To keep on track during flight, fruitflies discount the skyward view

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When small flying insects go off their intended course, they use the resulting pattern of motion on their eye, or optic flow, to guide corrective steering. A change in heading generates a unique, rotational motion pattern and a change in position generates a translational motion pattern, and each produces corrective responses in the wingbeats. Any image in the flow field can signal rotation, but owing to parallax, only the images of nearby objects can signal translation. Insects that fly near the ground might therefore respond more strongly to translational optic flow that occurs beneath them, as the nearby ground will produce strong optic flow. In these experiments, rigidly tethered fruitflies steered in response to computer-generated flow fields. When correcting for unintended rotations, flies weight the motion in their upper and lower visual fields equally. However, when correcting for unintended translations, flies weight the motion in the lower visual fields more strongly. These results are consistent with the interpretation that fruitflies stabilize by attending to visual areas likely to contain the strongest signals during natural flight conditions.

1. Introduction

Flight has helped drive the tremendous success of insects [1–3], but it subjects them to perturbations from flight errors and wind [4] that can cause collisions or missed targets. Analysing the motion patterns that result from self-motion, or optical flow fields, is a primary mechanism for correcting errors in position and heading [5–8]. Rotational and translational motions each add distinctive components to flow fields [9]. To detect an unplanned error in heading (rotation), a flier can use any object, near or far, that provides contrast, as the image motion at the retina is proportional to angular speed (and the sine of the angle from the axis of rotation). For example, rocks below, trees to the sides or clouds above all generate images that move on the retina during unintended rotation.

But, to detect an error in position (translation), a flier cannot rely on distant features, as their image motion is inversely proportional to their physical distance [10,11]. So, clouds, mountains and the sun provide no visual cue to signal unintended translation. Many insects fly in settings with nearby features below them (on the ground), and only far off features above (in the sky). Reflecting this, some insects have evolved vertically asymmetrical eyes, with different resolution or sensitivity in the upper and lower hemispheres [12,13]. Others show asymmetries in motion-sensitive neurons, with those responsive to rotational optic-flow-sensitive above the horizon, and those responsive to translational optic-flow-sensitive below [14]. Wild *Drosophila melanogaster* approach ripe and rotting fruit on the ground to search for food, mates and oviposition sites. We tested the hypothesis that they weight upper and lower features differently when correcting for unexpected motion, depending on whether the perturbation is rotational or translational.

2. Material and methods

A laboratory-reared population of *D. melanogaster* was fed on standard media under a 12 L : 12 D cycle at 21 °C. We cold-anaesthetized females 3–6 days after eclosion, then...
glued a tungsten rod to their back. As they warmed, we gave them a small piece of paper to manipulate with their legs, keeping them from beating their wings before an experiment began. After flies recovered for about an hour, we suspended them in the centre of a 200 mm Perspex cube, which delivered the visual stimulus, and removed the paper, causing them to initiate tethered flight.

From the centre of the cube, flies viewed a panoramic, perspective-corrected visual scene, described fully in previous work [15]. Back-projection screen material coated five sides of the cube, which were illuminated at 360 Hz by a projector, 5 feet away and a system of mirrors (figure 1a). The arena covers 10.46 of the entire 12.57 steradian visual field. We filled the space with small, randomly placed dots (1” diameter, 89% contrast, with an approx. 89 dots per steradian), and simulated deviations of either yaw rotation or sideslip translation (figure 1b), parameters known from previous work to produce strong corrective responses [8]. The dots moved for 8 s, over four cycles of a triangular waveform. Yaw displacements oscillated by 22°, and sideslip displacements were scaled such that the mean offset in the forward field was also 22°.

Figure 1. The experimental apparatus to measure fly optomotor responses. (a) Five perspective-corrected scenes are imaged onto the sides of a cube with a fast projector and a system of first-surface mirrors. (b) From the viewpoint of a tethered fly, objects appear to be moving in a continuous volume. Here, the lower dots are static, whereas the upper dots simulate lateral translation (sideslip) in time to a triangle waveform. Grey lines indicate dot trajectories, but were not rendered. (Online version in colour.)

Figure 2. Steering effort to upper and lower visual flow fields. (a) Traces indicate the mean responses to the first two cycles of each stimulus motion. Time advances downwards, the horizontal grey bars denote leftward motion in the forward visual field, and the traces show the mean ΔWBA with standard error of the mean indicated in light grey ((i–viii), n = 143; (ix)(x), n = 88). (b) Bars indicate the mean Pearson’s correlations between stimulus motion and ΔWBA as a measure of response strength. Error bars show the standard error, and the horizontal lines on top show the results of paired t-tests between groups, with n.s. indicating no statistical significance, *p < 0.05, and **p < 0.01. Stimuli (i(ii)) are controls, visual flicker with no motion and a moving vertical bar. Stimuli (iii–v) are yaw rotation, (vi–viii) are sideslip translation. Stimuli (ix) and (x) are yaw and sideslip, but opposing in upper and lower hemispheres, such that left in the lower occurs with right in the upper. Bars for (ix) and (x) show correlation to the lower hemisphere motion.
We quantified flight responses with a wing beat analyser. An infrared light above the fly cast shadows of the wings onto a pair of photodiodes below, which measured the left and right amplitude of each wing stroke [16]. Although the projection does not capture three-dimensional wing dynamics, the difference between the left and right wing beat amplitude ($\Delta$WBA, measured in volts) is proportional to yaw torque, and approximates steering effort [16,17]. Our stimuli followed a triangle wave through time, and we used the Pearson’s correlation between this and $\Delta$WBA to measure the influence of a visual stimulus on steering. For hypothesis tests, we used the Fisher transformation of correlations, which produces normally distributed samples appropriate for t-tests [18]. Trials appeared in random order, and between trials, flies tracked a vertical bar in closed loop for 2 s, to ensure they entered experiments in an actively steering behavioural state.

3. Results

We presented visual displacements of either yaw rotation or sideslip translation, in either the whole arena, just its lower or upper hemispheres, or opposing in the upper and lower hemispheres. We used two controls to determine the range of $\Delta$WBA responses. Visual flicker produces no net $\Delta$WBA response (figure 2b(i)), but a vertical bar (figure 2b(ii)) generates $\Delta$WBA that correlates strongly to bar motion.

Yaw flow fields constrained to just the lower or upper visual hemispheres produce no reduction compared with full field motion (correlation between stimulus and $\Delta$WBA response directions, $t = 0.048, p = 0.481$ and $t = 0.115, p = 0.454, n = 138$; figure 2b(iii–v)). Similarly, sideslip optic flow constrained to the lower visual hemisphere elicits a steering response indistinguishable from sideslip in the whole visual field ($t = 0.292, p = 0.386, n = 138$; figure 2b(vi)). However, sideslip flow in just the upper hemisphere generates a steering response significantly below whole field sideslip ($t = 1.83, p = 0.034$) and lower hemisphere sideslip ($t = 1.89, p = 0.030, n = 138$; figure 2b(vii)). It is not significantly distinguishable from mean correlation of zero, or no lateral response ($t = 1.365, p = 0.087, n = 138$).

We then presented opposing motion, left in the lower hemisphere paired with right in the upper and vice versa. When upper and lower yaw flow oppose, the resulting $\Delta$WBA is close to zero, consistent with stimuli that cancel one another in the final response (figure 2b(ix)). However, when upper and lower sideslip flow oppose, the resulting $\Delta$WBA correlates positively with the lower hemisphere motion, and negatively with the upper hemisphere (figure 2b(x)) (x differing from ix, $t = 2.42, p = 0.009, n = 88$). The responses to full field and lower field sideslip flow (figure 2b(vi)) are statistically indistinguishable from the response to lower field sideslip flow with opposing motion (figure 2b(x)); $t = 0.70, p = 0.242$ and $t = 1.17, p = 0.122$), but significantly different from the response to the upper flow fields ($t = 2.87, p = 0.002$ and $t = 4.42, p = 7 \times 10^{-7}$).

4. Discussion

During flight, flies detect errors and execute corrections. Detection depends largely, but not exclusively, on visual circuitry to analyse optic flow [14,19,20]. Corrections depend largely, but not exclusively, on wing beat kinematics and can be complex. Importantly, sideslip optic flow does not necessitate a sideslip mechanical response. Neither cars on ice nor aeroplanes in crosswinds can generate corrective sideslip forces, but can recover with forward motion and yaw. We have previously documented that visual slip, yaw and roll each produce unique $\Delta$WBA responses, but our goal here was simply to measure the magnitude of this corrective response, as it related to optic flow in the upper and lower visual fields. Here, we show that for fruitflies, visual yaw rotation of either the upper or lower hemisphere elicits $\Delta$WBA responses as strongly as the full visual field. This is not due to mechanical saturation, as moving vertical bars produce still stronger responses. Visual translation, by contrast, produces comparable responses when presented in the lower and full visual field, but little response when presented in the upper visual field. This is consistent with the visual ecology of a low-flying insect, in which features above or below can signal rotations, but only often the nearby ground can signal translation.

By contrast, insects high in the air, under a forest canopy, or in a cave, may have different needs. Insects are difficult to track when they are not at target sites, such as flowers or ripe fruit, so their total visual environment is difficult to estimate. Some may filter motion to match their typical environment, but some may filter dynamically, with changing environments. Previous results show *Drosophila* respond to translational optic flow depending on the relative speed of objects in it [15]. They regulate their corrective steering to rely on objects that seem closest, regardless of absolute image speeds, and might vary the spatial regions they rely on in a similar way. Other visual factors might also influence steering, such as small targets, when motion is restricted to a small area. As an insect navigates to a flower, accidental sideways motion alters the image position on the retina. Turning to reposition, the image puts the insect back on course. Even when a target is not visible, other senses aid in discovering errors in course [21].

How insects control sophisticated flight remains a puzzle, but the problem is not lack of sensory input. Even the coarse visual signal captured by compound eyes would quickly overwhelm the brain without substantial information processing and filtering. Our results indicate filtering in the corrective responses of *Drosophila* to translational optic flow that is not present for rotational optic flow. This may function in flies by restricting the visual search for evidence of sideways deviations to areas where it is rich in natural scenes.

Data accessibility. Data can be accessed at http://dx.doi.org/10.5061/dryad.jf150.

References


