# Report

# Optic Flow Cues Guide Flight in Birds

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## Summary

Although considerable effort has been devoted to investigating how birds migrate over large distances, surprisingly little is known about how they tackle so successfully the moment-to-moment challenges of rapid flight through cluttered environments [1]. It has been suggested that birds detect and avoid obstacles [2] and control landing maneuvers [3–5] by using cues derived from the image motion that is generated in the eyes during flight. Here we investigate the ability of budgerigars to fly through narrow passages in a collision-free manner, by filming their trajectories during flight in a corridor where the walls are decorated with various visual patterns. The results demonstrate, unequivocally and for the first time, that birds negotiate narrow gaps safely by balancing the speeds of image motion that are experienced by the two eyes and that the speed of flight is regulated by monitoring the speed of image motion that is experienced by the two eyes. These findings have close parallels with those previously reported for flying insects [6–13], suggesting that some principles of visual guidance may be shared by all diurnal, flying animals.

## Results and Discussion

We investigated the ability of budgerigars (*Melopsittacus undulatus*) to fly through narrow passages in a collision-free manner. The birds were trained to fly along a corridor where the walls were lined with stripes that were oriented horizontally or vertically (Figures 1A–1C). The birds' flight trajectories were recorded in three dimensions (3D) by a pair of high-speed stereo video cameras operating at a frame rate of 250 frames/sec and subsequently digitized and reconstructed using custom-written Matlab software (Mathworks, Inc.). Data were obtained from five birds, and 45–50 flights were recorded in each condition.

When the two walls were lined with vertical stripes, the birds flew along the middle of the corridor, never colliding with either wall (Figure 1A). In this situation, both walls induced strong image motion in each eye, because the stripes were oriented perpendicularly to the direction of flight. The mean trajectory position was not significantly different from the midline of the tunnel (p > 0.25, two-tailed t test). On the other hand, when

one wall was decorated with vertical stripes and the other with horizontal stripes, the birds flew significantly closer to the wall carrying the horizontal stripes (Figures 1B and 1C; p < 0.0001, one-tailed t test). In this case, the vertical-striped wall generated strong image motion, whereas the horizontal-striped wall induced little or no image motion, because the horizontal stripes were oriented parallel to the direction of flight. When one wall carried vertical stripes and the other was devoid of any visual texture (and therefore induced no image motion), the birds flew very close to the blank wall, occasionally colliding with it (Figure 2). Details of the statistical analyses of the data shown in Figure 1 and Figure 2 are given in Tables S1 and S2 available online. Examples of bird flights under the three conditions shown in Figure 1 are given in Movie S1, Movie S2, and Movie S3.

These results reveal that budgerigars negotiate narrow passages safely by steering a course such that the two eyes experience similar rates of image motion or "optic flow." When both walls carry visual textures that provide optic flow (as is usually the case in a natural environment), this strategy ensures that the bird flies a collision-free path through the middle of the passage. When flying closer to one wall, the corresponding eye would experience a greater magnitude of optic flow than would the other eye. This imbalance would cause the bird to veer away from the closer wall and to move toward the center of the passage, where the balance between the optic flows induced in the two eyes is restored. When only one of the walls presents strong optic flow, the birds move away from that wall in an attempt to restore the balance between the flows experienced by the two eyes.

Do birds use cues based on image motion to monitor and regulate the speed of their flight? In principle, when flying through a passage of constant width, the speed of flight can be regulated by ensuring that the eyes experience a more-or-less constant global magnitude of optic flow. An increase in the magnitude of the flow above a prescribed set point would signify an increase in flight speed, causing the bird to reduce its speed in order to restore the optic flow magnitude to its set point. Conversely, a decrease in the optic flow magnitude would cause the bird to produce a compensatory increase in flight speed.

To investigate whether birds use optic flow signals to regulate flight speed, we measured mean axial flight speeds in the tunnel under conditions in which the birds experienced optic flow signals of different strengths. The axial speed is the component of the flight speed parallel to the longitudinal axis of the tunnel. We varied strength of the optic flow that was experienced by the birds by decorating the walls with stripes that were oriented horizontally or vertically. Figure 3 shows profiles of flight speed versus position for individual trajectories (left-hand panels), and mean flight speeds (right-hand panels) for three different birds, for the conditions when the walls carry vertical stripes (red) or horizontal stripes (blue). In general, the speed of flight tends to increase after takeoff, reach a plateau, and then decrease when the bird has neared the end of the tunnel and is preparing to land or to make a U-turn and return to the experimenter's perch. We find that, for each of the birds, the mean axial flight speed is very significantly higher during flight through the horizontal-striped tunnel (LHRH: left horizontal, right horizontal), which provides weak or no optic flow signals, as compared to the

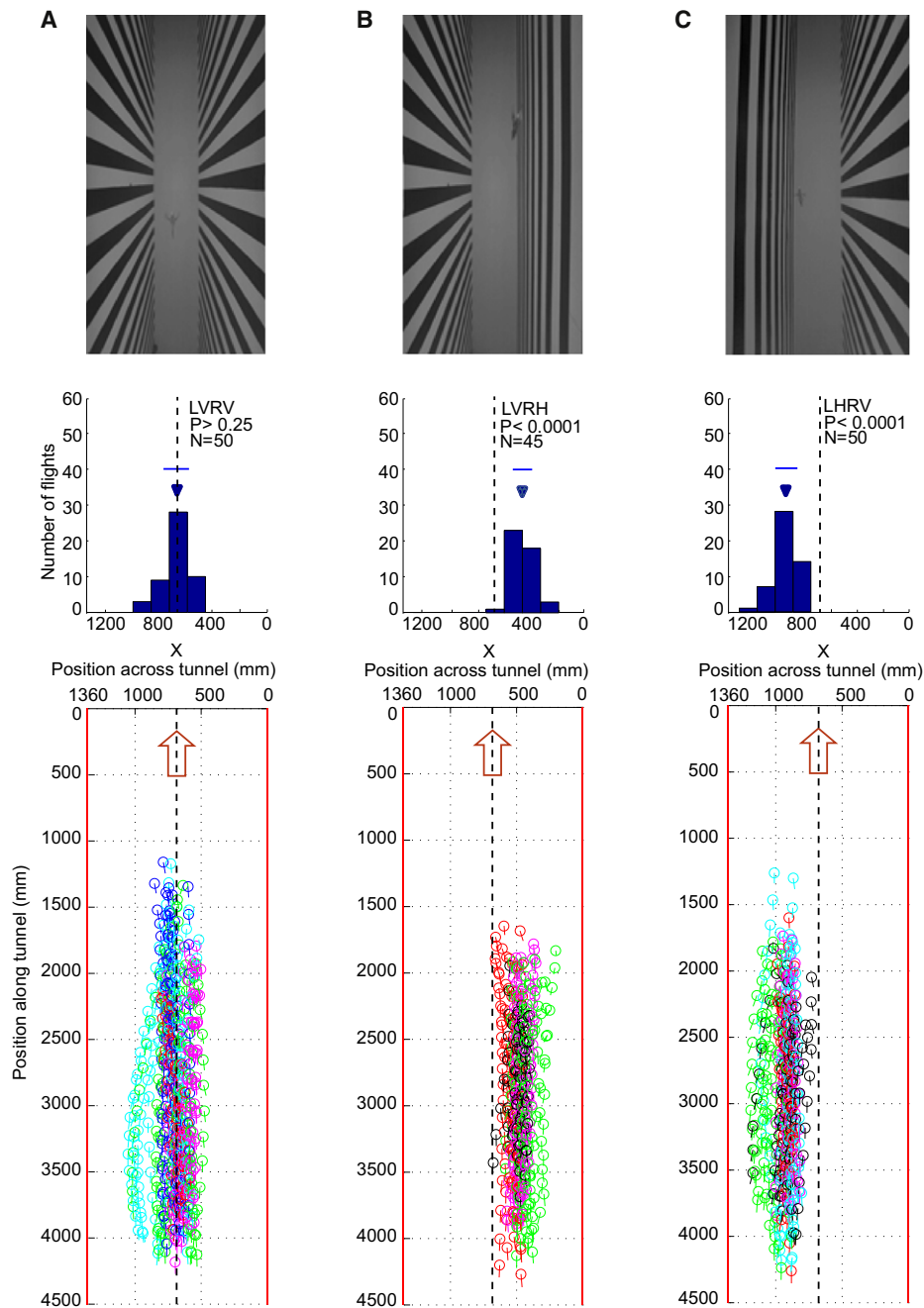*Correspondence: m.srinivasan@uq.edu.au

Figure 1. Bird Flight through Tunnels in which the Walls Are Lined with Vertical or Horizontal Stripes

Trajectories of budgerigars flying in a corridor in which both walls were lined with vertical stripes (A), the left wall was lined with horizontal stripes and the right wall with vertical stripes (B), and vice versa (C). The red arrow denotes the flight direction, which is from the bottom to the top in the images and the plots. The circles denote head position, and the lines denote body orientation. The dashed vertical line denotes the midline of the corridor. The histograms show the distributions of trajectory positions, the small arrowheads indicate the mean trajectory position, and the horizontal bars show the standard error of the mean (SEM) trajectory position. Data were analyzed from five birds, producing a total of 45–50 flights for each condition. P represents the results of t tests for a significant deviation of the mean trajectory position from the midline of the tunnel. The following abbreviations are used: LVRV, left vertical, right vertical; LVRH, left vertical, right horizontal; LHRV, left horizontal, right horizontal.

vertical-striped tunnel (LVRV: left vertical, right vertical), which provides strong optic flow signals (Table 1). This indicates that when the optic flow cues are impoverished, as in the LHRH condition, the birds fly faster in an attempt to restore the strength of the flow to that corresponding to the set point.

Figure 4 summarizes the results of measurements of mean axial flight speed in experiments in which the strength of the optic flow was varied by decorating the walls with various combinations of horizontal or vertical stripes. Four conditions were examined: (1) vertical stripes on both walls (LVRV), (2) horizontal stripes on both walls (LHRH), (3) horizontal stripes on the left wall and vertical stripes on the right wall (LHRV), and (4) vertical stripes on the left wall and horizontal stripes on the right wall (LVRH). Data were obtained from eight birds,
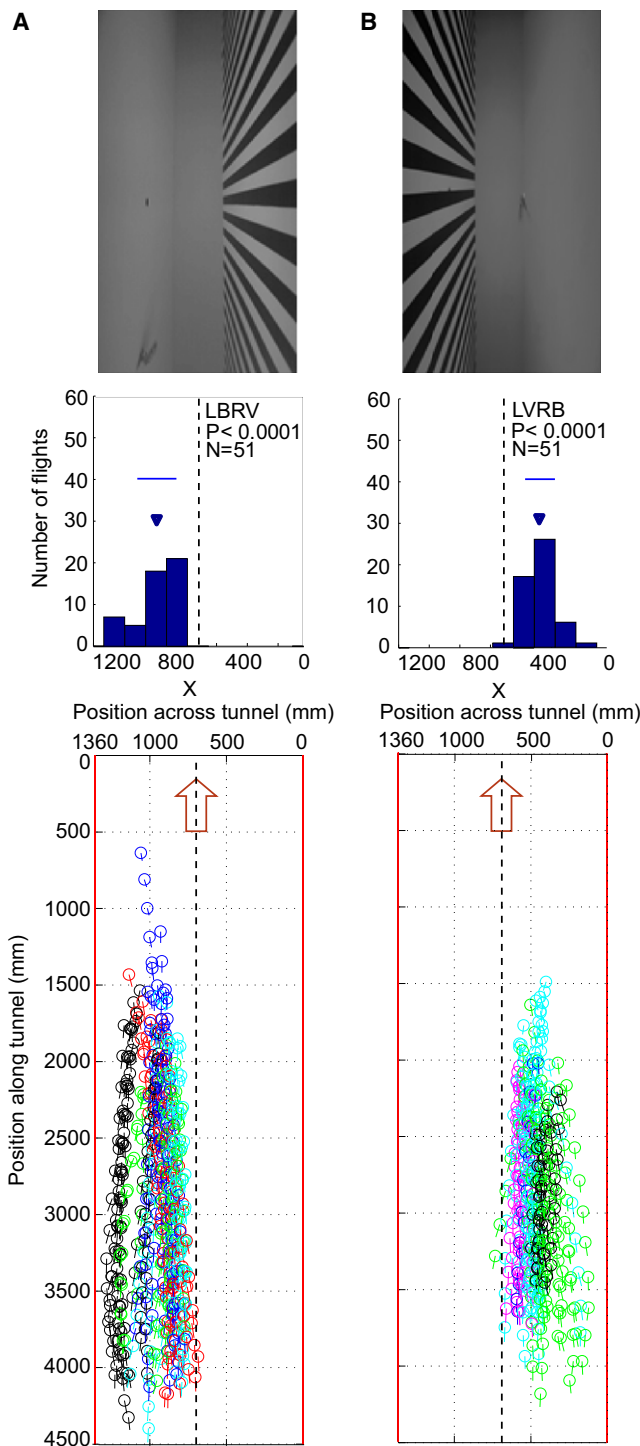
Figure 2. Bird Flight through Tunnels in which the Walls Are Blank or Lined with Vertical Stripes

Trajectories of budgerigars flying in a corridor in which the left wall was blank and the right wall was lined with vertical stripes (A) and vice versa (B). Other details are as in Figure 1. In each case, the birds flew significantly closer to the blank wall (p < 0.0001, t test). Data were analyzed from five birds, producing a total of 51 flights for each condition. The following abbreviations are used: LBRV, left blank, right vertical; LVRB, left vertical, right blank.

and 45–50 flights were recorded in each condition. Analysis of this data reveals that there is a significant variation of mean axial flight speed across the four conditions that were tested (p < 2 × 10$^{-16}$, one way analysis of variance [ANOVA]). The mean axial flight speed is lowest when both walls carry vertical stripes (LVRV), which provide strong optic flow signals. On the other hand, the mean axial flight speed is highest when both walls carry horizontal stripes (LHRH), which provide weak or no optic flow signals. The mean axial flight speeds measured in these two conditions are significantly different (p < 0.05, Multcompare analysis). This is consistent with the results of Figure 3, which showed detailed flight data from three individual birds, and supports the hypothesis that optic flow cues play a role in regulating axial flight speed. When one wall provides a strong optic flow signal and the other provides a weak signal (as in LHRV and LVRH), the birds fly at an intermediate speed that is between the maximum speed (corresponding to LHRH) and the minimum speed (corresponding to LVRV). This finding is again in agreement with the hypothesis, because the LHRV and the LVRH conditions provide global optic flow signals of intermediate strength, when summed over the two eyes. The mean axial flight speeds in the LHRV and the LVRH conditions are each significantly lower than in the LVRV condition and are each significantly higher than in the LHRH condition (p < 0.05 in each case, Matlab Multcompare test).

Similar results are obtained for the LBRV (left blank, right vertical) and LVRB (left vertical, right blank) conditions. Again, in each of these conditions only one wall provides optic flow, and, accordingly, the birds fly at an intermediate speed that is between the maximum speed (corresponding to LHRH) and the minimum speed (corresponding to LVRV) (Table S3).

Although the data displayed in Figure 3 and Figure 4 pertain to axial flight speeds, the results and the outcomes of the statistical analyses are similar for the total flight speeds (Table 1; Figures S1 and S2). This is because the flights are oriented primarily in the axial direction of the tunnel, making the axial flight speeds very similar to the total flight speeds.

What image velocities do the birds experience during flight in the tunnel? For a bird flying at an axial speed of V mm/sec at a distance of d mm from a wall, the angular velocity ω of the image of that wall in the lateral field of view (in a viewing direction at 90 degrees to the flight direction) is given by the following equation:

$$\omega = \left(\frac{180}{\pi}\right)\left(\frac{V}{d}\right)\text{degrees/second.}$$

Let us consider first the vertical-striped tunnel (LVRV), which provides the most robust optic flow. In this tunnel, the birds fly along the midline at a mean axial speed of V = 4,900 mm/sec. Because the distance to either wall is d = 680 mm, we can estimate from equation 1 that each eye would have experienced an average lateral image angular velocity of approximately 410 deg/s. In the LHRV condition, the mean axial flight speed is V = 5,602 mm/sec (Table S3) and the distance d to the vertical-striped wall on the right-hand side (the only wall that provides optic flow) is 934 mm (Table S2). In this case, we estimate the average angular velocity of the image in the lateral field of the right eye to be 344 deg/s. For the LVRH condition, the mean axial flight speed is V = 5,457 mm/sec (Table S3), and the distance d to the vertical-striped wall on the left-hand side (the only wall that provides optic flow) is 885 mm (Table S2), from which we estimate the average
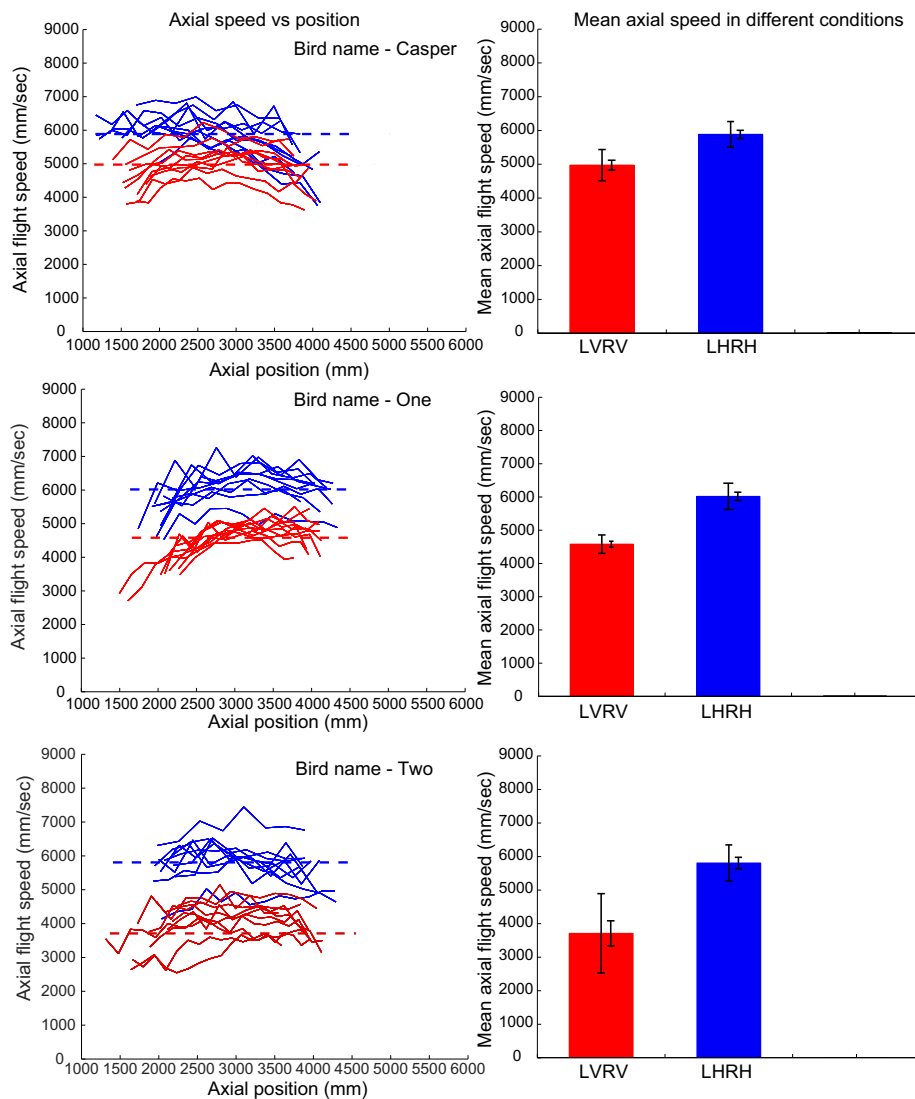
**Figure 3. Flight Speed Profiles**

Profiles of axial flight speed versus position for individual trajectories (left-hand panels) and mean axial flight speeds (right-hand panels) for the condition when both walls carry vertical stripes (LVRV, red) and when both walls carry horizontal stripes (LHRH, blue). The colored dotted lines in the left-hand panels and the correspondingly colored bars in the right-hand panels show the mean axial flight speed for each condition. In the right-hand panels, the error bars associated with each column depict the standard deviation (SD) (left) and the SEM (right). Data are shown for three different birds: Casper, One, and Two. The following abbreviations are used: LVRV, left vertical, right vertical; LHRH, left horizontal, right horizontal.

velocity of the image in the lateral field of the left eye to be 353 deg/s. Similarly, we can calculate from the data in Tables S2 and S3 that the LVRB condition produces an average image velocity of 311 deg/s in the left eye and the LBRV condition an average image velocity of 312 deg/s in the right eye.

These image velocities are of the same order of magnitude as the lateral image velocities experienced by honeybees (250–320 deg/s; [6, 7]) and by bumblebees (ca. 260 deg/s, calculated from a mean flight speed of 450 mm/sec in a tunnel of width 200 mm, as reported in [12]) during flight in tunnels lined with vertical stripes.

It is possible that our relatively short tunnel (7,280 mm long, approximately 36 budgerigar body lengths) prevented the birds from flying faster when they were deprived of optic flow in the LHRH condition. Thus, the differences in flight speed that were observed under the various conditions may

have been more pronounced if the birds had been flown in a longer tunnel. Nevertheless, the observation of significant pattern-induced variations in flight speed, even in these relatively short tunnels, indicates that optic flow cues play an important role in the control of flight speed in birds.

We cannot exclude the possibility that birds use additional cues to guide their flight through narrow passages, particularly when optic flow cues are not available. For example, when both walls are blank or lined with horizontal stripes, the birds may use geometrical cues based on the overall shape of the tunnel (as defined by its horizontal and vertical edges) to steer a middle course. In addition, the landing perch, or the boundaries of the end wall of the tunnel could provide cues related to image expansion and time to contact (e.g., [3–5]) that trigger and control the deceleration in preparation for landing. In principle, there are a number of additional strategies that the birds could

Table 1. Statistical Comparison of Flight Speeds under LVRV and LHRH Conditions

| Bird | Experimental condition | p (t test) |
|------|------------------------|-----------|
| Casper | Mean axial speed, LVRV versus LHRH | <0.0002 |
| | Mean total speed, LVRV versus LHRH | <0.0002 |
| One | Mean axial speed, LVRV versus LHRH | <0.0001 |
| | Mean total speed, LVRV versus LHRH | <0.0001 |
| Two | Mean axial speed, LVRV versus LHRH | <0.0001 |
| | Mean total speed, LVRV versus LHRH | <0.0001 |

Results of statistical comparisons (p, two-sample t test) of mean axial flight speeds and mean total flight speeds under conditions in which both walls of the tunnel carry vertical stripes (LVRV: left vertical, right vertical) or horizontal stripes (LHRH: left horizontal, right horizontal) for three different birds.

potentially use to control and regulate flight speed. Some examples are (1) ignoring all sensory input and simply maintaining a constant (predetermined) thrust, (2) using stereo ranging of objects directly ahead to monitor and ensure a constant velocity of approach, and (3) regulating flight speed by sensing air speed. Although we cannot exclude the possibility that these strategies are also being used, our results clearly indicate that optic flow cues definitely play a role in controlling flight speed and guiding flight through narrow passages. This is because manipulating the optic flow cues affects the birds' flight in ways that are predicted by this hypothesis.

Our findings demonstrate, for the first time, that birds use optic flow signals to (1) steer a collision-free path through narrow passages and (2) monitor and regulate their speed during flight in such passages. In these contexts, birds show a behavior that is very similar to that previously observed in honeybees [6–11], bumblebees [12], and flies [13], suggesting that some of the principles that underlie visually guided flight may be shared by all diurnal flying animals. They also pave the way for exploring the possible role of guidance based on optic flow in a variety of other avian flight maneuvers such as control of flight altitude and landing and estimation of distance flown, as has been demonstrated in insects [14–16].

### Experimental Procedures

#### Subjects
Adult male wild-type budgerigars (eight birds, approximately 1–2 years old) served as subjects for the experiments. The birds were obtained from different local breeders. Male budgerigars were identified by a characteristically green plumage and a blue coloration of the cere, whereas the female budgerigars were identified by a pink or brown cere. The birds were housed in pairs in identical cages of length 47 cm, breadth 34.5 cm, and height 82 cm and were not under acoustic or visual isolation.

#### Experimental Arena
The budgerigars flew indoors in a purpose-built, climate-controlled corridor (temperature: 23°C–25°C, relative humidity: 35%–40%) of dimensions 7,280 mm (length), 2,440 mm (height), and 1,360 mm (width). The walls were painted with Dulux low sheen acrylic paint (white 56289801), containing Wattyl Divinity Dye (product number IV68), which produced a color that was off-white (light cream) in appearance. The floor was painted with Dulux low sheen acrylic paint (white 56289801), containing Wattyl Pewter Cup Dye (product number IV113), which produced a color that was light gray in appearance.

Depending upon the experiment, each wall was either left blank or decorated with black, machine-cut cardboard stripes, 11 cm wide and separated by 11 cm edge to edge, oriented either vertically or horizontally (Figure 1). Illumination was provided by four lamps in the ceiling, with two 36 W fluorescent tubes (L 36 W/880 Osram Sky White FLH1) in each lamp, driven by a 40 kHz ballast to avoid any perception of flicker. The light levels, measured at the geometrical center of the tunnel, were 260 lux (each side wall), 1,230 lux (ceiling), and 145 lux (floor).
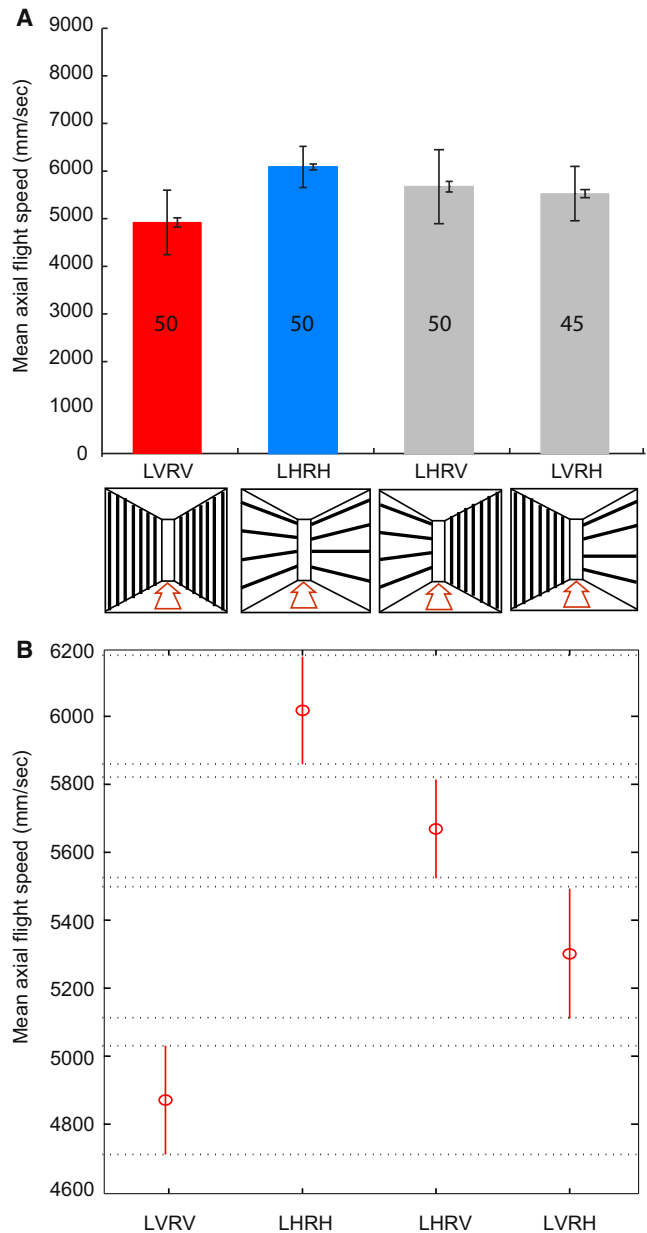


**A**



**B**

Figure 4. Axial Flight Speeds under Different Conditions

(A) Mean axial flight speeds of birds flying in tunnels in which both walls were lined with vertical stripes (LVRV), horizontal stripes (LHRH), horizontal stripes on the left and vertical stripes on the right (LHRV), or vertical stripes on the left and horizontal stripes on the right (LVRH). The error bars on each column depict SD (left) and SEM (right). Data were analyzed from a total of eight birds. The number of flights analyzed for each condition is shown in each column.

(B) Result of a Multcompare analysis (see Experimental Procedures) to test for statistical differences in flight speed among the four different conditions. The nonoverlapping error bars indicate that the mean axial speed in each condition is significantly different from that at each of the three other conditions, at the p < 0.05 level.

The following abbreviations are used: LVRV, left vertical, right vertical; LHRH, left horizontal, right horizontal; LHRV, left horizontal, right horizontal; LVRH, left vertical, right horizontal.

### Training of Birds
Male and female budgerigars were brought individually by the experimenter into one end of the corridor. They were induced to take off from a hand-held perch by rotating it slowly and were trained initially to fly to the other end of

the corridor to join a companion bird, kept in a cage. In the later stages of training, the companion bird was no longer necessary: the birds automatically took off and flew to the other end of the corridor when the perch was rotated and either landed on a perch at the far end or made a U-turn and returned to the experimenter's perch. For each bird, this shaping and training procedure took approximately 30–40 flights, spread over 3–5 days. Filming of the flights was then commenced.

### Filming of Flights
Flights of individual birds were captured in three dimensions using two high-speed video cameras (DRS lightning RDT, DRS Technologies Inc.) at a rate of 250 frames/sec. The cameras were controlled by a custom-configured desktop computer running special-purpose software (MiDAS 2.0, Xcitex, Inc.). One camera was placed at the center of the ceiling of the corridor, looking downwards. The other camera was placed at the center of the end wall of the corridor toward which the birds flew, and it looked horizontally along the axis of the corridor. Each camera, equipped with a wide-angle lens, had a field of view of 110 deg × 93 deg. Each flight yielded two synchronized image sequences, one representing an overhead view of the bird and the other a front view of the bird during its flight along the corridor. Although the cameras had relatively wide fields of view, the length of the flight segment that was captured by the overhead camera depended upon the height at which the bird flew—the greater the height, the shorter the segment. This is the reason for the variation in the lengths of the individual flights shown in Figure 1 and Figure 2.

### Camera Calibration
Stereo calibration of the cameras was carried out using a reference checkerboard pattern (check size 150 mm × 150 mm) in association with the J.Y. Bouguet Camera Calibration Toolbox for Matlab [17]. This procedure delivered the calibration parameters for each camera (including characterization of imaging distortions) and also determined the precise 3D position and orientation of one camera with respect to the other. The standard deviations of the positional errors along the x (width), y (height), and z (length) axes of the tunnel were 2.30 mm (0.65%), 5.49 mm (0.22%), and 20.72 mm (0.28%), respectively.

### Digitization and Reconstruction of Flight Trajectories
Flight trajectories were digitized frame by frame by using a custom-designed Matlab program and a mouse-driven cursor to manually track, and reconstruct in 3D, the positions of two points on the bird that were well defined and clearly visible in both camera views. These points were chosen to be (1) the head of the bird, which was clearly visible by virtue of the yellow patch that it carried and (2) the base of the bird's tail (the location where the tail is attached to the body), which was also clearly visible because of the abrupt narrowing of the body at this point. In Figure 1 and Figure 2, the circles represent head position and the line segments denote body orientation as determined from the two digitized points. For clarity of illustration, the resulting trajectories were subsampled prior to generating the plots of Figure 1, Figure 2, and Figure 3.

### Statistical Analysis of Data
One-sample t tests were used to check for statistically significant differences between the mean X positions of the flight trajectories and the X position of the midline of the tunnel for each of the conditions illustrated in Figure 1 and Figure 2, namely LVRV, LVRH, LHRV, LBRV, and LVRB. The procedure for this statistical analysis is described in [18].

A one-way ANOVA (Matlab function ANOVA1 from Mathworks) [19] and a Multcompare statistical analysis (Matlab function Multcompare from Mathworks) [20] were used to check for statistically significant variations in the mean axial flight speeds and the mean total flight speeds across the experimental conditions LVRV, LHRH, LHRV, and LVRH in Figure 4B and Figure S2B.

A two-tailed, two-sample t test for unequal variances (Matlab function t test2 from Mathworks) was used to check for statistically significant differences between the flight speeds (measured as mean axial speed or mean total speed) between the experimental conditions LVRV and LHRH, to obtain the results shown in Table 1.

### Supplemental Information

Supplemental Information includes two figures, three tables, and three movies and can be found with this article online at doi:10.1016/j.cub.2011.09.009.

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### Note Added in Proof

At the time this article went to press, the following new study was published, providing further evidence that flying insects use optic flow cues to control their flight speed: Portelli, G., Ruffier, F., Roubieu, F.L., and Franceschini, N. (2011). Honeybees' speed depends on dorsal as well as lateral, ventral and frontal optic flows. PLoS ONE *6*, e19486.