

## Spatial organization of visuomotor reflexes in *Drosophila*

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### Summary

In most animals, the visual system plays a central role in locomotor guidance. Here, we examined the functional organization of visuomotor reflexes in the fruit fly, *Drosophila*, using an electronic flight simulator. Flies exhibit powerful avoidance responses to visual expansion centered laterally. The amplitude of these expansion responses is three times larger than those generated by image rotation. Avoidance of a laterally positioned focus of expansion emerges from an inversion of the optomotor response when motion is restricted to the rear visual hemisphere. Furthermore, motion restricted to rear

quarter-fields elicits turning responses that are independent of the direction of image motion about the animal's yaw axis. The spatial heterogeneity of visuomotor responses explains a seemingly peculiar behavior in which flies robustly fixate the contracting pole of a translating flow field.

Key words: fruit fly, *Drosophila*, optic flow, vision, sensorimotor integration, wing kinematics, optomotor, motor control, LPTC, behavior, flight.

### Introduction

Motion processing is an essential component of the control systems that animals use to find food resources, detect predators and identify conspecifics (Land, 1999). The visual system of insects has long served as a useful model for studying general features of visual systems, including how sensory signals might be transformed into motor behavior (Borst and Haag, 2002; Egelhaaf et al., 2002; Frye and Dickinson, 2001; Srinivasan et al., 1999). Self-motion generates unique patterns of optic flow for all six translational and rotational degrees of freedom (Koenderink and van Doorn, 1987). Due to their robust behavior and stereotyped neural architecture, flies have proven particularly productive for providing key insights into the mechanisms by which visual systems use optic flow to stabilize gaze (Krapp, 2000; Miles and Wallman, 1993; Srinivasan and Zhang, 2000; van Hateren and Schilstra, 1999).

Within flies, early evidence for the use of visual motion in flight control emerged from the identification and analysis of the optomotor response (Götz, 1968). When placed within a vertically striped rotating drum, animals turn in the direction of the moving pattern – a response that acts to decrease the optic flow across the retina. In free flight or in walking, such a reflex is thought to stabilize locomotion by maintaining yaw velocity close to zero in the face of either external perturbations or morphological and physiological asymmetries (Götz, 1975; Heisenberg and Wolf, 1988). The optomotor response has been used extensively as a behavioral assay to

investigate the relationship between genes and visually mediated behavior in *Drosophila* (Blondeau and Heisenberg, 1982; Götz, 1985; Keller et al., 2002; Strauss, 2002). However, the combination of translational and rotational motion and the structural complexity of the visual world greatly complicate the pattern of flow seen by a moving animal. Natural optic flow results from both rotation and translatory self-motion of the animal, as well as the movements of objects within the environment. The complexity of natural visual dynamics is probably matched by specialized structure–function relationships within the hierarchy of visuomotor processing. By presenting fruit flies with patterns other than pure image rotation, we show that the visual system of these animals appears most sensitive not to full-field optomotor rotation about the vertical axis but rather to patterns of expansion and contraction generated during lateral translation.

### Materials and methods

#### *Open-loop experiments*

For all experiments, 1–3-day-old female *Drosophila melanogaster* were cold-anesthetized and tethered to a 0.1 mm tungsten rod with UV-activated glue. After several hours recovery, the animals were placed within an electronic flight arena consisting of a cylindrical array whose vertical extent consists of 24 rows of light-emitting diodes (LEDs). The luminance of active LEDs was 700 cd m<sup>-2</sup>, and the periodic

contrast of the display was approximately 91%. The details of both the tethering procedure and the electronic arena are described elsewhere (Lehmann and Dickinson, 1997; Tammero and Dickinson, 2002a). Because each LED of the arena subtends a discrete angle of  $5^\circ$ , pattern movement was approximated using apparent motion stimuli. The angular velocity of the pattern is determined by the amount of time between  $5^\circ$  jumps in the pattern. For each experiment, we programmed the arena to display a vertical square wave pattern with a spatial frequency of  $30^\circ$ . The horizontal motion of the pattern (around the yaw axis of the animal) could be independently controlled in the front and rear half-fields of visual space. When the direction of motion in both half-fields was identical, the fly received a full-field rotatory stimulus. If the direction of motion in one half-field was reversed, the display created a focus of expansion at  $90^\circ$  azimuth and a focus of contraction on the opposite side. When motion was confined to a single half-field, the opposite half-field displayed a stationary pattern.

To track the responses to motion in the display, the stroke amplitude and frequency of both wings was tracked optically using a wingbeat analyzer (Götz, 1987). We sampled the data at 1 kHz using a data acquisition board (National Instruments, Austin, TX, USA) and custom software written in MATLAB (Mathworks, Natick, MA, USA). We conditioned and normalized the wingbeat signals off line as described in a previous study (Tammero and Dickinson, 2002a). During each trial, the fly was presented with a motion stimulus lasting 4 s followed by a 5 s interval with no motion. Each experiment consisted of between 8 and 15 flies, each completing five sets of 50 trials.

#### *Torque measurements*

To measure the yaw torque that a fly generates, the flies were affixed to a modified tether. A 12 mm-long  $\times$  0.15 mm-diameter tungsten rod was placed inside an 8 mm-long polished stainless steel tubing (0.36 mm outer diameter, 0.18 mm inner diameter). Both the tubing and tightly nested rod were fixed in place at one end. The rod extended by 4 mm through the tubing at the free end. A small 1 mm $\times$ 1 mm $\times$ 0.1 mm-thick surface mirror was attached with cyanoacrylate to the protruding portion of the rod. Flies were tethered to the free end of the rod as they were with normal tethers. The stiff outer tubing minimized bending of the rod while permitting torsion generated by the tethered fly. Thus, as the fly modulated its yaw torque, the rod and mirror assembly rotated in torsion. Torsion was measured by aiming the beam of an He-Ne laser at the mirror, measuring the deflection of the reflected beam using a position-sensitive dual photodiode 'spot detector' (UDT SL5-2, capable of detecting displacements as little as 2  $\mu$ m). The signal from the photosensor was amplified and low-pass filtered at a cut-off of 1 kHz. The measured deflection of the beam was calibrated and found to be linear with respect to applied torque. During turning responses, the torque produced by the fly was calculated to twist the tether by less than  $10^{-6}$  rad.

#### *Closed-loop experiments*

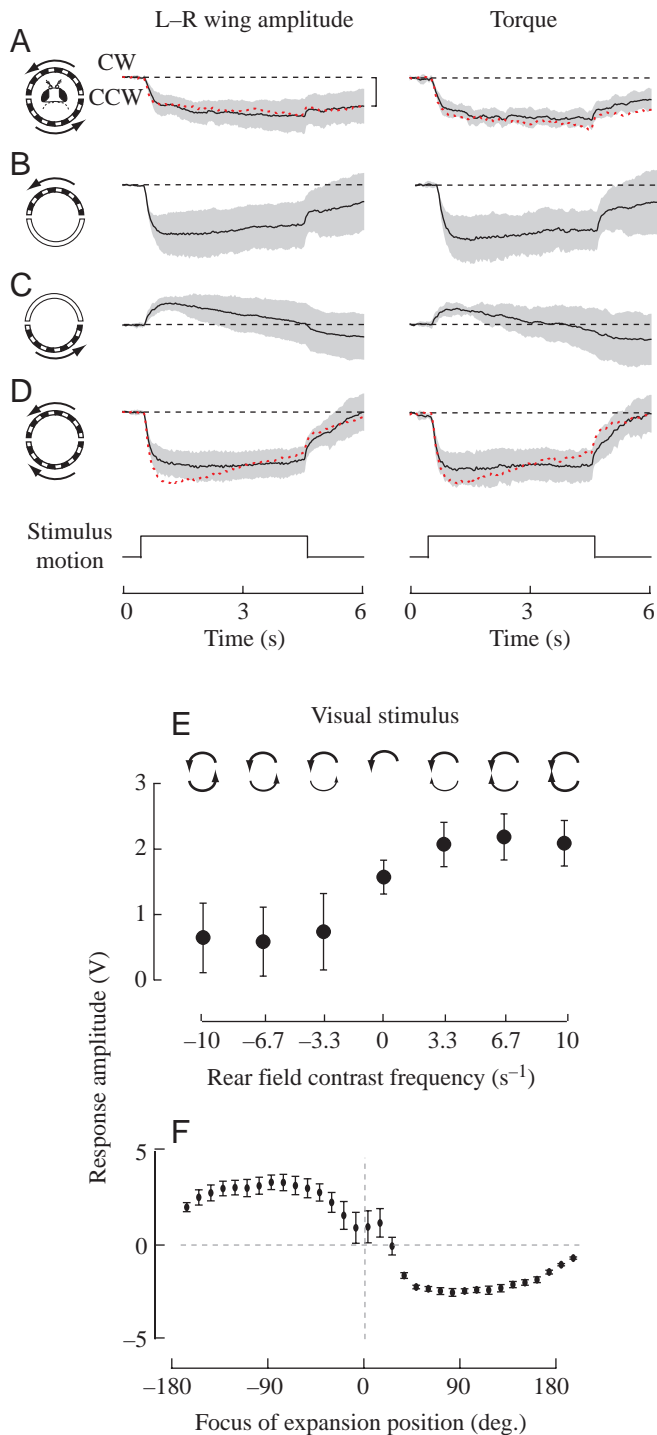
The methods for the closed loop experiments were identical to those used in the open loop, except that the difference between the left and right wingbeat amplitude was fed back to control the angular velocity of the display. The visual pattern placed in closed loop with the fly was either a full-field rotary pattern or a lateral expansion pattern, both of which extend over the full flight arena. In these experiments, a 3.5 V peak-to-peak 0.5 Hz sinusoidal bias was added to the feedback signal to challenge the fly's ability to control the display. Each trial lasted 180 s with the bias applied being switched on and off every 30 s. An individual experiment consisted of three trials with the rotary stimulus and three trials with the expansion stimulus.

## **Results**

### *Spatial organization, summation and gain of translation responses in open loop*

We investigated the spatial organization of visuomotor responses by placing tethered fruit flies within an electronic cylindrical arena that permitted independent motion within the front and rear regions of visual space. We monitored animal's responses to image motion by optically tracking the difference in stroke amplitude between the left and right wings and by simultaneously measuring yaw torque directly. Because in all cases these two signals were highly correlated, we refer to the behavior recorded by either method as the 'turning response'. The traces in Fig. 1A–D show the flies' responses elicited by a coherent yaw rotation at a temporal frequency of  $10\text{ s}^{-1}$ . The fly exhibits an optomotor response – a motor reflex by which the animal attempts to reduce the induced retinal slip speed. Surprisingly, when motion is confined to the front visual hemisphere, animals turn in the same direction, but the response magnitude is greater than if the flies are presented with full-field rotation (Fig. 1B). Furthermore, when the stimulus is confined to the rear hemisphere, flies turn against the direction of image rotation – a response that would increase flow across the retina in an unrestrained animal. Another distinct feature of the rear field response is that it decays more rapidly and eventually reverses polarity with the offset of image motion (Fig. 1C). The response to full-field rotation is closely approximated by the sum of oppositely signed reflexes (Fig. 1A, dotted red lines), which explains why it is attenuated relative to the front field response.

Combining identical pattern motion in the front visual hemisphere with motion in the opposite direction in the rear field approximates the pattern of optic flow during sideways translation (side-slip) with a coherent focus of expansion on one side of the animal and a focus of contraction on the other. The amplitude of the response to this lateral expansion/contraction pattern is larger than that elicited by either full- or frontal-field motion. Unlike full-field rotation, the response to the expansion/contraction stimulus does not represent a simple linear sum of separate front and rear responses (Fig. 1D, dotted red lines). Instead, the response reaches a lower plateau and



does not decay, as one would expect from the sum of separate front and rear field responses. This may result from morphological limits on the maximum wingbeat amplitude that the animal can exhibit during turns.

To further examine this interaction between motion in the rear and front visual hemispheres, we systematically varied the sign and magnitude of motion displayed behind the fly while keeping the motion in front of the fly constant (Fig. 1E). For each contrast frequency displayed to the rear field, the flies'

Responses to large-field motion stimuli presented in open-loop conditions. At the onset of image motion, the fly generates a bilateral change in wing stroke amplitude that is highly correlated with yaw torque. (A) Uniform rotation across the entire visual field elicits a turning response in the same direction as the stimulus. (B) Motion confined to the front half of the visual field elicits a larger response compared with the full-field stimulus. (C) Motion across the rear visual field elicits a turning response in the opposite direction. The sum of separate front and rear field responses (dotted red lines in A) closely approximates the full-field response. (D) A lateral expansion/contraction stimulus with motion in opposite directions in the front and rear visual fields elicits the largest turning response. The dotted red line shows the sum of the responses to individual stimuli indicated in B and C. Each trace represents mean  $\pm$  s.d. (shaded area) ( $N=10$ ). In all cases, contrast frequency changed from  $0 s^{-1}$  to  $10 s^{-1}$  according to the motion stimulus trace. The scale bars indicate 1 V for the wingbeat amplitude and  $10^{-8} N m$  for torque. Wingbeat amplitude signals were normalized (see Materials and methods). (E) Effect of rear field contrast frequency on turning response, measured from changes in wing stroke amplitude. Contrast frequency in the front field was held constant at  $10 s^{-1}$  while the value in the rear field varied from  $-10 s^{-1}$  to  $10 s^{-1}$ . Negative values indicate motion in the same direction as the front field. Data points represent the mean values of the response  $\pm$  s.d. ( $N=10$ ). (F) Turning response amplitude varies with the azimuth of the focus of expansion ( $N=5$ ). From  $-100 deg. s^{-1}$  to  $100 deg. s^{-1}$ , the turning response varies sigmoidally with the location of the focus of expansion. The response attenuates as the focus of expansion moves into the animal's rear field of view.

responses showed little change as long as the rear field pattern rotated in the same direction as the front field. When the rear field was stationary, the turning response increased by a factor of 2.4 times over the full-field rotation response. When the direction of motion in the rear visual field was in the direction opposite that of the front field, creating lateral foci of expansion and contraction, response magnitude increased to three times the full-field rotatory optomotor response. Thus, the response to front field motion is greatly elevated by any small counterdirectional motion behind the fly, whereas a small concurrent rotation causes a large decrease in the turning response. The effect shows a non-linear saturation, such that variation in the contrast frequency of the rear hemisphere has little influence on the magnitude of the turning response, as long as it is in the opposite direction as the front hemisphere.

To test whether responses to the expansion/contraction stimulus vary spatially, we measured the turning response while systematically changing the azimuth of the foci of expansion and contraction. For foci of expansion ranging from  $-100^\circ$  to  $100^\circ$  azimuth, the relationship between the turning response and stimulus position is sigmoidal (Fig. 1F). Thus, any time the focus of image expansion is displaced by more than  $20^\circ$  to one side, the fly generates a robust turning response away from the pole of expansion. Qualitatively, spatial variation in turning responses to a pattern of large-field (i.e. panoramic) expansion is similar to that measured for a small-field expanding object (Tammero and Dickinson, 2002a).

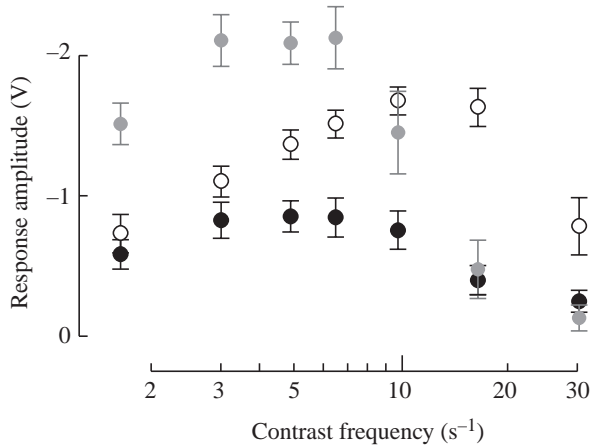


Fig. 2. The effect of contrast frequency on the front and rear field turning responses. The mean response amplitudes  $\pm$  S.E.M. for front (open symbols;  $N=12$ ) and rear (black symbols;  $N=13$ ) field motion reach a maximum at a contrast of  $10 \text{ s}^{-1}$  and  $6.7 \text{ s}^{-1}$ , respectively. Doubling the spatial period of the pattern (gray symbols;  $N=8$ ) results in a shift in the contrast frequency optimum. No response reversal indicative of aliasing was found within the tested range of spatial and temporal frequencies.

Responses to image motion in insects are thought to result from the spatial integration of directionally sensitive local elementary motion detectors (EMDs; Buchner, 1976; Buchner et al., 1978; Hassenstein and Reichardt, 1956). Due to their underlying architecture, EMDs are subject to aliasing due to the spatial separation of the detector elements (Buchner, 1976; Götz, 1964b), an effect that might explain the reversal of the optomotor response in the rear field of view. If, for example, the spacing of the rear field EMDs were substantially different from those in the front field, they might exhibit aliasing for image velocities that elicit a non-aliased response from front field EMDs. We tested this possibility by examining the dependence of both the front and rear responses on image velocity. Holding the spatial wavelength of the pattern at  $30^\circ$ , we found no evidence for a change in the sign of either the front or rear field responses at elevated image velocities (Fig. 2). Although the rear field response was more broadly tuned than the front field response, both showed a similar unimodal dependence on contrast frequency (the image velocity divided by the spatial wavelength). To further ensure that the sign of the turning response did not result from this spatial aliasing, we repeated the experiments with a  $60^\circ$  grating pattern, twice the initial spatial period. Although the lower spatial frequency resulted in larger amplitude responses, both the sign and magnitude of turning responses showed a similar dependence on contrast frequency. Taken together, these results suggest that both front and rear responses are mediated by EMDs with roughly similar spatial properties and that the reversed sign of the rear field response cannot be explained by spatial aliasing.

Optic flow fields generated during translation contain diametrically opposed poles of expansion and contraction. To

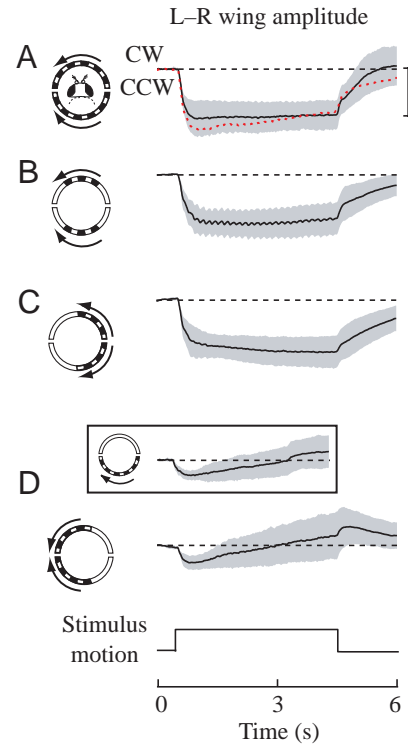


Fig. 3. Flies show similar responses to individual elements of the expansion/contraction pattern. Data (including scale bar) presented as in Fig. 1. (A) Mean responses to full-field expansion/contraction. (B) Responses to a pattern of translation without motion in the lateral fields of view produce expansion avoidance responses similar to the full-field pattern. (C) Responses to the focus of expansion and (D) contraction. For comparison, assuming bilateral symmetry, data from Fig. 1C are inverted and re-plotted here (inset). The sum of the responses shown in C and D (dotted red line in A) approximates full-field expansion/contraction responses ( $N=10$ ).

determine if the full-field response could be explained by particularly salient individual components of the flow (Fig. 3A), we presented animals with a series of visual patterns approximating only parts of a translatory optic flow field; i.e. the focus of expansion, the focus of contraction and the area in between those parts of the flow field (Fig. 3B–D). A stimulus in which the moving grating was eliminated over the lateral  $90^\circ$  azimuth on both sides of the fly (Fig. 3B) provided a pattern in which there were translational cues but no motion at the poles. The responses to this translating stimulus are similar to those elicited by a full-field expansion/contraction (Fig. 3A) or an isolated focus of expansion (Fig. 3C). By contrast, the response to an isolated focus of contraction is qualitatively different from the lateral expansion/contraction response. The turning response is smaller, never reaches steady state and changes sign after approximately 1.5 s (Fig. 3D). The responses to motion across the entire rear field followed a similar time course (Fig. 3D inset). The mathematical sum of responses to expansion and contraction presented individually slightly underestimates the response to both presented together (Fig. 3A, dotted red line). Together, these results demonstrate



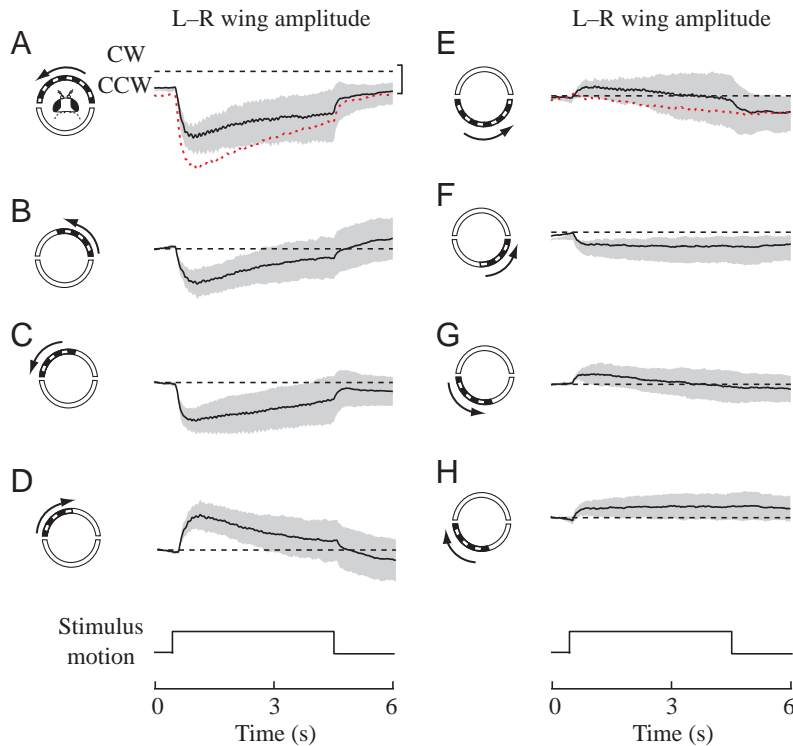


Fig. 4. Turning responses to motion in the rear quarter-fields are non-directionally selective. Motion across the front half-field (A) or the constituent quarter-fields (B,C) generates turning responses that follow the sign of image motion (D). Front quarter-field motion produces saturated responses, thus the sum of responses (dotted red line in A) exceeds responses to half-field motion. (E) Motion across the rear half-field generates counterdirectional turning responses. However, responses to motion restricted to constituent quarter-fields show a sign inversion (F,G). Both clockwise and counterclockwise motion centered in a rear quarter-field triggers clockwise turns (G,H). Assuming bilateral symmetry, data from F are inverted and re-plotted here. As a consequence, the sum of rear quarter-field responses (dotted red line in E) does not approximate the response to half-field motion. This indicates non-linear processing of binocular motion information in the rear part of the visual field.

that whereas either translational motion or a clear focus of expansion is sufficient to initiate a strong turning response, an isolated focus of contraction is not.

We further examined these phenomena by comparing responses to image motion restricted to individual quadrants of the fly's visual field. Like the response to image motion over an entire front half-field (Fig. 4A), the fly turns syndirectionally with motion over either quarter of the frontal visual field (Fig. 4B,C). Although the individual quarter-field turning responses are smaller in amplitude than the half-field response, the arithmetic sum of the two quarter-field responses exhibits a faster onset and larger amplitude than the half-field response, suggesting that the front field response is saturated (Fig. 4A, dotted red line). As expected, the responses to motion restricted to individual quarter-fields have the same polarity as image motion (Fig. 4D).

The responses to image motion over the rear-quarter fields, however, follow a different pattern. Whereas clockwise motion across the rear half-field generated counterclockwise turns (Fig. 4E), clockwise motion restricted to the right rear quarter-field generated clockwise turns (Fig. 4F). Due to this difference in polarity, the arithmetic sum of the rear quarter-field responses is much smaller in magnitude than the response to motion over the entire rear half-field (Fig. 4E, dotted red line). Remarkably, the initial polarity of rear quarter-field responses is independent of the direction of image motion. Motion presented to the left rear quarter-field triggered clockwise turns, regardless of the direction of motion (Fig. 4G,H). Thus, only progressive (front-to-back) motion in the rear field of view elicits responses against the direction of motion, opposite the polarity expected of the optomotor reflex

(compare panels B, C, F and G in Fig. 4). In addition, the temporal properties of rear field responses vary with stimulus direction. Whereas the response to progressive motion over a rear quarter-field steadily decays, the response to regressive motion over the same sector is sustained for the duration of the motion stimulus.

#### *Steady-state responses to translatory optic flow in sensorimotor closed loop*

How are open-loop expansion/contraction responses incorporated into a functional organization of the flight control system? We examined this question by allowing flies to control pattern velocity under closed-loop conditions. In these experiments, animals could control the sign and magnitude of either rotational velocity (i.e. optomotor closed loop) or expansion/contraction velocity by adjusting the difference between left and right wing stroke amplitude. We periodically challenged the fly's capacity to control pattern motion by adding a sinusoidal bias to the feedback signal. When flies controlled a full-field rotatory pattern, introduction of the sinusoidal bias causes them to lose control of pattern velocity, subjecting them to rapid shifts in image position (Fig. 5A). Flies were better able to reduce visual motion for a translating expansion/contraction pattern (Fig. 5B). To quantify a fly's ability to control image motion, we measured the variance in pattern velocity during consecutive 1 s windows throughout the flight sequence. Position variance was substantially smaller when flies controlled the lateral expansion/contraction pattern than when they controlled the rotatory pattern at identical gain (Fig. 5C). Thus, within the confines of the flight simulator, flies can better stabilize translatory flow than they can rotatory flow.

The magnitude, time course and polarity of open-loop turning responses to patterns of expansion/contraction indicate that flies robustly and continuously turn away from an expanding stimulus. Therefore, for a steadily translating flow field, bilaterally symmetrical collision avoidance reflexes

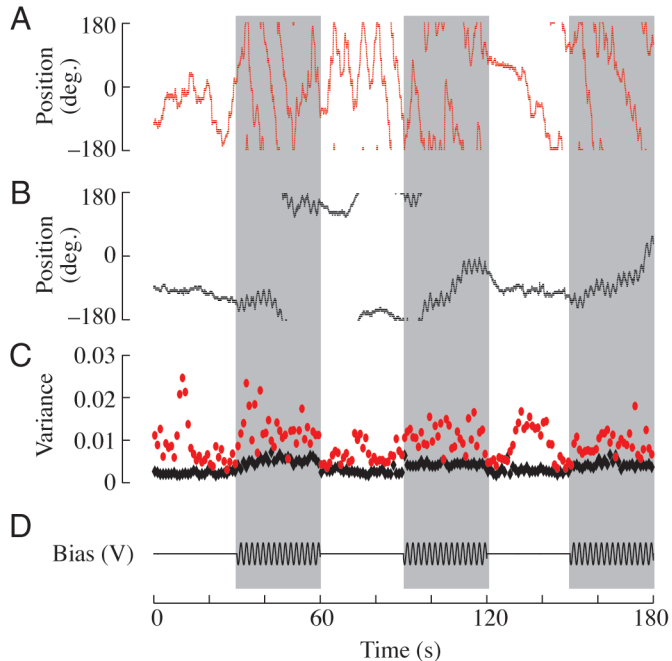


Fig. 5. Flies maintain better closed-loop control of an expansion/contraction pattern than a full-field rotatory pattern. The fly controls the direction and velocity of either a full-field rotational (A) or a lateral expansion/contraction pattern (B) by adjusting the difference between left and right wing stroke amplitude. (C) The fly's ability to hold the pattern steady is reflected by the variance in the position over a series of 1 s windows. (D) A sinusoidal bias is added to the feedback signal to challenge the fly's ability to control the pattern. The variance in position is much larger when the fly controls the position of a rotational pattern when compared to the expansion/contraction pattern.

should equilibrate only when the focus of expansion is centered directly behind the fly. To determine if flies stabilize a pole of expansion, we allowed flies to control the yaw velocity of an expansion pole under closed loop conditions. The strength of the fixation of pole of contraction is best seen in comparison with other closed-loop configurations. If permitted to control the yaw velocity of a rotating checkerboard, flies tend to generate rapid rotations of the pattern that are thought to be analogous to the saccadic turns executed in free flight (Fig. 6Ai). Although they may transiently orient towards a particular feature of the display, on average the flies do not stabilize, or fixate, any preferred position within the random pattern (Fig. 6Aii). By contrast, flies presented with a single vertical stripe in closed-loop tend to smoothly track the object and maintain its position frontally (Fig. 6B). However, the positional variation of object fixation is significantly larger than for fixation of a contraction pole at identical feedback gain (Fig. 6C). We further challenged the fly's ability to control the position of the expanding/contracting flow field by periodically reversing the direction of pattern motion on either side of the animal, thereby instantaneously switching the positions of the expansion and contraction poles.

Flies respond by rapidly turning away from the new pole of expansion, fixating the new pole of contraction (Fig. 7A).

What are the salient visual cues that flies use to locate the position of the foci of expansion and contraction? Flies execute steady-state collision avoidance responses to patterns of image translation without motion at the poles (Fig. 3B), suggesting that the fixation of the contraction pole results from balancing the spatial integral of image flow in the left and right hemispheres. Alternatively, flies might be tracking the apparent 'seams' of the flow field – the poles themselves. We tested these competing hypotheses by varying the spatial and temporal composition of image motion on one side of a drifting expansion/contraction pattern. The two treatments produced similar results. By either doubling the image velocity (Fig. 7B) or halving the spatial wavelength (Fig. 7C) on one side, the steady-state fixation responses were biased approximately  $20^\circ$  toward the side of the arena containing the lower contrast frequency. Therefore, flies appear to be balancing contrast frequency bilaterally rather than tracking the apparent position of the poles. This integration model also predicts that the time course of the response should vary with contrast frequency. For a bilaterally symmetric drifting pattern of expansion/contraction, increasing contrast frequency from 1.1 Hz to 6.6 Hz results in a 3-fold decrease in the delay to steady-state expansion avoidance (Fig. 7D). Therefore, both the spatial tuning and temporal dynamics of steady-state expansion responses depend upon the contrast frequency of the moving image.

## Discussion

In response to full-field image rotation during flight, flies turn in the direction of motion, a reflex consistent with the classic optomotor response (Fig. 1). However, when presented with motion restricted to the rear visual hemisphere, flies turn against the direction of motion, a reflex consistent with a collision avoidance response triggered by image expansion (which shall be referred to as 'expansion avoidance'; Fig. 1). Patterns of lateral expansion trigger compensatory turning responses three times larger than those elicited by full-field rotation. Furthermore, the time course and magnitude of full-field optomotor responses are nearly identical to the arithmetic sum of half-field translation responses (Fig. 1A, dotted red line). These results suggest that the flight control system in flies is more sensitive to patterns of translation generated during side-slip than to patterns of visual rotation. This selectivity to translatory patterns emerges from the response to progressive motion in the rear visual field (Fig. 4) and suggests a new interpretation of the optomotor reflex. The spatially heterogeneous sensitivity to translatory motion also explains the peculiar but robust frontal fixation of a contraction pole under closed-loop conditions (Figs 5, 6).

### *Importance of distinguishing translational and rotational flow for flight control*

Flies use patterns of rotational and translational optic flow

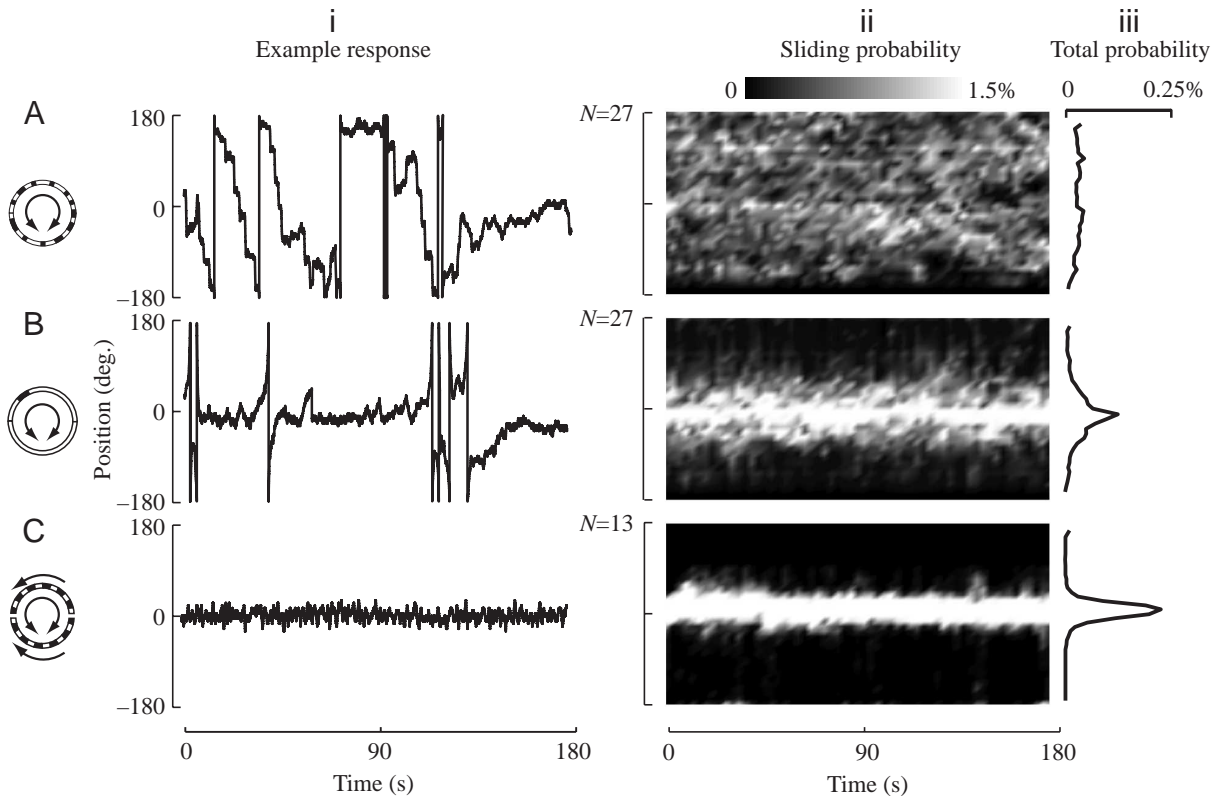


Fig. 6. In closed-loop conditions, flies show a powerful steady-state expansion avoidance reflex. By adjusting the difference between the right and left wing stroke amplitude, flies control the azimuth of (A) a random checkerboard pattern ( $N=27$ ), (B) a single vertical stripe ( $N=27$ ) and (C) the poles of a constantly expanding/contracting pattern of vertical stripes ( $N=13$ ). For each experimental treatment, example responses are plotted in the left column (i), time series averages are plotted in the center column (ii; indicated in grayscale) and total probability distributions are plotted in the right column (iii). For the grayscale plots, the white area indicates that flies maintained the rotating pattern in that particular position. On average, flies do not show preference for any single element of the random checkerboard pattern, whereas they tend to fixate the vertical stripe in front ( $0^\circ$ ). Flies show even more robust fixation of the poles of expansion/contraction. There is less variability in the fly's tendency to stabilize the poles of the expanding pattern in the rear field of view, thus the pole of contraction is fixed frontally.

to maintain stable flight within visually textured environments. The relative contributions of rotation and translation to the retinal optic flow field depend upon the fly's motions, the spatial organization of the visual world, as well as the respective geometrical constraints on optic flow. For example, body rotation in the absence of translation generates a flow pattern consisting of equal local velocity vectors along each meridian of the axis of rotation. Translation, by contrast, produces a field in which optic flow radiates outward along meridians from the focus of expansion towards the focus of contraction.

In response to panoramic image rotation, freely flying hoverflies (*Syritta pipiens*) turn in the same direction (syndirectionally) to minimize retinal slip (Collett, 1980). Counteracting rotational retinal slip, an example of the optomotor response, is thought to mediate stable forward flight in flies (Götz, 1975). During linear translation, image expansion triggers collision avoidance maneuvers during free flight in which *Drosophila* turn away from the pole of expansion (Tammero and Dickinson, 2002b). This reflex cannot be based solely on optomotor feedback because it

requires that the animal turns against the direction of image motion seen within a large portion of its visual field. Our results show that, when presented with horizontal motion restricted to either the front or rear hemisphere, *Drosophila* always turn in the direction of apparent translation (Fig. 1). Thus, for ambiguous patterns of optic flow, flies default to translation responses. Open-loop responses to translational expansion/contraction stimuli are three times larger than those generated by full-field rotation at an identical contrast frequency (Fig. 1E). This amplification of operational gain results in more robust closed-loop control over the velocity of expansion/contraction than to that of full-field rotation (Fig. 5). As a result of the spatial organization of visuomotor responses, when given a choice, the fly frontally fixates a steadily contracting flow field, a strange situation that illustrates a very low tolerance for image expansion (Fig. 6). As soon as an expansion pole is displaced laterally on the retina, the fly turns away. Thus, the only stable condition – the expansion pole positioned directly behind the fly – results in frontal fixation of the contraction pole. The positional variance during closed loop is substantially less for a pole of contraction than for a

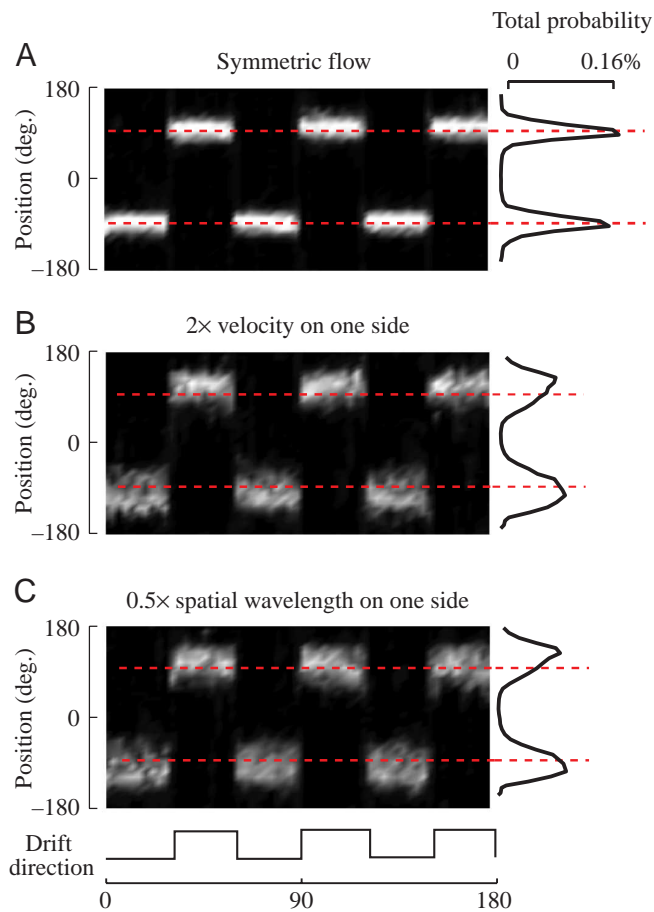


Fig. 7. Delay and steady-state balance of the expansion avoidance reflex depend upon the contrast frequency of large-field image motion. Flies had closed-loop control over the yaw position of the poles of expansion/contraction, while a pattern of stripes drifted at constant velocity. We periodically challenged the fly's closed loop responses to image expansion/contraction by

reversing the drift direction, therefore exchanging the position of the two poles. (A) At each direction reversal, flies rapidly turn away from the pole of expansion to fixate the pole of contraction frontally. In this figure, drift direction is indicated by the polarity of the stimulus waveform. Dashed lines indicate pole positions along the y-axis. (B) Either doubling the drift velocity or (C) halving the functional wavelength of the pattern on one half of the arena resulted in a 20° shift in fixation towards the side of the arena showing the slower drift speed. (D) Increasing the drift velocity results in shorter delay to the onset of steady-state responses ( $N=13$ ; ANOVA,  $F=14.7$ ,  $P<0.01$ ).

vertical stripe (Götz, 1968; Heisenberg and Wolf, 1979; Wolf and Heisenberg, 1990). To our knowledge, expansion avoidance generated by linear image translation is the most

robust visual reflex yet recorded in *Drosophila* and is therefore likely to be a fundamental component of the animal's flight control system.

#### Model for the spatial summation of translational flow fields

We propose the following model to summarize our findings (Fig. 8). The progressive (blue pathway) and regressive (red pathway) motion over each quarter of visual space is processed via an appropriate temporal filter. For example, progressive motion over the frontal visual field is processed by a filter ( $f_{fp}$ ) with both tonic and phasic step response characteristics (Fig. 4C). Similarly, the response of the filter sensitive to regressive motion in the front visual field ( $f_{fr}$ ) has transient and sustained components, although the sustained component is somewhat smaller than for that of progressive motion (Fig. 4B). The polarity of the response to frontal motion always matches the direction of image motion (Fig. 4B–D).

The processing of motion over the rear visual field is carried out in a similar fashion, with some distinct differences. The filter sensitive to progressive motion over the rear visual field ( $f_{rp}$ ) is dominated by the transient component, whereas the sustained component dominates the filter sensitive to regressive motion ( $f_{rr}$ ). The polarity of the turning responses does not, however, reverse when the direction of motion is reversed. Thus, both progressive and regressive motion over a rear quarter-field causes a turning response of the same polarity. The response to motion over the rear half-field does not result from the summation of the two rear quarter-fields (Fig. 4E, dotted red line). Rather, the response to progressive motion in one quarter-field appears to inhibit the response to regressive motion in the adjacent quarter-field when motion is presented across the rear half-field (Fig. 4). Finally, the output of each temporal filter is spatially summed, integrating motion over the fly's entire field of view. The final sum is then subject to saturation due to the mechanical and temporal limits on the control of wing kinematics. The model predicts that the sum of antagonistic translation commands results in a weak tendency of the fly to turn in the direction of full-field rotation – the classic optomotor response. By contrast, for a pattern of lateral translation producing opposing poles of expansion and contraction, similar rightward motion in the front field of view coupled with leftward motion in the rear field of view results in a stronger tendency to turn to the right – a collision avoidance response.

#### New implications for the neural mechanisms of visuomotor reflexes

For decades, visually mediated reflexes in insects have been used as behavioral assays to predict and examine structure–function relationships within the nervous system at both the cellular (Bishop and Keehn, 1967; Hassenstein and Reichardt, 1956) and molecular-genetic levels (Fischbach and Heisenberg, 1984; Götz, 1964a). The power of this integrative approach emerges from comparing the dynamics of intact behaviors with the physiological properties of individual neurons. The new interpretation of visuomotor reflexes



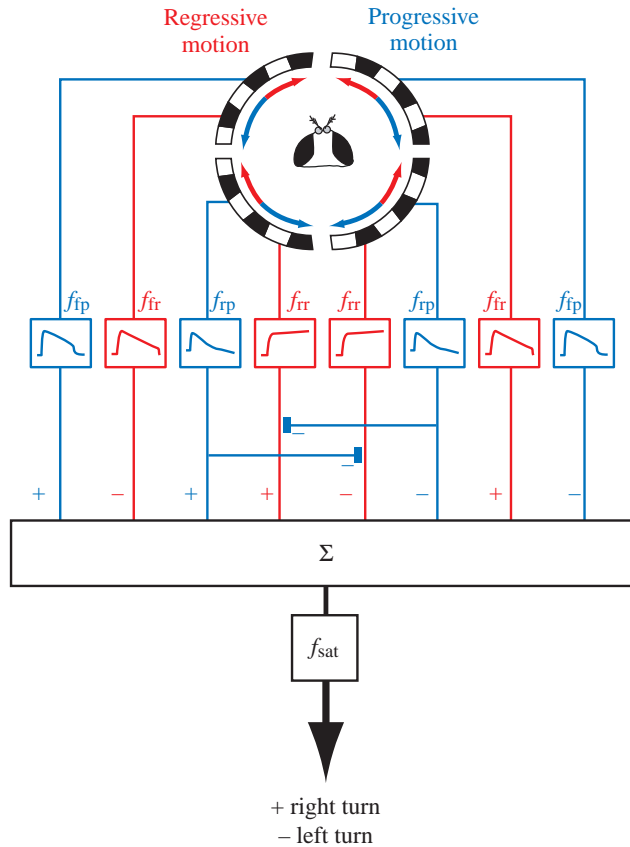


Fig. 8. Schematic model for the spatial organization of visuomotor reflexes in *Drosophila*. Image motion within individual quarter-fields is temporally filtered and spatially summed (see text for details). Motion across the frontal visual hemisphere results in a syndirectional turn, whereas motion in the rear results in a counterdirectional turn. By summation, full-field rotation results in a weak syndirectional turn. However, a pattern of expansion centered laterally produces a stronger turn away from the focus of expansion. Note that the polarity of turning responses to motion within the rear quarter-fields is independent of the direction of image motion.

presented here therefore initializes both a search for new physiological mechanisms and a reinterpretation of current advances.

Most electrophysiological studies of visual processing in flies have focused on a group of 60 or so motion-sensitive cells in the lobula plate (Hausen, 1984, 1993). Some of the lobula plate tangential cells (LPTCs) show local directional specificity for global patterns of optic flow (Krapp and Hengstenberg, 1996; Krapp et al., 2001). As yet, there have been few descriptions of LPTCs sensitive to expanding flow fields in flies. The Hx neuron responds strongly to patterns of translatory optic flow emanating from the caudo-lateral visual field (Krapp et al., 2001). Also, Hausen postulated that HS neurons probably participate in encoding self translation (Hausen, 1984, 1993). Furthermore, output regions in the central brain visit descending neurons that convey visual signals to the flight motor circuits within the thoracic ganglion (Strausfeld, 1976). Several neurons descending through

the cervical connective of the blowfly (*Calliphora erythrocephalia*) are sensitive to frontally positioned image expansion (Borst, 1991). In the locust *Schistocerca americana*, identified descending contralateral motion detector cells (DCMDs) may play a role in collision avoidance or escape behavior by firing in response to looming objects (Gabbiani et al., 1999; Gray et al., 2001; Judge and Rind, 1997). In the lobula plate of the hawk moth *Manduca sexta*, 'class 2 cells' respond to an expanding optic flow field (Wicklein and Strausfeld, 2000). It may be within similar premotor networks that the patterns of linear translation and expansion are encoded in flies.

Why should minimizing lateral translation or avoiding lateral expansion play such a dominant role in flight control? In both free-flight and tethered-flight conditions, fruit flies respond to a laterally positioned focus of expansion by turning away from the focus of expansion (Tammero and Dickinson, 2002a,b). This explains the tendency of *Drosophila* to saccade away from approaching walls in free flight, avoiding collisions. Consistent with free-flight behavior, tethered flies in visual closed loop show counterdirectional saccades that send an expanding object to the rear field of view. In the experiments described here, *Drosophila* appear to be treating the focus of expansion of a large field pattern as it does an expanding object, by turning away from the expanding flow field. By contrast, walking blowflies in which one eye has been occluded show a weak tendency to turn in the direction of the non-occluded eye, thus turning towards the focus of expansion (Kern and Egelhaaf, 2000). However, in flight, monocular animals do not show trajectories significantly different from their binocular counterparts. Strong differences in the temporal dynamics of image motion may contribute to varying behavioral strategies to stabilize gaze during locomotion in walking vs flying animals.

The most common source of lateral image motion and its associated expansion is side-slip during free flight, a situation that may occur if an animal is blown off course by a gust of wind. In response to such lateral translation, our results suggest that a fly would turn away from the laterally positioned focus of expansion, reflexively directing it away from any impending collision. Thus, this reflex and its underlying circuitry might be analogous to the centering response observed in bees (Srinivasan et al., 1991). A specific application of this reflex might be the maintenance of upwind flight, an essential component of long-distance odor tracking (Vickers, 2000). Mechanosensory structures such as filiform hairs or antennae cannot by themselves localize the upwind direction, because without an independent measure of ground speed a flying animal cannot easily distinguish an external wind from a self-generated component of airflow. Within the natural environment, the most likely source of side-slip is the drag that results from yaw relative to wind direction, an effect analogous to leeway on a boat. By turning to minimize lateral translation and fixate the focus of expansion in the rear field of view, an animal would tend to steer into the wind. The expansion avoidance reflex is thus a simple and robust means by which

the animal might avoid obstacles and also maintain an upwind direction.

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