NEURONAL MATCHED FILTERS FOR OPTIC FLOW PROCESSING IN FLYING INSECTS

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I. Introduction

A. Relative Motion and Optic Flow

Relative motions between the eyes and visual structured surroundings always result in retinal image shifts. Moving on a crowded place, for instance, will lead to a complex pattern of retinal image shifts which is induced by a "blend" of two different kinds of relative motions. Self-motion of an observer causes coherent wide field motion patterns covering the entire visual field of the observer. In contrast, external object

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motions within the visual field of an otherwise motionless observer result in image shifts which are usually locally confined. Both kinds of image shifts can be described in terms of velocity vector fields, called 'optic flow fields', where the local vectors indicate the direction and magnitude of the respective relative motion (Gibson, 1950; Nakayama and Loomis, 1974; Koenderink and van Doorn, 1987). In general, the resulting optic flow contains information which may be used to control visually guided behavior. First, the global structure of the optic flow depends on the observer's self-motion—the overall appearance of a flow field induced by a translation defers from a flow field generated during rotation (cf. Figs. 1B and 1C). And second, the magnitude of the translatory optic flow depends not just upon the respective translation speed but also on the distance between the observer and the visual structures of the surroundings. Objects close by result in higher image velocities than more distant ones. Thus, by analyzing the relative velocity differences within translatory optic flow fields, an observer may get information about the distribution of relative distances within the environment presently encountered. Both information about the present self-motion and the 3D layout of the environment is essential for a mobile observer. To control his locomotion adequately (e.g., to stabilize his motion path or to avoid bumping into obstacles), he needs to sense his current self-motion and to estimate the distance to possible obstacles. This holds true for all kinds of observers like humans, animals, and robots—if the latter are equipped with optical sensors. In this chapter, however, I will concentrate on optic flow processing in insects. The significance of optic flow processing for vertebrates, including humans, will be outlined in other chapters in this volume.

II. Visually Guided Behavior and Optic Flow Processing in Flying Insects

A. Trying to Explain Visually Guided Behavior on the Basis of Its Underlying Neuronal Mechanisms

Several species of flying insects show interesting visually guided behavior and have been investigated to find the neuronal basis for processing different aspects of optic flow (general overview: Wehner, 1981). In some cases, the behavioral and the neuronal level were brought together in a rather promising way. Object fixation and figure–ground discrimination (Reichardt and Poggio, 1976; Heisenberg and Wolf, 1984; Egelhaaf, 1985a, b, c; Warzecha et al., 1993; Kimmerle *et al.*, 1996), land-

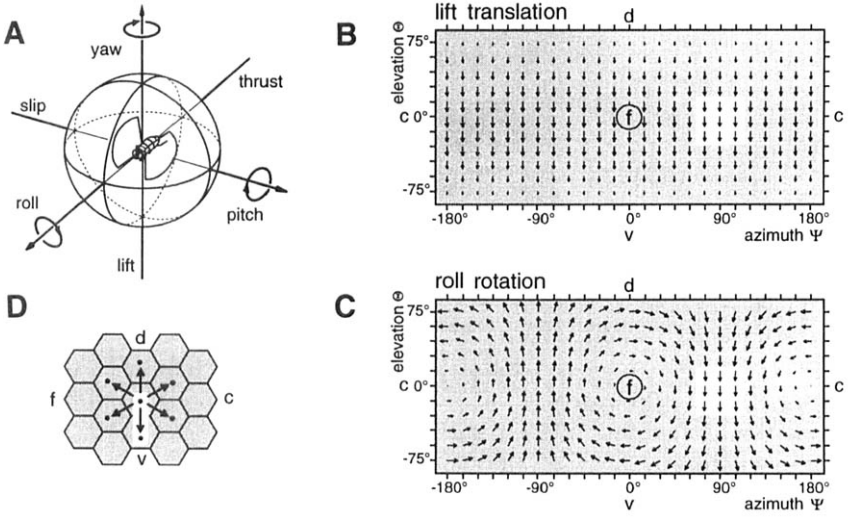

FIG. 1. Self-motion and self-motion-induced optic flow. (A) Self-motion in 3D space can be described in terms of its translation (thrust, slip, lift) and rotation (roll, pitch, yaw) component along and around the animal's three major body axes (body axis, transverse body axis, and vertical body axis). (B) Optic flow field induced by a pure lift translation. It is plotted in a Mercator map of the whole visual field where each location is specified by two angles (i.e., the horizontal azimuth ψ and the vertical elevation θ). The encircled f in the center denotes the direction along the positive body axis of the animal; the left and right halves show the left and right visual hemisphere, respectively (d = dorsal, v = ventral, c = caudal). Due to the Mercator projection, the dorsal and ventral parts of the spherical visual field are highly overemphasized in the map. Each single arrow indicates the direction and velocity of the respective local image shift. In translatory optic flow fields, all velocity vectors are aligned along great circles connecting the focus of expansion (at d) with the focus of contraction (at v). For further explanations, see text. (C) Optic-flow field induced by a pure roll rotation, plotted in the same way as the lift-flow field. In a rotatory flow field, local velocity vectors are aligned along parallel circles centered around the axis of rotation (here: corresponding exactly with the body axis f). Globally, we can easily distinguish the structure of translatory and rotatory flow fields. (D) A set of six local motion detectors (EMDs) analyzing retinal image shifts resulting from relative motion at the same location in the visual field. Arrows connecting the black dots indicate the different preferred directions of the EMDs. Note that the EMD analyzing vertical image shifts (white frame) at $\psi = 90°$ and $\theta = 0°$ may be strongly excited in either case—if the animal is performing a lift or roll self-motion (compare the white areas within the respective flow fields). Modified from Krapp *et al.* (1998).

ing (Wagner, 1982; Borst and Bahde, 1988; Borst, 1991) and chasing behavior (Wagner, 1986; Böddeker *et al.*, 1998; Wachenfeld, 1994) in flies, for instance, are controlled by visual cues which rely on particular aspects of optic flow. Dragonflies have developed visual interneurons which are thought to extract particular features from the optic flow to control prey-

ing (Mayer, 1957; Olberg, 1981; O'Carroll, 1993; Frye and Olberg, 1995). In the hawk moth, visual interneurons were found to respond to particular self-motion-induced optic flow components which may be involved in their visually controlled feeding behavior (i.e., hovering in front of a flower and sucking nectar like hummingbirds) (Herrera, 1992; Farina *et al.*, 1994; Kern and Varjú, 1998; Kern, 1998). Although it is well known that hymenoptera, first of all honeybees, are capable of solving a great variety of visually controlled tasks based on optic flow processing (Lehrer, 1994, 1997; Srinivansan *et al.*, 1996; Srinivasan and Zhang, this volume), comparatively little is known about the underlying neuronal basis. This rather arbitrary list of examples for different visually guided behaviors in different insects could be continued at length. Nevertheless, in the following I will confine myself to the neuronal basis of the optomotor behavior and gaze stabilization in the fly. In general, the optomotor behavior in flying insects describes the capability of compensating for involuntary course deviations which may be due to gusts of wind or flying through turbulent air, respectively. This capability has been investigated in several insect species including, for instance, flies, locusts and bees, at the behavioral (Wehner, 1981; Lehrer, 1994; Collett *et al.*, 1993; Buchner, 1984; Götz, 1983a,b; Heisenberg and Wolf, 1993; Rowell, 1988; Robert, 1988; Gewecke, 1983; Preiss, 1991) and as well as the neuronal level (Hausen and Egelhaaf, 1989; Gewecke and Hou, 1993; Goodman *et al.*, 1990; Reichert and Rowell, 1986; Rind, 1990; Milde, 1993). In this chapter, gaze stabilization refers to the tendency of insects to keep their eyes aligned with the external horizon by means of rotatory head movements (Hengstenberg, 1991)—a behavior thoroughly investigated in other visually oriented animals and humans (Carpenter, 1988; Dieringer, 1986).

B. The Fly as an Experimental Model System

Among insects and with respect to visual information processing, the fly turned out to be a rewarding experimental animal to address questions of general interest. The fly visual system has been investigated extensively by means of behavioral experiments on the one hand, and by applying neuroanatomical as well as electrophysiological techniques on the other. Often, both the behavior and its underlying neuronal basis can be studied quantitatively in the very same system under similar or even the same stimulus conditions. The combination of the neuronal and the behavioral description level allows us to estimate the system's adaptation regarding the performance in particular behavioral tasks. It is evident, of course, that this kind of neuroethological approach can be

ideally pursued in systems where distinct behaviors can be correlated with the activity of identified neuronal circuits or even single nerve cells.

III. How to Gain Self-Motion Information from Optic Flow

A successful performance of both optomotor response and gaze stabilization behavior relies on information about the instantaneous self-motion. In addition to using the mechanosensory signals of the halter system, which measures the velocity of self-rotations (Hengstenberg, 1993), the fly is thought to gain information about the self-motion by exploiting the instantaneous optic flow (Hausen and Egelhaaf, 1989).

A. Features of Rotatory and Translatory Optic Flow

As already mentioned in the introduction, self-motion can be described in terms of translation and rotation. The resulting optic flow field is a linear combination of the translatory and rotatory component induced by the respective motion along and around the three main body axes (Fig. 1A). Translations (thrust, slip, lift) and rotations (roll, pitch, yaw) generate different optic flow fields over the insect's eyes. The local flow vectors in translatory optic flow fields are oriented along meridians connecting the focus of expansion (i.e., the direction point d in the translation is pointing at, Fig. 1B) with the focus of contraction which is the opposite pole of the flow field. Figure 1B shows the optic flow induced by a lift translation plotted along azimuth ψ and elevation θ in a Mercator map of the visual field. The flow field generated during a rotation around the body axis (roll) is shown in Fig. 1C. A general feature of the rotatory flow structure is that all local vectors are aligned along parallel circles centered around the axis of rotation (in this case the axis coincides with point f in Fig. 1C). Within both flow fields (Figs. 1B and 1C), no image shift occurs at the poles. With increasing distance from the poles, the magnitude of the flow vectors increases as well and gets maximum at the equator of translation or rotation (i.e., exactly between the two poles). The local translation vectors additionally depend on the distance between the eyes and the objects in the environment; objects close by generate bigger flow vectors. In the calculated optic flow field shown in Fig. 1B, the same distance was assumed at all location. Rotatory optic flow is distance invariant. In "real" flight situations, the rotatory and translatory components are linearly superimposed and may result in rather complex optic flow fields.

B. How to Get the Global Difference by Local Measurements: The Idea of Neuronal Matched Filters

Globally, we can easily distinguish the flow fields induced by the different self-motions shown here. Visual motion, however, is sensed locally by elementary movement detectors (EMDs; Hassenstein and Reichardt, 1956; Reichardt, 1987; Borst and Egelhaaf, 1989). Each location in the visual field is analyzed by a set of EMDs along at least six different preferred directions. These preferred directions reflect the arrangement of the optical axes of neighboring ommatidia within the fly's compound eye (Fig. 1D; Buchner, 1976; Götz *et al.*, 1979). At the level of a single motion detector, however, it is ambiguous whether the image shift exciting the EMD is due to a translation or a rotation. Such an area where the local optic flow is quite similar for different self-motions is marked in the optic flow fields shown in Figs. 1B and 1C. One way to make the problem less ambiguous is to integrate selectively the outputs of EMDs whose preferred directions correspond to the directions of the local flow vectors at each point in visual space. Figure 2 demonstrates the scheme of

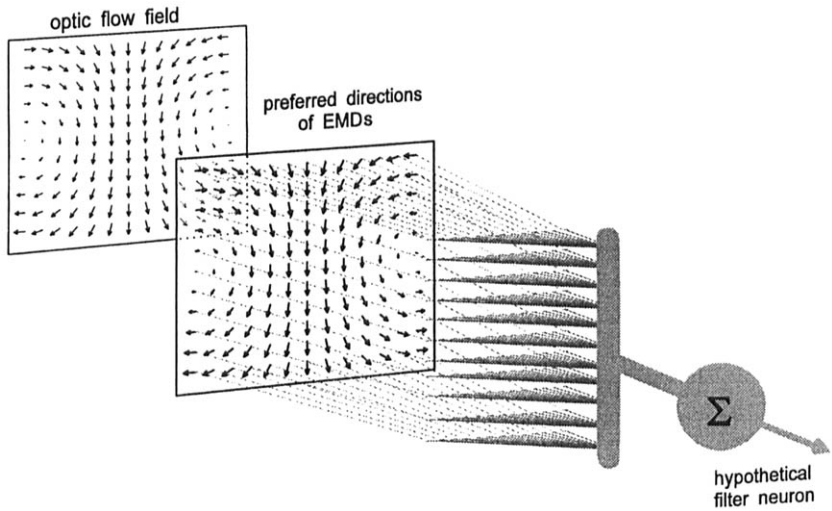

Fig. 2. A hypothetical filter neuron integrates selectively signals of EMDs whose preferred directions correspond to the direction of local flow vectors from a roll flow field over the right eye. This filter neuron with a receptive field that makes up the right visual hemisphere would be strongly excited by a roll rotation around the body axis to the left. Modified from Krapp *et al.* (1998).

a hypothetical filter neuron designed to sense the optic flow over the right eye induced by a rotation to the left around the body axis (roll). Based on this model, some qualitative features of such filter neurons can be expected: these kinds of neurons need to be motion sensitive and directionally selective. They should have extended receptive fields—the larger the receptive field, the better it can be expected to distinguish between different optic flow fields and thus different self-motions. And finally, the distribution of local preferred directions should match the direction distribution of local optic flow vectors.

We have known for a long time that individually identifiable interneurons which respond to wide field motion live within the fly visual system (Bishop and Keehn, 1967; Bishop *et al.*, 1968; MacCann and Dill, 1969; Dvorak *et al.*, 1975; Hausen, 1976). Their big receptive fields and their directionally selective motion response made these so-called tangential neurons good candidates for being involved in the control of optomotor responses and gaze stabilization. After a short introduction into the visual system of the fly, I will try to further explain why some of these neurons are most likely concerned with optic flow processing.

IV. The Fly Visual System

A. Organization of the Visual Neuropils

The fly visual system is organized in retinotopically arranged columns (Strausfeld, 1976, 1989; Bausenwein and Fischbach, 1992) and consists of the retina plus three successive neuropils, called lamina, medulla, and lobula complex. In diptera, the lobula complex is subdivided into the anterior lobula and the posterior lobula plate. With respect to the visual analysis of self-motion, the lobula plate was identified to be the highest processing stage. In the lobula plate, about 60 tangential interneurons have been found so far (Hausen and Egelhaaf, 1989; Hausen, 1984). They are stacked along the anterior-posterior extent of the neuropil within four directional input layers representing horizontal front-to-back, horizontal back-to-front, vertical upward, and vertical downward motion (Buchner and Buchner, 1984). They are thought to integrate the outputs of many movement-detecting small field elements on their dendritic arborizations (Borst and Egelhaaf, 1992). Some tangential neurons are heterolateral spiking elements (Hausen, 1976, 1984). They pick up local visual information within one lobula plate and convey it to the con-

tralateral part of the bilateral symmetric visual system. Other tangential neurons are thought to be pure output elements. In *Calliphora vicina* (previously *Calliphora erythrocephala* Meig.), 13 of these output neurons can be subdivided into two different groups called HS neurons (HS = horizontal system) and VS neurons (VS = vertical system; Hausen, 1976, 1982a; Hengstenberg, 1977; Soohoo and Bishop, 1980; Pierantoni, 1976; Eckert and Bishop, 1978; Hengstenberg *et al.*, 1982).

B. Wide Field Motion-Sensitive Neurons in the Third Visual Neuropil: The Tangential Neurons

Like most of the other tangential neurons, the HS and VS neurons can be individually identified by single-cell-staining methods (Strausfeld *et al.*, 1983; Hengstenberg *et al.*, 1983). Together, the dendritic arborizations of both neuronal subgroups cover the whole lobula plate. The HS divides the visual field into three slightly overlapping areas. The dorsal neuron HSN (N = north) has its receptive field in the upper part of the ipsilateral visual hemisphere, the middle one HSE (E = equatorial) analyzes motion in the equatorial visual field, and the ventral neuron HSS (S = south) monitors the lower part of the visual hemisphere. The dendrites of the HS neurons arborize in the anterior input layers of the lobula plate. Accordingly, on average, these neurons are excited by ipsilateral front-to-back motion. Ipsilateral back-to-front motion inhibits the HS neurons. The HSN and HSE are additionally sensitive to back-to-front motion within the contralateral hemisphere (Hausen, 1982b).

The vertically oriented dendrites of the 10 VS neurons overlap slightly more than those of the HS neurons. Dendritic fields of the VS neurons cover the lobula plate from the distal (VS1) to the proximal margin (VS10) of the neuropil (Hengstenberg *et al.*, 1982). Most of the dendritic arborizations of the VS neurons ramify within the most posterior input layer of the lobula plate, which corresponds with a predominant sensitivity to vertical downward motion (Hengstenberg, 1982). However, some dorsal dendritic branches of VS1 and VS7–VS10 invest the more anterior layers mediating horizontal direction selective inputs (Hengstenberg *et al.*, 1982).

Both, the HS neurons and the VS neurons respond predominantly to visual stimulation with graded membrane potential changes which may be accompanied by irregular superimposed spikes (Hengstenberg, 1977). Motion along their respective preferred direction results in a depolarization of the membrane, whereas motion along the antipreferred, or null direction, causes a hyperpolarization.

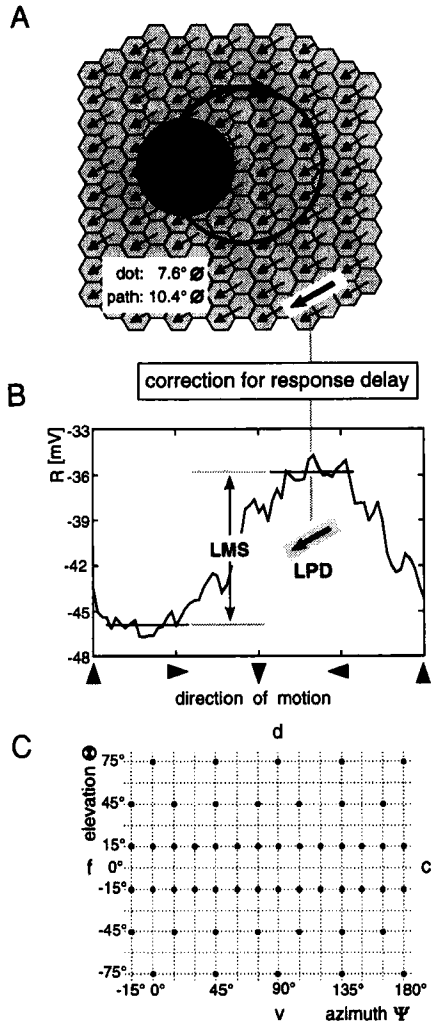

FIG. 3. Stimulation procedure to investigate the receptive field organization of direction-selective wide field neurons. (A) A black dot is moved along a circular path at constant velocity (2 cycles per second). Small arrows within the hexagonal pattern, which schematizes the ommatidium lattice, indicate the preferred directions of EMDs converging on an intracellularly recorded tangential neuron. (B) When the direction of dot motion coincides with the local preferred direction of the EMDs, the response of the recorded neuron becomes maximal; motion in the opposite direction results in a hyperpolarization of the membrane potential. The local preferred direction is determined by comparing the responses to dot motion in clockwise and counterclockwise direction and estimating the response delay. From the corrected tuning curve, the local preferred direction can be obtained by applying circular statistics, or determining the phase shift of the first harmonic of the Fourier transform. The local motion sensitivity is defined by the difference between the LPD quadrant and the opposite quadrant of the tuning curve (thick horizontal lines indicate the quadrants). (C) Measuring positions. The LPDs and LMSs are determined at the positions labeled by small black dots. Data at intermediate positions were obtained by interpolations. Modified from Krapp and Hengstenberg (1997) and Krapp *et al.* (1998).

C. Behavioral Deficiencies in Flies with Ablated or Degenerated Tangential Neurons

Various kinds of evidence suggest that HS and VS neurons are involved in the control of the optomotor response and gaze stabilization. (i) Detailed neuroanatomical descriptions of the fly brain (Strausfeld, 1976, 1989;) provide insight into the neuronal wiring of the motion pathway. The output regions of the HS and VS neurons are connected via descending neurons to the flight motor centers in the thoracic compound ganglion and, partly, directly to motoneurons of the neck motor system (Gronenberg *et al.*, 1995; Gronenberg and Strausfeld, 1990; Milde *et al.*, 1987; Strausfeld and Gronenberg, 1990; Strausfeld *et al.*, 1987). (ii) Electrophysiological investigations in *Calliphora* showed that the response of these neurons increases with pattern size (Haag *et al.*, 1992; Hausen, 1982b; Hengstenberg, 1982). (iii) Microsurgical lesion experiments in adults or laser ablation of the HS precursor cells resulted in predictable failure of the animal's optomotor response (Geiger and Nässel, 1981; Hausen and Wehrhahn, 1983). (iv) The HS and VS neurons are not developed in the neurological *Drosophila* mutant omb^{H31} (Heisenberg *et al.*, 1978; Pflugfelder and Heisenberg, 1995). This defect selectively affects optomotor responses (Heisenberg *et al.*, 1978; Götz, 1983a,b) and gaze stabilization (Hengstenberg, 1995), whereas the response to small objects is still normal (Bausenwein *et al.*, 1986).

In summary, these findings suggest that the VS and HS neurons in the fly visual system are key elements to process self-motion-induced optic flow and to generate signals for optomotor control and gaze stabilization. However, until recently, it was not known if the receptive field organization of these neurons showed any specialization with respect to this task. In this context, results from early investigations on the VS neurons were quite interesting. In the dorsolateral receptive field, some of these neurons did show responses to horizontal pattern movements (Hengstenberg, 1981). That was a first hint that at least VS neurons may process optic flow in a more specific way rather than extracting only vertical downward motion. To find out if the idea of a neuronal matched filter, proposed in the introduction, may be realized in the fly visual system the local response properties of several tangential neurons were investigated in detail recently.

V. Mapping the Local Response Properties of Tangential Neurons

By applying a fast visual stimulation procedure (Fig. 3), the local directional tuning curves of individually identified tangential neurons

were measured at about 50 different positions within the visual field (Krapp and Hengstenberg, 1997). From the tuning curves, the local preferred direction (LPD) and the local motion sensitivity (LMS) could be obtained (Fig. 3B). These response parameters were mapped as arrows at the respective measuring positions into a Mercator projection of a little more than one hemisphere of the fly's visual field (Fig. 3C). All positions are determined by their azimuth ψ and elevation θ. The orientation of each arrow gives the local preferred direction, and the length denotes the relative motion sensitivity.

Figure 4 shows the morphology and the response fields of HSN and VS10. The dendritic arborizations of the HSN cover the dorsal part of the neuropil (Fig. 4A). As already shown for the HS neurons by Hausen (1982b), both position and extent of the dendritic branching pattern of the VS neurons are very similar in different individuals. The response fields show the distribution of LPDs and LMSs as determined for the right visual hemisphere and one vertical stripe of the frontal left visual hemisphere (Figs. 4B and 4D; ($\psi = -15°$). Two global features of the response fields are striking. First of all, they extend over wide parts of the ipsilateral hemisphere including the frontal region of binocular overlap at $-15°$ azimuth. Second, the LPD distributions are by no means homogeneous within the response fields. Instead, the LPDs clearly depend on the respective measuring position.

Although, on average, the LPDs within the HSN response field are aligned horizontally, there are considerable deviations from this orientation especially in the frontodorsal and caudal part of the visual field. Purely horizontal LPDs are confined to the lateral and equatorial region of the response field (cf. Fig. 4B, ψ about 90°). In different studies, it was found that in the frontodorsal eye region the LPDs of the HSN and HSE are tilted upward, whereas the LPDs of the HSS and HSE in the frontoventral eye region are tilted downward, relative to the horizontal (cf. Fig: 4B; Hausen, 1982b; Hengstenberg *et al.*, 1997).

The interpretation of the HS response fields is somewhat difficult. On the one hand, as Hausen pointed out (1993), the distribution of LPDs is reminiscent of the dorsal half of a translatory optic flow field. The focus of expansion of such a field would lie at about the frontolateral equator within the contralateral hemisphere. On the other hand, this neuron is thought to receive a rotation-specific input from spiking heterolateral elements (Hausen, 1982a). Thus, it is excited by optic flow generated during rotations around the yaw axis as well. From his investigations and the way tangential neurons in general were thought to integrate ipsilateral and heterolateral wide field motion, Hausen (1993) inferred that these neurons do not specifically discriminate between the

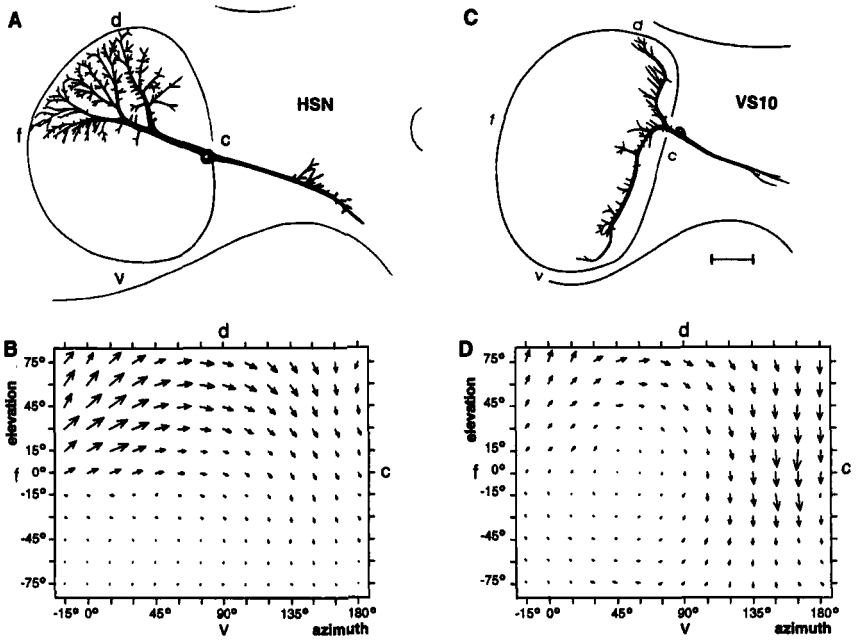

FIG. 4. Morphology and response fields of the HSN neuron and the VS10 neuron. (A) Morphology of the HSN neuron as reconstructed from frontal serial cross sections shown in the contour of the third visual neuropil (lobual plate; the neurons were stained with the intracellular fluorescent dye Lucifer Yellow). The main dendrites of HSN are aligned horizontally and cover the medial to superior part of the lobula plate. The letters f, c, d, and v refer to the retinotopical organization of the neuropil. (C) Morphology of the VS10 neuron, presented in the same way as HSN. Note that the main dendrites of the VS neuron are oriented vertically and are confined to the proximal region of the neuropil. (B) The HSN response field is composed of the whole dorsal hemisphere. In the ventral hemisphere, this neuron does not respond to motion at all. The orientation of each single arrow indicates the local preferred direction and its length gives the local motion sensitivity normalized to the maximum response. The HSN is most sensitive to motion in the frontodorsal visual field. From the global LPD distribution, it is hard to infer which particular self-motion would be sensed most effectively by this neuron. This neuron may contribute to the analysis of different self-motions as proposed by Hausen (1981) (see text). (D) The VS10 response field covers almost the whole visual hemisphere. Even in the frontoventral visual field where the sensitivity is strongly reduced, LPDs can be measured which are consistent with the overall structure of the response field. The neuron is highly sensitivity to vertical downward motion in the caudolateral visual field. However, note that all possible LPDs are present. Within this response field, the LPD distribution shows a strong similarity with an optic flow field induced by a rotation around a horizontally aligned body axis which lies between the pitch and the roll axis (θ about 0° and ψ about 45–60°). As all other VS neurons, VS10 responds more strongly to motion in the dorsal than in the ventral part of the visual field. (C) and (D) are modified from Krapp *et al.* (1998).

rotatory and translatory optic flow components. The new, more detailed data of the local response properties (Fig. 4B; Hengstenberg *et al.*, 1997, Krapp, unpublished results) do not contradict this statement regarding the HS neurons. However, it needs to be reformulated with respect to some other lobula plate neurons (see conclusions).

The dendritic field of the neuron VS10 covers the proximal parts of the neuropil. Its vertical main dendrite arborizes within the most posterior input layer. Some of the dorsal dendrites, however, invade the more anterior input layers which convey signals encoding horizontal motion. A comparison of Figs. 4A and 4C demonstrates the horizontal orientation of the main dendritic branches in HS neurons versus the vertical orientation of the main dendrites of the VS neurons. Another general difference concerns the strong sensitivity to more or less horizontal motion (HS) in contrast to maximum motion responses to vertical downward motion of the VS neurons (cf. Figs. 4B and 4D). Moreover, the VS10 response field shows a marked similarity to a rotatory optic flow field with a presumed axis of rotation at an azimuth of about 45–60° and an elevation of about 0° (Fig. 4D). Even though the HSN response field may not be specialized for sensing a particular optic flow field, the VS10 response field apparently is. Even in the ventral parts of the receptive field where the motion sensitivity is comparatively low, the local preferred directions fit almost perfectly the direction distribution of a global rotatory flow structure. Thus the response field suggests that VS10 is adapted to analyze the momentary optic flow for components induced by a particular self-rotation. Its "preferred axis of rotation" appears to lie between the roll and the pitch axis. The response fields of the other nine VS neurons were also found to mimic rotatory structures induced by self-rotations around horizontally aligned body axes. The different preferred axes of rotation for the ten VS neurons could be estimated from the response fields by applying a least-square algorithm developed by Koenderink and van Doorn (1987). All VS axes are aligned horizontally and scattered along the azimuth (Fig. 5). A slight clustering can be seen for VS8–VS10. The VS4–VS7 axes are more or less aligned with the animal's roll axis, whereas the VS1 and VS2 axes are close to the pitch axis. The preferred rotation axis of VS3 lies between the roll and the pitch axis. The response fields of all VS neurons are highly reliable at the interindividual level (Krapp *et al.*, 1998).

These findings suggest that the VS neurons are adapted to sense self-rotations. However, there is a particular difference between the sensitivity distribution within the response fields and the velocity distribution within rotatory optic flow fields. The velocity distribution within optic flow fields is symmetrical with respect to the equatorial plane. If the roll

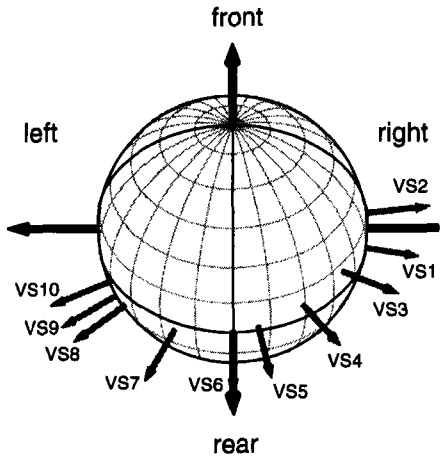

FIG. 5. Preferred axes of rotation of the VS neurons. To calculate the respective axes of rotation from all measured response fields, an iterative least-square algorithm developed by Koenderink and van Doorn (1987) was applied to determine the motion parameters from a "noisy" optic flow field. The plotted arrows represent the mean axes obtained from at least three (up to 12) response fields per neuron type. These preferred axes of rotation are plotted in the visual unit sphere as seen from the rear and above. All rotation axes (gray arrows) are aligned horizontally. The preferred axis of VS6 coincides with the body axis (roll) and the preferred axes of VS1 and VS2 close below and above the transverse body axis (pitch).

flow field shown in Fig. 1C is compared with the VS response fields shown in Figs. 4D and 6A, it appears that the sensitivity within the response fields is asymmetrically distributed. In the ventral part, the sensitivity is smaller than in the dorsal. This observation, which holds true for all VS neurons, was the starting point for a more quantitative approach to understanding the functional significance of the response fields of the VS neurons (see next section).

A different type of response field was measured in another spiking tangential neuron, the so-called neuron Hx (Fig. 6C; Krapp and Hengstenberg, 1996). In contrast to the global rotatory structure within the VS response fields, the Hx response field shows the global structure of a translatory optic flow field. A focus of expansion can be seen at an azimuth of about 135° within the equatorial plane. The results obtained from the Hx show that, within the lobula plate, there are also tangential neurons whose response field is similar to a global translatory structure.

It should be noted that the sensitivity distributions within the translatory Hx response field is inverted with respect to the rotatory response

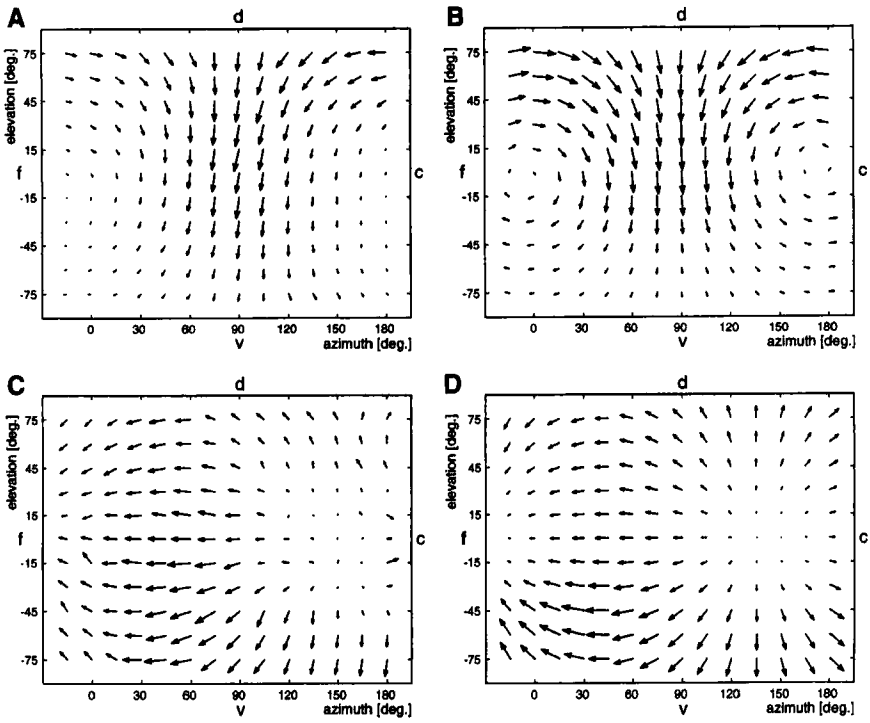

FIG. 6. Response fields and matched filters. (A) Averaged VS6 response field obtained from experiments in five different animals. The preferred axis of the VS6 roughly corresponds to the body axis (roll axis). (B) Weighted direction template corresponding to a particular stage of optic flow processing as derived for an optimal matched filter approach. (C) Response field of the Hx neuron. Note the completely different global structure compared to the VS response field. This response field is highly reminiscent of a translatory optic flow field with a focus of expansion at about $\psi = 135°$ and $\theta = 0°$. Note that Hx is more sensitive to motion in the ventral than in the dorsal visual field. (D) The weighted direction template calculated in the same way as in (B) but for the respective processing stage of a matched filter for translatory self-motion. Note the good correspondence between the measured response field and the weighted direction templates as derived from the theoretical model. See text for further explanations. Modified from Franz and Krapp (submitted).

fields measured in the VS neurons. The Hx responds more strongly to motion stimuli in the ventral than in the dorsal visual field (cf. Fig. 6C).

Until now, not all lobula plate tangential neurons could be investigated with respect to their individual receptive field organization. Only about half of a total of about 60 tangential neurons are characterized so far.

VI. Response Fields and Matched Filters for Optic Flow Processing

A. Matched Filters without Prior Assumptions about Environment and Self-Motion

The matched filter concept originally proposed in the field of image processing (Rosenfeld and Kak, 1982) was later adapted for information processing in biological systems (Wehner, 1987). A "classical" matched filter as applied in image processing is a device whose output is proportional to the cross correlation between the current input and a particularly specified stimulus pattern. Thus a matched filter is not a binary coding device whose output is only different from zero if the input exactly fits the specified stimulus pattern. Instead, input patterns similar but not identical to the specified one will result in a measurable output, too. In this context, the specified stimulus pattern corresponds to a direction template [i.e., a particular distribution of local preferred directions (cf. Fig. 2)], combined with an appropriate set of local weights.

Applying the iterative least-square procedure proposed by Koenderink and van Doorn (1987) Dahmen *et al.* (1997) studied the principal limits of estimating the self-motion parameters from noisy optic flow fields. To extract both the rotation vector and the direction of translation, the authors derived a classical matched filter model. The self-motion estimation is based on a weighted average over the projections of local flow vectors into a direction template. In contrast to the iterative procedure of Koenderink and van Doorn, the approach of Dahmen *et al.* (1997) consists of a "one-shot" mechanism which turned out to be formally equivalent to the first iteration step of the iterative procedure.

The receptive fields of some tangential neurons seems to be organized in a way which is reminiscent of the classical matched filter concept (i.e., to be adapted to sense a specific optic flow field). However, if self-motion is to be estimated, this may be not the optimal strategy. The same combination of rotation and translation in different environments may induce different optic flow fields because the translatory component depends on the distance distribution. Thus many matched filters would be necessary to sense the same self-motion in different 3D layouts.

B. Matched Filters with Prior Assumptions about Environment and Self-Motion

Recently an approach different from the Koenderink and van Doorn procedure and the "one-shot" mechanism was chosen; it was aimed at

understanding the particular response field organization of the VS neurons (Franz *et al.*, 1998). In contrast to previous attempts, this approach assumes certain statistics with respect to the distances distribution between the eyes of the fly and the objects in the environment. In addition, assumptions were made about the fly's average flight velocity and the distribution of translation directions occurring during its flight. The resulting type of matched filter was designed to sense particular self-rotations or translations from the momentary optic flow rather than to match a specific optic flow field. In a first processing step, the momentary optic flow is projected into a direction template (e.g., a distribution of EMDs similar to that shown in Fig. 2, but with unit sensitivities). In this case, for instance, the filter would be constructed to sense "roll"-rotations. The local flow projections contain information about the current rotation around the filter axis. However, this information is corrupted by noise and errors of the motion detection process. Furthermore, the local flow projections are contaminated by the current translatory flow, the magnitude of which depends on the respective object distance. Local object distances, however, are not always the same in different environments encountered by the fly but may unpredictably vary around a mean distance. In a second processing stage, therefore, the projections are weighted depending on how much the self-rotation estimation is affected by these factors. The resulting local estimates are subsequently summed in an output stage whose signal then indicates the rotation around the filter axis (Franz and Krapp, submitted).

As derived from the model, local estimations of the rotatory flow component need to be weighted. These local weights were adjusted in such a way as to minimize the variance of the filter output induced by noise and the distance-dependent variability of the translatory flow. The optimal weight distribution was determined under the assumption that during flight the fly's distance toward the ground is closer than toward visual structures in the dorsal visual field. As a consequence, the relative variability of the translatory flow is higher in the ventral than in the dorsal visual field where the translatory flow is reduced because all visual structures are farther away. In addition, it was assumed that directions of voluntary and involuntary translations performed by the fly are broadly distributed with a center of mass that coincides with the fly's body axis. These assumptions were formalized and, including the respective filter axis, used as parameters for the model. From the model, analytic expressions were derived describing matched filter structures which could be compared to the measured response fields. Figures 6B and 6D demonstrate that the global structure of the response fields can be reproduced quite well by the model. Both the local preferred directions and the local motion sensitivities of the VS6 and the Hx neuron

are in good agreement with the matched filter models of the respective self-motion sensors. By applying a χ^2 fitting procedure, significant correspondence could be shown between the response fields of VS4–VS6 and the respective theoretical weight distributions (for VS6 see Figs. 7A and 7B).

Although all VS neurons show the dorsoventral anisotropic sensitivity distribution, fitting the matched filter model to the other VS neurons only led to qualitative similarities between model structures and response fields. This is because the weak motion sensitivity in the frontal response field of the neurons VS7–VS10 (for VS10 see Fig. 4D) and in the caudal response field of the neurons VS1–VS3 is not predicted by the model. Nevertheless, neurons of the two groups may complement each other by converging at a later processing stage. Combining the VS1 inverted response field and the VS10 response field, for instance, resulted in a structure perfectly well suited to sense rotations around the transverse body axis ("pitch"-rotation).

Another interesting outcome of the comparison between the response fields and the filter model is that, for fitting the experimental data of the VS neurons, the parameter describing the simplified distance model assumes about the same value. This suggests that all VS neurons make the

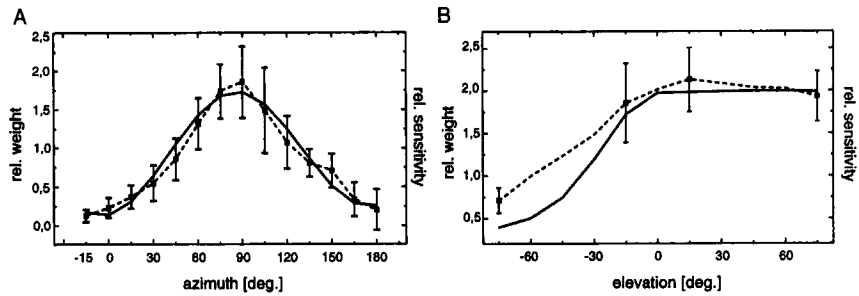

FIG. 7. Cross sections through the optimal weight distribution and the measured sensitivity distribution averaged over five VS6. (A) Section along the azimuth at an elevation of −15°. The measured sensitivities are given by filled squares connected with the dashed line; errorbars denote standard deviations. Theoretical weights are described by the solid line. (B) Cross section along the elevation at an azimuth of 90° through the same weight and sensitivity distributions. The calculated weights are optimized to minimize the filter's output variability given a roll self-rotation in combination with different self-translations. The good accordance of the weights predicted by the model with the experimentally determined sensitivities suggests the dorsoventral anisotropic sensitivity distribution to be a measure of adaptation for processing rotatory self-motions (for further explanations see text). Modified from Franz and Krapp (submitted).

same assumptions about the average distance distributions they are usually encountering.

From these investigations it can be concluded that the tangential neurons apparently extract neither a particular self-motion parameter nor a parameter combination according to the classical matched filter concept. The classical matched filter concept assumes the input organization of the filter to be literally matched to a unique input pattern. The VS neurons, however, can be considered as a generalization of the classical matched filter concept. Although the distribution of the LPDs within their response fields is obviously adapted to a particular rotatory optic flow field, the respective sensitivity distributions are not matched to one unique velocity field. Instead, the sensitivities seems to be adapted to sense an entire class of flow fields, namely those induced by a rotation around a particular axis in combination with a broad distribution of possible translations.

It should be noted that, due to the broad directional tuning of the EMDs, the VS neurons also can be expected to respond, although more weakly, to rotations around axes close to their respective preferred filter axis. In addition, local EMDs do not distinguish between rotatory and translatory optic flow (see Fig. 1). If confronted with a lift translation, for instance, most of the VS neurons may be excited as well. A more specific representation of the momentary self-rotation around a distinct axis could be computed at a later integration stage by subtracting respective correction signals. Such signals may be estimated by other visual wide field neurons and/or by mechanosensory systems like the haltere system, for instance, which senses self-rotations. The processing stage pooling these signals could, in principle, represent the respective self-rotation vector. It may be located at the level of the descending neurons, the interneurons within the motor centers, or the motoneurons.

VII. Conclusion

Rotatory self-motion components are inevitable consequences of locomotion. The resulting optic-flow component, however, does not contain any information about the 3D layout of the environment. This information is only present within translatory optic-flow fields. Thus for all kinds of long-range and short-range distance estimation tasks, a pure translatory optic flow field is desirable (Srinivansan *et al.*, 1996; Land and Collett 1997; Srinivasan, 1993). One possibility to, at least, reduce the rotatory component in the optic flow is to compensate for it by

means of stabilizing head movements and steering maneuvers. These measures can be observed in the fly but also in other visually oriented animals, including humans. Of course, to generate the compensatory actions, the respective rotatory self-motion needs to be determined by the sensory systems and transformed into an adequate motor control signal.

The studies reviewed in this chapter suggest that identified interneurons in the fly visual system are adapted to analyze rotatory or translatory optic flow fields (VS neurons and Hx). From their receptive field organization alone, this categorization does not include the HS neurons. It is conceivable that HS neurons are utilized to sense both translation and rotation as has been proposed by Hausen (1981) and will be discussed below.

The VS neurons and the Hx neuron cannot be expected to be insensitive to flow components induced by other than their own respective preferred self-motions. Nevertheless, each neuron is specialized to sense a particular class of optic flow fields. For VS neurons, for instance, each class is defined by its preferred axis of rotation which may be combined with any translations in different environments. The receptive field organization of these neurons shows two adaptations which may have evolved on a phylogenetical time scale: (i) The asymmetric sensitivity distribution within the response fields. This distribution reflects the assumptions about the average distance distributions implemented in the fly visual system (i.e., on average, the distances are closer toward the ground, which makes immediate sense). Furthermore, the local flow estimates are weighted according to their respective reliability, reducing the variability of the neurons response to its respective self-motion axis. (ii) The distribution of the local preferred directions within the response fields reflects the direction distribution of velocity vectors within a class of optic flow fields all induced by a particular self-motion.

The output of a single VS neuron or of combinations of VS neurons needs to be corrected for "apparent rotations." Such apparent rotation may be due to translatory self-motions and to rotations around axes other than the preferred axis of the respective VS neuron. The signals necessary to correct for these erroneous response contributions could be supplied by other wide field neurons. The translation along the body axis and the transverse body axis, for instance, could be estimated by the two Hx neurons living in the left and right lobula plate. Hx has a preferred axis of translation which lies exactly between the body axis and the transverse body axes. Thus, in combination, the two Hx neurons would form a system with two orthogonal measuring axes. The difference of the two Hx outputs could indicate the translation along the transverse body axis, whereas the sum reflects the translation along the

body axis. Generally, if the rotatory and translatory correction signals are estimated by other tangential neurons, as proposed for the Hx, reciprocal connections between neurons sensing the respectively different self-motion component need to be assumed. Such connections among the tangential neurons still need to be demonstrated electrophysiologically.

In this context the HS neurons could, in principle, supply correction signals for translations and rotations by appropriately combining their outputs. The HSN in combination with HSS could sense rotations around the transverse body axis (pitch) if the HSS signal is subtracted from the HSN signal (or vice versa). They could also monitor thrust translation if the sum of the outputs is considered. The sum of the HSN and HSS signals, however, may indicate rotations of the animal around the vertical body axis (yaw). The latter possibility is supported by the finding that HSN is also excited by a contralateral spiking wide field element which respond strongly to back-to-front motion. Together, the ipsi- and contralateral inputs to the HSN neuron mediated a high sensitivity to yaw rotation. The HSE neuron may be involved in sensing translatory or rotatory self-motions as well. Like the HSN, it receives contralateral input from spiking elements which are sensitive to back-to-front motion. This input is ineffective during thrust translation because the contralateral element is inhibited in this case, but would facilitate the neurons' response to yaw rotations. Regarding the self-motions presumably sensed by the HS neurons, Hausen (1981) already came to the same conclusions.

Correction signals encoding fast self-rotations may also be supplied by the haltere system (Nalbach, 1994). Because the dynamic range of the haltere system is shifted toward higher angular velocities, it is thought to complement the visual self-motion estimation (Hengstenberg, 1991). By measuring Coriolis forces like a gyroscope, this mechanosensory system is particularly sensitive to fast self-rotations (Nalbach, 1994).

Why are self-rotation and self-translation not represented as a vector at the level of the tangential neurons already? One reason might be that as long as the signals of the VS neurons are kept separately, they could be combined among each other—or with other tangential neurons—to monitor the self-motion along any intermediate motion axis. Such an ensemble coding of self-motion could take place at later processing stages in the nervous system. An advantage of this coding strategy could be to keep the sensory-motor transformation flexible. Information from particular sensory measuring axes could be selected according to the requirements of particular pairs of muscles to be controlled.

Meanwhile the investigations on the visual system of the fly under

steady-state conditions did result in a good understanding of some basic aspects regarding optic flow processing. Based on findings with respect to the elementary movement detection and visually controlled stabilization behavior, robots which are capable of autonomously navigating within their respective environments have been designed (Franceschini *et al.*, 1992).

The functional interpretation of the receptive field organization adapting the tangential neurons for optic flow processing is based on the assumption that retinal image shifts are represented in terms of local motion vectors. Part of the theoretical approaches assumed that the output of the local motion analysis will be proportional to the velocity of the respective image shift. In addition, both approaches take for granted that the results of the local motion estimates are summed up in a linear fashion at an integrating processing stage. For insect visual systems, however, it was found that local motion analysis is achieved by elementary motion detectors whose output is not simply proportional to velocity (Egelhaaf and Reichardt, 1987) but also depends on pattern properties like spatial wavelength and contrast (Egelhaaf and Borst, 1993). Hence, it remains unclear how biological sensory systems cope with highly dynamic stimuli as encountered, for instance, by the fly during free flight. It is by no means easy to predict the signals of the tangential neurons under such natural conditions. Moreover, a "gain control" mechanism has been found for the spatial integration properties of the tangential neurons corresponding to the integration stage in the models. The response of the neurons increases with increasing pattern size but saturates at different levels, depending on the respective velocity (Borst *et al.*, 1995; Single *et al.*, 1997). Further experiments using whole field optic flow stimuli will show whether or not the matched filter concept is an appropriate interpretation of the local receptive field organization of the tangential neurons.

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