Robustness of the tuning of fly visual interneurons to rotatory optic flow

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ABSTRACT

The sophisticated receptive field organization of motion-sensitive tangential cells in the visual system of the blowfly Calliphora vicina matches the structure of particular optic flow fields. Hypotheses on the tuning of particular tangential cells to rotatory self-motion are based on local motion measurements. So far, tangential cells have never been tested with global optic flow stimuli. Therefore, we measured the responses of an identifiable neuron, the V1 tangential cell, to wide-field motion stimuli mimicking optic flow fields similar to those the fly encounters during particular self-motions. The stimuli were generated by a ‘planetarium-projector’, casting a pattern of moving light dots on a large spherical projection screen. We determined the tuning curves of the V1-cell to optic flow fields as induced by the animal during 1.) rotation about horizontally aligned body axes, 2.) upward/downward translation, and 3.) a combination of both components. We found that the V1-cell does not respond as specifically to self-rotations as had been concluded from its receptive field organization. The neuron responds strongly to upward translation and its tuning to rotations is much coarser than expected. The discrepancies between the responses to global optic flow and the predictions based on the receptive field organization are likely due to nonlinear integration properties of tangential neurons. Response parameters like orientation, shape and width of the tuning curve are largely unaffected by changes in rotation velocity or a superposition of rotational and translational optic flow.
INTRODUCTION

To perform adequate motor actions a mobile observer requires information about both its self-motion and the 3D layout of the environment. Visually orientating animals, including man, obtain such information by exploiting optic flow induced during self-motion (Gibson 1979, Koenderink and van Doorn 1987, Warren et al. 2001). The global structure of optic flow depends on the performed self-motion: rotation about the longitudinal body axis, for instance, causes optic flow that is directed downward in the lateral visual field of one eye but upward in the lateral field of the other (Fig. 1A). During upward translation the optic flow in the whole visual field is directed downward (Fig. 1B). While the global structure of rotatory and translatory flow fields can be distinguished quite easily, there may be ambiguities at a local scale (cf. Fig. 1A/B, shaded squares in left part of middle panels). Obtaining unambiguous information requires neuronal mechanisms that combine local motion information from large parts of the visual field in an appropriate way.

In vertebrates and invertebrates, neurons responding to optic flow have been found to have large receptive fields (e.g. Leonard et al. 1988, Ibbotson 1991, Wicklein and Varju 1999, Wylie and Frost 1999b). In the fly visual system about 50-60 individually identifiable tangential cells integrate output signals of many local motion sensitive elements from large parts of the receptive field (reviews: Hausen and Egelhaaf 1989; Egelhaaf et al. 2002; Borst and Haag 2002). The local preferred directions within the receptive field of each tangential cell are not homogeneously oriented but match the orientation of velocity vectors in a particular optic flow field (review: Krapp 2000). The local preferred directions within the receptive field of tangential cells belonging to the vertical system (VS-cells; Hengstenberg et
al. 1982), for instance, match the orientation of velocity vectors in optic flow fields induced during self-rotations of the animal. Their receptive field organization was concluded to be adapted to sense self-rotations about horizontally aligned body axes (Krapp and Hengstenberg 1996). This is also true for the tangential cell investigated in this study, the V1-cell, although it does not receive input directly from local motion sensitive elements, but from three VS-cells (Kurtz et al. 2001; Warzecha et al. 2003). Thus its receptive field structure resembles, as the receptive fields of VS-cells, the structure of a rotatory rather than a translatory flow field (Fig. 1C). Accordingly, the V1-cell can be expected to be tuned to a rotation of the fly about a horizontally aligned axis. These hypotheses on the tuning of tangential cells to particular types of self-motion are based on local motion measurements. Verification of the predictions based on the local responses necessitates a stimulus covering large parts of the receptive field and approximating the local structures of an optic flow field.

In most studies investigating the response characteristics of optic flow neurons, simplifications have been made concerning the extent and/or the fine structure of optic flow stimuli. Relatively simple grating or dot patterns have been generated on displays, by rotating drums or by banks of light emitting diodes (e.g. fly: Hausen 1982; bee: Ibbotson et al. 1991, dragonfly: Olberg 1981; locust: Baader 1991; crab: Johnson et al. 2002; cat: Sherk et al. 1995, monkey: Duffy and Wurtz 1991). In the present study we used a ‘planetarium-projector’ generating a pattern of moving light dots which more closely approximates realistic global optic flow. Although similar devices have been used in electrophysiological experiments on rabbits and pigeons (Simpson et al. 1988, Wylie et al. 1998), for technical reasons it was not possible, so far, to superimpose rotation and translation induced optic flow. Our ‘planetarium
projector’ overcomes these limitations in that it allows us to combine translatory and rotatory optic flow.

With this stimulus device we measured for the first time the activities of a particular fly tangential cell, the V1-cell, to realistic wide-field optic flow induced during different self-rotations and self-translations of the animal and a combination of both. We tested the specificity of the V1-cell to its preferred self-motion and how well the tuning of the cell can be predicted on the basis of its local response properties.
METHODS

PREPARATION AND ELECTROPHYSIOLOGY

All experiments were performed on 1 to 3 day old female blowflies (*Calliphora vicina*) bred in our laboratory culture. To avoid inbreeding the culture is refreshed several times a year with animals, which were caught in the wild. Before dissection, the animals were briefly anaesthetized with CO$_2$. Legs and wings were removed and the animal was fixed to a holder. Wounds were closed with wax to prevent the animal from desiccation. The head was aligned by adjusting it according to the symmetrical deep pseudopupil (Franceschini 1975) in the frontal region of both eyes. To access the lobula plate the head capsule was opened from behind and fat tissue, air sacs and tracheae were removed. By adding saline solution (chemical composition: e.g. Karmeier et al. 2001), the nervous tissue was kept moist. All experiments were performed at a temperature between 24 and 27°C.

The V1-cell can be identified unambiguously on the basis of its sensitivity to vertical downward motion in the visual field contralateral to the neuron’s output ramifications in the lobula plate (Hausen 1976, Krapp and Hengstenberg 1997). From the output ramifications we recorded extracellularly the spike activity of V1 using tungsten electrodes. The electrode tips were sharpened electrolytically and insulated with varnish resulting in impedances between 2 and 8 MΩ. A tip-broken glass capillary was used as ground electrode and to supply the brain with saline solution. Recorded signals were processed by standard electrophysiological equipment and were sampled into a PC at a rate of 10kHz using a Data Translation board (DT 3001). Programs
for data acquisition were written in HP VEE (Hewlett-Packard Co.). All data were evaluated offline using MATLAB (The Mathworks, Natick, MA).

**VISUAL STIMULATION**

Optic flow stimuli were generated by a planetarium projector (Fig. 2A) comparable to those used in electrophysiological experiments on rabbits and pigeons (Simpson et al. 1988, Wylie and Frost 1993). Our projector consisted of a small, hollow metal globe (diameter: 120 mm), the surface of which was drilled with numerous small holes (30 within a solid angle of 90°). A small halogen light source was positioned in its center, casting a field of dots on the wall of a large, spherical projection screen (diameter: 1.2 m). The projected light dots were patches of non-homogenous light with a mean luminance of 30 cd/m². Their size ranged from 1.9° x 3.8° to 3.8° x 3.8° as seen from the animal. Step motors (SIG Positec BERGERLAHR, Phytron) rotated the metal globe about three axes of a Cartesian coordinate-systems. One horizontal axis allowed for continuous rotation. About the other two axes periodic rotatory movements could be performed in the range of about ±15°. Rotations of the metal globe resulted in coherently moving light patterns on the projection screen, mimicking rotatory optic flow. At the same time the light source inside the metal globe could be moved along three axes (up/down, right/left, forward/backward). The wide-field stimulus covered the entire dorsal-equatorial visual field except a small dorsal area of 22.6° in diameter and a caudal area directly behind the animal. Relative to the eye equator the caudal area amounted to ±30° and ±35° in its horizontal and vertical extend, respectively. The fly’s field of view was extended ventrally down to an elevation of –45° and for a range of approximately 120° along the azimuth (extended visible section; Fig. 2D). The area in which no visual motion was presented is linked to the horizontal rotation axis of
the device and therefore changed its azimuth as different axes of rotation are tested. The maximum speed with which we could move the light source within the metal globe mimicked the animal translating at 0.35 m/s in an environment where the distance between its eyes and any visual contrasts amounted to 1 m. This corresponded to an angular velocity of 39°/s at the flow field equator. Rotational velocities ranged from 39°/s to 1223°/s.

**DETERMINING TUNING CURVES**

The fly was positioned in the center of the projection sphere, slightly above the metal globe as indicated in Fig. 2A. Rotatory tuning curves were obtained by recording the neuron’s activity induced during simulated rotations about horizontal axes spaced at 45°. The curved arrows in Fig. 2A indicate the direction of simulated self-rotation of the fly. Flow fields induced by self-rotations in opposite directions (e.g. 0° and 180°) were generated by rotations of the metal globe in clockwise and counterclockwise direction, respectively. Therefore, to determine the tuning curves we effectively rotated the metal globe about 5 different axes of the planetarium projector. The stimulus consisted of 500 ms of motion in one direction, a stationary phase of 5 seconds, followed by 500 ms of motion in the opposite direction. Average responses for each animal were obtained from 2 motion sweeps in either direction. We defined the responses to motion by subtracting the mean spike rate recorded within 500 ms before stimulus onset, from the mean spike rate measured within a 100 ms time window during motion. To account for the time dependence of the responses we determined the activity for two time windows (Fig. 2B, \( t_1 \) and \( t_2 \), starting 40 ms and 200 ms after stimulus onset, respectively. The starting time of the second window was constrained by the limited duration of the stimulus for combined motion. The average responses obtained during \( t_1 \) are plotted as a function of the orientation of the rotation
axis (Fig. 2C). To facilitate the quantitative analysis of the experimental data we applied a least square algorithm to fit a truncated cosine function to each of the measured tuning curves. The fits were based on four parameters; i.e. phase shift, amplitude, cut-off and offset. From the fits we obtained three parameters, which characterize the tuning of the neuron: 1.) the ‘preferred axis of rotation’ corresponds to the azimuth resulting in the maximum in the fitted tuning curve. 2.) As the maximal neuronal response we consider the maximum of the fit, and 3.) we define the width of the tuning curve by its width at half maximum height of the fit. We additionally calculated a sensitivity index (for definition, see Fig. 2C).

CONTROL EXPERIMENTS

As a result of the design of the stimulus device the projected optic flow field was restricted in size (cf. Fig. 2A & 2D). Additionally, a change of the projector orientation results in a change of the position of the extended visible section. To test whether these restrictions affect the tuning curves, we measured two tuning curves each of which was based on 5 different orientations of the projector. For the first curve (curve1 in Fig. 2E), the projector was oriented in a way so that the extended visible section of the flow field was projected into the most sensitive part of the neuron’s receptive field (extended visible section centered at -135°, -90°, -45°, 0° and 45°). The second curve (curve2 in Fig. 2E) was obtained by applying the opposite orientations (extended visible section centered at 45°, 90°, 135°, 180° and -135°). Although the resulting tuning curves show differences in the respective activity, both, the ‘preferred axis’ and the width are similar. The positions of the projector used to derive the first curve were used in subsequent experiments.
The local preferred directions and local motion sensitivities were determined by using a stimulus procedure introduced by Krapp and Hengstenberg (1997). In short, a small black dot (diameter: 7.6°) was moved at constant speed on a circular path (diameter: 10.4°), thus covering only a small part of the visual field. When the instantaneous direction of dot motion coincided with the local preferred direction, the response was maximal. The local motion sensitivity is given by the difference between the average response to motion in an interval of ±45° relative to local preferred direction and the average response to motion in an interval of equal size relative to the null direction; i.e. 180° apart from the local preferred direction. To quantify the similarity between the receptive field and the optic flow field, both fields were normalized with respect to the maximum local motion sensitivity or the maximum local velocity vector, respectively. The value obtained by projecting the optic flow field into the response field of the neuron indicates the similarity between both structures. To account for the restricted size of the stimulus local scalar products of only those positions in the visual field were included in the integration, which were visible to the fly upon stimulation with the ‘planetarium projector’. Distortions due to the Mercator-projection (see legend of Fig. 1) were compensated for by appropriate weighting of the local scalar products. Contributions from the left and right visual field were summed separately. To account for the rectification caused by spike generation the contributions were set to zero if they became negative. Contributions from either side were added. Tuning curve parameters and the sensitivity index were derived directly from the calculated curves.
RESULTS

To examine the tuning of the fly tangential cell V1 to rotatory self-motion we measured its activities to flow fields mimicking rotations of the animal about different horizontally aligned body axes. The preferred axis of rotation, the width at half modulation height of the tuning curve and the sensitivity index were derived from fits to the experimentally obtained tuning curves. These parameters were used to quantify the tuning while the angular velocity was varied or translatory optic flow was added to the rotatory flow. Unless otherwise stated the data represent the mean and standard deviation obtained from 5 animals. The measured tuning curve parameters were compared to those obtained from the tuning curves calculated from local measurements.

TUNING TO PURE ROTATION

The dependence of the V1 response on the axis of rotation was tested for a wide range of velocities (39°/s, 123°/s, 390°/s, and 1223°/s). Within both an early and a later time window of the response the resulting tuning curves coincide largely. They have a peak in the range between approximately 55° and 65° in azimuth (Fig.3, response t1 and t2; Table 1). On both sides of the peak the sensitivity decreases. The width of the tuning curves at half-maximal amplitude is relatively broad (Table 1). Although the rotation velocity shows only little effect on the overall shape of the tuning curves, the response amplitudes in both time windows depend on velocity as has been described for other tangential cells before (Hausen 1982, Maddess and Laughlin 1985, Egelhaaf and Borst 1989).

To compare the tuning curves obtained with wide-field optic flow with the prediction based on the local preferred directions and local motion sensitivities within the receptive field of the V1-
cell, the experimental data were fitted by a truncated cosine function (see Fig. 4 for the fit for a velocity of 123°/s). The overall shape of the two curves is similar and the curves overlap greatly. However, three differences between the curves are obvious: 1.) the ‘preferred axis of rotation’ of the predicted and the measured curve differ by ~20°. 2.) The spike rate measured with the wide-field stimulus is never reduced to the resting level. 3.) The tuning curve measured with wide-field motion is broader than predicted. These findings are corroborated by experiments done on another tangential cell (V2, N=1). The V2-cell receives retinotopic input and conveys motion information via a thin axon to the contralateral lobula plate where it forms output ramifications (Hausen 1984). V2 is most sensitive to upward motion in the lateral visual field and is suggested to sense roll rotations. The differences between the predicted and the measured tuning curves of the V2-cell are basically the same as those described for the V1-cell (Fig. 4, inset).

RESPONSE TO PURE LIFT TRANSLATION

The response field of the V1-cell resembles the structure of a flow field induced by a rotation about the neurons ‘preferred axis’. However, the vectors in an optic flow field induced during upward (positive) lift-translation match the local preferred directions in the V1-response field around an azimuth of –30° (Fig. 1 B). Accordingly, some activity is predicted for a positive lift translation: it amounts to approximately 43% of that predicted for rotations about the ‘preferred axis’ of the V1-cell (Fig. 5). The predicted specificity for rotatory optic flow is not found in the measured neuronal responses. The activities to a lift-translation inducing maximal angular displacements of 39°/s amount to 92% of those evoked by a rotation about the ‘preferred axis’ at 39°/s for both time windows.
TUNING TO ROTATION AND SUPERIMPOSED LIFT TRANSLATION

So far, tuning to optic flow has only been characterized for purely rotatory or translatory optic flow. In behavioral situations both motion components are usually superimposed. The structure of flow fields induced during a pure rotation or during combined rotational and translational movements may differ considerably. Because of the V1-cell’s sensitivity to positive lift translation we chose to superimpose rotations with positive and negative lift-translations. Both stimuli induce maximum angular displacements of the pattern of $39^\circ$/s, corresponding to a rotation of $39^\circ$/s and a translation at 0.35m/s. The superimposed lift-translation has the strongest effect on the rotation flow field in the equator of the visual field, where the downward motion component is doubled or cancelled out, respectively (Fig. 6A). The predicted activities reflect this effect of the superimposed lift-translations: the activity increases when a positive lift and decreases when a negative lift is superimposed. The ‘preferred axes of rotation’, the width and the overall shape of the predicted curves are hardly affected (Fig. 6B, upper panel).

The effect of a superimposed lift-translation is much stronger for the measured activities: compared to the tuning curve obtained for pure rotation, the activity during rotations combined with a positive lift-translation is stronger for most axes of rotation, particularly for those axes where there are only small responses to a pure rotation (Fig. 6B, lower panel). Despite these differences in the shape of the tuning curves the ‘preferred axes of rotation’ and the width of the curves are only slightly affected. The combination of rotations and a negative lift-translation results in almost negligible responses for all axes of rotation. We were not able to compute the tuning curve parameters for this motion combination.
By superimposing a lift-translation of 0.35 m/s on rotations of all tested angular velocities (39°/s, 123°/s, 390°/s, 1223°/s), we changed the ratio of rotation:translation from 1:1 to 32:1. The shape of the tuning curves is relatively invariant when the rotation velocity is increased. The maximum response amplitude elicited by a rotation about the cell’s preferred axis depends on the rotation velocity but is hardly affected by a superimposed lift-translation (Fig. 7D-7F). The differences in the widths of the curves are relatively small compared to the overall tuning widths of the cell. Table 1 summarizes the tuning curve parameters for all stimulus conditions.
DISCUSSION

To gain information about self-motion from optic flow, tangential cells in the fly visual system have to pool the signals of many retinotopic inputs from extended parts of the visual field. Experiments using local motion stimuli indicate that the receptive field organization of some TCs is adapted to this task: the distribution of local preferred directions matches the distribution of velocity vectors in optic flow fields induced during certain self-motions (Franz and Krapp 2000, review: Krapp 2000). Predictions based on the local motion measurements were tested here for the first time with realistic optic flow generated by a novel planetarium-like visual stimulator.

In the following we will discuss 1.) the differences between the measured and predicted specificity of the V1-cell to its preferred self-motion and possible reasons for the differences and 2.) the tuning characteristics of the V1-cell in the context of encoding of self-motion from optic flow.

PREDICTION OF NEURONAL ACTIVITIES FROM LOCAL RESPONSE PROPERTIES

The tuning curves predicted on the basis of local motion measurements do not agree in all aspects with the experimentally determined tuning curves. The predictions capture qualitatively the general shape of the experimental tuning curves (Fig. 4) and the overall effect of a superimposed lift translation (Fig. 6). The difference between the measured and predicted ‘preferred axis of rotation’ is likely to be a consequence of the different set-ups in which the respective experiments were performed. However, there is a marked difference in the predicted and measured specificity to a rotation about the neuron’s ‘preferred axis’: the measured tuning curve is broader (Fig. 4), the response to a rotation about the neuron’s ‘preferred axis’ and to a
positive lift-translation are in the same range (Fig. 5), and the impact of a superimposed lift translation is stronger than predicted (Figs. 6 and 7). These differences are most likely due to linear integration of local motion contributions in our model, which we tried to keep as simple as possible. Some nonlinearities known for fly tangential cells concern the computation of motion by local motion detectors and the spatial pooling of the motion detectors’ outputs by the tangential cells. 1.) The output of the local motion detectors is not proportional to velocity. It first increases with increasing velocity, reaches an optimum and then decreases again. It also depends on pattern properties like spatial wavelength and contrast (review: Egelhaaf and Borst 1993). Even the time course of a summed array of local motion detectors is proportional to pattern velocity only for relatively slow velocity changes (Egelhaaf and Reichardt 1987; Egelhaaf and Borst 1993). 2.) The output of tangential cells is proportional to the number of activated local motion detectors only for small numbers. For greater numbers of inputs the neurons show a ‘saturation-like’ characteristic (Borst et al. 1995, Hausen 1982, Hengstenberg 1982). This nonlinearity does not represent an output saturation at the level of TCs, but has been interpreted as a ‘gain control’ mechanism because the level at which the response ‘saturates’ depends on pattern velocity (Borst et al. 1995, Single et al. 1997; review: Egelhaaf and Warzecha 1999).

As a consequence of these nonlinearities the V1-cell is likely to be activated maximally not only during a rotation about its ‘preferred axis’, but also if the structure of the optic flow field does not perfectly match the structure of the receptive field. In contrast, the activity predicted from the local response properties becomes maximal only if the optic flow field perfectly matches the structure of the receptive field. The predicted activities are smaller if the optic flow field does not perfectly match the distribution of local preferred directions. It is most likely that the nonlinear integration properties of the tangential cells result in the measured lack of
specificity to rotatory self-motion, i.e. the broad tuning curves, the strong response to a positive lift-translation and the stronger impact of superimposed translations.

In conclusion, the receptive field organization, as determined with local motion stimuli, is a good indicator of the preferred self-motion of a neuron but does not provide appropriate information about the neuron’s specificity for its preferred self-motion. A similarly small specificity to a neuron’s preferred self-motion was found in different studies in invertebrates and vertebrates that analyze specificity by characterizing the cells with either, rotatory and translatory optic flow stimuli (e.g. Hausen 1981, Kern et al. 2001, Horstmann et al. 2000, Ibbotson and Goodman 1990, Kern 1998, Duffy and Wurtz 1991, Tanaka et al. 1989). Studies where a stimulus device was chosen that could generate either translatory or rotatory optic flow could not provide appropriate information about the specificity to the preferred self-motion (e.g. Wylie and Frost 1999a, Simpson et al. 1988, Tanaka and Saito 1989).

TUNING CHARACTERISTICS OF THE V1-CELL IN THE CONTEXT OF ENCODING SELF-MOTION FROM OPTIC FLOW

To characterize the tuning of the V1-cell to its preferred self-motion we have applied flow field combinations that are critical for the neuron rather than visual stimuli as encountered by the animal during every-day flight. The fly may hardly encounter a pure lift-translation and some of the generated rotation velocities are relatively slow compared to the velocities in normal flight situations (Schilstra and Hateren 1999, Hateren and Schilstra 1999). Furthermore, we simulated optic flow patterns within an environment assuming a uniform distance distribution. Nevertheless this systematic analysis helps to understand principles of encoding self-motion in the fly visual system. The findings from this study clearly show that a given activity level of the neuron does
not provide unambiguous information about the stimulus. The magnitude of the cells response
depends on rotation velocity (Fig. 3) and is in the same range for pure upward lift and for a
rotation about the ‘preferred axis’ (Fig. 5). Thus the same activity level in the V1-cell can be
elicited, for instance, by a slow rotation about the ‘preferred axis’, by a fast rotation about a non-
optimal axis or by a translational self-motion. Variability in the neuronal response even further
limits the precision with which self-motion can be detected (e.g. Warzecha and Egelhaaf 1999).

These response ambiguities can be resolved, at least partly, if we take into account that self-
motion information is conveyed by a population of tangential cells each responding best to a
particular self-motion. A rotation about a particular axis induces a specific pattern of neuronal
population activity. A change in rotation velocity or translatory motion superimposed on the
rotation would have a similar effect on the activities of all neurons in the ensemble. The relative
activities of the neurons are likely to be less affected. If the tuning width or the ‘preferred axis of
rotation’ of the neurons in the ensemble would depend on rotation velocity or on superimposed
translation, it would be much more difficult to detect the axis of rotation from the pattern of
population activity. Therefore, an invariant tuning width and ‘preferred axis of rotation’ seem to
be advantageous for a robust neuronal representation of self-motion information.
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**REFERENCE LIST**


FIGURES

FIGURE 1

A/ Rotation

B/ Translation

C/ Response field V1

Self-motion induced optic flow and response field of the V1-cell. Optic flow induced during a rotation about a horizontal (A), or a upward translation along the vertical body axis (B). Flow fields are illustrated in spherical coordinates of the visual field (left) and their projections onto Mercator maps (right). Positions in the Mercator map are specified by the angles of azimuth (\(\Psi\)) and elevation (\(\Theta\)); \(\Psi<0\) denotes left, \(\Psi>0\) the right visual hemisphere (f=frontal, c=caudal, d=dorsal, v=ventral). Each single arrow indicates the direction and velocity of the respective local image shift. Note that, due to the Mercator projection, the dorsal and ventral parts of the spherical visual field are highly overemphasized in the map. Rotation induces optic flow where local image shifts are aligned along parallel circles.
centered with the axis of rotation (AOR; A, left). In contrast, local image shifts induced by translation are aligned along great circles connecting the focus of expansion (FOE) with the focus of contraction (FOC; B, left). (C) V1 response field. Binocular response field reconstructed from experiments in 4 animals. Orientation of each single arrow indicates the local preferred direction and its length gives the local motion sensitivity normalized to the maximum response. The V1 response field comprises almost the entire visual field. Maximum sensitivity is found in the azimuth range of -15° to -45° around the eye’s equator. The local preferred directions of V1 continuously change from vertical downward in the frontolateral, to horizontal in the dorsolateral, to oblique vertical upward in the dorsocaudal visual field. The organization of the receptive field is more similar to the structure of a rotatory than to that of a translatory flow field thus indicating that the V1-cell should be more sensitive to a self-rotation.
**Figure 2**

(A) Experimental set-up. The light source positioned in the center of a small metal globe (diameter 120 mm) casts through small holes in the globe a field of light dots on a large spherical projection screen (diameter 1.2m; not shown). The fly is positioned in the center of the projection screen, above the metal globe. Rotation of the metal globe results in rotatory optic flow and translation of the light source within the metal globe results in translatory optic flow being projected to the screen. Tuning curves are obtained for rotations about horizontally aligned body-axes spaced 45°. The figure shows the coordinate system used in subsequent figures. Rotation of the metal globe about the 0° axis corresponds to a self-rotation of the animal about the longitudinal body-axis to the right, rotation of metal globe about the 180° axis to rotation of the animal about the same axis to the left. (B) The activity of the V1-cell to a rotation about the 45° axis at 390°/s plotted over time. The activity is smoothed with a
sliding window of 40 ms width. The resting activity of the neuron is set to zero. The
horizontal bar below the x-axis indicates the stimulus period. To determine tuning curves, the
average activity to a rotation about each axis was determined in two 100 ms time windows \( t_1 \)
and \( t_2 \), starting 40 ms and 200 ms after motion onset respectively (vertical bars). (C) The
average activity obtained within \( t_1 \) is plotted over the axis of rotation. To determine the
parameters of interest a cosine function was fitted to the data (see METHODS for detail).
\( \text{PAR} = \text{azimuth of ‘preferred axis of rotation’}, \text{ obtained from cosine fit; } \text{ACT} = \text{maximum activity obtained from cosine fit; } \text{WHH} = \text{width at half maximum height; } \text{SI} = \text{sensitivity index, } \text{MIN} = \text{minimum of the fit.} \) In this and the subsequent figures the ‘preferred axis of rotation’ is indicated by an arrow pointing to the x-axis. (D) Due to the construction of the projector, the metal globe is partly screened at three out of four sides (c.f. A), leading to a restricted projection of the optic flow fields. The gray area within the V1 response field indicates the area not visible to the fly at a rotation axis of 45° and –135° respectively. Note that a change of the orientation of the projector results in a change of the area visible to the animal. (E) To test for the effect of this screening we measured two tuning curves, each based on 5 different orientations of the rotation axis of the projector (see METHODS for detail).
Tuning curves measured with wide-field optic flow stimuli for 4 different rotation velocities. Experiments were done in 11 animals, each tested for 1 to 3 stimulus conditions. Mean activity and standard deviation obtained from 5 (rotation velocity: 39°/s, 123°/s and 390°/s) or 4 animals (rotation velocity: 1223°/s) are plotted over the respective axis of rotation. The resting spike activity is set to zero. Arrows indicate the ‘preferred axis’ for each tuning curve as obtained from the cosine fit. The V1-cell is broadly tuned to a rotation about an axis intermediate between the longitudinal (0°) and the transverse (90°) body axis. The mean ‘preferred axis’ is at 60° azimuth, the individual axes differ from the mean by maximally 5.25° (rotation velocity: 39°/s). Compared to the activity to a rotation about the ‘preferred axis’ at 39°/s the activities to velocities of 123°/s and 390°/s differ by an amount of 1.2 and for a velocity of 1223°/s by 0.7, respectively. The largest difference in the width of the tuning curves amounts to 5.7% (rotation velocity: 1223°/s) of the mean width for all
conditions. The shape of the tuning curves obtained for the two time windows $t1$ and $t2$ (inset) are basically the same.
FIGURE 4

Cosine fit to the tuning curve measured upon wide-field rotatory optic flow at 123°/s (resting spike activity set to zero) and tuning curve computed from local motion measurements (c.f. METHODS). The calculated curve is scaled to the maximum of the fit, the predicted ‘preferred axis’ is located at the maximum of the calculated tuning curve. The small vertical bars left and right to the maximum of the fit indicate the angular deviation of the ‘preferred axis of rotation’. Even if the overall shape of the two curves is similar, some differences are obvious: the ‘preferred axis’ of the calculated and the measured curve differs by 20° and the width of the calculated curve is smaller by 23% compared to the measured width. In addition, the neuron’s spiking activity is not reduced to resting activity for a range of rotation axes (-180° - -45° and +150° - +180°) as predicted. Similar differences between measured tuning curve and tuning curve calculated from local motion measurements where found for another tangential cell, the V2-cell (inset).
Figure 5

Specificity for rotation

Response to a rotation about the ‘preferred axis’ of the V1-cell at 39°/s (left) and activity induced during positive lift-translation (right). In contrast to the measured activity (open black symbols), the model (filled gray symbols) predicts a weaker response to a pure lift translation than to a rotation about the neuron’s ‘preferred axis’. Values are normalized to the response to rotation.
Effect of lift-translation superimposed on rotatory flow. (A) Optic flow fields induced by a pure rotation about the measured ‘preferred axis’ of the V1-cell ($\Psi = 60^\circ$). Rotatory movements were superimposed by positive and negative lift-translations with the same angular velocity in the equator of the visual field ($\Theta = 0^\circ$). Shaded area in each flow field indicates the part of the receptive field where the V1-cell is most sensitive to downward motion. For the pure rotation (upper panel) the local velocity vectors are pointing downward in this area. Superposition of positive lift (middle panel) leads to an increase, superposition of
negative lift (lower panel) to a decrease of the downward motion component in this area. (B) Tuning curves predicted from the local response properties of the V1-cell (upper panel) and tuning curves obtained for pure rotation at 39°/s and for rotations superimposed with lift-translations inducing angular displacements of 39°/s in the equator of the visual field (lower panel). Data for pure rotation are the same as in Fig. 4. The overall shape of the predicted tuning curves is the same, the response amplitude and the width of the curves are affected by the superimposed lift-translation. For the measured curves the ‘preferred axis’ obtained from the tuning curve to rotation superimposed by positive lift-translation is shifted by 10° from the ‘preferred axis’ for pure rotation. Compared to the width of the tuning curves obtained with pure rotation the width for the combined motion is smaller by 7%. The combination of rotations and negative lift-translations results in almost negligible responses for all axes of rotation.
Tuning curve parameters, mean and standard deviation (smaller than symbol size if invisible). The symbols in the left part of each panel indicate values for rotation superimposed with a negative lift-translation, symbols in the middle part are values for pure rotation and symbols in the right part are values for rotation superimposed with positive lift-translation. Sketches below each panel schematize those sections of the respective optic flow stimulus, which affect the neuron’s area of maximum sensitivity to downward motion (corresponding to the gray area in Fig. 6A). Upper panels: parameters for the tuning curves measured with
rotations of 39°/s (open symbols) and calculated curves (filled symbols) shown in Fig. 6B. Since combination of rotation and negative lift nearly leads to total inhibition of the measured response, tuning curve parameters were not determined for this motion combination. (A) Activity to rotation about ‘preferred axis’ for measured tuning curve and for the predicted curve scaled to the measured data. Values are normalized to the activity to pure rotation. (B) Width of measured and calculated tuning curves, (C) Sensitivity index of measured and calculated curve. Lower panels: parameters for tuning curves obtained from stimuli combining rotations and lift-translation at different velocity ratios (rotation:translation: 39°/s:39°/s = open triangles, 123°/s:39°/s = filled squares, 390°/s:39°/s = open circles, 1223°/s:39°/s = filled diamond). Data for combinations with 1223°/s rotation velocity obtained from 4 animals. (D) Activity to rotation about ‘preferred axis’ for all stimulus combinations, values normalized to response to pure rotation at 39°/s. The activity is affected by the rotation velocity as described in Fig. 3. For all stimulus combinations the response to rotation superimposed with a negative lift is smaller than to the pure rotation. (E) Superposition of a lift-translation on rotations with different velocities has no consistent effect on the width of the tuning curves. (F) Sensitivity index for all motion combinations. Except the sensitivity index obtained from a motion combination of lift and rotation at 39°/s the width of the curves and sensitivity index are hardly affected by a change in the rotation velocity or superposition of a lift-translation.
TABLE 1

Table 1. Tuning curve parameters and SI for all stimulus combinations

<table>
<thead>
<tr>
<th>r=39°/s; t=39°/s</th>
<th>r=123°/s; t=39°/s</th>
<th>r=390°/s; t=39°/s</th>
<th>r=1223°/s; t=39°/s</th>
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<tbody>
<tr>
<td>motion components</td>
<td>motion components</td>
<td>motion components</td>
<td>motion components</td>
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<tr>
<td>PAR[°]</td>
<td>65±7</td>
<td>75±7</td>
<td>-</td>
</tr>
<tr>
<td>ACT[sp./s]</td>
<td>162±21</td>
<td>180±29</td>
<td>-</td>
</tr>
<tr>
<td>WHH[°]</td>
<td>153±10</td>
<td>143±11</td>
<td>-</td>
</tr>
<tr>
<td>SI[rel.units]</td>
<td>.95±.08</td>
<td>.68±.05</td>
<td>-</td>
</tr>
</tbody>
</table>

Tuning curve parameters obtained from cosine fits to data measured with global motion stimuli, mean ± standard deviation. PAR = ‘preferred axis of rotation’; ACT = activity to rotation about preferred axis; WHH = width at half maximum height; SI = sensitivity index.

The translation velocity used in the experiments corresponds to an angular velocity of 39°/s in the flow field equator. Combination of rotation at 39°/s with negative translation leads to almost negligible responses. Therefore the tuning curve parameters for this motion combination have not been calculated.