Motion Detection and Visual Orientation: A Combined Behavioral, Neuronal and Theoretical Analysis of the Fly's Visual System

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Visual orientation greatly relies on the extraction of the global motion patterns received by the eyes when an animal moves around in its environment. Since these motion patterns are determined by both the animal's own movements as well as the three-dimensional structure of the visual environment, they contain a wealth of information on these features. If evaluated properly by the nervous system this information can be used in visual orientation. Global retinal motion patterns are particularly conspicious in fast moving animals, and especially in flying ones. Their visual systems, therefore, can be expected to be highly adapted to evaluate motion information.

This is one reason that the fly proved to be a good model system for analyzing the neuronal computations by which global retinal motion patterns are extracted and transformed into muscular activity patterns controlling orientation behavior. Three visual orientation tasks depending on the evaluation of different types of motion patterns have been thoroughly analyzed in this respect (e.g. Reichardt 1986; Egelhaaf et al. 1988; Borst and Bahde 1989; Hausen and Egelhaaf 1989). (i) Coherent rotational image displacements of the entire visual surround may signal deviations of the animal from its course and induce compensatory optomotor turning responses. (ii) Small-field motion and relative motion between different parts of the retinal image indicate the existence of moving or stationary objects and may be used as visual cues to control orientation responses towards these objects. (iii) Expansion of the retinal image in all directions indicates that the animal approaches an obstacle and may elicit landing responses. For all these tasks it is now possible on the basis of a combined behavioral, electrophysiologcial and theoretical analysis to bridge at least part of the gap between the performance of the whole animal under natural conditions and the underlying computational principles as operating at the neuronal level.

Principal steps of motion information processing

How are global retinal motion patterns encoded by the visual system of the fly? The direction and velocity of motion are not represented explicitly at the level of the retinal input. Instead, the only primary information available to the visual system is given by the time-dependent brightness values of the retinal image as sensed by the two-dimensional array of photoreceptors. From spatio-temporal coherences in these brightness patterns, motion information is computed in a series of processing steps. Essentially three principal steps of motion information processing could be shown to transform the retinal input to motor control signals. (i) Detection of local motion in the retinal image by large retinotopic arrays of movement detectors. (ii) Extraction of the various global retinal motion patterns by appropriate spatial integration of the local motion information. (iii) Matching of the dynamical properties of these representations of global retinal motion to the needs faced by the fly in free flight.

Local motion detection

The initial explicit representation of motion information in the nervous system is computed by local movement detectors. These are organized in parallel in retinotopic arrays covering the visual fields of both eyes and extract a kind of spatio-temporal

cross-correlation of the local light intensitiy fluctuations at neighboring points in the retinal image (Reichardt 1961, 1987; Buchner 1985). The movement detectors have two input elements which feed two mirror-symmetrical subunits (Fig.A). 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 subunits' outputs. Owing to the delay and multiplication-like interaction, the subunits are already directionally selective. Nevertheless, they may also respond to some extent to input signals which are not due to 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). This motion detection scheme has been confirmed in the motion detection system of the fly by both behavioral and electrophysiological experiments (e.g. Götz 1964; Buchner 1985; Reichardt 1987; Egelhaaf et al. 1989). Interestingly, the same basic scheme has been successfully applied to account also for motion detection in vertebrates including man (see e.g. Santen and Sperling 1984; Emerson 1987). This suggests that motion detection in quite different species is based on essentially equivalent computations.

What cellular mechanisms are responsible for these computations characterized so far only in formal terms? The simplest possibility to account in cellular terms for the multiplication and subtraction stage of the formal model would be the appropriate synaptic interaction of only two cells. For the subtraction stage this simple scheme is most likely to be realized by a combination of an excitatory and an inhibitory synapse; there is evidence that the latter synapse is GABAergic (Egelhaaf and Borst 1989b). It is much less straightforward to realize the multiplication-like interaction of the two detector input signals by synaptic interactions. This is suggested by the various cellular models proposed for this computation (Srinivasan and Bernard 1976; Torre and Poggio 1978; Grzywacz and Koch 1987). Mostly discussed among these models with respect to motion detection in different species is the 'shunting inhibition model' (Torre and Poggio 1978; Koch et al. 1986; Schmid and Bülthoff 1988). It relies on the nonlinear interaction of an excitatory and an inhibitory synapse (Torre and Poggio 1978). Model simulations combined with electrophysiological and pharmacological experiments made it rather unlikely that this type of synaptic interaction represents the cellular equivalent of the multiplication nonlinearity in the motion detection system of the fly (Egelhaaf and Borst 1989b; Borst and Egelhaaf, this vol.). Further pharmacological dissection of the fly's motion detection system is obviously required. Thereby, one should keep in mind that the multiplication-like interaction in the formal model may not be the result of an interaction of only two cells, but an emergent property of more complex wiring schemes.

Whatever the cellular mechanisms underlying movement detection might exactly be, very detailed knowledge has been accumulated during the last years about what information on the moving visual scene is represented explicitly by the local movement detectors. Most importantly, movement detectors as realized in the visual system of the fly are not pure velocity sensors that correctly indicate the direction and velocity of local motion. Instead, their responses are strongly influenced by the textural properties of the moving pattern such as its spatial frequency content and contrast (Reichardt 1961, 1987; Götz 1964; Buchner 1985). Moreover, the response of a local movement detector is not constant but modulated in time, even if the stimulus pattern moves at constant velocity. The time course of the response modulations depends in a characteristic way on both the velocity and texture of the pattern (Reichardt and Egelhaaf 1988; Egelhaaf et al. 1989). This is one reason why a local motion detector on its own does not yield reliable information on the direction and velocity in which the different segments in the retinal image are moving. Thus, additional processing steps are required to extract less ambiguous motion estimates from the activity patterns of the retinotopic arrays of movement detectors.
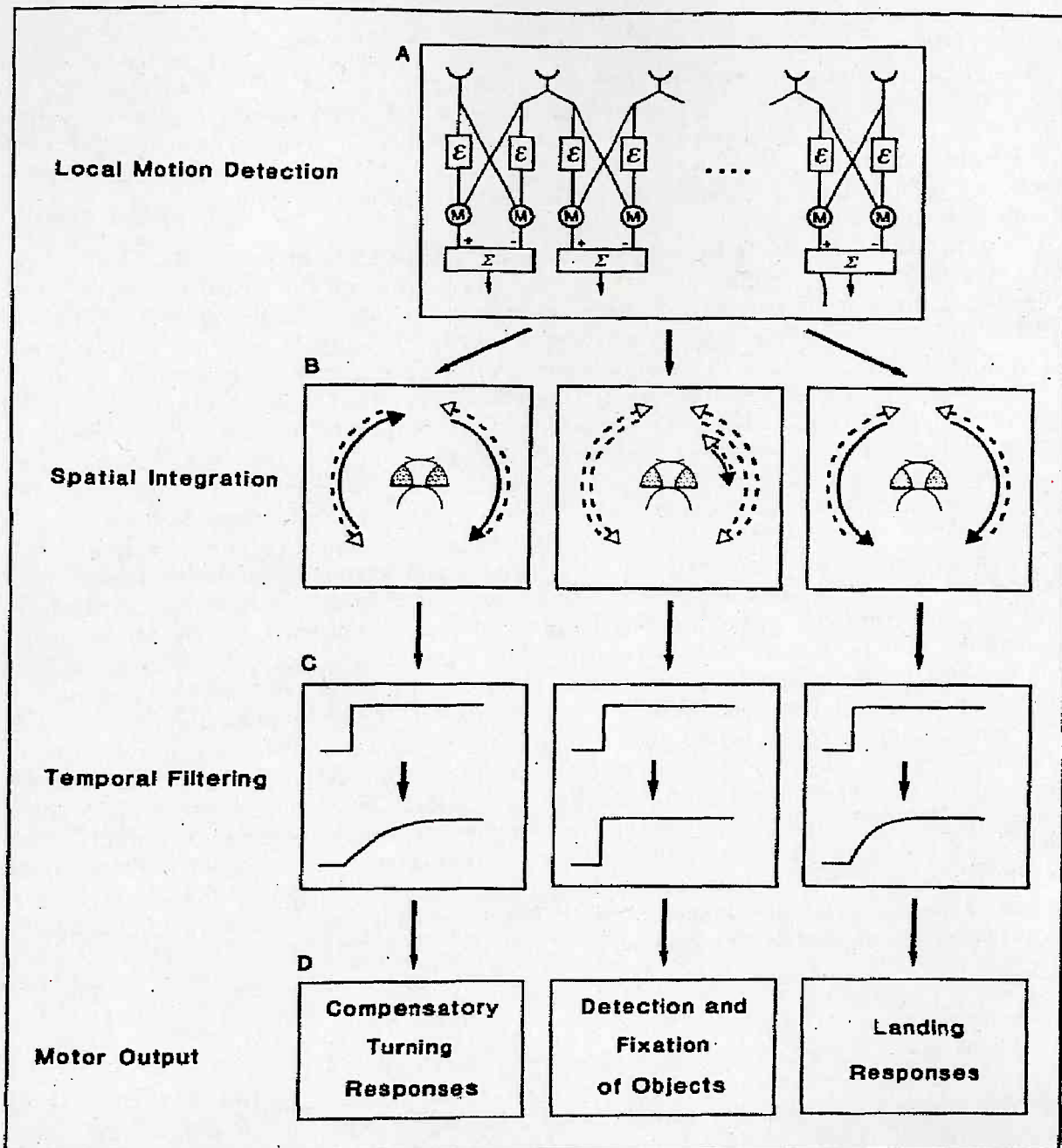
Extraction of global retinal motion patterns

How the fly extracts information on the global retinal motion patterns as induced during different flight maneuvers from the ambiguous local motion measurements has been analyzed at both the behavioral and neuronal level (Reichardt 1986; Buchner 1985; Egelhaaf et al. 1988; Borst and Bahde 1989; Hausen and Egelhaaf 1989). Appropriate intra- and interocular spatial integration of local motion information form the basic computational principle underlying this processing step. There are mainly two reasons for the significance of some sort of spatial integration. (i) Since a large number of local movement detectors control only a few motor output variables (e.g. the different rotational and translational velocity components) some sort of spatial convergence has to be expected. (ii) Spatial integration is the simplest means of getting rid of the time-dependent modulations of the local movement detector responses (see above, Egelhaaf et al. 1989).

This kind of spatial integration is achieved in the posterior part of the third visual ganglion. Here, the point-to-point representation of visual space is abandoned by about 50 large interneurons which can be identified individually in each animal owing to their highly invariant physiological and anatomical properties (Hausen and Egelhaaf 1989). These cells scan either the entire visual field or at least large sections of it and pool the output of small columnar elements. The columnar elements are likely to represent the local movement detectors. Hence, the large-field cells in this part of the brain are activated by motion in a particular preferred direction, and are inhibited by motion in the respective opposite direction. The specific tuning of these large-field elements to different global retinal motion patterns is eventually shaped by specific intra- and interocular interactions.

Three types of cells and basic interaction schemes should be mentioned here (Fig.B). (i) The HS-cells are excited by direct retinotopic input of ipsilateral local movement detectors mediating front-to-back motion. Due to synaptic connections from a large-field cell of the contralateral side of the brain, part of the HS-cells also respond to back-to-front motion in the contralateral visual field. This simple wiring scheme makes the HS-cells particularly sensitive to rotatory large-field motion about the animal's vertical axis as is induced during deviations from the flight course (Hausen 1982a,b). There is good evidence for an involvement of these cells in the control of corrective steering maneuvers (Hausen and Wehrhahn 1983; Egelhaaf et al. 1988; Hausen and Egelhaaf, 1989). (ii) The FD-cells are most sensitive to small-field motion and to relative motion of an object with respect to its background. They are excited by retinotopic input of movement detectors from one eye. Their specific tuning to small-field and relative motion is due to specific inhibitory interactions with ipsi- and contralateral elements responsive to large-field retinal image displacements. Both electrophysiological and behavioral evidence speaks in favor of a role of the FD-cells in discriminating objects from their background and in mediating orientation responses towards them (Egelhaaf 1985a,b; Egelhaaf et al. 1988). (iii) Recently, a novel type of cells was found in the cervical connective which connects the optic lobes with the motor control centers. These cells respond best to pattern expansion as may occur when a fly approaches an object. They are excited by front-to-back motion in the visual field of both eyes and are likely to play a role in mediating landing responses (Borst, this volume).

Hence, at the spatial integration stage the two-dimensional representation of local motion as provided by the movement detectors segregates into different pathways that convey specific information on different global retinal motion patterns. By relatively simple computations those aspects are extracted from the retinal motion fields which are relevant in certain situations in free flight.

Local Motion Detection

A

Spatial Integration

B

Temporal Filtering

C

Motor Output

D

| Compensatory Turning Responses | Detection and Fixation of Objects | Landing Responses |

Principal steps of motion information processing in the fly visual system. (A) Detection of local motion by large retinotopic arrays of movement detectors; only three detectors are shown here; for a description of their properties, see text. M denotes the multiplication stage and ε the movement detector filter (B) The initial representation of local motion segregates into three pathways which extract different global motion patterns: Rotatory large-field motion (left diagram); relative motion of an object and its background (middle diagram); pattern expansion (right diagram). The arrows indicate the direction selectivities of the extraction mechanisms on the right side of the visual system; filled and open arrow-heads indicate excitation and inhibition, long and small arrows large-field and object motion. (C) Temporal tuning of the representations of rotatory large-field motion and pattern expansion by some kind of low-pass filters with different time constants. The signals before and after the filters are shown in response to an onset of motion. (D) The different pathways are involved in mediating different components of orientation behavior.

Tuning of the dynamical response characteristics

The retinal motion patterns as induced during various types of flight maneuvers are not only characterized by their different global geometries but also by specific dynamical features. For instance, houseflies do not turn smoothly in free flight when purposely changing course, but make several rapid turns instead (Wagner 1986); these turns lead to rotatory retinal large-field motion in the respective opposite directions.

The dynamical features of the global retinal motion patterns characteristic of the free-flight situation are reflected in the dynamical properties of the visual pathways which handle these motion patterns. Specific dynamical tuning is achieved only after the spatial integration stage (Fig.C). The dynamical properties of the integrating units in the third visual ganglion seem to be determined by their local movement detector input. By comparing the responses of the HS-cells with the corresponding behavioral compensatory turning responses, some kind of temporal low pass filter could be postulated somewhere between the third visual ganglion and the final motor control centers (Egelhaaf 1987). This processing stage attenuates the peculiar response transients in the spatially integrated movement detector output (Egelhaaf and Reichardt 1987; Egelhaaf and Borst 1989a). Hence, only slow changes of the direction of retinal image motion as may result from external disturbances and asymmetries in the flight motor are compensated for by corrective steering maneuvers. In contrast, active turns of the fly which are usually brief and fast (Wagner 1986) are not impeded by compensatory reactions. This type of frequency filtering thus 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). Hence this system remains operational during active turns of the animal. In the pathway carrying information on retinal image expansion and controlling the initiation of landing responses temporal frequency filtering plays also a decisive role. In thorough behavioral experiments the movement detector output signals could be shown to be temporally integrated before passing a threshold element which eventually elicits the landing response (Borst and Bahde 1986, 1988, 1989). Interestingly, neurons in the cervical connective were found to represent this kind of temporally integrated signals (Borst, this volume).

Conclusions

The processing steps in the fly visual system involved in the control of even intricate motion-dependent visual orientation tasks seem to be well within the computational capabilities of fairly simple neuronal circuits. Motion information is first extracted by retinotopic arrays of local movement detectors and then segregated by differential spatial integration and temporal filtering into parallel pathways. These pathways are tuned to the characteristic properties of the global retinal motion fields as induced during certain flight maneuvers. Despite the relative simplicity of these mechanisms, the computational problems which they solve are of widespread relevance. Hence, it may be not surprising that computational processes as revealed in the fly play also a role in other biological vision systems including man. This has been demonstrated most convincingly for the mechanisms underlying local motion detection (e.g. Santen and Sperling 1984) but also with respect to the evaluation of global retinal motion patterns by separate specifically tuned pathways (for discussion, see Egelhaaf et al. 1988). Common principles of information processing may thus exist not only at the level of single nerve cells but also at the level of computations performed by neural circuits.

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