Dendritic Structure and Receptive-Field Organization of Optic Flow Processing Interneurons in the Fly

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Krapp, Holger G., Bärbel Hengstenberg, and Roland Hengstenberg. Dendritic structure and receptive-field organization of optic flow processing interneurons in the fly. *J. Neurophysiol.* 79: 1902–1917, 1998. The third visual neuropil (lobula plate) of the blowfly *Calliphora erythrocephala* is a center for processing motion information. It contains, among others, 10 individually identifiable ''vertical system'' (VS) neurons responding to visual wide-field motions of arbitrary patterns. We demonstrate that each VS neuron is tuned to sense a particular aspect of optic flow that is generated during self-motion. Thus the VS neurons in the fly supply visual information for the control of head orientation, body posture, and flight steering. To reveal the functional organization of the receptive fields of the 10 VS neurons, we determined with a new method the distributions of local motion sensitivities and local preferred directions at 52 positions in the fly's visual field. Each neuron was identified by intracellular staining with Lucifer yellow and three-dimensional reconstructions from 10-μm serial sections. Thereby the receptive-field organization of each recorded neuron could be correlated with the location and extent of its dendritic arborization in the retinotopically organized neuropil of the lobula plate. The response fields of the VS neurons, i.e., the distributions of local preferred directions and local motion sensitivities, are not uniform but resemble rotatory optic flow fields that would be induced by the fly during rotations around various horizontal axes. Theoretical considerations and quantitative analyses of the data, which will be presented in a subsequent paper, show that VS neurons are highly specialized neural filters for optic flow processing and thus for the visual sensation of self-motions in the fly.

INTRODUCTION

Optic flow

Locomotion of animals or robots through varying surroundings may affect their body equilibrium and the orientation toward their goal. To stabilize gait and course, reliable information about self-motion is required continuously. Locomotion through optically structured environments generates chracteristic patterns of retinal image shifts. These patterns can be described as vector fields where the length of each local vector gives the velocity and its orientation the direction of the respective image shifts (Koenderink and van Doorn 1987; Nakayama and Loomis 1974). The global structure of these vector fields depends on the momentary ''mode'' of locomotion, i.e., translation or rotation. Therefore such ''optic flow fields'' are considered a rich source of self-motion information (Gibson 1950).

Meanwhile, the analysis of optic flow has been studied at different levels: for instance, from first principles in computer vision (review Barron et al. 1994; Bülthoff et al. 1989), and in technical and biological systems where constraints of their design and tasks must be taken into account. Biologically inspired models using optic flow to determine self-motion or the direction of heading (e.g., Lappe and Rauschecker 1994; Perrone 1992) are based on studies in humans (e.g., Morrone et al. 1995; Warren and Hannon 1988), primates (e.g., Duffy and Wurtz 1991, 1995; Lagae et al. 1994; Tanaka and Saito 1989), cats (e.g., Rauschecker et al. 1987), and pigeons (e.g., Wylie and Frost 1990).

Behavioral studies in insects have demonstrated their superb maneuverability even in complex habitats like forests and shrubbery. They accomplish demanding aerial tasks like chasing prey, mates, or competitors (Collett and Land 1978; Land and Collett 1974; Wehrhahn et al. 1982), or when hovering in front of wind-swept flowers (Farina et al. 1994). Their ability to exploit optic flow has been investigated in depth (Collett et al. 1993; Hausen and Egelhaaf 1989; Hengstenberg 1993; Srinivasan 1993; Srinivasan et al. 1996). The comparatively small number of individually identifiable neurons in their visual nervous system allows to record from them repeatedly in different individuals. This makes them ideally suited to study the neural processing of optic flow (Egelhaaf and Borst 1993; Gronenberg et al. 1995; Hausen 1993; Krapp and Hengstenberg 1996; Milde 1993).

Flying insects maintain a distinct flight posture with the back directed upward. They can translate along their body axes (Fig. 1*A*: thrust, slip, lift) and rotate around the same axes (Fig. 1*A*: roll, pitch, yaw). Each of these motions generates a characteristic optic flow pattern on the eyes (Fig. 1*B*: lift translation; Fig. 1*C*: roll rotation). It can be visualized either by a surface view of the visual unit sphere, which only shows one-half the visual space at a time (e.g., Fig. 4*C*), or, for example, by a Mercator map of the entire visual space (Fig. 1, *B* and *C*). In this map the area of the visual space is increasingly distorted toward the poles (Fig. 1, *B* and *C*: d, v). However, the angles for azimuth (ψ) and elevation (Θ) are specified in an orthogonal coordinate system that is everywhere veridical. During pure translation, all local flow vectors are aligned radially, i.e., along the meridians that connect the focus of expansion (Fig. 1*B*: d) with the focus of contraction (Fig. 1*B*: v). During rotation all local flow vectors are aligned along parallel circles around the axis of rotation (Fig. 1*C*: f). For both types of self-motion, the local velocity is zero at the respective poles, and maximum midway between the poles (Fig. 1*B* along $\Theta = 0°$, Fig. 1*C* along $\psi = \pm 90°$). Any real self-motion, where translation and rotation may be performed at the same time, generates a more complex optic flow field composed of the linear sum of the translatory and rotatory flow (Koenderink and van Doorn 1987).

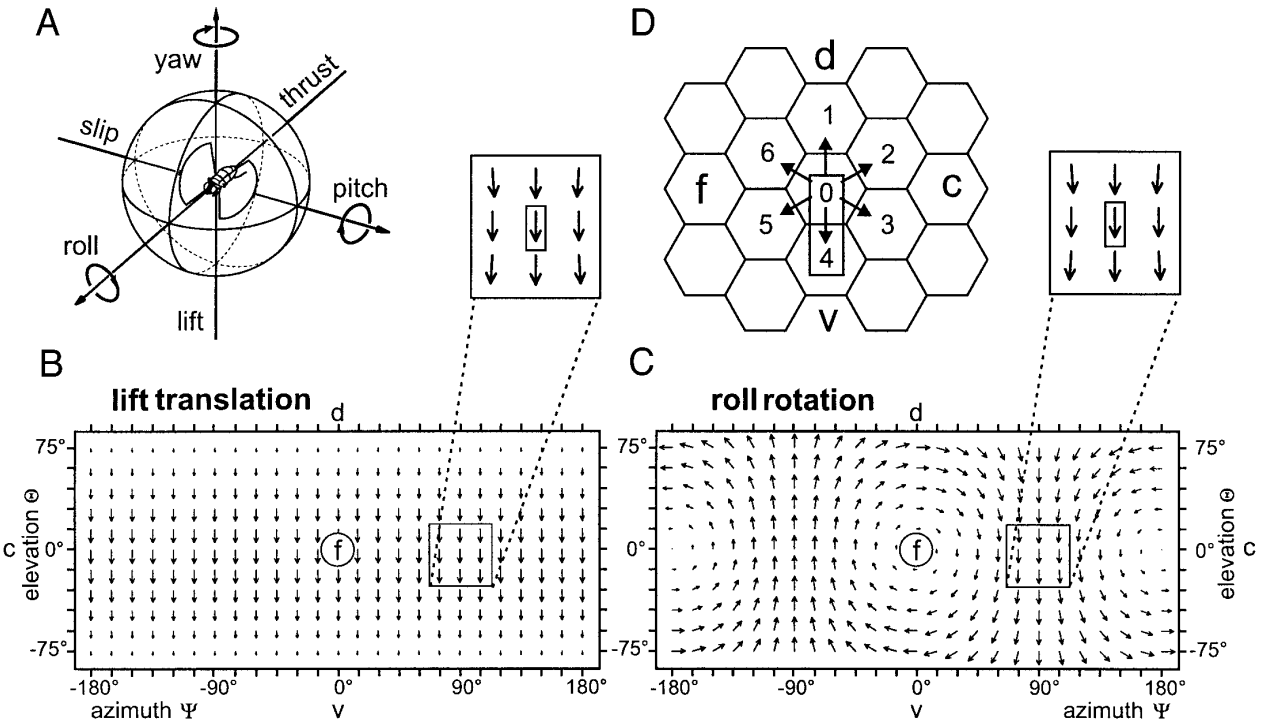


FIG. 1. Global structure of translatory and rotatory optic flow fields, and the local analysis of visual motion. *A*: motions of the fly can be described by their translatory (thrust, slip, lift) and rotatory components (roll, pitch, yaw) around the 3 body axes (longitudinal, transverse, vertical). The different motion components induce different optic flow fields over both eyes of the moving animal. For simplicity, equal distances from the objects in a structured environment are assumed. This is indicated by showing the fly in the center of the visual unit sphere. *B* and *C*: optic flow field caused by a lift translation along the vertical body axis (*B*), and a roll rotation around the longitudinal body axis (*C*). Optic flow patterns are transformed from the visual unit sphere into Mercator maps to show the entire visual space. Positions in space are defined by the angles of azimuth (ψ) and elevation (Θ). The encircled f (frontal) denotes the straight-ahead direction of the fly; c, caudal; d, dorsal; v, ventral in the visual field. Note that in this representation the area is increasingly overrepresented toward the poles (d, v). Globally the 2 optic flow fields can easily be distinguished from one another. In the visual system, however, motion is analyzed by sets of small-field motion detectors. *C* shows schematically a small part of the fly's compound eye, and arrows indicate the 6 preferred directions of the predominant local motion detectors. Note that the vertical downward detector is equally excited by an upward lift translation or a roll rotation to the left (see magnified sections of the optic flow fields). Thus local motion signals are not sufficient to distinguish different flow fields unambiguously.

Motion detection in insects

In insects, motion is detected locally, i.e., within small areas of ~5° diam, a by a nonlinear interaction between adjacent visual elements (for reviews see Borst and Egelhaaf 1993; Egelhaaf and Borst 1993; Reichardt 1987). Two unidirectional subunits most probably constitute a bidirectional motion detector (Hassenstein and Reichardt 1956). Such a detector is excited by motion in its preferred direction and is inhibited by motion in its null direction (Borst and Egelhaaf 1993; Franceschini et al. 1989; Götz and Buchner 1978). For each part of the eye, and thus for each small location in visual space, motion is detected in at least six different directions, corresponding to the arrangement of visual elements in the eye (Fig. 1*D*) (Götz et al. 1979; Hausen 1993). With respect to the underlying self-motion, however, the response of local motion detectors can be ambigous. The magnified sections of Fig. 1, *B* and *C*, for example, show that local downward motion in the right lateral visual field can be generated either by upward lift translation (Fig. 1*B*) or by roll rotation to the left (Fig. 1*C*). Because of such ambiguities, local motion signals cannot be used directly for motor control.

The ambiguities can be overcome by a selective wide-field integration of local motion signals. Figure 2 illustrates a qualitative model of a hypothetical filter neuron tuned to sense roll rotation. Such filter neurons can be expected to have certain properties. *1*) They should have an extended receptive field: the larger the field, the better is the tuning to a specific optic flow (Koenderink and van Doorn 1987). *2*) They should be motion sensitive and directionally selective. *3*) The distribution of local preferred directions within their receptive field should resemble the specific aspects of the optic flow field induced by particular self-motion.

Visual system of the fly

Figure 3*A* shows a schematized horizontal section through the brain of the fly. The visual system, supplied by the compound eyes, consists of the retina and three visual neuropils: the lamina, the medulla, and the lobula complex. In diptera, the lobula complex is divided into the anterior lobula and the posterior lobula plate. Local motion information is processed in separate retinotopically arranged columns that extend through all layers of the three neuropils (Bausenwein and Fischbach 1992; Strausfeld 1976, 1984). In Fig. 3*B* the retinotopical mapping of the ipsilateral visual hemisphere at the level of the lobula plate is shown (Hausen 1993). The lobula plate contains ~60 individually identifiable visual interneurons (Hausen 1984, 1993), each of which is known

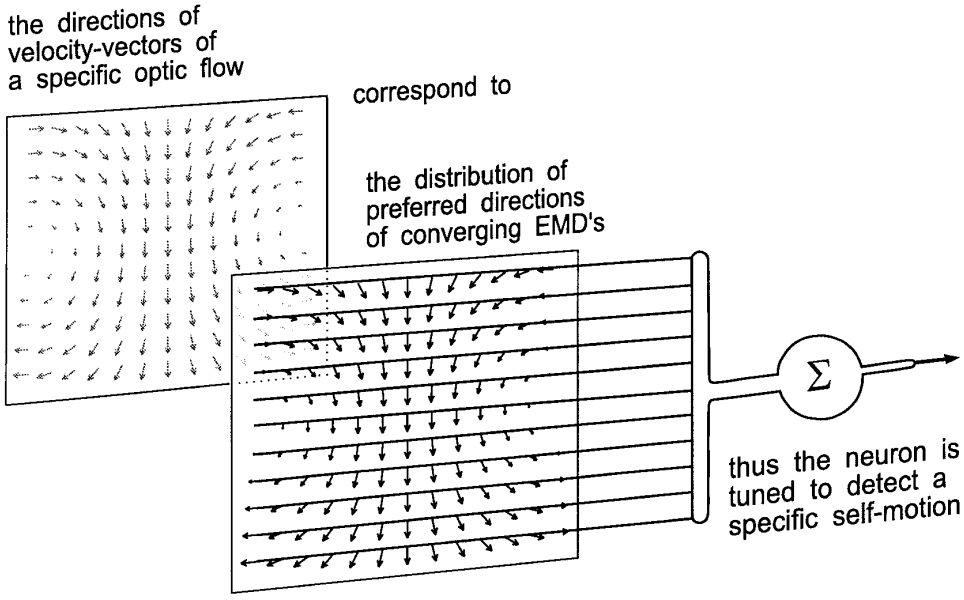


FIG. 2. Hypothetical filter neuron to sense a particular self-motion. Local motions of an optic flow field, for example roll rotation, activate locally those motion detectors with appropriate preferred directions. A wide-field neuron selectively collects and spatially integrates the signals of these motion detectors. Hence it would be most sensitive to that particular optic flow and consequently to the self-motion that caused the flow.

to integrate the signals of many motion detectors on its extended dendritic arborization (Borst and Egelhaaf 1992).

Experiments in *Drosophila,* combining specific motion stimulation with activity-dependent labeling, showed that the lobula plate is organized, anterior to posterior, in four directionally specific input layers (Buchner and Buchner 1984). The most anterior layer consists of input elements preferring horizontal front-to-back motion. The next layer is specific for horizontal back-to-front motion and is followed by a layer dedicated to vertical upward motion. The most posterior layer contains local input elements signaling vertical downward motion.

Some of the tangential cells transfer visual information between the left and right lobula plates (''heterolateral elements'') (Hausen 1984, 1993). Others send their axons to the lateral protocerebrum, one of the main output regions of the visual system (Strausfeld 1976). From the brain output regions, visual information is conveyed either via descending interneurons to the motor control centers in the thoracic compound ganglion or directly to motor neurons innervating the neck muscles (Gronenberg et al. 1995; Gronenberg and Strausfeld 1990; Milde et al. 1987; Strausfeld and Gronenberg 1990; Strausfeld et al. 1987).

Among the 60 tangential neurons, the lobula plate contains 2 small subgroups of prominent neurons: 3 cells of the ''horizontal system'' (HS; Fig. 3*C*) (Hausen 1982a,b), and 10 of the ''vertical system'' (VS; Fig. 3, *D* and *E*) (Hengstenberg et al. 1982).

The three HS neurons together occupy the whole retinotopic area of the lobula plate. Each of them covers roughly one-third of the dorsoventral extent of the neuropil with some overlap (Fig. 3*C*). Correspondingly, their receptive fields cover the dorsal, equatorial, and ventral areas of the ipsilateral visual hemisphere. The dendrites of the HS neurons arborize in the anterior layers of the lobula plate. HS neurons are excited by front-to-back motion and inhibited in the reverse direction. The dorsal (HSN) and equatorial neurons (HSE) are also excited by contralateral back-to-front motion (Hausen 1982b).

The group of 10 VS neurons also occupies the whole retinotopic area of the lobula plate (Fig. 3*D*). Their dendritic fields are more or less stripelike and oriented dorsoventrally (Fig. 3*E*). The dendrites are stacked from the distal to the proximal side of the lobula plate and overlap considerably (Fig. 3*D*; directions, see *B*). The most distal neuron *VS1* and the proximal group *VS7–VS10* have fan-shaped arborizations in the dorsal lobula plate (Fig. 3*E*). The main dendrites and ventral arborizations are located in the posterior layers of the lobula plate, but the fan-shaped dendrites are located in the anterior layer, like those of the HS neurons (Hengstenberg et al. 1982). Most cell bodies of the HS and VS neurons are located near the proximal margin of the lobula plate (Fig. 3, *C* and *D*). Their axons terminate in the so-called optic foci of the ipsilateral protocerebrum.

VS neurons are excited by downward motion (preferred direction) and inhibited by upward motion (null direction) in the ipsilateral visual hemisphere. They respond to visual motion stimuli with graded membrane potential changes. These changes can be accompanied by irregular superimposed spikes if the neuron is stimulated with motion in its preferred direction (Hengstenberg 1977). Motions in the neurons' null direction cause hyperpoarizing changes of its membrane potential. Preliminary data suggested that some VS neurons also process horizontal motion information (Hengstenberg 1981). The functional organization of the receptive fields of the different VS neurons, however, remained unclear because of technical limitations.

HS and VS neurons are thought to contribute to the control of self-motion. Their responses increase with pattern size (Haag et al. 1992; Hausen 1982b; Hengstenberg 1982). After unilateral microsurgical deletion or laser ablation of the precursor cells of the HS neurons, *Calliphora* lacked normal optomotor behavior on the manipulated side (Geiger and Nässel 1981; Hausen and Wehrhahn 1983). In the neurological mutant omb^{H31} of the fruitfly *Drosophila,* the HS and VS neurons are not developed (Heisenberg et al. 1978; Pflugfelder and Heisenberg 1995). Although these animals have normal vision and respond to small objects (Bausenwein et al. 1986), they fail to respond to wide-field motion in course control (Götz 1983; Heisenberg et al. 1978) and gaze stabilization (Hengstenberg 1995).

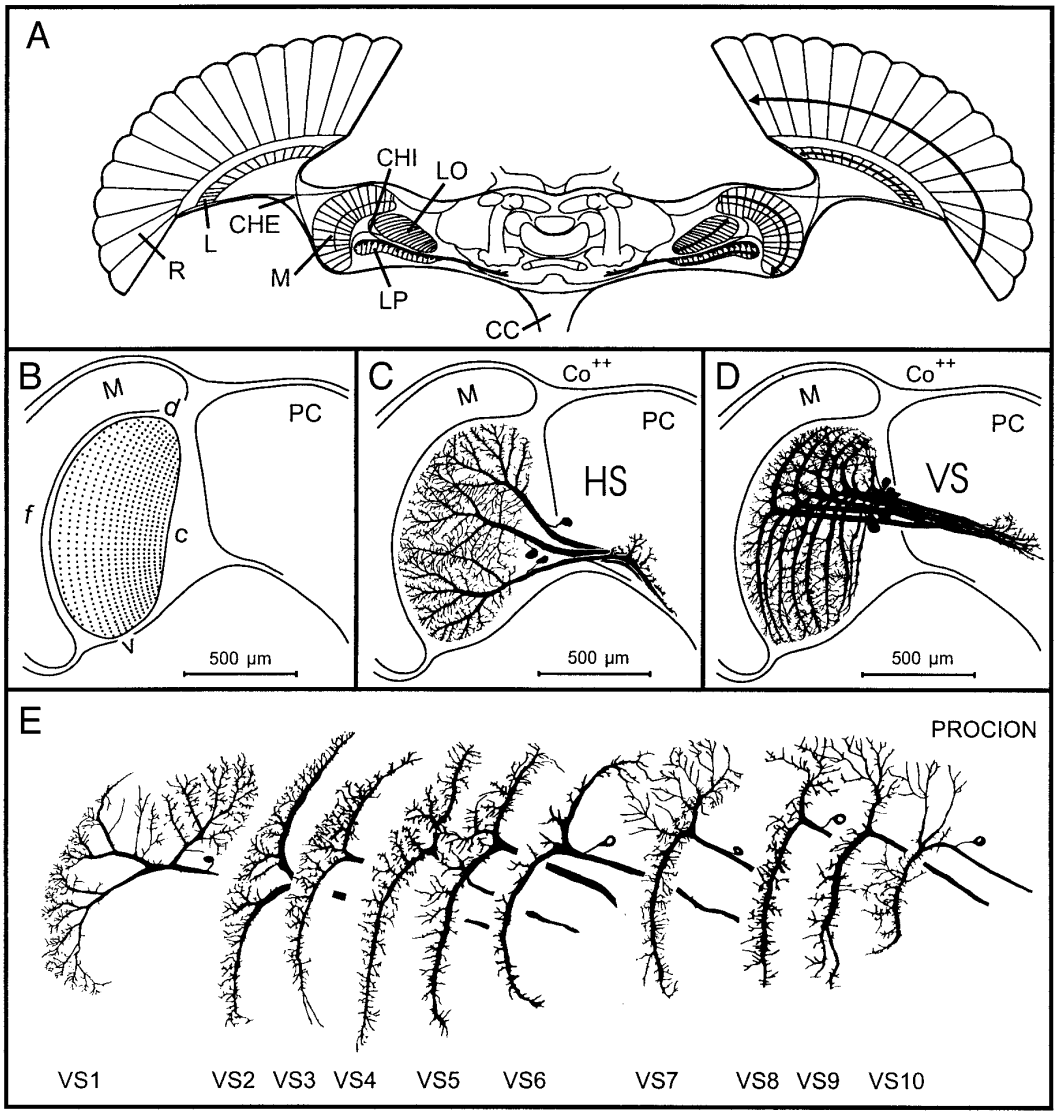


FIG. 3. Visual system of the blowfly. *A*: schematic horizontal section showing the retina (R) and the 3 visual neuropils: lamina (L), medulla (M), and the bipartite lobula complex with the anterior lobula (LO) and the posterior lobula plate (LP). Fiber tracts (CHE, CHI) connecting the neuropils preserve the retinotopic arrangements of columns where local visual signals are processed. Some wide-field output neurons of the lobula plate converge on descending neurons that transfer signals through the cervical connective (CC) to motor neuropils of the thoracic compound ganglion (not shown) (modified after Hausen 1984). *B*: retinotopic representation of the right visual hemisphere within the right lobula plate viewed from anterior (modified after Hausen 1993) (f, frontal; c, caudal; d, dorsal; v, ventral). *C*: 3 neurons constitute the ''horizontal system (HS).'' Their dendritic arbors fill the anterior layers of the lobula plate, and each extends over roughly $\frac{1}{3}$ of the neuropil (from Hausen 1982a). *D*: the 10 neurons of the ''vertical system'' (VS) have their arborizations mainly in the posterior layers of the neuropil. Their dendritic fields are vertically oriented stripes, stacked from the distal to the proximal margin of the lobula plate and, taken together, cover again the whole retinotopic extent of the neuropil. *E*: individual dendritic arbors of the 10 VS neurons drawn apart to reveal their distinct structures. The more fan-shaped dorsal branches of *VS1* and *VS7–VS10* are located in the anterior layers of the lobula plate. Reconstructions were made after cobalt staining (*C* and *D*) or procion yellow injections (*E*). *C–E* modified after Hengstenberg et al. (1982).

These results suggested that the HS and VS neurons play a significant role in the control of self-motion. The experiments were, however, insufficient to specify the particular role of the individual neurons or to elucidate the functional principles behind their design. We addressed these questions by mapping the local preferred direction (LPD) and the local motion sensitivity (LMS) using tiny stimuli (<1% of the unit sphere) presented successively at many positions in the receptive fields of VS and other neurons. The response maps obtained for the different neurons, which were identified by fluorescent dye injection, can be quantitatively analyzed and compared with a variety of calculated optic flow fields. A small part of this study has been published in a short communication (Krapp and Hengstenberg 1996).

METHODS

Preparation

One- to three-day-old female blowflies (*Calliphora erythrocephala*, Meigen) were used for the experiments. The animals were briefly anesthesized with CO_2; their legs and wings were removed and the wounds closed with wax. The flies were mounted on a

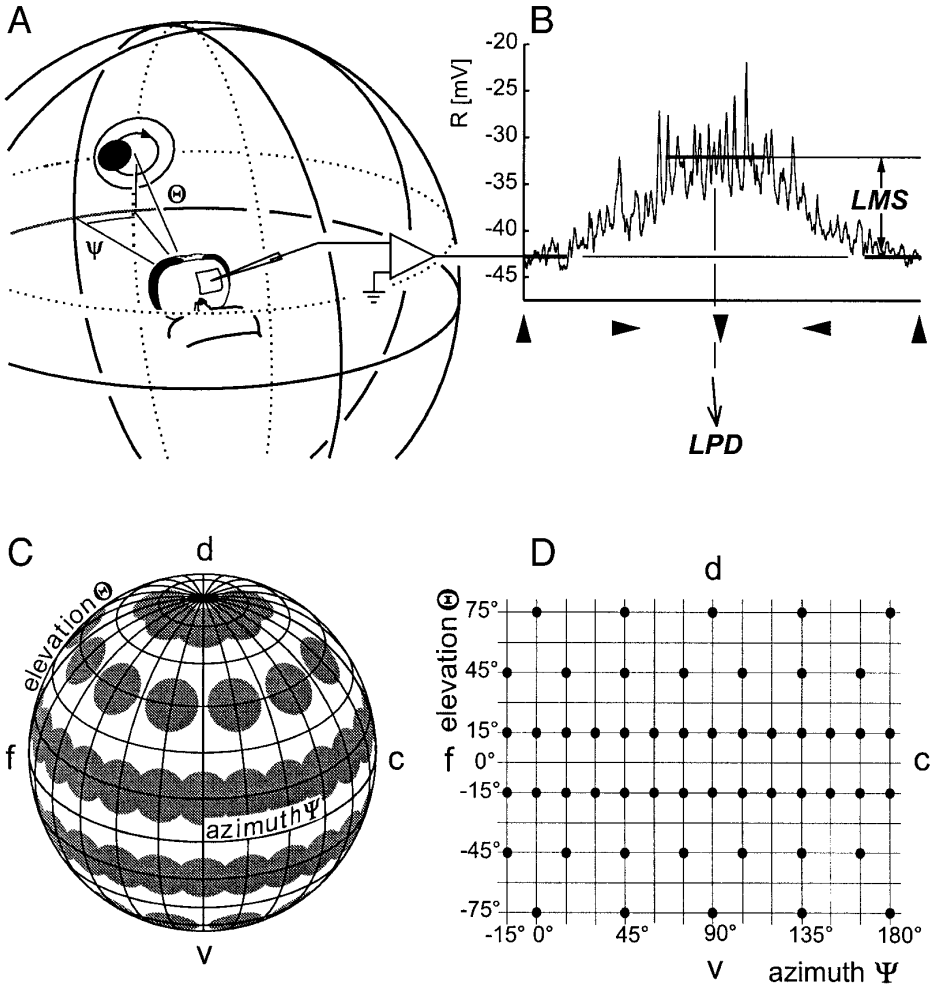


FIG. 4. Determination of the local preferred direction (LPD) and the local motion sensitivity (LMS). *A*: a black dot (7.6° diam) is moved at constant speed (2 cycles/s) on a circular path (10.4° diam) at a particular position in the visual field that is specified by the angles of azimuth ψ and elevation Θ (modified from Krapp and Hengstenberg 1996). *B*: when the direction of dot motion coincides with the local preferred direction of a recorded neuron, its response becomes maximum. After correction for the response delay, the LPD is determined by circular statistics. LMS is defined as the difference between the mean value of the quadrant centered on LPD and that of the opposite quadrant (thick lines). Arrowheads below the recording trace indicate the momentary direction of dot motion during a stimulus cycle. *C*: stimulus positions and areas plotted on the left visual hemisphere to illustrate the actual positions and extent of the stimuli. *D*: Mercator map of the right hemisphere plus the frontal stripe of binocular overlap in the contralateral hemisphere ($\psi = -15°$). Stimulus centers are indicated by dots. Note the increasing distortions of distance and area toward the poles (d, v). c, caudal; d, dorsal; f, frontal; v, ventral.

holder fitting into the center of a spherical stimulator (Fig. 4*A*) (Krapp and Hengstenberg 1997). Their eyes were aligned with the coordinates of the stimulator by adjusting the head according to the symmetrical pseudopupil (Franceschini 1975) and then fixing it in place. The fly's thorax was bent ventrad relative to the horizontally aligned head. Access to the optic lobe was gained by cutting a window of 0.5 × 1 mm into the back of the head capsule, and removing the overlying air sacs and tracheae. The esophagus and muscles of the mouth parts were removed to prevent brain movements, and the wounds were sealed with wax. The visual input to neurons recorded in the right lobula plate was restricted to the ipsilateral eye by occluding the left eye with nontoxic black acryl paint. The preparation was kept moist by adding saline solution (Hausen 1982a).

Electrophysiological recordings

For intracellular recordings, glass capillaries (Clark, GC 100F-10 500 PCS) were pulled on a Brown Flamming puller (Sutter Instruments, *P* 87). Their tips were filled with 3% Lucifer yellow CH (Sigma) in 1 M LiCl for intracellular staining, and the shaft was filled with 1 M LiCl. The input resistance of the recording electrodes ranged between 40 and 60 MΩ. A hydraulic micropositioner (David Kopf Instruments, M 650) was used to place the electrode in the tissue and to help penetrate the cell. Most of the neurons were recorded by penetrating their axons close to the proximal margin of the lobula plate. The recorded resting potentials ranged between −38 and −50 mV; occasionally small potential drifts <3 mV over 10–15 min were observed, which did not noticeably affect the results. In a few cases, stable recordings were obtained up to 90 min. The signals of the recorded cells were preamplified 10-fold by a high-impedance amplifier ($10^{12}\Omega$, workshop of the MPI) in balanced current-clamp mode and sampled by a computer (IBM PC 386) via an I/O-board (Data Translation, DT 2801). Because the VS neurons responded with graded membrane potential changes, we sampled their activity at a rate of 0.72 kHz. This rate was high enough to measure the VS neuron's directional tuning over an angular range of 360° at a resolution of 1°. Neuronal signals and reference pulses elicited during each stimulus cycle were additionally stored on a digital audio tape (Bio-Logic, DTR 1800). The responses of spiking neurons played back from tape were sampled at 10 kHz and converted into unit pulses for further analysis. All software for stimulus control, data acquisition, and evaluation was programmed in ASYST 4.0 (Macmillan Software).

Visual stimulation

To determine the LPDs and LMSs, a black dot (visual diameter, 7.6°) on a white background was moved at 2.0 cyles/s along a small circular path (10.4° diam). When the momentary direction of the dot motion coincides with the LPD of the recorded neuron, it responds maximally (Fig. 4*B*). Phase-locked summation of three response cycles to clockwise dot motion and the same number of response cycles to counterclockwise stimulations are used to eliminate the phase shift due to the response delay. The LPD is defined by the mean vector of the response applying circular statistics (Batschelet 1981); the LMS is defined by the difference between the mean response of the neuron within the quadrant centered

on the preferred direction and the mean response in the opposite quadrant (see Fig. 5*A*). The procedure allows us to measure the local motion tuning and determine the LPD and LMS within <10 s. The adaptation of this procedure to the fly's visual system as well as the validity and robustness of the obtained results have been demonstrated previously (Krapp and Hengstenberg 1997).

Mapping the distributions of LPD and LMS within the visual field

Local motion tuning curves were measured at 52 positions in the visual field; Fig. 4*C* shows the stimulated areas plotted on the left half of the visual unit sphere. It illustrates the actual spatial distribution and overlap of the stimulated regions. In the pole regions there is an overlap of ~40%; in the equatorial region it amounts to 20%. Each position is defined by the angles for azimuth ψ and elevation Θ of its center. The Mercator map of the right visual hemisphere ($0° < \psi < 180°$) plus a vertical stripe of the left hemisphere ($-15° < \psi < 0°$) shows again the measuring locations (Fig. 4*D*; dots). The position $\psi = 0°$, $\Theta = 0°$ denotes the location directly in front of the fly (line of sight). The local motion responses are plotted as arrows that originate at the sites of measurement; their orientation indicates the LPD, and their length indicates the LMS. LMSs are normalized to the maximum local response of the cell. To give a better impression of the global distribution of the LPDs and LMSs in the Mercartor projection, we completed the response maps of Figs. 5–9 by interpolating between the actually measured data. The interpolated data were obtained by weighting the measured values inversely propotional to their distance on the sphere. The measured data were left unchanged and marked with small dots in Figs. 5, 6, 7, and 9.

Histology

Intracellular staining with Lucifer yellow was performed by injecting a small hyperpolarizing current (−1 to −2.5 nA DC) during the measurements, with the bridge current balanced carefully to cancel the current-induced voltage offset. We tested current injections up to −6 nA without observing any changes in the structure of the neuronal response fields.

After the experiments the preparations were inspected by fluorescence microscopy (Zeiss, Axiophot, fluorescein isothiocyanate filter combinations) to identify the recorded neurons. When the staining appeared good enough in vivo, the brain was prefixed (4% formaldehyde in Millonig's buffer) (Strausfeld et al. 1983) for 10–15 min, removed with the compound eyes from the head capsule, and fixed for another 60 min. The subsequent steps for embedding the preparation in Spurr's epoxy medium were slightly modified after Strausfeld et al. (1983). Series of 10-μm frontal sections were made from the preparation and photographed on daylight color transparency film (Kodak, Elite 200 ASA) under the fluorescence microscope. Camera lucida drawings and three-dimensional (3-D) stereo reconstructions of the neurons were made from the slides using the PC program package HISTOL (Hengstenberg et al. 1983). The 3-D reconstructions were particularly helpful to identify the different types of VS neurons and to judge the location of their dendritic arborizations within the directionally specific input layers of the lobula plate.

RESULTS

Within 3 yr, the response fields of 90 identified VS neurons could be mapped completely. This corresponds to a success rate of ~25%; each type of VS neuron was investigated between 3 and 17 times. Neither the response fields nor the reconstruction of the neurons were complemented with data obtained from more than one animal. One-third of the stained neurons were reconstructed from serial sections, the remaining cells were identified by in situ fluorescence microscopy of live preparations.

The left sides of Figs. 5–7 show camera lucida drawings of the respective VS neurons within the outlines of the right lobula plate as seen from anterior. The maps of the right visual hemisphere plus the frontal strip of binocular overlap in the left hemisphere are shown on the *right* as seen by the fly. The change of perspective between neurons and response maps eliminates the mirror inversion by the outer chiasm (cf. Fig. 4*A*: CHE). This allows us to correlate directly the spatial organization of the dendritic field within the neuropil with the spatial organization of the respective response distributions: f, frontal; c, caudal; d, dorsal; v, ventral (cf. Fig. 3*B*).

Anatomy and response field of the VS neurons

The easiest VS neuron to identify is *VS1* (Fig. 5*A*). It has an extended, vertically oriented main dendrite ramifying in the distal part of the neuropil and sampling visual information from the frontal to frontolateral visual field. In addition, it has a characteristic second dendritic arbor originating from the axon within the central region of the neuropil (Fig. 5*A*, ∗). It spreads dorsally to dorsocaudally. The overall appearance of this VS neuron and, indeed, that of all the other VS neurons shown in this work is very similar to that described by Hengstenberg et al. (1982) (cf. Fig. 3*E*). This is remarkable because the respective flies originate from different wildtype strains that are separated by 15 yr and have an undefined genetic background.

VS1 has a huge response field covering the complete dorsal, and equatorial, parts of the frontoventral visual hemisphere, including the meridian at $\psi = -15°$. This neuron was known to be strongly excited by vertical downward motion in the frontal part of the visual field and to horizontal back-to-front motion in the dorsolateral visual field (Hengstenberg 1981). This finding is confirmed in the present study. However, the neuron's responses to vertical upward motion in the caudal to dorsocaudal part of the visual field is an unexpected new result. The response field of *VS1* clearly shows some important characteristics of a rotatory flow field around the transverse axis (pitch rotation; see Fig. 1*A*): large vertical responses along the frontal meridian at $\psi = 0°$, next to no response at $\psi = 90°$, $\Theta = 0°$, and a roughly tangential orientation of most local responses around this pole. In the ventral and the caudal-equatorial parts of the visual field, the neuron does not respond to motion. The site and extent of the dendritic arborizations correspond very well with the mapping of the response properties of this neuron.

The dendritic arborizations of the *VS2* neuron (Fig. 5*B*) are confined to a narrow vertical stripe of the distal part of the neuropil. Its response field appears smaller than that of *VS1*. Like *VS1, VS2* responds best to motion directed vertically downward in the frontal visual field. In addition, there is a weak but measurable response to oblique vertical upward motion in the dorsocaudal visual field. Because all local responses are normalized linearly with respect to the largest one (at $\psi = 0°$, $\Theta = 15°$), the well-ordered arrangement of the small responses in the dorsocaudal area of the response field can hardly be recognized at the scale of the figure. The finding that the LPD at $\psi = 0°$, $\Theta = 75°$ is oriented exactly opposite

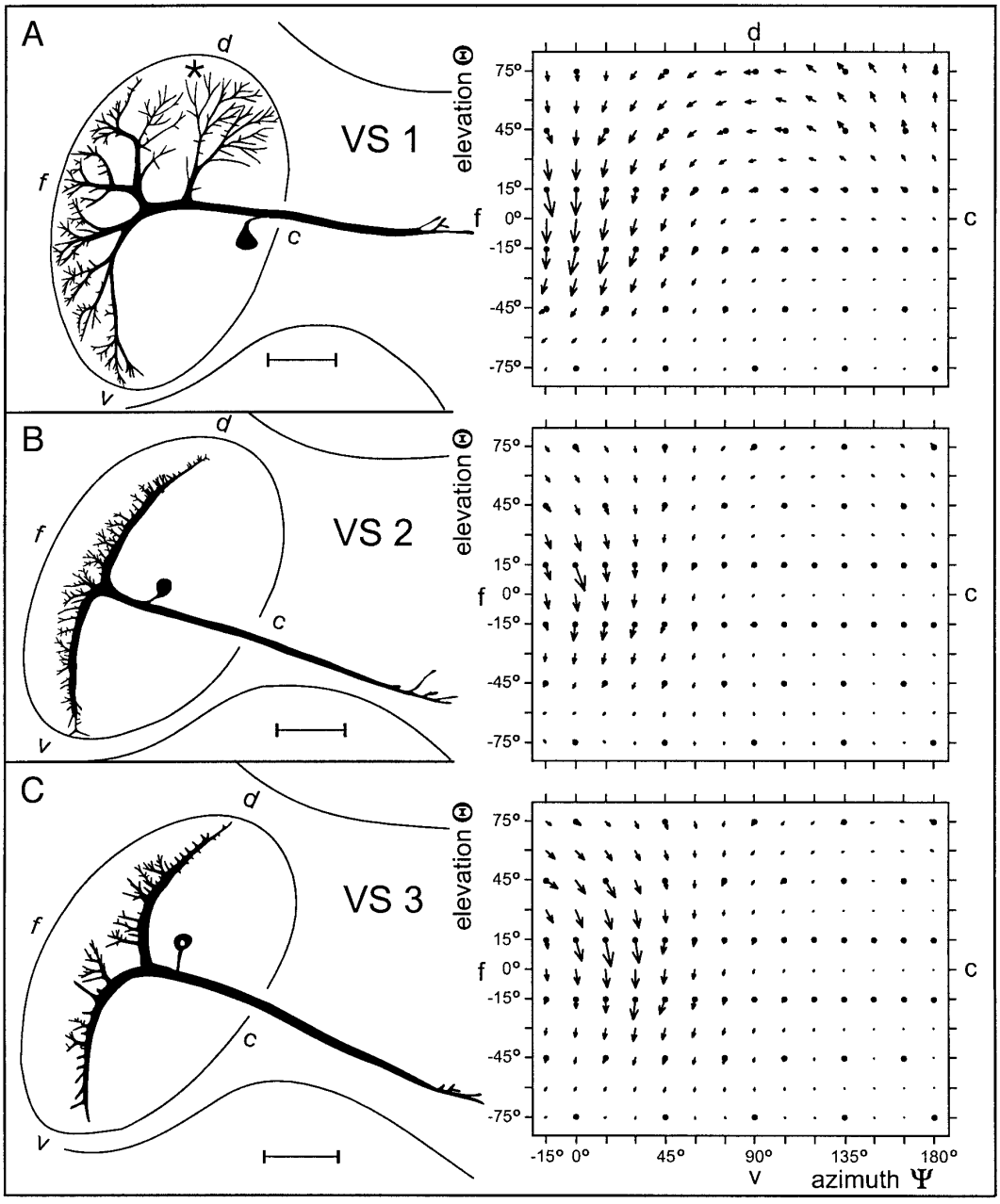


FIG. 5. Anatomy and response fields of the neurons *VS1–VS3*. *A*: *VS1* has a bistratified dendritic arborization: the main dendrite along the distal margin of the lobula plate lies in the posterior neuropil layers. The fan-shaped dorsal dendrite (*) extends toward the dorsal and proximal margin of the neuropil and is placed in the anterior layer of the neuropil. Local motion responses are plotted as arrows in the map of the ipsilateral (right) hemisphere. The orientation of the arrows indicates their LPD. Their length corresponds to the normalized LMS. Measuring positions are marked with small dots; arrows between measuring positions (cf. Fig. 5) were interpolated (cf. METHODS). The response field of *VS1* reflects the dendritic branching pattern in the retinotopic neuropil. Motion sensitivity is concentrated in the frontal equatorial part of the visual field but extends in the dorsal part to positions directed backward. Note the gradual change of LPDs from vertical downward in the frontal field through horizontal back-to-front in the dorsolateral field to almost vertical upward in the caudal region. *VS1* does not respond to motions in ventrocaudal areas of the visual field. *B*: *VS2* has a stripelike dendritic arborization in the distal part of the neuropil that is confined to the posterior layers of the lobula plate. Correspondingly, its response field is restricted to the frontal visual field and downward motion sensitivity is again concentrated near the straight-ahead direction ($\psi = 0°$, $\Theta = 0°$). There are, however, weak but distinct responses to upward motions in the dorsocaudal visual field. *C*: the main dendrites of *VS3* are placed a little more medially in the neuropil. The response maximum to downward motion is equally displaced laterally. The small responses in the dorsal visual field change their LPDs along the azimuth gradually from front to back at $\psi = 0°$ to the reverse at $\psi = 180°$. Note that in all 3 response fields the mean sensitivity in the ventral visual field is smaller than in the dorsal part. Scale bars, 150 μm.

to that at $\psi = 180°$, $\Theta = 75°$ is again reminiscent of a rotatory structure. Here, too, the main sensitivity in the visual field corresponds to the dendritic field of the cell within the neuropil.

The main dendrite of the *VS3* neuron (Fig. 5*C*) lies a little more proximally within the neuropil than those of *VS1* and *VS2*. Correspondingly, the main sensitivity of the neuron to

vertical downward motion is slightly shifted frontolaterally. This shift leads us to expect the putative axis of rotation to be in an azimuth range between $\psi = 105°$ and $\psi = 120°$. Otherwise the global structure is very similar to the response field of the *VS2*. For both *VS2* and *VS3* the extent of the dendritic arborization in the retinotopic array of the lobula plate seems inadequate to account for the motion sensitivities found in the dorsocaudal area of the response fields (see DISCUSSION).

The pronounced maximum of sensitivity in the vicinity of $\psi = 0°$, $\Theta = 0°$ is a significant common feature of the response fields of *VS1*, *VS2*, and *VS3*. There the sensation of pitch rotations would be least disturbed by the translatory optic flow caused by forward locomotion in confined surroundings (Collett 1980).

Although the main dendrite of the *VS4* neuron (Fig. 6*A*) is only slightly more proximal and the arborization invests only a confined area of the neuropil, the general appearance of the response field is markedly different from those shown in Fig. 5. The response field covers more than the ipsilateral visual hemisphere. The main sensitivity lies at an azimuth of $\psi = 75–90°$, corresponding fairly well with the site of the main dendrite in the neuropil. This response field shows a remarkable similarity to an optical flow field induced by a roll-rotation of the fly around its longitudinal body axis (Fig. 1, *A* and *C*). But the optic flow field is not only symmetrical with respect to the distribution of the orientations of the velocity vectors but also with respect to their magnitudes. In the neuronal response field, however, the sensitivities in the ventral part are clearly smaller than in the dorsal part of the field.

The main dendrite of the *VS5* neuron (Fig. 6*B*) ramifies approximately in the middle of the lobula plate; the dorsal main dendrite is bent a little bit more proximally than in *VS4*. As we might expect, the response fields of *VS4* and *VS5* are hard to distinguish from one another (cf. Fig. 6, *A* and *B*). The response field of *VS5* also resembles a rotatory optic flow field induced by a roll motion, but again there is a dorsoventral asymmetry of LMSs.

Figure 6*C* shows on the *left* the main dendrite of the *VS6* neuron arborizing slightly more proximally than those of the *VS4* and *VS5* dendrites. This shift corresponds with a shift of the stripe of main sensitivity to an azimuth of $\psi = 90°$. Thus *VS6* is best adapted to extract the rotatory component from the momentary optic flow field caused by a roll rotation. A dorsoventral asymmetry in the sensitivity distribution is observed in this response field as in those of the other VS neurons.

The morphology of the *VS7* neuron (Fig. 6*D*) differs from that of *VS6* in two respects. First, the rich arborizations of the main dendrite ramify again more proximally within the neuropil. And second, several second-order dendrites of the dorsal main branch spread out distally within the neuropil (Fig. 6*D*, $*$). The *VS7* response field comprises the whole ipsilateral visual hemisphere plus the contralateral stripe of binocular overlap at $\psi = -15°$. The main sensitivity of the neuron to vertical downward motion at an azimuth of $\psi = 120°$ corresponds with the position of the main dendrite within the neuropil. The meridian of main sensitivity is separated by $\sim 90°$ from a singular point in the response field at $\psi = 30°$, $\Theta = -15°$. All LPDs are oriented tangentially around this particular point, even the very small ones that are hard to recognize at this scale of the figure. This clearly demonstrates the rotatory structure of the response field. *VS7*, too, has the dorsoventral asymmetry with respect to the sensitivity distribution.

The vertical main dendrite of the *VS8* neuron (Fig. 7*A*) ramifies in the more proximal parts of the lobula plate. The dorsal dendritic arborizations bend distally, investing the medial parts of the neuropil. These arborizations are situated in the anterior layer of the lobula plate. Again, the main sensitivity of the neuron to downward motion at an azimuth of about $\psi = 135°$ corresponds nicely with the more proximal site of the main dendrite in the lobula plate. Compared with the dendritic field, i.e., the area of arborization, the response field of *VS8* is surprisingly large. The rotatory structure of the response field becomes most obvious for this neuron: there is a distinct singularity at $\psi = 45°$, $\Theta = -15°$ and the sensitivity maximum is separated by 90° from this center of rotation. The dorsoventral sensitivity asymmetry is present in the *VS8* as well. The huge receptive field, spanning more than the ipsilateral hemisphere, can certainly not be accounted for by the limited extent of the dendritic arborization in the retinotopic lattice of the lobula plate. This raises intriguing questions about the input circuitry of *VS8* and other VS neurons (see DISCUSSION).

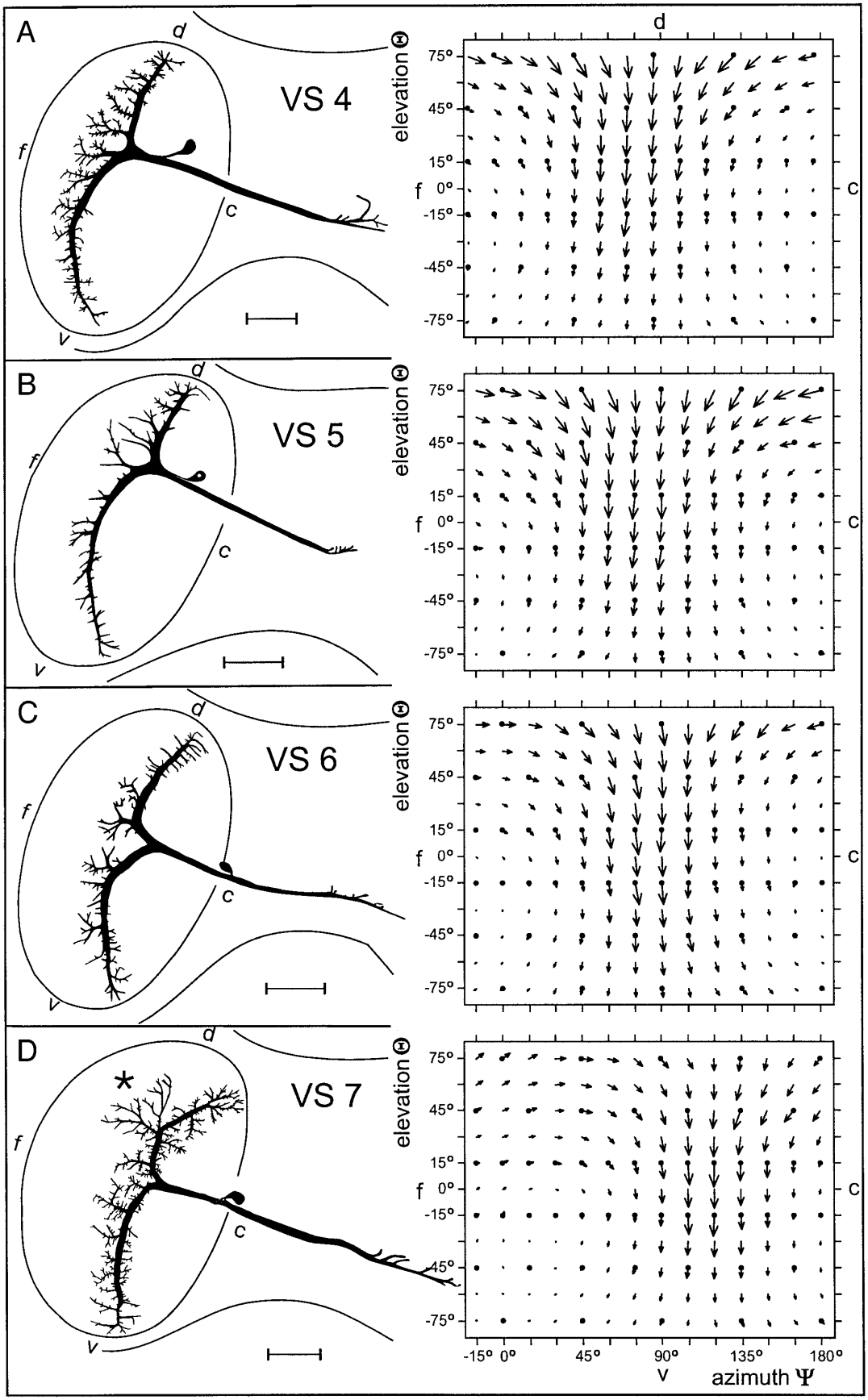
The anatomy of the *VS9* neuron (Fig. 7*B*) as well as the sites of its dendritic arborizations within the neuropil are similar to those of *VS8*. The singularity is slightly shifted laterally (i.e., between $\psi = 30°$ and $\psi = 45°$), and the main sensitivity to vertical downward motion is observed at an azimuth of about $\psi = 150°$. The overall rotatory structure within the *VS9* response field can be recognized just as well as in that of *VS8*. The same is true of the dorsoventral sensitivity gradient.

The main dendrite of the *VS10* neuron (Fig. 7*C*) is located and arborizes at the proximal margin of the lobula plate; again, the dorsal branch is bent distally. The same holds true for the tip of the ventral dendrite, although there it is less pronounced. In keeping with the proximal site of the main dendrite, the greatest sensitivity to downward motion is found at an azimuth of about $\psi = 165°$. The singularity of the *VS10* is also slightly shifted; it lies between $\psi = 45°$ and $\psi = 60°$. Like those of *VS8* and *VS9*, the response field of *VS10* nicely shows a rotatory structure. Its sensitivity distribution also displays a dorsoventral asymmetry. Here, too, we are prompted to ask how this neuron can possibly receive motion information from the frontal parts of the visual field.

A common feature of *VS8*, *VS9*, and *VS10* is the concentration of a large proportion of the overall motion sensitivity in the vicinity of $\psi \approx 165°$, $\Theta = 0°$. This corresponds roughly with the focus of contraction of forward translation at $\psi = 180°$, $\Theta = 0°$. Again it would seem, as in the case of *VS1–VS3*, that this arrangement is best suited to extract pitch rotations with a minimum of disturbance from translatory optic flow components generated during forward flight.

Constancy of the response fields of the VS neurons

To demonstrate the interindividual constancy of the response fields and the reliability of the measurements, we give different measures of variability. First, Table 1 lists the axes of rotation and their scatter. These were determined


A
VS 4
B
VS 5
C
VS 6
D
VS 7
d
f
c
v
elevation Θ
75°
45°
15°
0°
-15°
-45°
-75°
-15° 0°
45°
90°
135°
180°
azimuth Ψ

from the response fields by a modified least-square algorithm proposed by Koenderink and van Doorn (1987) for the estimation of self-motion parameters from noisy optic flow fields. Second, Fig. 8 shows on the *left* the mean response fields of a *VS1*, *VS6*, and *VS8* obtained from experiments in five different flies. The contour plots on the *right* show the respective mean angular deviation (Batschelet 1981) of the LPDs for all measuring positions as determined for each of the three VS neurons. The scatter is surprisingly small in areas of high motion sensitivity and much larger in those of low sensitvity.

Hx neuron—a wide-field neuron sensitive to translatory self-motion

A common feature of all VS neurons is the striking similarity of their response fields to rotatory optic flow fields. To demonstrate that the lobula plate does not only contain neurons adapted to sense rotations, Fig. 9 shows the anatomy and response field of another wide-field neuron that differs fundamentally from the VS neurons. The dendritic arborization of the Hx neuron extends throughout the whole neuropil. Visual information is conveyed by action potentials via a thin axon to the contralateral protocerebrum where the neuron has axon terminals close to the output region of the contralateral HS and VS. The response field of Hx shows a singularity at about $\psi = 135°$, $\Theta = 0°$ which is as clear as, for example, that of *VS8*. However, in the field of Hx, the LPDs are oriented radially, and not tangentially with respect to the singularity. Such a structure is typical for translatory optic flow fields. The neuron is most sensitive to horizontal back-to-front motion in a region ~90° away from the singularity ($\psi = 45°$), which is what we might expect if the neuron were adapted to the sensation of translatory optic flow. In contrast to the dorsoventral decrease of sensitivity of the VS neurons, the sensitivity of the Hx neuron increases slightly in this direction.

The results of this study may be summarized as follows. *1*) For the VS neurons, the site of the main dendritic arborizations within the lobula plate corresponds with the region of greatest sensitivity to vertical motion within the visual field. This reflects the retinotopic organization of the neuropil very nicely. In several instances, however, the extent of the response fields of neurons, *VS8–VS10* in particular, cannot be fully predicted from the arborization patterns of their dendrites within the neuropil. *2*) The VS neurons have huge response fields, in some cases exceeding the area of one visual hemisphere. *3*) The response fields are complex in nature; i.e., the neurons not only respond to vertical downward motion but, in the case of *VS8–VS10*, at various locations to motion in all possible directions. *4*) The response fields are similar to the optic flow fields that would be induced by rotations of the fly around horizontally aligned body axes; i.e., pitch, roll, and intermediate rotations. For all VS neurons the singularity of the response field and the zone of maximum sensitivity are separated by ~90°. *5*) All VS neurons show a dorsoventral gradient of motion sensitivity; in the dorsal part the neurons respond stronger to motion stimuli than in the ventral visual field. *6*) In the two groups of VS neurons (*VS1–VS3* and *VS8–VS10*) that respond to rotations about roughly transverse axes, the peak of motion sensitivity is concentrated near the flow field singularities for forward translation. *7*) In contrast to the VS neurons, the response field of Hx shows a translatory structure, and its motion sensitivity is higher in the ventral than in the dorsal part of the visual field.

DISCUSSION

We have studied in detail the receptive-field organization of each of the 10 neurons constituting the so-called ''vertical system (VS)'' and that of one other wide-field neuron (Hx) in the third visual neuropil (lobula plate) of the blowfly. Our attempt was to distinguish between two proposals concerning the functional roles of these neurons. *1*) The wide-field integration of many local motion signals yields a mean, more or less vertical preferred direction for linear motion (Eckert and Bishop 1978). *2*) VS neurons may be specifically tuned to sense particular components of optic flow by fine, local adjustments of their small-field response properties (Hengstenberg 1981). Our present results show clearly that the receptive fields of the VS neurons are tailor-suited to sense rotatory optic flow, each neuron for a distinct axis of rotation. Other tangential neurons in the lobula plate of the fly specifically sense other components of optic flow. The Hx neuron, for instance, would be suited to sense a particular translatory self-motion.

Disclosure of the receptive-field structure by sequential application of local stimuli

Our method for revealing the functional structure of the receptive field requires that the neurons respond sufficiently well to local motion stimuli. In spiking neurons with low spontaneous activity and a high firing threshold, the charac-

FIG. 6. Anatomy and response fields of the neurons *VS4–VS7*. *A*: *VS4* has a rich stripelike arborization in the posterior layers of the lobula plate, and its main dendrites are placed a little more medially than in *VS3*. Its response field comprises more than the ipsilateral hemisphere. The largest responses are obtained for downward motion along $\psi = 75°$. At other locations in the dorsal half, the LPDs seem to flow toward this line, and diverge from it in the ventral half. Minima of motion sensitivity are found ahead of and behind the fly, slightly below the horizon. *B*: the dendritic arrangement and response field of *VS5* are very similar to those of *VS4*, except for a minute lateral shift of the main sensitivity. *C*: the deeply bifurcated main dendrite of *VS6* is placed approximately in the middle of the lobula plate and lies in the posterior neuropil layers. Its response field covers again the whole ipsilateral hemisphere and exhibits most clearly ½ of the global structure of an optic flow field for roll rotation (cf. Fig. 2*B*). *D*: the main dendrites of *VS7* are located close to those of *VS6* in the middle of the lobula plate. Most of the smaller branches are found in the posterior layers of the lobula plate, but the fan-shaped twigs protruding from the dorsal dendrite toward the distal neuropil margin (*) invade the anterior layers where horizontal motions are processed. The main sensitivity to downward motion of *VS7* is shifted to an azimuth of $\psi = 120°$. In the dorsofrontal visual field, significant responses are elicited by horizontal front-to-back motions, and in the ventrofrontal field smaller responses to the reverse direction of motion. The global structure of the response field is very similar to a rotatory optic flow field around an axis of rotation at about $\psi = 30°$, $\Theta = -15°$. The neurons *VS4–VS7*, like *VS1–VS3*, respond more strongly to motion in the dorsal than in the ventral half of the visual field. Scale bars, 150 μm.

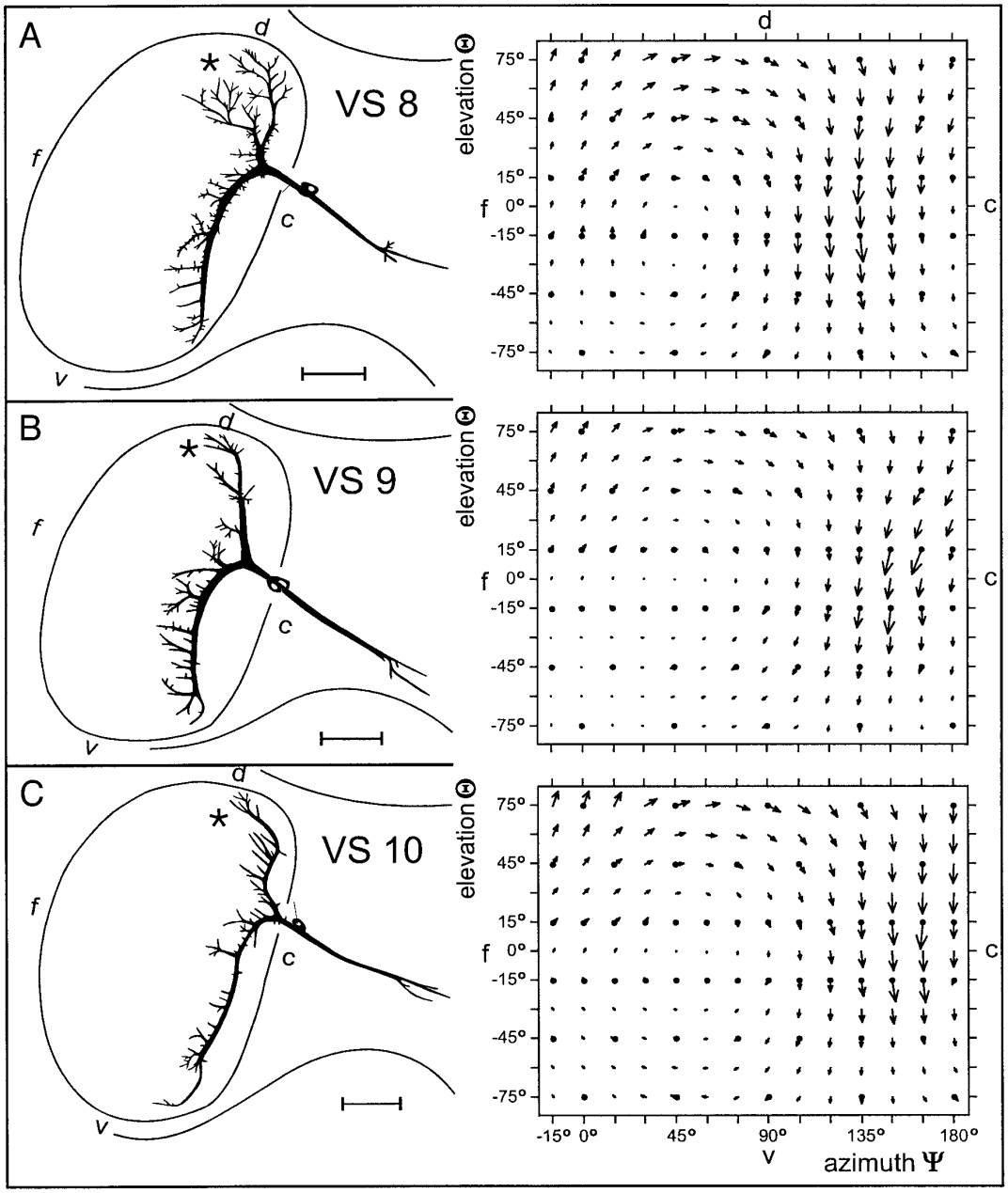


FIG. 7. Anatomy and response fields of the neurons *VS8–VS10*. *A*: the main dendrites of *VS8* lie near the proximal margin of the lobula plate. The narrow ventral dendrites lie in the posterior neuropil layers, but the broad dorsal arborization (*) invades the anterior layers. The response field clearly shows a rotatory structure with a singularity at $\psi = 45°$, $\Theta = -15°$, and a belt of downward sensitivity at $\psi = 135°$. The responses to front-to-back motions in the dorsolateral field may be mediated by the broad dorsal dendrite, but the responses to upward motions in the frontal visual field cannot simply be reconciled with the anatomy of *VS8* (see DISCUSSION). *B*: *VS9* is similar to *VS8* in its placement in the lobula plate. Its dorsal dendrite (*), although less broad, extends distally and invades the anterior layers of the neuropil. The response field is very similar to that of *VS8* except that the peak of downward sensitivity is shifted to $\psi = 150°$. Here again, the dendritic structure does not explain off-hand the responses to upward motions in the frontal visual field. *C*: *VS10* has thin dendrites close to the proximal margin of the lobula plate. The branching pattern is similar to that of *VS9*. The response field clearly shows a rotatory structure with a singularity at about $\psi = 60°$, $\Theta = 0°$ and correspondingly the largest responses to downward motion at $\psi = 150°$. Again, the sizeable responses to upward motion in the dorsofrontal field are not obvious from the dendritic structure of *VS10*. As in the other VS neurons, the sensitivity of *VS8–VS10* is larger in the dorsal than in the ventral visual field. Scale bars, 150 μm.

terization of receptive-field areas with low responsiveness may therefore be difficult. For example, descending neurons in the cervical connective, eliciting the landing response, were found to respond only if both eyes were stimulated simultaneously (Borst 1991). However, all spiking neurons encountered so far in the lobula plate had a spontaneous activity high enough ($\geq$10 spikes/s) to reveal even small local responses (e.g., Fig. 9) (Krapp 1995). The VS neurons respond to visual stimuli with graded membrane potential modulations. Therefore in these cases the problem of sub-

TABLE 1. *Reliability of axes of rotation of the 10 VS neurons*

Neuron	Number	Azimuth	Elevation
VS1	8	90°	12 ± 11°
VS2	7	89°	−10 ± 13°
VS3	9	51°	−11 ± 20°
VS4	9	29°	−7 ± 13°
VS5	12	10°	−2 ± 6°
VS6	6	0°	3 ± 9°
VS7	9	336°	5 ± 11°
VS8	10	309°	9 ± 11°
VS9	17	300°	12 ± 9°
VS10	3	291°	12 ± 13°

Values in Elevation are means ± SD, taking into account both the variation of azimuth and elevation for the respective rotation axis in a right-handed coordinate system. The axes of rotation were estimated by a least-square algorithm to determine the self-motion parameters from noisy optic flow fields (Koenderink and van Doorn 1987).

threshold responses does not exist. The reduced signal-to-noise ratio of small local responses increases only the scatter of measurements and may be overcome, if required, by increasing the number of stimulus cycles.

A different question is raised by the comparatively large amplitudes of the responses to local stimulation (e.g., 10 mV modulation of the membrane potential; Fig. 4*B*). With simultaneous stimulation at many locations of the receptive field, as expected for real self-motions in structured surroundings, the linear sum of very many local motion signals would by far exceed the dynamic range of VS neurons. It has been shown previously that, in VS neurons, overload of the output is prevented by a reduction of gain with increasing area of stimulation (Haag et al. 1992; Hengstenberg 1982). Several different biophysical mechanisms have been proposed to account, in concert, for this deviation from linearity (Hengstenberg 1982; Kirschfeld 1989).

Identification of the VS neurons and the reproducibility of their response fields

The recorded neurons were marked by dye injection in all experiments. Each VS neuron could be unambiguously identified by its characteristic branching pattern in the lobula plate as determined in a previous neuroanatomic study (Hengstenberg et al. 1982). For all VS neurons the location of the main dendrites in the retinotopic mosaic of the lobula plate corresponds well with the azimuth of the vertical zone of maximum motion sensitivity in the visual field. This close relationship between the neuronal morphology and the physiological results allows fairly safe predictions about the identity of a VS neuron even before its histological reconstruction is made. With appropriate caution, it also enables us to identify weakly stained neurons. Two pairs of VS neurons (*VS4-VS5* and *VS9-VS10*), however, cannot be identified safely by physiological criteria alone. Their response fields are so similar that they may be confused (Figs. 6, *A* and *B*, and 7, *B* and *C*).

How are the complex structures of the response fields generated?

Our results show that both the LPDs and the LMSs are unevenly distributed within the receptive fields of all tangential neurons studied so far. This raises the question of how these uneven distributions come about.

Locally, motion is detected by a nonlinear interaction between signals from adjacent elements of the retinal lattice (Fig. 1*D*) (cf. Egelhaaf and Borst 1993; Hassenstein and Reichardt 1956). For yaw turns, interactions between next-but-one neighbors are also effective, although to a lesser extent, but interactions across the rows of the retinal lattice are very small in the light-adapted state, if at all present (Buchner 1976; Hausen 1993; Schuling et al. 1989). Motion is detected along all three axes of the hexagonal retinal lattice, and probably everywhere in the compound eyes (Buchner et al. 1978; Götz et al. 1979). The orientation of the facet rows, and thus of the motion detectors, changes over the compound eye (Franceschini et al. 1979; cf. Hausen 1982b). Hence two explanations could account for the observed variation in local preferred direction across the receptive fields of VS neurons.

1) The LPD at any particular location could be due to the weighted average of all elementary motion detectors present at this location. This would require the wide-field neuron to have access to all local motion signals at each retinotopic location. This, in turn, means either that the terminals of small-field neurons would have to invade the neuropil layer containing the dendritic branches of the wide-field neurons or, conversely, that their dendritic branches would have to invade the neuropil layers where the small-field neurons terminate (see 2). According to this explanation, any useful LPD could be created anywhere and everywhere in the receptive field, irrespective of the local orientation of the retinal lattice.

2) Alternatively, the local preferred directions of wide-field neurons could be caused by selection of only the appropriate motion detector signals from the local set of six directions. In this case the LPDs of all wide-field neurons should reflect the lattice orientation for every given location in the eye.

At present, the cellular identity of those small-field neurons providing motion input to the lobula plate and the nature of their signals relative to the model of motion detection have not yet been established unambiguously (Bausenwein and Fischbach 1992; Douglass and Strausfeld 1996; Egelhaaf and Borst 1993; Franceschini et al. 1989; Hausen 1993). Four layers of directional preference have been demonstrated in the lobula plate of *Drosophila* by activity labeling of small-field neurons stimulated by pattern motion in different directions (Buchner and Buchner 1984). Correspondingly, HS neurons and other cells responding to horizontal motion are situated in the anterior layers of the lobula plate. VS neurons and other cells responding to vertical motions have their main branches, and large parts of their arborization, in the posterior layers of the lobula plate (Hausen 1993; Hengstenberg et al. 1982). The bidirectionality of the responses of HS and VS neurons requires that each of them occupies at least two of the four ''directionality'' layers.

Several VS neurons (*VS1, VS7–VS10*) have bistratified arborizations. Their main dendrites are located in the posterior layers of the neuropil, and more or less vertical LPDs prevail in the corresponding parts of their receptive fields (Figs. 5–7). Their dorsal arborizations, and smaller parts of their ventral arborizations, are situated in the anterior neuropil layers, and correspond to receptive-field areas with more or less horizontal preferred directions (Figs. 5*A*, 6*D*, and 7, *A–C*). It was never shown in any of the HS and

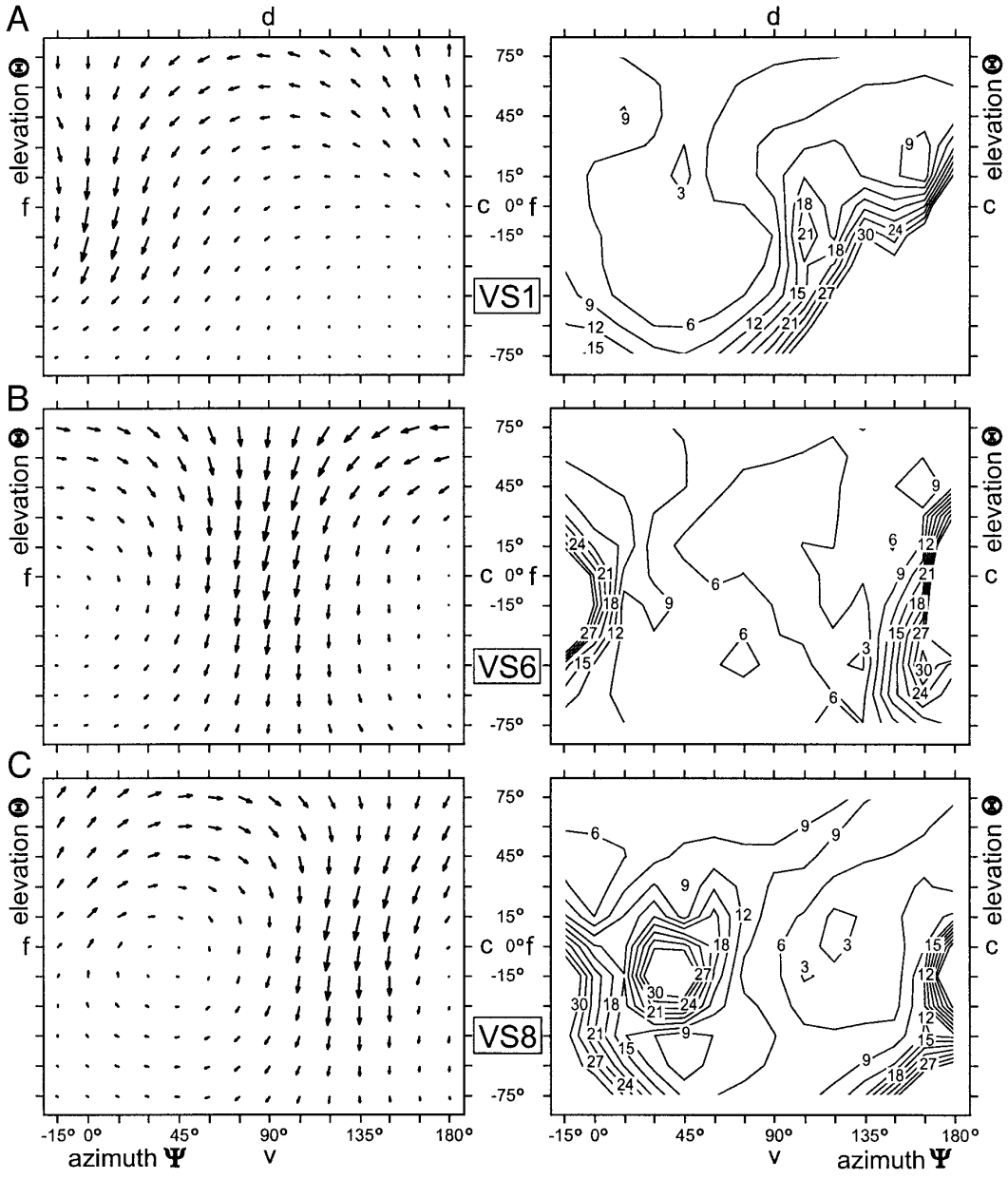


FIG. 8. Reproducibility of the neuronal response fields. Mean response fields obtained in 5 different animals. The contour plots on the *right* show the mean angular deviation of the LPDs at the respective measuring locations. *A*: results for *VS1*. *B*: results for *VS6*. *C*: results for *VS8*. Note the extraordinarily low angular deviations in the regions of high motion sensitivity. Only in regions where the neurons are literally ''blind''; e.g., aroung the rotational axis, the deviation is considerably increased. The same degree of consistency is found in the other 7 VS neurons when repeatedly recorded in different individuals.

VS neurons, by any staining procedure, that their dendritic arborizations extend locally through the whole depth of the neuropil (Bishop and Bishop 1981; Eckert and Bishop 1978; Hengstenberg et al. 1982, 1983; Strausfeld and Seyan 1985).

The combination of this finding with the directionality layering mentioned above makes it very unlikely that the LPDs of VS neurons are generally due to a weighted average of local motion signals with all possible directions. Instead it favors the view that the LPDs are mainly caused by selection of the appropriate small-field signals, as proposed by Hausen (1982b) for other lobula plate neurons. A close comparison between the LPDs in different VS neurons and the local orientation of the lattice of the optical axes at corresponding positions will be necessary. Such a comparison may show whether this simple model is sufficient to account for the observed receptive-field structures.

The simplest model for the organization of the lobula plate, as stated above, implies that the receptive field of any particular VS neuron is delineated by the outline of the receptive fields of the small-field units converging on that VS neuron. This is assumed to be indicated by the extent of its dendritic arborization within the retinotopic lattice of the neuropil. In contrast to this view, however, our results show that most VS neurons also respond to stimuli in areas of the visual field that are not reached by their dendrites in the corresponding areas of the lobula plate: *VS2* and *VS3* respond weakly but characteristically to oblique upward motions in the dorsocaudal visual field (Fig. 5, *B* and *C*). *VS4–VS7* respond to hori-

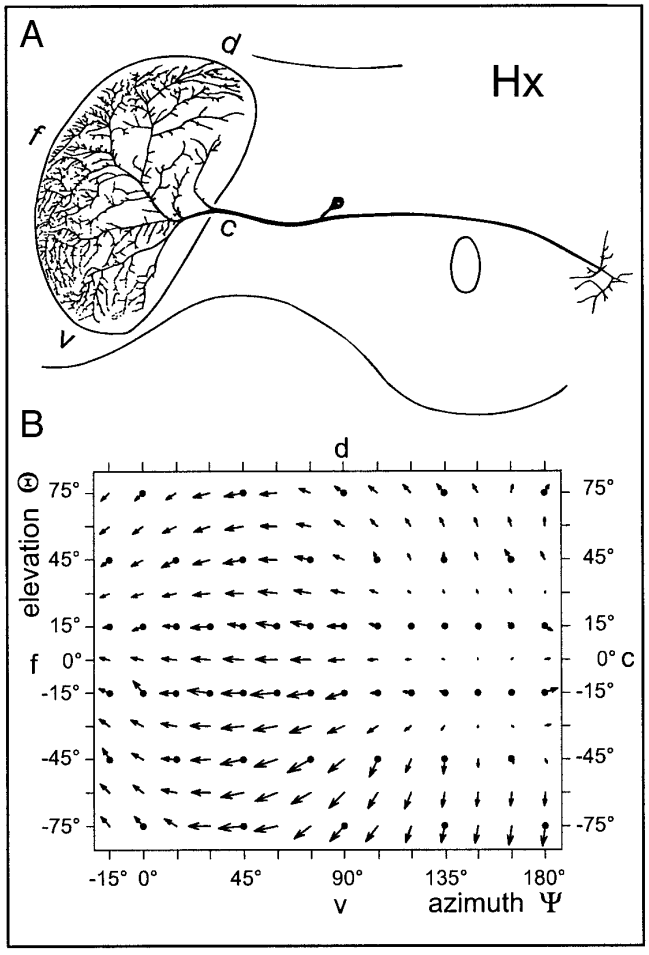


FIG. 9. Anatomy and response field of the neuron Hx. *A*: the dendritic arborization of this neuron extends over almost the whole area of the lobula plate. Its thin axon passes across the sagittal midline to the contralateral protocerebrum and terminates in the vicinity of the HS and VS axon terminals. *B*: in keeping with its structure, the response field of Hx comprises the entire ipsilateral hemisphere and includes the contralateral zone of binocular overlap along $\psi = -15°$. Hx responds maximally to horizontal back-to-front motion at azimuths of $\psi = 45°$, and minimally near $\psi = 135°$, $\Theta = 0°$. All LPDs are arranged radially around this singularity. This global structure is very similar to that of a translatory optic flow field. Note also that in contrast to the VS neurons, the overall motion sensitivity of the Hx neuron is higher in the ventral half than in the dorsal half of the visual field.

zontal motions in the dorsofrontal and dorsocaudal visual field (Fig. 6, *A–D*). Most notably, *VS8–VS10* respond significantly to upward motion in the anterior visual field, even in the contralateral hemisphere (Fig. 7, *A–C*).

Spurious responses in ''remote'' areas of the receptive field might be caused by stray light or reflections of the moving stimulus. This possibility seems very unlikely because of the following reasons. *1*) The whole setup was lined with dull black cloth. *2*) Artifacts of this kind should be similar in different neurons for the same stimulus position. This we did not observe. *3*) Stray light responses should be reduced at increased ambient illumination, but the unexpected local responses persisted under normal room light conditions. We are therefore confident that the response fields of VS neurons reflect the true functional organization of these cells.

The lack of congruence between dendritic fields and response fields might also be explained if the VS neurons were incompletely stained in our experiments. But neither in the best stainings of this study nor in previous studies with different staining procedures have much farther reaching arborizations been observed in VS neurons (Bishop and Bishop 1981; Eckert and Bishop 1978; Hausen 1984; Hengstenberg et al. 1982; Strausfeld and Seyan 1985). An alternative possibility is that these unexpected responses may indicate an input additional to the direct ipsilateral small-field inputs of VS neurons. *1*) The presumed small-field units could have far-reaching lateral interactions importing specific motion information from remote areas of the visual field. *2*) Similarly, such transfer may be achieved by amacrine cells of the lobula complex (cf. Hausen 1993; Strausfeld 1976). *3*) Finally, VS neurons may not be completely isolated from one another. There may be either dendrodendritic contacts in the lobula plate neuropil, as in case of the figure/ground discrimination circuit (Egelhaaf et al. 1993; Warzecha et al. 1993), or contacts in the region of the axon terminals. This problem needs further clarification by specific investigations.

Are VS neurons matched filters to sense self-motions?

The uneven distributions of LPD and LMS in the response fields of all VS neurons show a striking similarity to rotatory optic flow fields (Fig. 1*C*). This is most obvious for *VS6* (Fig. 6*C*), whose axis of rotation nearly coincides with that of the theoretical example (Fig. 1*C*). The tangential alignment of the LPDs around the singularities of the response fields, i.e., around the presumed axis of rotation, can be easily seen in the response fields of *VS1* (Fig. 5*A*) and *VS8–VS10* (Fig. 7, *A–C*). The same arrangement is present in the response fields of *VS4–VS7* (Fig. 6, *A–D*), but, because of the characteristic distortions of the Mercator projection, it is graphically not as obvious. Very clearly, the response fields of VS neurons do not have the characteristic features of a purely translatory optic flow field (Fig. 1*B*). We conclude therefore that the 10 VS neurons are specific neural filters, in the sense of Fig. 2, for simultaneously extracting from the ongoing optic flow the rotatory motion components around different, approximately horizontal axes.

The response fields of VS neurons, however, show in common two interesting deviations from the mathematical structure of pure rotatory optic flow fields. *1*) All VS response fields have a general dorsoventral gradient of motion sensitivity (Figs. 5–7), which is, of course, not present in the corresponding rotatory optic flow field (e.g., Fig. 1*C*). This may reflect an adaptation to the vertical asymmetry of the real world and its unequal distribution of contrast. *2*) The response fields of *VS1–VS3* and *VS8–VS10* show a concentration of motion sensitivity near the roll axis (Fig. 1; $\psi = 180°$, $\Theta = 0°$ to $\psi = 0°$, $\Theta = 0°$) but much lower sensitivities at the top ($\psi = 90°$, $\Theta = 75°$) of the visual field. In an optic flow field for rotation around the transverse axis ($\psi = 90°$, $\Theta = 0°$), the flow velocity would be equal all around the equator of rotation connecting the positions mentioned above. This difference between optic flow fields and neuronal response fields probably reflects an adaptation to the fact that flies usually move forward while they rotate. Pitch and yaw turns (Fig. 1*A*) can be sensed best where the corresponding rotatory flow is least disturbed by the translatory flow of forward motion, i.e., straight ahead and

straight behind (Collett 1980). A similar concentration of sensitivity to straight-ahead motion has been observed in HS neurons, corroborating this view of a functional regionalization of the fly's visual field (Hengstenberg et al. 1998).

In Fig. 9 it is immediately obvious that the response field of the Hx neuron has the global structure of a translatory optic flow field. In contrast to VS neurons, its sensitivity is larger in the ventral part of its receptive field and is not concentrated in a small area. Eventually we expect to find more cells of this type among the 60 tangential neurons of the lobula plate.

The characteristics of the Hx neuron demonstrate that the functional tuning of wide-field neurons in the visual system of flies is not a trivial consequence of the structure of the compound eye. Together with the results on the VS neurons, they favor the view that the functional specificity of these ''filter neurons for optic flow'' is achieved by subtle local tuning of synaptic contacts of single neurons.

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