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Visual Sensation of Self-Motions in the Blowfly *Calliphora*

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Abstract - Insects flying across their habitat generate in their eyes complex motion patterns. They contain information about the animal's instantaneous direction and speed of locomotion as well as about the three-dimensional layout of the surroundings. In flies, visual motion is analyzed by large arrays of small field motion detectors. For each location in visual space, motion is detected in different directions. Local motion signals of distinct preferred directions are projected retinotopically into different layers of the lobula plate (third visual neuropil). There, neurons with extended dendritic arborizations across the retinotopic input array select from different depths of the neuropil many local signals, each corresponding to a particular direction of motion at a particular location in visual space. Spatial integration of thousands of well-selected local inputs over tailor-suited areas of visual space would allow to create specific filters for distinct optic flow patterns. By intracellular recordings from wide-field neurons, receptive field mapping with local motion stimuli and cell identification by dye injection and 3-D-reconstruction we demonstrate the ways how flies overcome the multiple ambiguities of local motion signals and generate useful representations of different self-motions.

1.Habitats and lifestyles of blowflies:

Sheep blowflies (*Lucilia* spec.) live in open country, e.g. sheep pasture; hence their visual surroundings are simple and coarsely structured. Blue bottles (*Calliphora* spec.) live in shrubland at forest edges or even within not too dense forests (Colyer and Hammond 1968). Their habitat is characterized by many obstacles to be circumvented.
The visual surroundings are richly by structured and the global features of sky and ground are often masked by vegetation. Blowflies (Fam. Calliphoridae), in general, have thus to be able to manoever artistically through unknown and very complex surroundings, i.e. to perceive quickly and reliably their motions in space in order to control their flight attitude and flight trajectory as required. To facilitate this perceptual task, flies stabilize the orientation of their eyes, relative to the surroundings, against voluntary and unexpected rotations of their body (Hengstenberg 1991 and this volume).

2. Motion in space and optical flow patterns:

Flies have, like other animals, a preferred body posture when walking an the ground and a similar attitude when flying through still air: the body axis is more or less horizontal and the back is directed upwards (Fig. la). Flying insects have, in principle, all six degrees of freedom to move in space: they can translate along their body axes (lift, side-slip, thrust) and rotate about these axes (yaw, pitch, roll; Fig. 1 a) or perform certain combinations of these motions.

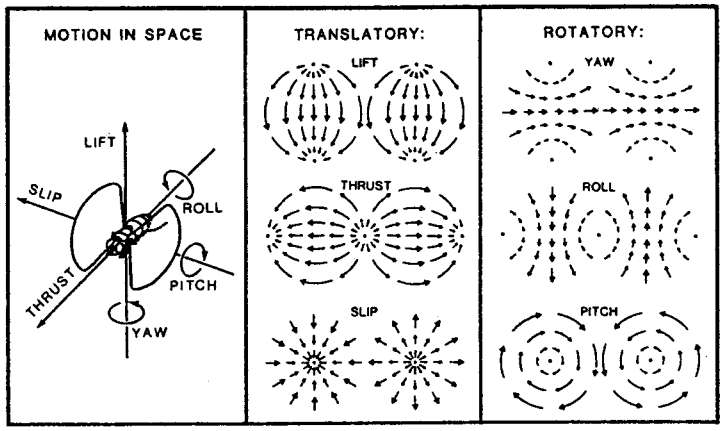

Fig. 1:
Motion in space and retinal motion patterns. (**a**) Degrees of freedom of a flying insect. (**b**) Retinal motion patterns caused by translations along the fly's principal axes. (**c**) Retinal motion patterns caused by rotations about the fly's principal axes.

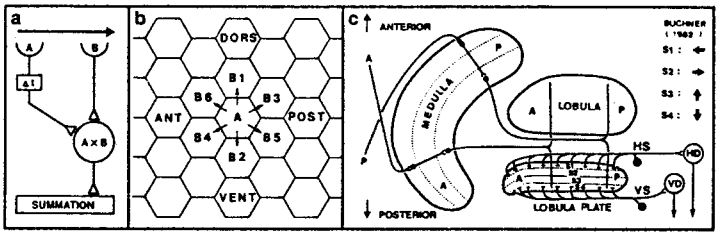

Fig. 2:
Elementary motion detection in insects (**a**) Functional structure of a unidirectional motion detector. (**b**) Motion is sensed along all directions of the facet array. (**c**) Local motion signals of different preferred directions are transferred to different layers of the lobula plate (see inset).

The visual field of the fly's two compound eyes covers almost the whole sphere around the animal. Each eye surveys roughly its respective hemisphere with a narrow zone of binocular overlap along the mid-sagittal plane and a small blind area at the back of the visual field where the fly's body obstructs vision straight backwards.
The principal motions (Fig. 1 a) create, in the eyes, characteristic motion patterns that are illustrated, in a cartoon fashion, in Fig. lb, c. The hemispherical visual fields of the two eyes are shown as circular areas, as if peeled off the fly's eyes, and flattened into a transverse plane in front of the animal. Fig. lb illustrates flow patterns caused by translatory motions of the fly: upward lift (top), forward thrust (middle) and slip to the right (bottom). Fig. lc illustrates flow fields of rotatory motions: yaw turn to the left (top), roll to the right (middle) and upward pitch (bottom). Each of these motion patterns is characterized by the arrangement of its motion axis (Fig. lb: dots = focus of expansion/contraction; Fig. 1c: dots = center of rotation) and a typical flow pattern, where arrows of different size are meant to indicate motions of different speed. Translatory motion patterns (Fig. lb) depend upon the distance of visual objects and vanish if things are infinitely far away. Hence for Fig. lb a finite distance of the surroundings was assumed. Rotatory motion patterns (Fig. 1c) are independent of distance but the apparent speed across sampling stations of finite separation on the eye (see below) depends upon the latitude of the region considered from the equator.
Optic flow thus depends upon the three-dimensional layout of the surroundings, on the instantaneous motion and on the direction of gaze (Koenderink and van Doorn 1987). Conversely, extraction of translatory components from the complex flow pattern provides information about the three-dimensional layout of the surroundings. Motion discontinuities reveal steps in depth, as occurring at the edges of objects. Rotatory flow components, on the other hand, reveal unambiguously body-rotations of the fly because they are independent of object distance. Fast and reliable sensation of body rotations would allow the fly in the first place to control its body attitude in order to keep balance and additionally to stabilize the orientation of its eyes in order to reveal and probably make use of the translatory flow components (Hengstenberg et al. 1986, Srinivasan 1993, Colett et al. 1993).
In this paper we demonstrate how certain neurons in the visual system of the blowfly *Calliphora* extract specific rotatory components from arbitrary optic flow patterns. Before dealing with this issue, however, it is necessary to introduce briefly the anatomy of the fly's eyes and visual nervous system, as well as some of our present knowledge about the process of visual motion detection.

3. Anatomy of the fly's visual system

Flies have two kinds of eyes: (1) the three dorsal ocelli are small camera eyes with a single, underfocussed wide-angle lens and a few hundred photoreceptors; they are best suited to sense global brightness in the dorsal hemisphere (Schuppe and Hengstenberg 1993). (2) the two large compound eyes consist, in *Calliphora*, of about 2 x 6000 ommatidia, overlooking the two lateral hemispheres. Each ommatidium has its own little lens which provides for a small receptive field of about 2° diameter and thus allows to resolve spatial details. An ommatidium contains 8 photoreceptors which fall in two classes;

the peripheral receptors R1-R6 are mainly used for motion detection and two . central photoreceptors R7, R8 which serve other, less well defined purposes (Heisenberg and Buchner 1977, Heisenberg and Wolf 1984, Hardie 1985).
The optic lobes of the central nervous system consist of three successive areas (neuropils): the outermost lamina ganglionaris, the medulla and the lobula complex which, in flies, consists of two parts, the anterior lobula and the posterior lobula plate.
All three neuropils are retinotopically organized i. e. they consist of a repetitive multitude of similar small field neurons that preserve the two-dimensional organization of the retina. The restricted lateral extent of their arborizations (Strausfeld 1976) and the small receptive fields found in electrophysiological recordings (Devoe and Ockleford 1976, Gilbert and Strausfeld 1992, Gilben, Penisten, Devoe 1991) suggest that these neurons perform local interactions which are, however, only partly understood due to the technical difficulties associated with recordings from these very small fibres.
At several depths of the visual neuropils tangential neurons contact extended areas of the retinotopic array of smallfield neurons (Strausfeld 1976, Fischbach and Dittrich 1989) and seem to collect layer-specific information over large parts of the visual field. Some of these have big enough fibres to be thoroughly studied by intracellular recordings. This is especially true for motion sensitive tangential neurons of the lobula plate (Hausen 1993).

4. Elementary motion detection by small-field columnar neurons

Studies of the optomotor turning response of the beetle *Chlorophanus* (Hassenstein and Reichardt 1956) have revealed that motion is detected in insects by a second order nonlinear interaction between input signals arising in two adjacent facets of the compound eye. Directional specificity is achieved by delaying one of the two input signals.
The simplest, unidirectional structure fulfilling these requirements is illustrated in Fig. 2a. Since the beetle's response was found to be bidirectional, an antisymmetrical scheme was proposed to account for the observed behaviour (Reichardt 1961). Recently it was shown that the subtraction stage of this scheme increases the directional specificity by elimination of non-directional signals of the imperfect detector stages (Egelhaaf and Borst 1993).
Different physiological mechanisms for the essential step of motion detection have been proposed (rev. Franceschini et al. 1989). At present, however, physiological evidence is still too sparse to finally decide which mechanism is used by the fly. Similarly it is not quite clear which small field neurons perform the essential operation of motion detection. (Egelhaaf and Borst 1993, Hausen 1993). The application of modern methods of optical microstimulation (Franceschini et al. 1989), whole cell patch recording, optical recording of calcium fluxes (Borst and Egelhaaf 1992), genetic microsurgery (Pflugfelder and Heisenberg 1994 in press), immune cytology (Buchner et al. 1988) and computer-assisted neuroanatomy (Bausenwein et al. 1992) will probably allow to settle these questions in the near future.

Studies of different optomotor responses in walking and flying flies have revealed that pattern motion is sensed along all principal directions of the facet array and probably everywhere in the fly's visual field (Fig. 2b; Götz 1964, Götz et al. 1979).
Local motion signals of any one direction class (Fig. 2b) are directed to the lobula complex in a retinotopic manner (Strausfeld 1976, Fischbach and Dittrich 1989) and are represented in distinct layers of the lobula plate (Fig. 2c; Buchner und Buchner 1984). Local motion signals, however, cannot be directly used for motor control because they are ambiguous in several respects:
(1) The direction of motion is uncertain within ± 90° of the preferred direction. The detector output depends on the cosine of the angle between the direction of motion and the preferred direction of the detector. Therefore each output value corresponds to two possible input directions of stimulus motion. This problem can be solved by comparison of detector signals with preferred directions that share the same receptive field (Reichardt et al. 1988).
(2) The speed of motion is uncertain for similar reasons: the output of a directionally specific motion detector is zero in the absence of motion and at infinite speed, and has a working range inbetween. Therefore, again, each output value corresponds to two possible input speeds. Comparison of signals from detectors overlapping receptive fields the same preferred direction but different sampling bases or different delays would allow to solve this problem (Buchner 1984).
(3) Finally, local motion signals are ambiguous with respect to the type of self-motion by which they may have been generated. A vertical downward motion at the equator in the left lateral visual field, for example, may either be caused by an increase in lift (translatory Fig. 1b top) or by a roll turn to the right (rotatory; Fig. 1c, middle). Similarly, a horizontal front-to-back motion in the right lateral field may be caused by forward progression in confined surroundings (translatory; Fig. lb, middle) or by a yaw turn to the left (rotatory; Fig. 1c, top). These ambiguities can be resolved by comparison of motion signals arising from diametrically opposed parts of the visual field (Götz 1972, Kern et al. 1993).

5. Wide-field integration of motion in the third visual neuropil

The lobula plate (Fig. 2a) contains numerous tangential neurons. They have flat, often fan-shaped dendritic arborizations which spread over large areas of the neuropil and correspond to large receptive fields (Hausen 1993). The dendritic arborizations are located in distinct depths of the neuropil and this correlates with distinct preferred directions: neurons lying more anteriorly respond preferentially to horizontal pattern motion and more posteriorly situated cells prefer vertical motions in the visual field (Hausen 1993, Hengstenberg 1982). Axons of tangential neurons may project to different brain areas, to the contralateral optic lobe or terminate in small "optic foci" on the postero-lateral side of the brain. Here are also the input areas of descending neurons which transfer visual and other signals through the neck to motor coordination areas in the thoracic compound ganglion (Gronenberg and Strausfeld 1990, Gronenberg and Strausfeld 1992). Two groups of tangential neurons of the lobula plate are particularly conspicuous because of their comparatively thick fibres:

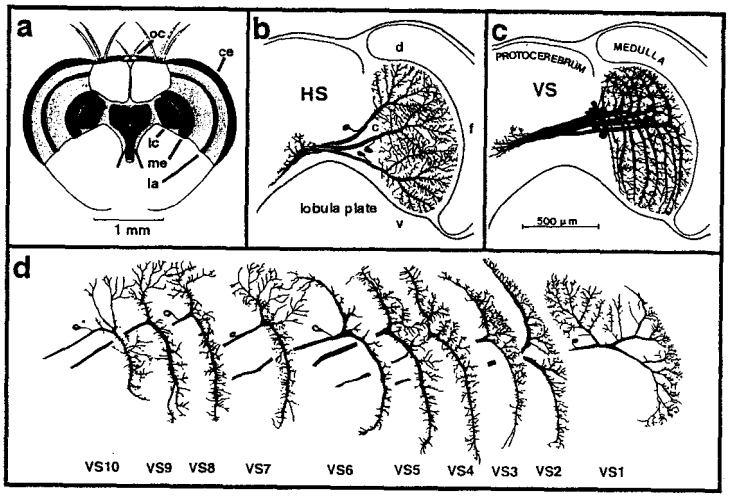

Fig. 3:
Neurons of the horizontal (HS) and vertical system (VS). (**a**) Rear aspect of the fly's brain, showing the location of the ocelli (oc) and compound eyes (ce), the three visual neuropils: lamina (la), medulla (me), lobula complex (lc) and central brain areas with the neck connectives. (**b**) The three HS-neurons in the anterior layer of the lobula plate; letters indicate visual field coordinates: d = dorsal, v = ventral, f = frontal, c = caudal. (**c**) VS-neurons in the posterior layer of the lobula plate. Cobalt stainings courtesy K. Hausen. (**d**) Individual structures of dendritic arborizations of the VS-neurons revealed by intracellular recording and staining.

The "Horizontal System" (HS;Fig. 3b) consists of three neurons and the "Vertical System" (VS; Fig. 3c, d) of usually ten cells. Fig. 3a shows a fly's head in frontal aspect from behind with the brain dissected free. Eyes and neuropils are shown in black and fibre tracts are shaded grey.

The bean shaped area in Fig. 3b shows the anterior layer of the right lobula plate with indications of the visual field coordinates (d = dorsal, v = ventral, f = frontal, c = caudal). Each of the three HS-neurons spans completely the fronto-caudal extent of the lobula plate. The dorso-ventral extent of the lobula plate is, however, divided among the three HS-neurons: HSN occupies the dorsal third, HSE the equatorial third and HSS the ventral third with some overlap of dendritic fields at the borders. The inconspicuous cell bodies lie at the medial border of the lobula plate, detached from the main fibres as usual in insects. The HS-axons terminate with a few stubby collaterals in the ventrolateral protocerebrum (Fig. 3b; Hausen 1993).

The 10 VS-neurons (Fig. 3c,d) occupy the posterior layers of the lobula plate. Their dendritic fields span the whole dorso-ventral extent of the lobula plate but in stripes of limited fronto-caudal extent. The dendritic arborizations show characteristic features that can be recognized in different individuals and justify a specific labeling of each VS-neuron (Fig. 3d, bottom). A particuliar feature of VS1 and VS7-VS10 is that their broader dorsal dendrites invade the anterior layers of the lobula plate. The cell bodies of VS-neurons form a cluster at the medial border of the neuropil and the axons project as a bundle to a target area a little more dorsal than that of the HS-neurons (Hengstenberg et al. 1982, Strausfeld and Seyan 1985).

Intracellular recordings from HS- and VS-cells reveal that these neurons respond mainly with graded changes of membrane potential although they are capable of generating action potentials (Dvorak et al. 1975, Hengstenberg 1977, Hausen 1984).

Both, HS- and VS-neurons respond bidirectionally to visual motions in the ipsilateral hemisphere: VS-cells are excited by vertical motion (but see below). HS-cells are excited by vertical motion and inhibited by the reverse motion; they are additionally excited by contralateral back-to-front motion. The responses increase with pattern size are invariant against contrast polarity and depend upon the speed of motion much like different optomotor responses (Hausen 1993, Hengstenberg 1982, Egelhaaf and Borst 1993). These findings suggest that HS- and VS-neurons monitor self-motions of the fly and may play a. crucial role in the control of posture and locomotion. This conjecture was corroborated by different experiments made to eliminate HS- and VS-neurons:

(1) Transsection of the axons on one side and subsequent study of turning responses showed that pattern motion towards the operated side did no more evoke an optomotor following response whereas motion towards the control side released a normal response as in intact animals (Hausen and Wehrhahn 1983).

(2) Laser ablation of the precursor cells of HS- and VS-neurons in the larval stage of *Musca* produced adult flies lacking these neurons on the operated side and showing severe deficits in turning responses with wide-field motion towards the operated side (Geiger and Nässel 1982).

(3) *Drosophila* mutants (omb' rbs) which fall to make HS- and VS-neurons during metamorphosis show none of the characteristic responses to wide-field pattern motion

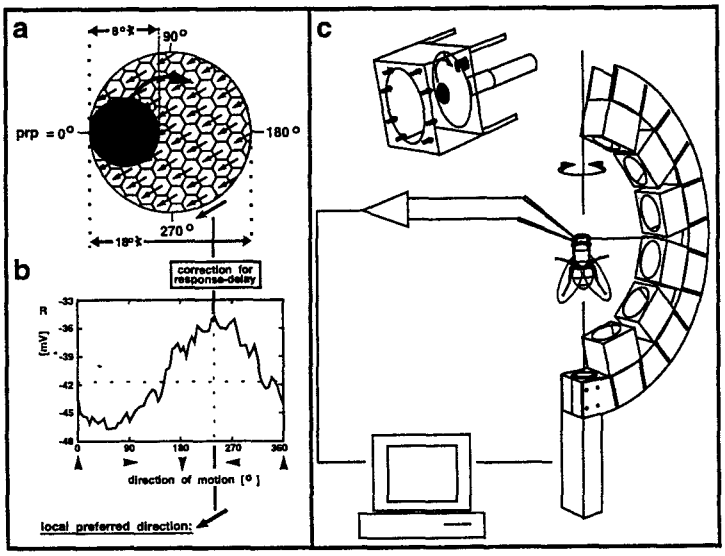

Fig. 4:
Mapping of local motion tuning. (**a**) Circulating dot stimulus passing quickly through all directions of motion. (**b**) Local motion tuning curve, specifying directional preference (center of gravity) and local motion sensitivity (modulation) of the response. (**c**) Pivoted stimulus meridian, carrying six "dot-circulators" allows to map local motion responses almost everywhere in visual space.

(Heisenberg and Wolf 1984, Pflugfelder and Heisenberg 1994, Hengstenberg 1991). HS- and VS-neurons are obviously important for the sensation and control of selfmotions but the specific role of single neurons could not be revealed by these experiments.

6. Functional specification of single tangential neurons

The characteristic abilities of single neurons are revealed by mapping their motion sensitivity and directional preference throughout the receptive field (Hengstenberg 1981). Local motion stimuli are presented at many places in the visual surround and cell responses are recorded intracellularly. Neurons are unambiguously identified by fluorescent dye injection and 3D-reconstructions from serial sections (Hengstenberg et al. 1983).
Local preferred direction and motion sensitivity are measured quickly and accurately by a specifically developed stimulus (Fig. 4a): a single black dot (8°-) is moved on a circular path (10°-) at constant speed (2cps) somewhere in the visual field. Whenever the direction of dot motion coincides with the preferred direction of motion detectors, looking at that spot and feeding into the recorded neuron, the response becomes maximal. At the opposite position of the dot path, the response becomes minimal. Reversing the direction of dot motion allows, by comparison of responses, to eliminate the effects of dot location and of the response delay. One such local motion tuning curve (Fig. 4b) can be measured within 5 seconds; its center of gravity gives the local preferred direction and its modulation is a measure of local motion sensitivity (Menzel and Hengstenberg 1991, Krapp and Hengstenberg 1992).
Figure 4c shows a stimulator with six "dot-circulators" (Fig. 4c, inset) that can be activated singly, in sequence or simultaneously in defined phase relationships. The devices are mounted on a meridian that can be rotated about the vertical. Thereby local motion stimuli can be almost applied everywhere in the fly's visual field (Krapp and Hengstenberg 1993).
Figure 5 shows motion response maps and camera lucida drawings of three representative VS-neurons. The dendritic arborizations in the right lobula plate are shown in frontal aspect to facilitate comparisons with the response maps. The retinotopy of the lobula plate is illustrated by letters, outside of the neuropil, designating locations in the visual field and in the motion response maps (d = dorsal, v = ventral, f = frontal, c = caudal).
The response maps are Mercator-projections of the ipsilateral hemisphere. Measurements were taken at the positions marked by circles. The local motion responses are represented as arrows originating at the site of measurement. The direction of the arrow indicates the local preferred direction and its length indicates the motion sensitivity, normalized to the maximum response. At positions where no measurements had been made, interpolated arrows were filled in. The Mercator- projection is veridical for angles relative to the circles of longitude and latitude. For surface area, however, it is non-veridical: it over-represents area with increasing elevation. Therefore the dorsal and ventral areas of response maps are overemphasized and must be interpreted with consideration.

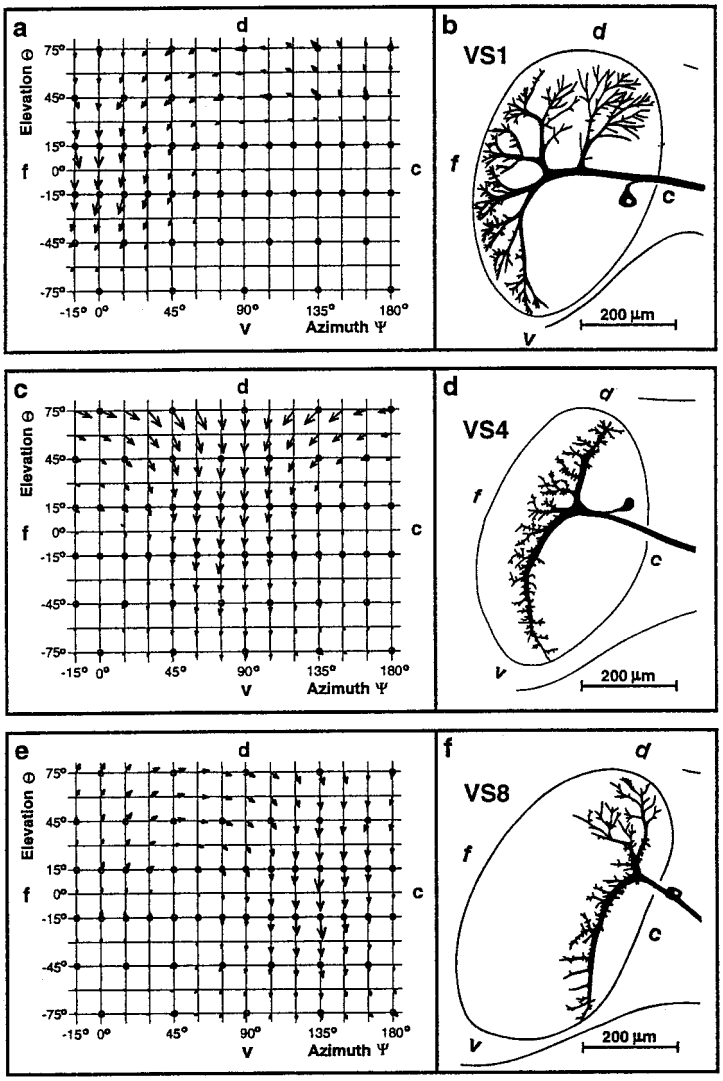

Fig. 5:
Dendritic structures and motion response maps of different VS-neurons. Mercator projection of the ipsilateral hemisphere. Stimulus positions are marked by small circles. Arrows indicate the local preferred direction. The length of the arrows represents local sensitivity, normalized for the maximum response. Arrows without circles are interpolated. Note that each of the three VS-neurons is maximally excited by a distinct rotation about a horizontal axis.

The VS1-neuron (Fig. 5b) occupies frontal and dorsal areas of the lobula plate; frontal branches are situated in the posterior layer associated with vertical motions and the medio-dorsal branch lies in the anterior layer associated with horizontal motions (cf section 5; Hengstenberg and Hengstenberg 1980). The response map of VS1 (Fig. 5a) shows a high sensitivity to downward motion in frontal parts of the visual field, responses to back-to-front motion in dorso-lateral parts and weak but significant responses to upward motion in the dorso-caudal region. This distribution of motion sensitivity and directional preference agrees very well with the notions about the general architecture of the lobula plate (section 5; Hausen 1993) and the detailed structure of this neuron. Apparently, VS1 is strongly excited by counterclockwise pattern rotation about the transverse axis ($\Psi = 90°$, $\Theta = 0°$) i.e. during upward pitch turn of the fly.

The VS4-neuron (Fig. 5d) occupies a strip-like area of the lobula plate, extending from the dorsal to the ventral margin of the lobula plate, centered near the middle of the fronto-caudal extent, and the dendrites are located in the posterior layer, associated with vertical motions. The response map of VS4 (Fig. 5c) shows a belt of high sensitivity to downward motion in the lateral part of the visual field ($60° < \Psi < 105°$ at $0 = 0°$). The consistency of directional tuning along the meridian of maximal sensitivity ($75° < \Theta < 90°$) is quite amazing. In the dorsal half of the field the overall motion sensitivity is larger than in the ventral half. The response pattern widens in angular extent with increasing elevation and the local preferred directions turn increasingly towards the horizontal: a front-to-back component is added in the fronto-dorsal quadrant ($\Psi < 90°$; $\Theta > 0°$) and a back to front component in the caudo-dorsal quadrant $\Psi > 90°$; $\Theta > 0°$). This motion response pattern suggests that VS4 is maximally excited when the fly rolls to the left (compare Fig. 1c, middle).

VS8 (Fig. 5f) occupies more caudal areas of the lobula plate with a strip-like ventral dendrite situated in the posterior layer and a dorsal fan-shaped arborization situated in a more anterior layer. The response map of VS8 (Fig. 5e) reveals a belt of downward motion sensitivity along a caudo-lateral meridian ($\Psi = 135°$). Front-to-back motions in dorso-lateral areas and even upward motions in dorso-frontal parts of the visual field contribute to the response of the cell. lt seems that VS8 is maximally excited if the fly turns downwards about an oblique horizontal axis originating at $\Psi = 45°$, $\Theta = -15°$.

The response maps shown in Fig. 5 and those of the other VS-cells demonstrate that these neurons are vigorously excited by rotations of the fly about different horizontal axes. It should be stressed, however, that the motion response patterns of VS-neurons are not exact neural representations of optical flow patterns. In Fig. 6 are compared the measured motion response pattern of the neuron VS6 (Fig. 6a) and the calculated optic flow pattern for a roll turn to the left (Fig. 6b). It is obvious that optic flow as shown in Fig. 6b would maximally excite VS6, but although the directions of roll flow are also well represented in the ventral part of the receptive field, the motion sensitivity in this area is much reduced. lt is not clear at present whether VS-neurons are meant to extract exclusively rotatory components of optic flow and are therefore ventrally insensitive, where translatory flow prevails during locomotion (Collett 1980, Preiss 1991).

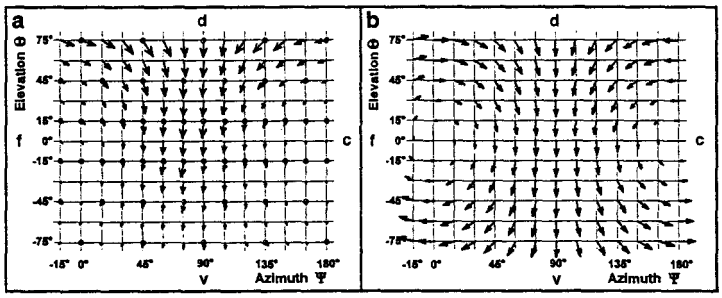

Fig. 6:
Motion response pattern compared to optic flow pattern. (**a**) ipsilateral map of local motion responses of VS6 (**b**) computed optic flow pattern for a roll turn to the left. Note the striking similarity in the direction of flow but the reduced sensitivity in the ventral part of the response field of VS6.

Alternatively the response profiles of VS-neurons could be exquisitely tuned to a mixture of rotatory and translatory components that may occur during flight or may be best suited for motor control.

7. Discrimination of rotations from translations

A local motion signal does not indicate whether it has been caused by a translation or a rotation of the fly (see section 4). Therefore such signals cannot be used directly for motor control. Signals from diametrically opposite areas of the visual field have the same sign in case of translation and opposite signs in case of rotations. Hence best discrimination is achieved by convergence of the appropriate signals from the corresponding areas of the visual field (Götz 1972, Kern et al. 1993).
HS-neurons are known to receive input from the contralateral eye which makes them most sensitive to yaw rotations (Hausen 1984, .1993). Figure 7 shows a receptive field map of the equatorial horizontal neuron (HSE) in the right lobula plate. On the ipsilateral side (Fig. 7; $\Psi < 0°$) the cell responds to horizontal front-to-back motions within an equatorial zone ($-45° < \Theta < 45°$) and over the whole azimuth range of the eye ($0° < \Psi < 180°$). This corresponds nicely with the extent of the dendritic arborization of HSE in the lobula plate (Fig. 3b). Stimuli in the contralateral hemisphere (Fig. 7; $\Psi < 0°$) are effective in the mirror-symmetrical part of the visual field. The preferred directions are tilted fronto-ventrally but there is a considerable sensitivity to horizontal back-to-front motions.
Selectivity for rotations can be further enhanced when rotatory motion is sensed in a region of the visual field where rotation components are large and translation components are small (Collett 1980, Junger and Dahmen 1992). For a flying insect, and yaw rotations, there are two such exceptional areas: one straight ahead and the other straight behind the fly, but there it cannot see very well.
Do HS-neurons make use of this topological asset? In Fig. 7a the length of the arrows indicating the local motion sensitivities is scaled logarithmically to show the homogeneous orientation of preferred directions even in areas with low sensitivity. When this accentuation is not made and the responses are plotted linearly (Fig. 7b) it becomes obvious that HSE is maximally motion-sensitive in straight ahead direction ($\Psi = 0°$, $\Theta = -15°$) and that a comparatively small area of 30° x 30° , centered around the gaze axis ($\Psi = 0°$, $\Theta = 0°$), dominates the overall response of HSE.
The huge size of the receptive field of the HSE-neuron, the prevailing sensitivity to horizontal motion, the appropriate convergence of signals from the ipsi- and contralateral eye and the sensitivity maximum straight ahead make this neuron most sensitive to yaw turns of the fly to the left. None of there processes acts as a logical discriminator. All add up to increase gradually the neuron's specificity for one kind of self-motion.
Similar mappings are presently being made for the other two HS-neurons (HSN, HSS) for the ten VS-neurons (Krapp in prep.) and other tangential neurons that can be recorded long enough. The neurons VS4-VS6 which respond to downward motion in the lateral part of the ipsilateral hemisphere (Figs. 5, 6) could be complemented by contralateral downward motion resulting in a preference for lift translations or by

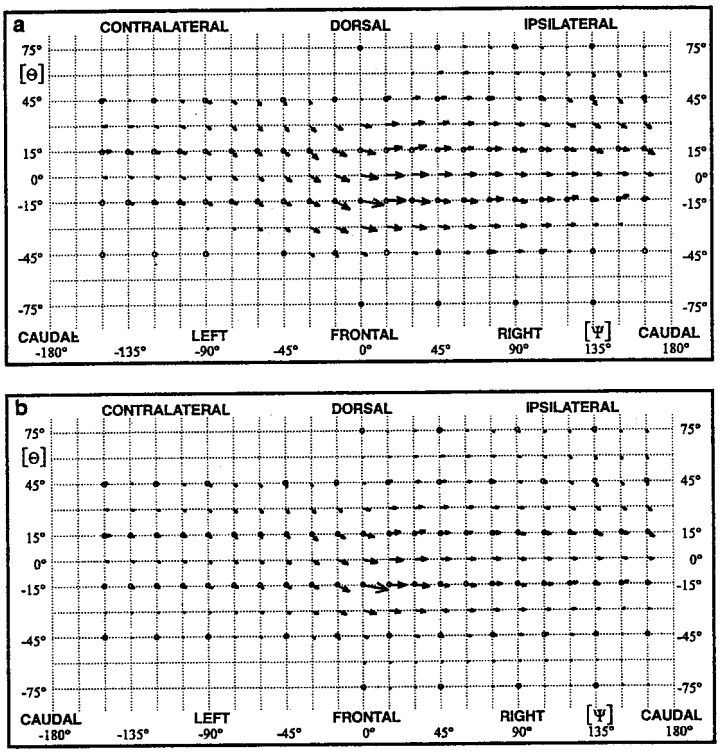

Fig. 7:
Binocular motion response field of the equatorial horizontal neuron HSE. In the contralateral hemisphere stimulation was restricted to elevations of $-45° < \Theta < 45°$ for technical reasons. (**a**) Response amplitudes scaled logarithmically to accentuate the distribution of preferred directions even in areas of low motion sensitivity. (**b**) Response amplitudes scaled linearly to show the region of high sensitivity around the straight ahead direction ($\psi = 0°$, $\theta = 0°$). Note the gigantic size of the receptive field, its mirror-symmetrical extent in the two hemispheres, the essentially horizontal directions (but see text) and the sensitivity maximum straight ahead. This combination of properties makes the HSE-neuron in the right lobula plate most sensitive to yaw turns to the left.

contralateral upward motion to yield a specificity for roll rotations. VS1-VS3 which respond to downward motion along a frontal meridian (Krapp and Hengstenberg 1994) could be supplemented by upward motion along the posterior meridian to create a preference for upward pitch rotations. None of these interactions has to be made necessarily on HS- or VS-neurons. That could equally take place an dendrites of descending neurons. If convergence does take place on tangential neurons of the lobula plate, as in case of HSE (Fig. 7), the specific role of that neuron for the sensation of selfmotions and its possible role in locomotor control can be stated more clearly.

Conclusions

The functional organization of wide-field motion-sensitive neurons in the fly can be revealed by mapping sequentially the responses to local motion stimuli at many places in the receptive field. The motion response map of a certain neuron shows the particular seif motion of the fly by which that neuron would be maximally excited.
The experiments show further that the high specificity is achieved gradually by a combination of different mechanisms: (1) selection of small-field motion signals from specific areas of the visual field, (2) selection of a signal with an appropriate preferred direction from the ensemble of local signals, (3) weighting of the local signals according to the desired sensitivity distribution, (4) wide-field spatial integration and (5) convergence of wide-field signals from ipsi- and contralateral hemispheres.
The functional representations of different self-motions in single tangential neurons can be conveniently used by the fly for the control of posture and locomotion.

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