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MINI REVIEW

MOTION COMPUTATION AND VISUAL ORIENTATION IN FLIES

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Abstract—1. Visual orientation greatly relies on the evaluation of the motion patterns received by the eyes when the animal moves around.

2. In a combination of behavioral, neurophysiological and pharmacological analysis and modelling, the mechanisms are established by which the visual system of the fly extracts three types of-basic retinal motion patterns.

3. Coherent retinal large-field motion as is induced during deviations of the animal from its course, image expansion occurring when the animal approaches an obstacle, and relative motion which is induced when a nearby object is passed in front of its background.

4. Separate neuronal networks are specifically tuned to each of these motion patterns and make use of them in three different orientation tasks: in compensatory course stabilization, the control of landing behaviour and the fixation of objects.

INTRODUCTION

Motion information plays a prominent role in visual orientation in many animal species. An animal is confronted with motion whenever an object moves in its visual field. This, however, may not be the only source of motion information. Although we are usually not aware of this, motion stimuli also occur in a stationary environment when the animal is moving. This is because during self-motion the retinal images are continually displaced. The resulting retinal motion patterns depend in a characteristic way on the trajectory described by the animal as well as on the particular three-dimensional structure of the visual environment.

Consider, for instance, three commonplace situations: (1) when an animal deviates from its course, the retinal image of the entire visual environment is coherently displaced in the opposite direction (Fig. 1 left hand diagram); (2) in contrast, the approach towards an obstacle leads to an expansion of the retinal image. This means that all elements in the image move centrifugally away from the point the animal is heading for (Fig. 1 middle diagram); (3) when the animal passes a nearby object in front of a more distant background, the retinal images of the object and the background move at different velocities. This leads to discontinuities in the retinal motion field (Fig. 1 right hand diagram). All these retinal motion patterns induced by self-motion are particularly pronounced in fast moving animals and, especially, in flying ones.

Why should an animal such as a flying insect make efforts to evaluate these different types of motion patterns? The answer is that they can tell the animal much about its own motion and also about the structure of its environment. This information may then be used to guide visual orientation: (1) rotatory large-field motion may signal to the animal unintended deviations from its course. A system extracting this type of motion pattern could thus be an integral part of an autopilot which compensates for these deviations by corrective steering manoeuvres; (2) image expansion signals that the animal is approaching an obstacle. A system evaluating this type of motion pattern may control behavioural responses such as landing behaviour by initiating a deceleration and an extension of the legs to avoid crash-landing; (3) finally, discontinuities in the retinal motion field and small-field motion indicate nearby stationary or moving objects. Mechanisms sensitive to this type of motion pattern, therefore, may be part of a fixation system which induces turning reactions towards objects.

The mechanisms underlying the extraction of these retinal motion patterns and their transformation into the appropriate motor activity have been analysed in some detail in flies mainly in the housefly *Musca domestica*, the blowfly *Calliphora erythrocephala* and the fruitfly *Drosophila melanogaster*. For two reasons, the fly has proved to be particularly suitable in this respect: (1) since the fly's orientation behaviour relies heavily on motion information, its visual system was found to be highly specialized with respect to motion vision; (2) the nervous system of at least the relatively big blowfly *Calliphora erythrocephala* is amenable to an analysis on the basis of nerve cells which can be identified individually in each

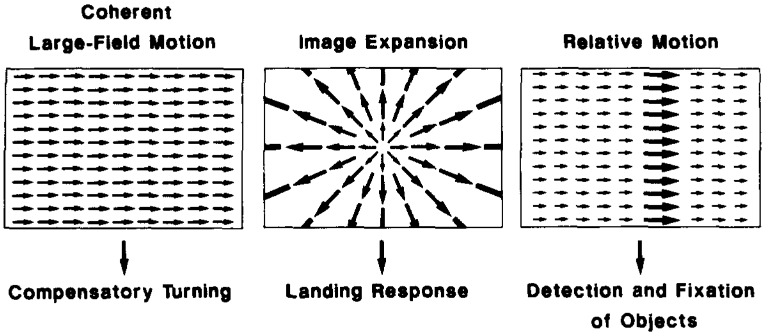

Fig. 1. Retinal motion patterns induced by self-motion of the animal and the visual orientation responses which may be controlled by them. Deviations of the animal from its course lead to coherent displacements of the retinal images of both eyes. This visual information can be used to control compensatory turning reactions (left diagram). When the animal approaches an obstacle the different elements in the retinal image move centrifugally. This image expansion signals an impending collision and may control the initiation of, for instance, landing behaviour (middle diagram). When the animal passes a nearby object in front of a more distant background, discontinuities in the retinal motion field are induced. Relative motion thus indicates small objects and may be used to mediate turning responses to these objects (right diagram). The retinal motion patterns are given here only schematically.

animal. This is a great advantage for an understanding of biological information processing in terms of neuronal circuits.

MAIN FEATURES OF THE NERVOUS SYSTEM OF THE FLY

The transformations of the moving retinal images into the appropriate motor activity are the consequence of specific biophysical properties of nerve cells and their connection patterns. Figure 2 summarizes schematically those features of the fly's nervous system which are most relevant in the present context. It shows a schematic horizontal cross-section through the nervous system with the large compound eyes and the three visual ganglia as well as the motor control centres in the thoracic ganglia. The retinal images are initially transformed by a sequence of successive retinotopically organized layers of columnar nerve cells. At the level of the third visual ganglion, large-field elements integrate the output of the columnar neurones; these large-field cells either connect to other brain areas or, via descending neurones, to the motor control centres. All of these large-field cells respond selectively to motion in a particular direction. As will be shown later, they play an important role in extracting the different types of retinal motion patterns. Owing to their extraordinary structural constancy and highly invariant physiological properties, they can be identified individually

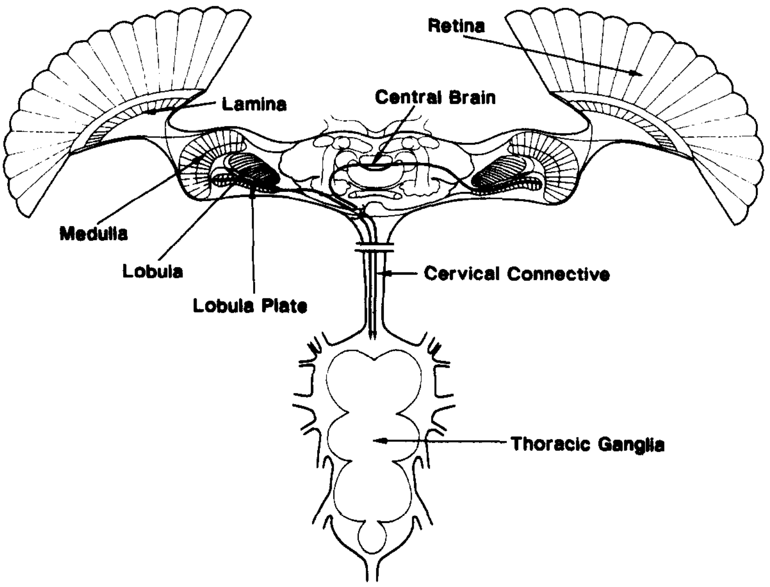

Fig. 2. Schematic horizontal cross-section through the nervous system of the fly with the retina, the three visual ganglia lamina, medulla and lobula complex (which is subdivided into the anterior lobula and the posterior lobula plate), the central brain and the thoracic ganglia with the motor control centres. Modified from Hausen (1984).

in each animal. Besides these large-field cells, much is known about the fine structure of almost the entire visual pathway from the photoreceptors to the muscles which mediate the different behavioural responses. In addition, the functional properties of part of these structures are well known, too (for detailed recent reviews see Franceschini, 1975; Strausfeld, 1976, 1989; Heide, 1983; Hausen, 1984; Hardie, 1985; Laughlin, 1989; Hausen and Egelhaaf, 1989). Recently, successful attempts have also been made to analyse the molecular specificity of different brain areas and individual nerve cells. For instance, a wealth of information has been accumulated by immunohistochemical techniques on the distribution of the different neurotransmitters (see reviews by Hardie, 1989; Nässel, 1991).

LEVELS OF ANALYSIS AND EXPLANATION OF VISUAL ORIENTATION OF THE FLY

All this detailed knowledge, however, is not sufficient to understand what computations are performed by all these neuronal circuits. Since the functions of nervous systems manifest themselves in behaviour, a behavioural analysis is required before one can tell what has to be explained at the underlying neuronal level. However, the behavioural and the neuronal level are usually too far apart to explain the one immediately by the properties of the other. Instead, some intermediate level of explanation is often needed. The problem of how the fly processes motion information was, therefore, approached not only at the behavioural and neurophysiological levels but, in addition, modelling was successfully applied to bridge the gap in between.

The performance of the animal under free-flight conditions may be a natural starting point for this kind of analysis and has actually been studied to some extent (e.g. Land and Collett, 1974; Wehrhahn *et al.*, 1982; Wagner, 1985; Zeil, 1986). Free-flight behaviour, however, is often much too complex for a sufficiently detailed input–output analysis intended to elucidate the underlying information processing mechanisms. Therefore, most behavioural experiments were done on tethered flying animals under well defined and sufficiently simple visual stimulus conditions to allow stimulus–response relationships to be quantitatively established. Fortunately, the fly is sufficiently cooperative to exhibit certain basic visually induced orientation responses under such restrictive conditions.

In this way a systematic analysis was done on the landing responses as well as two types of turning reactions: compensatory course stabilization and orientation towards objects. The different types of visually induced turning responses were monitored by mounting the tethered fly when in flight to a torque meter and stimulating it with patterns of different size which could be moved with various velocities in different directions (Fig. 3) (Fermi and Reichardt, 1963; Götz, 1964; Buchner, 1984; Heisenberg and

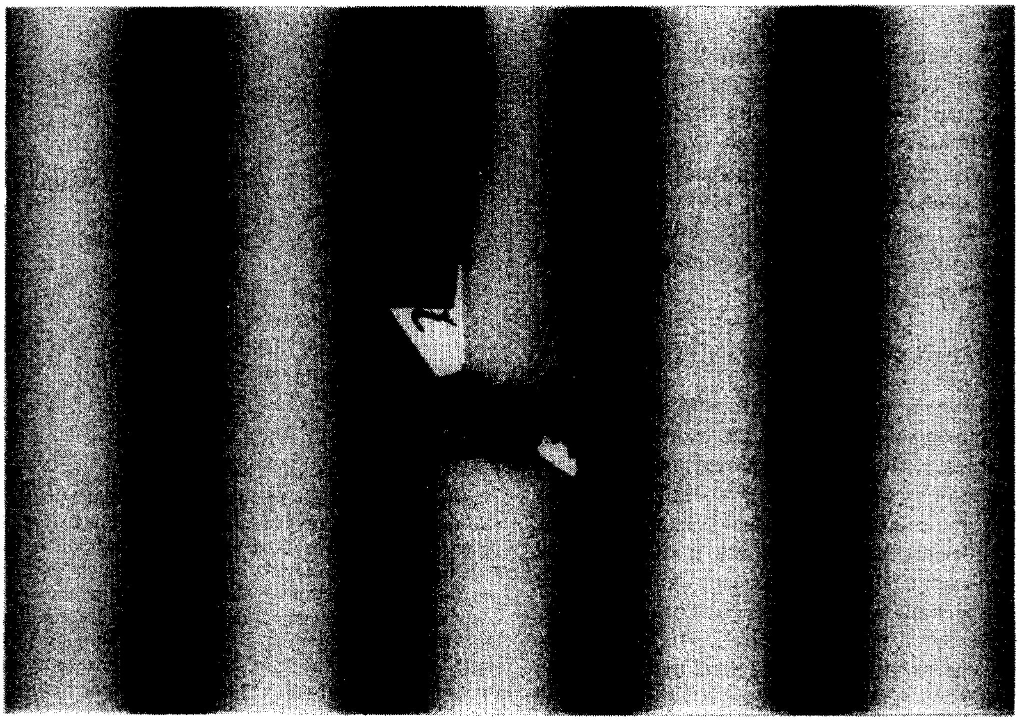

Fig. 3. Stimulus situation of the fly in a behavioural experiment done in tethered flight. The fly when in flight is tethered at a torque meter (not shown) with a cardboard triangle glued to its thorax between two pattern monitors.

Wolf, 1984; Reichardt, 1986; Egelhaaf *et al.*, 1988). Essentially the same stimulus conditions were employed to investigate the visual release mechanisms of landing (Borst and Bahde, 1989; Borst, 1990). In these experiments the extension of the fly's forelegs, a fixed-action pattern which characterizes the initial phase of the landing response (Goodman, 1960; Borst, 1986) and is accompanied by a deceleration of the animal (Borst and Bahde, 1988b), was monitored by means of a light barrier.

From this sort of behavioural analysis models of the underlying mechanisms could be derived. In part, the mechanisms were formulated as phenomenological theories by relating formally the different retinal input parameters, such as the retinal velocity or position of an object, to particular motor output variables, such as the fly's turning velocity (Reichardt and Poggio, 1976; Poggio and Reichardt, 1976; Buchner, 1984; Reichardt, 1986). Alternatively, these models were formulated as circuits which specify explicitly the different computations (Reichardt *et al.*, 1983; Egelhaaf, 1985a,c; Borst and Bahde, 1988a; 1989; Reichardt *et al.*, 1989).

From these models, predictions were derived with respect to the underlying neuronal substrate. These permitted the designation, as a search profile, of the appropriate visual stimuli for an identification of those neurones which may correspond to the different elements in the formal models (Egelhaaf, 1985b,c; Egelhaaf *et al.*, 1988; Hausen and Egelhaaf, 1989; Borst, 1990). On this basis, it was possible to model in terms of synaptic interactions and transmitters some of the operations previously specified in formal terms. Again, these hypothetical mechanisms were challenged experimentally. The application of pharmacological techniques allowed specific components of the system to be functionally disabled and for visual responses to be examined in their absence (Schmid and Bülthoff, 1988; Egelhaaf *et al.*, 1990; Egelhaaf, 1990; Warzecha *et al.*, 1993. The outcome of this multi-faceted analysis of the different computations performed by the fly's motion pathway can now be summarized.

STAGES OF MOTION COMPUTATION

Since we see motion without mental effort, it may not be immediately obvious that motion vision is by no means a trivial computational problem. This, however, may become clear if we realize that the only information available to the visual system is given by the time-dependent brightness values of the retinal image as sensed by the photoreceptors. From these continually changing brightness patterns, an explicit representation of motion information has to be computed by the nervous system. Therefore, one has to be aware that "retinal motion fields" are first of all the result of geometrical projections done by human investigators and not something available to the animal *a priori*.

In the present context, essentially three principal steps of motion computation are particularly important in transforming the retinal input into the corresponding behavioural output: (1) motion in the different parts of the retinal image is computed in parallel by two-dimensional retinotopic arrays of local movement detectors; (2) from their signals, various retinal motion patterns are extracted by spatial integration over arrays of appropriately directed local movement detectors; (3) the dynamic properties of these representations of retinal motion are tuned by temporal filtering to the needs of the fly in free flight.

LOCAL MOVEMENT DETECTION

Motion in different parts of the visual field usually does not have the same direction and velocity (Fig. 4 upper diagram). As a first step of motion analysis, therefore, a local representation of all the different motion vectors has to be computed. This is done in parallel by local movement detectors. These are organized in two-dimensional retinotopic arrays which cover the entire visual field (Fig. 4 middle diagram). On the basis of a behavioural analysis,

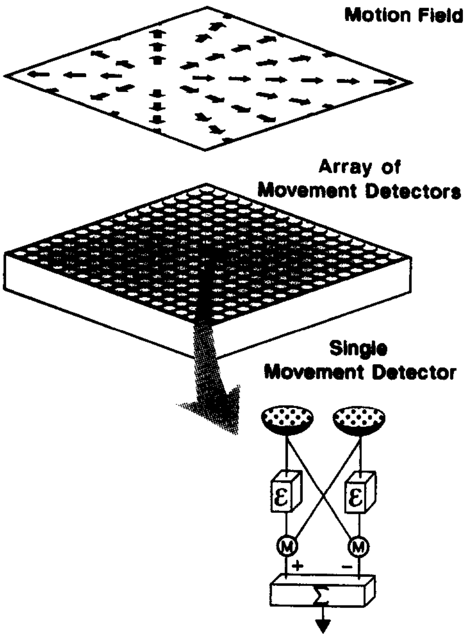

Fig. 4. In the first step of motion analysis, motion in different parts of the visual field is computed in parallel by two-dimensional arrays of local movement detectors. In the upper diagram an example of a retinal motion pattern is shown. The middle diagram shows a two-dimensional array of movement detectors. The bottom diagram shows a correlation-type movement detector as a representative of a local motion detection mechanism. In its simplest form, its input is given by the light intensities as measured at two points in space. In each subunit, the detector input signals are multiplied (M) with each other after one of them has been delayed by a time interval (eee). The outputs of both mirror-symmetrical subunits are then subtracted to give the final output signal of the detector.

Reichardt and Hassenstein proposed many years ago a formal model of such a local movement detector, the so-called correlation-type movement detector (Fig. 4 bottom diagram) (Hassenstein and Reichardt, 1956; Reichardt, 1961; Buchner, 1984; Reichardt, 1987; Borst and Egelhaaf, 1989). It consists of two mirror-symmetrical subunits, the output signals of which are subtracted from each other. Each subunit has two input channels which interact in a nonlinear way after one of the signals has been delayed by some sort of temporal filtering. A multiplication was proposed for the nonlinear interaction.

The mechanism of motion detection

How a correlation-type movement detector acquires its direction selectivity is illustrated in Fig. 5. For simplicity, this is done here separately for a single detector subunit (Figs 5a,b) and a complete detector (Figs 5c,d). As can be seen in Figs 5a and b, a detector subunit is directionally selective to some extent, since its responses differ for motion in opposite directions. This difference is due to the fact that during motion in the preferred direction, the detector input signals are shifted by the delay in such a way that they tend to coincide at the multiplication stage leading to a large response amplitude (Fig. 5a). In contrast, during motion in the null direction the time interval between the two signals when arriving at the multiplication stage increases resulting in only small responses (Fig. 5b). Nevertheless, if a movement detector were just realized in this way, it would also strongly respond to correlated input signals which are independent of the direction of motion, such as fluctuations in the mean light intensity (Van Santen and Sperling, 1985; Egelhaaf *et al.*, 1989a; Borst and Egelhaaf, 1990). This is reflected by the positive responses induced by motion in both the preferred and null direction (Figs 5a,b). By composing the movement detector of two oppositely directed units the outputs of which are subtracted, the direction-independent response components are eliminated (Fig. 5c,d). If the detector is perfectly

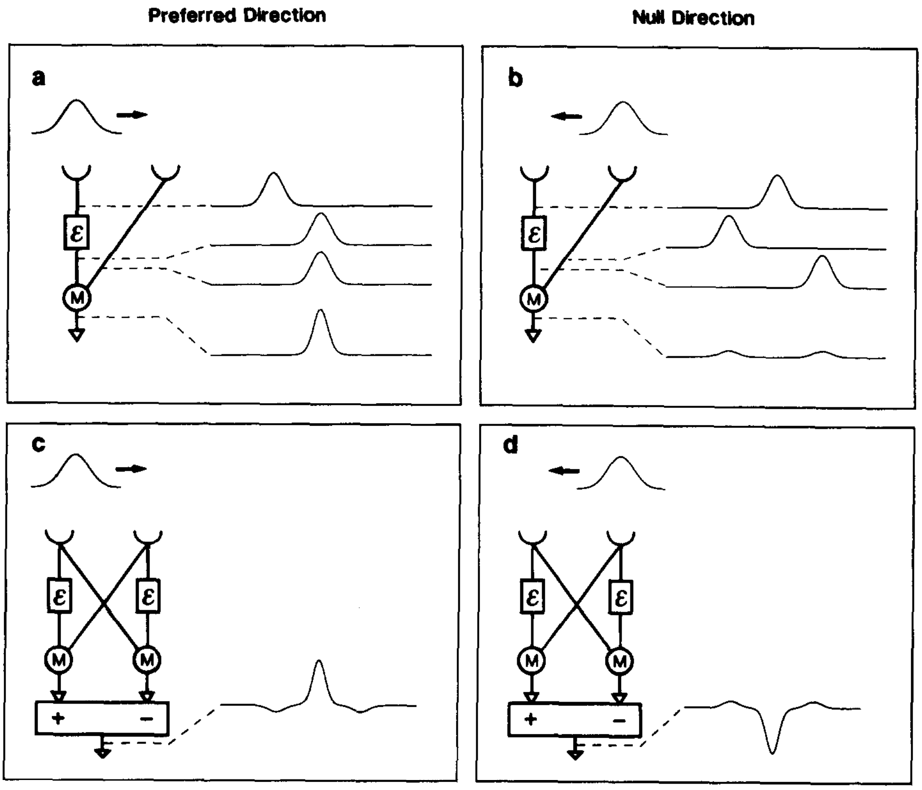

Fig. 5. Computation of motion by a correlation-type movement detector. To facilitate an understanding of the different operations performed by the detector,—the output of a single detector subunit to motion in opposite directions is considered first (a,b). The signals conveyed at the different processing stages are shown at the right of each subunit. When the stimulus pattern passes the two detector input channels, they are activated one after the other with a certain time shift. (a) When the pattern moves in the preferred direction, the temporal separation of the signals in both input channels may be compensated for by the delay. In this way both signals may coincide at the multiplication stage giving rise to a large response. (b) When the stimulus moves in the null direction, the temporal sequence of the signals in both channels is reversed. The delay further increases their separation in time, which results in only small responses. (c,d) By subtracting the output signals of the two oppositely directed detector subunits, those response components that are due to correlated input signals which are independent of the direction of motion and still present in the subunit output are eliminated. When the subtraction stage is perfectly balanced, the responses to motion in opposite directions have the same amplitude and time course but different signs.

symmetrical, it responds to motion in opposite directions with the same amplitude but with opposite sign (Egelhaaf *et al.*, 1989a).

The performance of the local movement detectors in the fly's visual system can be approximated surprisingly well by this formal scheme under both steady-state and transient conditions (Götz, 1972; Zaagman *et al.*, 1978; Mastebroek *et al.*, 1980; Buchner, 1984; Reichardt, 1987; Egelhaaf and Reichardt, 1987; Reichardt and Egelhaaf, 1988; Borst and Egelhaaf, 1989, 1990; Egelhaaf and Borst, 1989, 1992; Egelhaaf *et al.*, 1989a). Of course, the brain performs these computations by synaptic interactions between different nerve cells. The cellular basis of the different computations specified in the motion detector model is currently under intensive investigation. So far, pharmacological experiments using agonists and antagonists of various transmitters lead to the conclusion that GABA is likely to be involved at the subtraction stage of the two detector subunits, but the synaptic mechanism responsible for the nonlinear interaction between the input lines still needs to be clarified (Egelhaaf *et al.*, 1990). In the present context, however, it is more important to summarize what information about the visual surround is represented by these mechanisms.

Information represented by a local movement detector

Movement detectors do not provide an exact measurement of the local pattern velocity. Their responses also depend in a characteristic way on the structure of the stimulus pattern (Götz, 1964; Buchner, 1984; Reichardt, 1987; Borst and Egelhaaf, 1989). This is illustrated most strikingly by the time-course of a single movement detector's response to constant pattern motion. In Fig. 6 model predictions of a local movement detector are compared with the corresponding experimental data of motion detectors in the fly's visual system. The stimulus consists of a grating pattern with a sinusoidally modulated brightness. It is alternately moved with a constant velocity in the detector's preferred and null direction. Although the pattern velocity is constant, the movement detector responses are modulated over time in a characteristic way. As is predicted for a multiplication-like interaction between the movement detector input channels, the responses to a grating pattern with sinusoidal brightness modulation contains essentially only the fundamental and second harmonic of the temporal frequency of the stimulus (Egelhaaf *et al.*, 1989a,b). The close similarity of the predicted and the experimentally determined responses demonstrates the extraordinary predictive power of the formal movement detector model. Most important from a functional point of view, these results reveal that local movement detectors are not pure velocity sensors; their responses depend also in a characteristic way on the pattern structure. The mean response amplitude, however, signals to some extent the polarity of stimulus motion (see later). In the example shown in Fig. 6, negative responses indicate front-to-back motion, whereas positive responses indicate back-to-front motion.

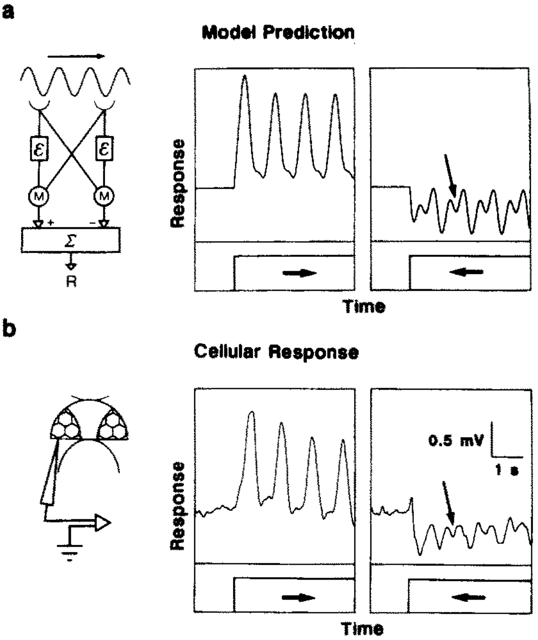

Fig. 6. Local movement detector responses to sinusoidally modulated gratings moving with a constant velocity in the preferred (left diagrams) and null direction (right diagrams). (a) Model simulation of a single correlation-type movement detector (see inset). (b) Electrophysiologically determined responses in the visual system of the blowfly *Calliphora erythrocephala*. The responses are graded membrane potential changes intracellularly recorded in one of the directionally selective HS-cells in the lobula plate. Since this cell type integrates local detector responses from large parts of the visual field, temporally modulated responses are obtained when spatial integration is prevented. This is achieved by moving the sinewave grating behind a small vertical slit, so that only a fraction of a spatial wavelength is seen by the fly at a given time. As predicted by the correlation model, the experimentally determined responses consist of virtually only the fundamental and second harmonic frequency components of the temporal frequency of the stimulus pattern which was 1 Hz. The second harmonic in the responses is indicated by arrows. Data taken from Egelhaaf *et al.* (1989a).

In the example shown in Fig. 6, a rather simple stimulus pattern was used: its brightness was modulated in only one direction and it moved along the axis of the movement detector. Things become more complicated if, as is usually the case, the animal is confronted with two-dimensional stimuli moving in arbitrary directions. To represent motion in two dimensions, it is not sufficient to have a single movement detector at each retinal location. Instead a pair of differently oriented detectors is needed. Their responses can then be combined to form a response vector which may be regarded as a two-dimensional representation of the corresponding motion vector. Since the response of each detector of a pair does not only depend on the velocity component along its respective axis but also on the structure of the stimulus pattern, the direction of the response vector may deviate from the direction of pattern motion. The output of pairs of movement detectors therefore do not, in general, encode correctly the direction and velocity of a moving object (Reichardt, 1987; Reichardt *et al.*, 1988; Reichardt and Schlögl, 1988). Thus, additional processing steps are required to gain meaningful motion information from the output of local movement detectors and, in particular, useful representations of the different retinal motion patterns.

EXTRACTION OF DIFFERENT RETINAL MOTION PATTERNS

Significance of spatial integration

Specific information about the different retinal motion patterns is extracted by intra- and interocular spatial integration over appropriately oriented local movement detectors. This simple computational strategy is appropriate because a large number of local movement detectors controls only a few motor output variables, such as the different rotational and translational velocity components or the movements of the legs. Indeed, some sort of spatial convergence has to take place between the local movement detectors and the final motor output anyway.

Moreover, spatial integration also eliminates the temporal modulations of the local movement detector responses. Since neighbouring movement detectors look at different spatial phases of the stimulus pattern, their responses are phase-shifted in time. Therefore, the temporal modulations disappear after spatial integration (Fig. 7) (Egelhaaf *et al.*, 1989a). Hence, spatial integration is a simple means of recovering, at least within a certain dynamic range (Egelhaaf and Borst, 1989), the time course of pattern velocity. Nevertheless, the mean response amplitude still depends in a characteristic way on the structure of the stimulus pattern (Götz, 1964; 1972; Buchner, 1984; Reichardt, 1987).

How should the nervous system integrate over the local movement detectors? The different types of motion patterns are characterized by different velocities in the different parts of the visual field (see Fig. 1). Hence, the easiest way would be to pool those movement detectors which have their preferred directions approximately oriented along the different directions of motion. If, for convenience, only the horizontal axis of the eye is taken into account, the following predictions may be derived: elements extracting rotatory coherent large-field motion should be excited by front-to-back motion in the visual field of one eye and by back-to-front motion in the other visual field. Elements tuned to retinal image expansion should respond best to front-to-back motion in the visual field of both eyes. The sensitivity of both systems to their corresponding motion patterns would be further enhanced if they were inhibited by motion in the respective reverse directions. Predictions for elements responding to small-field and relative motion are somewhat more complicated. They should be excited by movement detectors sensitive to front-to-back motion in the visual field of one eye. To prevent these elements from responding also to large-field stimuli moving in the same direction, they have, in addition, to be inhibited by large-field elements with the appropriate preferred directions.

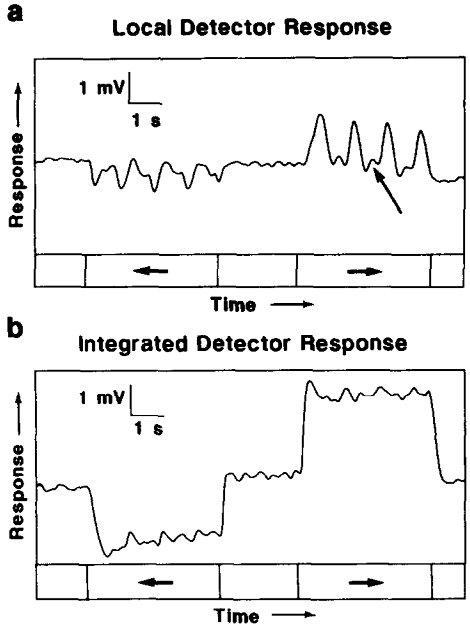

Fig. 7. Local and spatially integrated responses of biological motion detectors to sinusoidally modulated gratings drifting with a constant velocity. Graded changes in the membrane potential as recorded intracellularly from one of the directionally selective HS-cells in the lobula plate of *Calliphora erthrocephala.* (a) The local detector responses were recorded as described in the legend of Fig. 6 using the slit technique. The responses to motion in both the null and preferred direction show the characteristic response modulations although the pattern velocity is constant. (b) When large parts of the receptive field of the cell are stimulated by motion and one spatial wavelength of the pattern is seen by the eye, the response modulations virtually disappear. Only after spatial integration is the time course of the response about proportional to the time course of pattern velocity. Data taken from Egelhaaf *et al.* (1989a) and from Borst and Egelhaaf (1989).

Elements sensitive to large-field motion, relative motion and image expansion

From electrophysiological experiments, neuronal elements are known which meet these predictions and thus represent the different motion patterns which are under consideration here. It is mainly at the level of the posterior part of the third visual ganglion, the lobula plate (see Fig. 2), where large-field elements integrate spatially the signals of two-dimensional retinotopic arrays of local movement detectors with appropriate preferred directions. All these elements are activated by motion in a particular direction and are inhibited by motion in the respective opposite direction. Some of these interneurones are output elements of the visual ganglia, some connect to the contralateral half of the brain, and still others are centrifugal elements projecting from the brain back to the visual ganglia, thereby elaborating the response properties of the spatially integrating elements (Hausen, 1981, 1982a,b, 1984; Hengstenberg, 1982; Eckert and Dvorak, 1983; Egelhaaf, 1985b,c; Hausen and Egelhaaf, 1989). The lobula plate thus represents a main centre of motion computation and is therefore a good starting point for searching for the predicted elements which extract the different types of retinal motion patterns. Two functional classes of output elements of the lobula plate are particularly important in the present context, since they are specifically tuned to coherent rotatory large-field motion and to small-field and relative motion, respectively. These are the horizontal cells (HS-cells) (Hausen, 1982a,b) and figure detection cells (FD-cells (Egelhaaf, 1985b; Warzecha *et al.*, 1993).

There are three HS-cells which cover the dorsal, medial, and ventral parts of the lobula plate (Fig. 8a). According to the retinotopic organization of the visual pathway (see Borst and Egelhaaf, 1992), they scan the dorsal, medial and ventral parts of the ipsilateral visual field. In the ipsilateral brain, the HS-cells are connected to descending neurones which project to motor control centres in the thoracic ganglia (Strausfeld and Gronenberg, 1990; Gronenberg and Strausfeld, 1990). As a consequence of their local motion detector input, all three horizontal cells are excited by motion from the front to the back in the ipsilateral visual field. Their responses increase, though not linearly, with an increasing size of the stimulus pattern (Fig. 8b). Due to synaptic input from another identified large-field element of

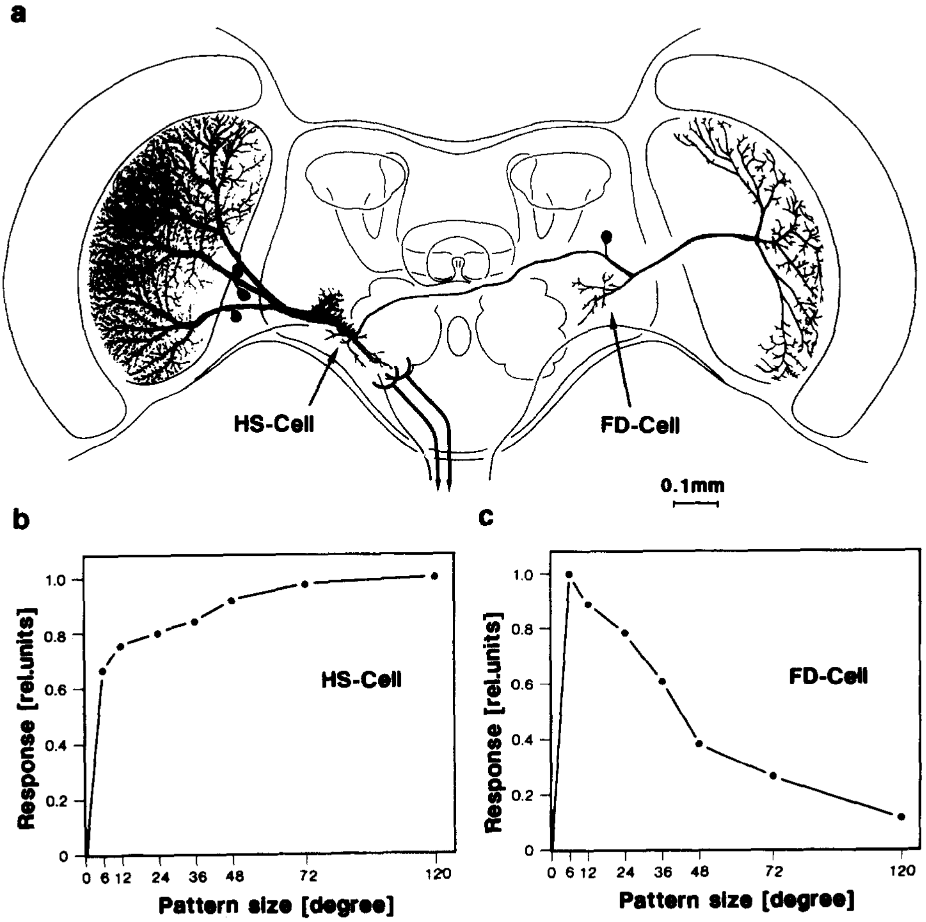

Fig. 8. Spatial integration properties of neural elements in the lobula plate of the blowfly *Calliphora erythrocephala* extracting coherent rotatory large-field motion (HS-cells) and relative and small-field motion (FD-cells). (a) Frontal projection of arborizations of the three HS-cells (shown in the left optic lobe) and one of the FD-cells, the FD1-cell (shown in the right optic lobe). The HS-cells were reconstructed from cobalt stainings (courtesy Klaus Hausen), the FD1-cell from intracellular Lucifer Yellow labelling taken from Egelhaaf, (1985). (b,c) Dependence of the mean response amplitude of a HS-cell and a FD1-cell on the size of the stimulus pattern. The pattern was a random texture the angular horizontal extent of which was varied (for details see Egelhaaf, 1985c); (b) unpublished; (c) taken from Egelhaaf (1985c). The response of the HS-cell reaches its maximum for motion of large patterns, whereas the FD-cell responds strongest when a small pattern is moved in its receptive field.

the contralateral lobula plate, some of the HS-cells also respond to motion from the back to the front in the contralateral visual field (Hausen, 1982a,b). This input organization makes the HS-cells particularly sensitive to coherent rotatory large-field motion about the animal's vertical axis. These cells may thus signal deviations of the animal from its course. There is good experimental evidence that the HS-cells are part of the fly's autopilot which compensates for unintended turns of the fly from its course. This conclusion is based on comparisons of the response properties of HS-cells with behavioural experiments on intact flies (Hausen, 1981; Wehrhahn and Hausen, 1980; Reichardt *et al.*, 1983; Wehrhahn, 1985; Egelhaaf *et al.*, 1988; Hausen and Egelhaaf, 1989; Reichardt *et al.*, 1989), on flies after microsurgical lesioning (Hausen and Wehrhahn, 1983; Hausen and Egelhaaf, 1989) or laser ablation (Geiger and Nässel, 1982) of the HS-cells, and on *Drosophila* mutants lacking the HS-cells (Heisenberg *et al.*, 1978; Heisenberg and Wolf, 1984).

The FD-cells are an anatomically heterogeneous group of at least four output elements of the lobula plate. As an example, the FD1-cell shown in Fig. 8a covers with its extended dendritic tree the lateral part of the lobula plate and consequently responds to motion in large parts of the fronto-lateral visual field. Its preferred direction is from the front to the back. All FD-cells are selectively tuned to small-field motion. Their response amplitudes reach their maxima during stimulation with a small pattern and decline again when the stimulus pattern becomes larger (Fig. 8c) (Egelhaaf, 1985c). This suggests that the FD-cells are inhibited by large-field motion. The inhibitory effect is induced not only by large-field motion in front of the ipsilateral eye, but also by large-field motion in the contralateral visual field (Egelhaaf, 1985b; Warzecha *et al.*, 1993). Thus, the FD-cells are selectively tuned to the motion of a small object and may signal its displacements against the background. The close similarity between the functional properties of the FD-cells and the dependence of visually induced turning responses on the different stimulus parameters suggests that the FD-cells may control orienting turns of the animal towards objects (Egelhaaf, 1985c; Reichardt *et al.*, 1989).

Visual interneurones extracting a representation of image expansion from the activity profiles of the retinotopic array of movement detectors have, so far, not been found at the level of the third visual ganglion. In the cervical connective (see Fig. 2), however, cells have been found which are responsive to retinal image expansion (Chillimi and Taddei-Ferretti, 1981; Borst, 1989b, 1991). They also respond to unilateral front-to-back motion, but not as strongly as to the bilateral stimulus. That back-to-front motion in the visual field of either eye is an inhibitory stimulus for these cells, suggested by the finding that their response to rotatory motion is considerably weaker than to unilateral front-to-back motion (Fig. 9). These elements thus respond strongest when the animal approaches an obstacle such as a potential landing site. Since their responses depend in a very similar way on the different parameters of the motion stimulus as the corresponding landing responses determined in behavioural experiments, it is suggested that they are part of the neuronal circuit initiating landing behaviour (Borst, 1989b, 1990).

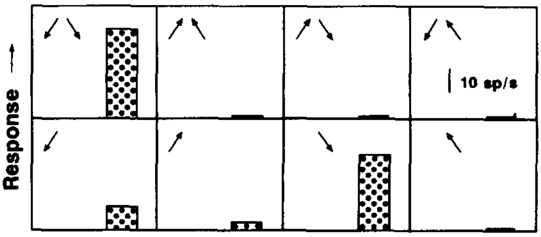

Fig. 9. Spatial integration properties of elements in the blowflys cervical connective extracting a representation of image expansion. The stimulus consisted of two grating patterns positioned symmetrically in front of the two eyes. In the upper diagrams both patterns were moved (direction of motion is indicated in the insets). In the bottom diagrams, the stimulus pattern in front of only one eye was moved, while the respective contralateral pattern was kept stationary (see insets). The cell is excited by front-to-back motion in front of either eye and inhibited by motion in the reverse direction. As a consequence, the cell does not respond to rotatory large-field motion but responds best to image expansion. Data taken from Borst (1989b).

Spatial tuning of FD-cells

The characteristic spatial tuning of elements sensitive to coherent rotatory large-field motion and image expansion can be explained by assuming that their responses are simply formed by a combination of their ipsi- and contralateral inputs. Such a simple wiring scheme cannot account for the specific response characteristics of FD-cells, since they become both activated and inhibited by ipsilateral motion depending on the size of the stimulus pattern (Egelhaaf, 1985b). This feature, together with the finding that FD-cells are also inhibited by contralateral motion (see above), can be explained in the most parsimonious way by assuming that the FD-cells are activated within the confines of their excitatory receptive fields by the retinotopic array of local movement detectors and, in addition, are inhibited by a binocular large-field element with the appropriate preferred direction (Fig. 10a).

Computer modelling demonstrates that such a mechanism indeed works and is sufficient to explain the properties of the FD-cell. On the basis of this circuit, not only the selective tuning of the FD-cell to small field motion, but also the characteristic time course of the responses to synchronous and relative motion of an object and its background can be modelled (Egelhaaf, 1985c).

In recent experiments the large-field inhibitor of a particular FD-cell has been identified. It is one of

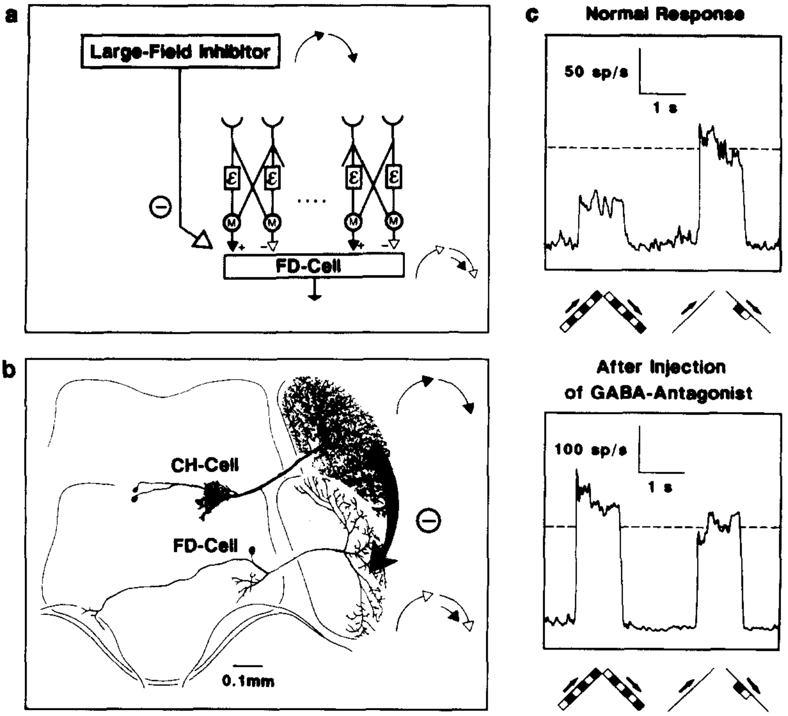

Fig. 10. Mechanism underlying the tuning of the FD1-cell in the blowfly to small-field motion. (a) Model of the mechanism: the FD-cell is assumed to integrate over the array of local movement detectors within the confines of its excitatory receptive field and to be inhibited in some way (either presynaptically at the level of the local movement detectors or postsynaptically (see Egelhaaf, 1985c) by an element sensitive to coherent rotatory large-field motion in front of either eye. (b) Anatomy of the (FD1-cell and its likely large-field inhibitor, the CH-cells (FD-cell taken from Egelhaaf, 1985b, 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 (Sigma, St Louis, MO, 100 nl of 1 mM solution injected in haemolymph over the lobula plate). Stimuli were electronically generated on two monitor screens mounted symmetrically in front of the eyes (see inset); a squarewave grating was used as stimulus pattern; the small-field stimulus had an angular horizontal extent of 17°, the large-field stimulus of 68 in front of either eye. Abbreviations. sp/s: spikes per sec. Before injection of the GABA-antagonist the cell responds in its characteristic way, i.e., with a larger response amplitude to small-field than to large-field motion. After injection of the GABA-antagonist the mean spike frequency in response to motion increases dramatically; most important, the response amplitudes are now somewhat larger during large-field motion than during small-field motion. Data from Egelhaaf (1990).

a pair of cells, called CH-cells. The CH-cells are another type of large-field elements which reside, as the FD-cells, in the lobula plate (Fig. 10b) (Hausen 1976a,b; 1981; Eckert and Dvorak, 1983; Hausen and Egelhaaf, 1989; Egelhaaf *et al.*, 1993). The CH-cells are excited by rotatory binocular large-field motion just as was proposed for the inhibitor element of the FD-cells. Furthermore, it is suggested by immunohistochemical labelling that the CH-cells are GABA-ergic and thus exert an inhibitory influence on postsynaptic elements (Meyer *et al.*, 1986).

The initial experimental evidence that the CH-cells may, in fact, inhibit a particular FD-cell has been obtained by application of an antagonist of GABA (Egelhaaf, 1990; Warzecha *et al.*, 1993). The outcome of such an experiment is illustrated by the spike frequency histograms in Fig. 10c. Before application of the GABA-antagonist the cell responds with a higher spike frequency to small-field motion than to large-field motion. However, some time after the GABA-antagonist is injected the response profiles change considerably. Most important in the present context, the response amplitude is now somewhat larger during large-field than during small-field motion. Thus, the sensitivity of the FD-cell to the motion of small objects disappears. To decide which one of the CH-cells inhibits the FD1-cell, a more specific ablation technique was used. A single CH-cell was individually filled with a fluorescent dye and photo-ablated while the activity of the FD1-cell was recorded. Photo-ablation of only one of the CH-cells led to an elimination of the FD1-cell's specific sensitivity for small moving objects (Warzecha *et al.*, 1992, 1993). Hence, the characteristic spatial tuning of the FD1-cell is mediated by a single large-field element via GABAergic synapses.

TEMPORAL TUNING

The different types of motion patterns, however, are not only characterized by their specific geometrical properties. They can also be expected to have specific dynamic features. Of course, these are also largely determined by the animal's own direction and velocity. For instance, in free flight, coherent rotatory large-field image displacements induced by self-motion of the fly are brief and rapid. This is because the animal does not turn its body axis smoothly when changing course, but makes several rapid turns instead (Wagner, 1986).

Is the processing of the different retinal motion patterns tuned in some way to their dynamic properties or, alternatively, are the temporal properties of the motion pathway mainly determined by the dynamic properties of the local movement detectors? At the level of the lobula plate, the different motion-sensitive elements still have the same dynamic properties as their movement detector input elements (Egelhaaf and Reichardt, 1987; Egelhaaf and Borst, 1989). In contrast, at the behavioural level the dynamic properties of the different motor control systems differ considerably. Indeed, in both the pathway mediating corrective steering manoeuvres and the landing system, the temporal properties of the signals are severely altered after the spatial integration stage.

Frequency filtering in the motion pathway

In the fly's autopilot as well as in its landing system the spatially integrated signals are temporally processed by a leaky integrator or, which is equivalent from a formal point of view, a low-pass filter (Egelhaaf, 1987; Borst and Bahde, 1989; Borst, 1989a, 1990).

Figure 11a relates the temporal properties of compensatory turning reactions as recorded in tethered flight to those of the HS-cells, the corresponding element at the spatial integration stage by which these turning reactions are controlled. The stimulus consisted of a large-field pattern which was oscillated sinusoidally about the fly. While the mean turning amplitudes of the fly are largest at low oscillation frequencies, the corresponding cellular responses at the spatial integration stage are largest at much higher frequencies. These data suggest some sort of temporal low-pass filter in the pathway tuned to coherent rotatory large-field motion which severely attenuates the high frequency components in the response. Temporal tuning is accomplished by neuronal computations somewhere between the lobula plate and the steering muscles which mediate the compensatory turning responses, rather than by the mechanical properties of the flight torque generating mechanisms. This is suggested by recent combined behavioural and electrophysiological experiments, where the flight steering muscles were found to fall into two functional classes according to the responses they mediate. The muscles mediating corrective turning responses show different dynamic properties from the muscles responsible for orientation turns towards small objects. These different dynamic properties closely parallel the corresponding behavioural response components (Egelhaaf, 1989).

The experiments leading to evidence for a leaky temporal integrator in the pathway controlling landing are necessarily different. This is because, in

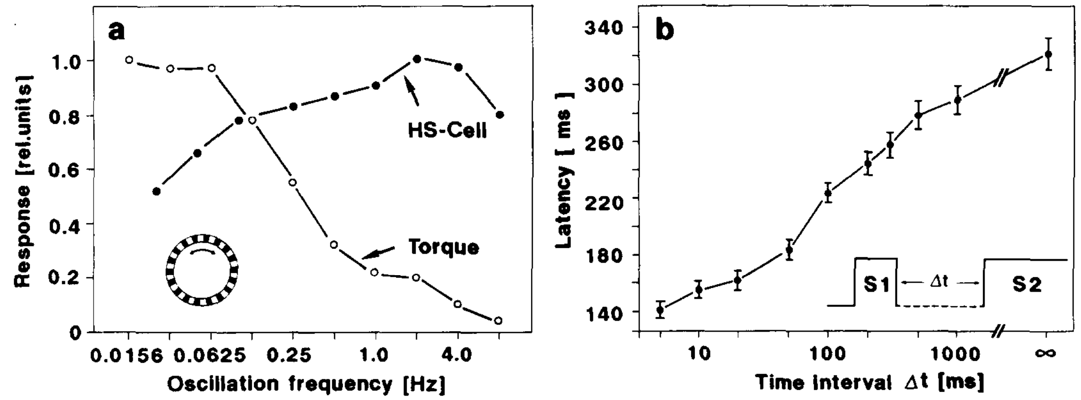

Fig. 11. Temporal tuning of the system mediating compensatory turning reactions (a) and the landing system (b). (a) Average amplitude of optomotor yaw torque (open symbols) and of the response of a HS-cell (filled symbols) as a function of the oscillation frequency of a cylindrical drum covered with a striped pattern (see inset). The behavioural and cellular responses depend in a different way on oscillation frequency. While the behavioural response is strongest at low frequencies, the corresponding cellular response has its optimum at 2 Hz. This difference suggests a kind of low-pass filter somewhere between the lobula plate and the final motor output in the system mediating compensatory turning responses (data of torque responses from Egelhaaf, 1987, electrophysiological data, Egelhaaf, unpublished). (b) Latency of the landing response as a function of the time interval between a subthreshold prestimulus S1 of 150 ms duration and a test-stimulus S2. In both cases, the pattern moved from the front to the back. For an interstimulus interval of only 5 msec the response latency is reduced to 140 msec as compared to 320 msec without prestimulus (data point on the right of the diagram). The effect of S1 on the latency decays with an increasing inter-stimulus interval. Note that even after 1 sec, a significant influence of S1 can still be measured. This suggests a leaky integrator in the landing system with a time constant of several hundred millisec (data from Borst, 1990).

contrast to the control systems for the different types of turning responses, no continuous time-dependent behavioural output signal of the landing system is available. Since the extension of the legs which accompanies the initiation of landing is an all-or-none response as described previously (Borst, 1986), only its occurrence can be monitored. However, the latency of this response varies with the stimulus strength in a graded way. In the experiment shown in Fig. llb the latency of the landing response is shortened if a test-stimulus is preceded by an appropriate subthreshold pre-stimulus. The effect decreases with increasing interval between pre- and test-stimulus (Borst and Bahde, 1989; Borst, 1989a, 1990). These results agree with the assumption of a leaky temporal integrator in the landing system. Taking the dynamic properties of the movement detectors into account (Borst and Bahde, 1986; Egelhaaf and Borst, 1989), the pre-stimulus would not be expected to affect the latency following the test-stimulus without such a temporal processing stage. Interestingly, the neurones in the cervical connective which are sensitive to image expansion (see above) show a marked difference in the time-course of their response when compared to lobula-plate neurones. In contrast to the cells in the lobula plate, they reach their maximum response level only some time after a stimulus pattern has started moving (Fig. 12) (Borst, 1990). When pattern motion is stopped, they also show a slow decay of their response lasting for more than 1 sec. Hence, these cells yield a representation of the time course of retinal image expansion which has been processed by a leaky temporal integrator.

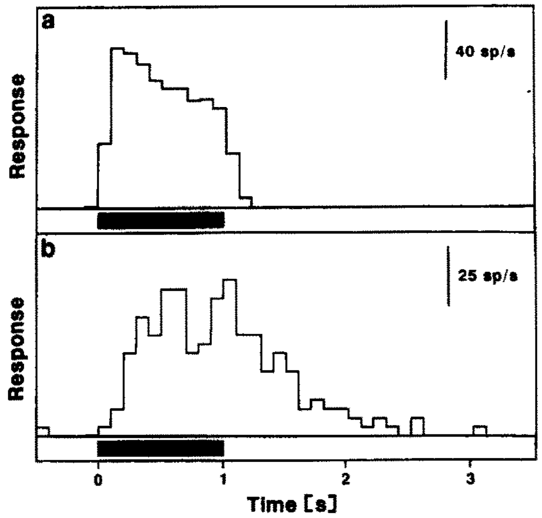

Fig. 12. Dynamic response properties of a typical neurone in the lobula plate (H1-cell) (a) and an element in the cervical connective responding best to image expansion (b) (see Fig. 9). The stimulus consisted of a grating pattern which moved during the time indicated with a constant velocity in the cells preferred direction. The neurone in the cervical connective differs from the lobula plate cell in that its response rises slowly at stimulus onset and decays slowly after the end of the motion stimulation. In this type of neurone the motion information is already spatiotemporally integrated. Abbreviations. sp/s: spikes per sec. Data shown in (b) from the same cell as in Fig. 9; taken from Borst (1989b).

Functional significance

Although temporal processing in both the pathways mediating corrective steering manoeuvres and landing responses can be formally characterized in essentially the same way by a leaky temporal integrator (or a low-pass filter), its functional significance is likely to differ considerably.

Active turns of the fly in free flight are brief and rapid (Wagner, 1986). The resulting retinal large-field motion, consequently, is also characterized by fast changes in its direction. Owing to the dynamic tuning of the fly's autopilot, these deviations from the course are not much compensated for by corrective steering manoeuvres (Egelhaaf, 1987). Hence, the temporal tuning stage in the pathway extracting rotatory large-field motion might be a simple computational means to prevent the visual consequences of active turns being compensated for by the autopilot. This is only possible because the visual system is carefully tuned to the specific dynamic properties of the retinal motion patterns that are generated under natural conditions both actively and passively.

In contrast, in the landing system, a leaky temporal integrator in combination with a threshold device is required to convert the stimulus strength into a wide range of response latencies. A weak stimulus, such as a slowly expanding pattern, leads only to a slow increase in the temporally integrated signal and thus to a large response latency, whereas a strong stimulus, such as a pattern expanding with a higher velocity, leads to a rapid increase in the temporally integrated signal and thus needs less time to reach threshold. Consequently, a temporal integrator ensures that the fly initiates landing earlier, when it approaches a potential landing site with a higher velocity than with a lower one and thus provides safe landing.

CONCLUSIONS

The features of the different retinal motion patterns which are important for flight control are extracted in a series of processing steps (Fig. 13). (1) The initial explicit representation of motion is computed in parallel by retinotopic arrays of local motion detectors. (2) This representation then segregates into different pathways which are selectively tuned to the different retinal motion patterns and feed different control systems of visual orientation behaviour. This spatial tuning is achieved by appropriate intra- and interocular spatial integration. (3) Before exerting their influence on the motor control centres, the signals are tuned by appropriate temporal filtering to the characteristic dynamic properties of the retinal motion fields as induced during the different flight manoeuvres.

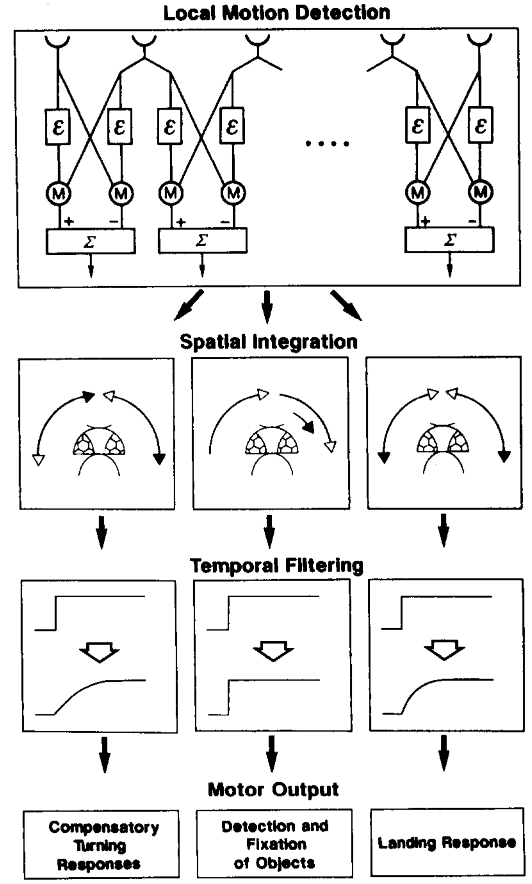

Fig. 13. Summary diagram of the principal steps of motion information processing in the fly visual system. Local Motion Detection: detection of local motion by large retinotopic arrays of movement detectors; only three detectors are shown; for an explanation of the abbreviations, see legend of Fig. 4. Spatial Integration: the initial representation of local motion segregates into three pathways which extract different retinal 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; filled and open arrow-heads indicate excitation and inhibition, long and small arrows large-field and small-field motion, respectively. Temporal Filtering: temporal tuning of the representations of rotatory large-field motion and pattern expansion by some sort of low-pass filters with different time constants. The signals before and after the filters are shown schematically in response to an onset of motion. Motor Output: the different pathways are involved in mediating different types of orientation behaviour.

In this way three flight control systems have been characterized. One of them responds best to coherent rotatory large-field motion of the entire visual surround. As part of the fly's autopilot, it signals deviations of the animal from its course and mediates corrective steering manoeuvres. Another system signals retinal image displacements of relatively small objects. It thus detects these objects and controls orientation responses towards them. The third control system responds best to image expansion when the animal approaches a potential landing site and releases landing.

All these computational problems are not specific to the fly but have to be solved quite generally by motion vision systems. It would be interesting to know whether there are also common solutions to these problems. With respect to the computations underlying local motion detection, there is rather good evidence from electrophysiological, behavioural and psychophysical studies for essentially the same mechanism even in animals as phylogenetically distant as insects and man (for a review see Borst and Egelhaaf, 1989). Moreover, there also seem to be common strategies of extracting the different types of retinal motion patterns, as is suggested by the fact that in other insects (e.g. Palka, 1972; Collett and King, 1975; Olberg, 1981; DeVoe *et al.*, 1982) as well as various vertebrate species (e.g. Simpson, 1984; Allman *et al.*, 1985; Frost, 1986; Saito *et al.*, 1986; Tanaka *et al.*, 1986) neuronal elements were found which represent specifically these motion patterns.

These similarities indicate common mechanisms of motion information processing, and thus substantiate the significance of using comparatively simple systems, such as the fly, to elucidate the underlying neuronal mechanisms.

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