temporal low-pass filters play a role are the landing system of the fly (see BORST, this volume) and the eye following system of monkeys (MILES and KAWANO 1987). In any case, the fly is one of the few examples where it has been possible so far to trace at least some important computations underlying neuronal information processing from the behavioral level to the level of biophysical mechanisms.

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