The Journal of Experimental Biology 213, 1625-1632

doi:10.1242/jeb.038802

Minimum viewing angle for visually guided ground speed control in bumblebees

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Accepted 26 January 2010

SUMMARY

To control flight, flying insects extract information from the pattern of visual motion generated during flight, known as optic flow. To regulate their ground speed, insects such as honeybees and *Drosophila* hold the rate of optic flow in the axial direction (front-to-back) constant. A consequence of this strategy is that its performance varies with the minimum viewing angle (the deviation from the frontal direction of the longitudinal axis of the insect) at which changes in axial optic flow are detected. The greater this angle, the later changes in the rate of optic flow, caused by changes in the density of the environment, will be detected. The aim of the present study is to examine the mechanisms of ground speed control in bumblebees and to identify the extent of the visual range over which optic flow for ground speed control is measured. Bumblebees were trained to fly through an experimental tunnel consisting of parallel vertical walls. Flights were recorded when (1) the distance between the tunnel walls was either 15 or 30 cm, (2) the visual texture on the tunnel walls provided either strong or weak optic flow cues and (3) the distance between the walls changed abruptly halfway along the tunnel's length. The results reveal that bumblebees regulate ground speed using optic flow cues and that changes in the rate of optic flow are detected at a minimum viewing angle of 23–30 deg., with a visual field that extends to approximately 155 deg. By measuring optic flow over a visual field that has a low minimum viewing angle, bumblebees are able to detect and respond to changes in the proximity of the environment well before they are encountered.

Key words: bumblebee, flight control, flight speed, ground speed, vision.

INTRODUCTION

For safe and reliable navigation, flying insects require information about their current position, speed and orientation in space and information about the proximity of surfaces in their environment. This information is extracted, to a large extent, from the pattern of visual motion that is generated on the retina during flight. This pattern of apparent motion is called optic flow and comprises two components; rotational optic flow – caused by rotations *about* the roll, pitch or yaw axes – and translational optic flow, generated by translations *along* the roll, pitch or yaw axes (Koenderink, 1986). Unlike rotational optic flow, the translational optic flow varies with the distance to surfaces and the translational speed of the viewer with respect to these surfaces, i.e. surfaces that are closer generate higher image angular velocities than those that are further away. Properties of translational optic flow, such as the direction and velocity of motion in the visual scene, can thus provide cues for detecting the proximity of objects in the environment as well as information about the translational movement of the viewer (Gibson, 1950; Koenderink and van Doorn, 1987; Whiteside and Samuel, 1970).

Several investigations have revealed that translational optic flow cues are important for ground speed control in insects. In this context, ground speed is defined as the forward speed of the insect with respect to the ground, in contrast to its speed with respect to the air (airspeed). Honeybees (Baird et al., 2005; Srinivasan et al., 1996) and *Drosophila* (David, 1982; Fry et al., 2009) regulate their ground speed by holding constant the rate of translational optic flow in the axial, or front-to-back, direction (this type of optic flow will be referred to as axial optic flow). This strategy will ensure that ground speed is high when flying in an open field, where distances to surfaces are large, and low during flight through dense vegetation, where distances to surfaces are small and the chance of collision high. Maintaining a constant image velocity on the retina may therefore function as a useful mechanism for ensuring that the speed of flight is automatically adjusted to a level that is safe and appropriate to the environment.

One interesting consequence of this strategy of ground speed control is that its performance varies with the angle at which axial optic flow is measured. When an insect flies from an open field into dense foliage, the apparent rate of axial optic flow will increase, causing the insect to decrease its ground speed. However, the point at which this change in proximity is first detected will vary with the minimum viewing angle (defined here as the angular deviation from the frontal direction of the longitudinal axis of the insect) at which changes in axial optic flow are perceived (Fig. 1). The lower the minimum viewing angle, the earlier the change in the surroundings that lie ahead will be detected. Early detection of a change in environment is advantageous because it would allow an insect to adjust its ground speed well before entering a new environment. This would be especially important when approaching dense, cluttered environments where a decrease in flight speed would increase the chances of detecting and avoiding nearby obstacles. One disadvantage of detecting changes in optic flow at a low viewing angle however, is that the magnitude of optic flow decreases non-linearly with decreasing viewing angle (Gibson, 1950), making the absolute difference in optic flow generated by a change in the environment more difficult to perceive. Furthermore, the signal will be more vulnerable to noise and detection errors. Increasing the minimum viewing angle at which changes in optic flow are detected would limit these errors, but would decrease the time between detecting a change in environment and entering the new environment – potentially increasing the chance of collisions. Despite the influence of viewing angle on the function of a visually guided ground speed control strategy, very little is known about where in the visual field

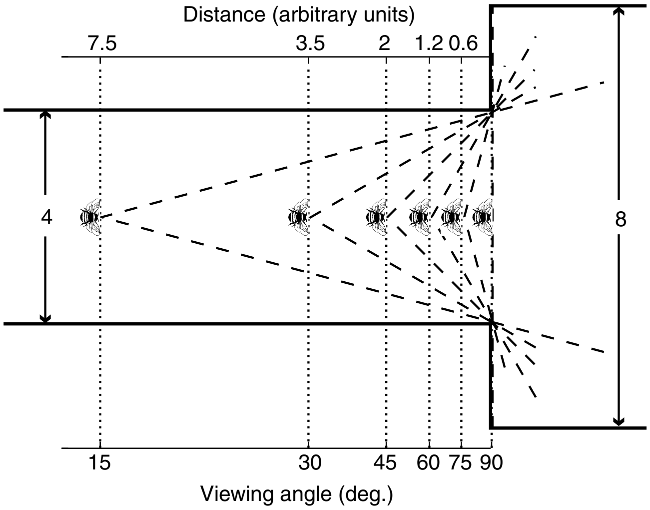

Fig. 1. Illustration of the relationship between the angle at which axial optic flow is measured and the distance at which a change in the proximity of the environment can be detected. Black lines represent the walls of an experimental tunnel. Dotted lines indicate the distance (top scale) at which the change in tunnel width first becomes apparent for each given viewing angle (defined as the angular deviation from the longitudinal body axis, bottom scale) for a bee flying along the midline of the tunnel.

flying insects first start to measure optic flow for ground speed control.

One of the few behavioural experiments to investigate the visual angle at which optic flow for flight control is being measured was performed by Srinivasan et al. (Srinivasan et al., 1991). The aim of the study was to identify the region of the eye that was involved in the centring response – a behaviour in which honeybees balance the optic flow in each eye in order to fly between nearby obstacles. Honeybees appeared to respond to the presence of a black bar in an otherwise white experimental tunnel only when the bar passed the lateral region of the eye, indicating that the minimum viewing angle at which honeybees detect and respond to changes in optic flow lies in the lateral region of the visual field. This result is also consistent with the findings of an earlier study, which showed that honeybees use the image motion from landmarks in the lateral visual field to locate a frontally positioned target (Lehrer, 1990). These results indicate that, in honeybees, the lateral region of the visual field plays an important role in mediating optic-flow-driven tasks such as centring and short-range goal localisation.

The importance of viewing angle on the function of optic-flow-based behaviours has recently been demonstrated for visually guided unmanned aerial vehicles (UAVs). Hrabar et al. (Hrabar et al., 2006) showed that, in an environment consisting of parallel walls, the stability of the centring response in a UAV depends upon the angle at which optic flow is measured. In another study, Beyeler et al. (Beyeler et al., 2009) showed that the performance (measured as the flight duration before crashing) of a UAV using optic flow to avoid obstacles also changes significantly with the angle at which optic flow is measured. Both of these studies concluded that optimal performance was achieved when optic flow was measured at a single viewing angle of 45 deg. Interestingly, these empirical results from UAVs are in contrast to the more lateral viewing measured from the centring response in a flying insect (Srinivasan et al., 1991).

Riley et al. (Riley et al., 1999) hypothesised that bumblebees regulate their ground speed by holding constant the rate of axial optic flow from the ground beneath them. When flying in windy conditions, bumblebees do not maintain a constant ground speed. Instead, they tend to fly slower and lower in head winds, and faster and higher in tail winds. Based on these observations, the authors hypothesised that, to maintain constant the rate of optic flow beneath them when flying in strong head winds, bumblebees would have to decrease their height above the ground until the apparent rate of optic flow reaches the desired set point of the visual system. Similarly, in strong tail winds bumblebees would experience an increased rate of optic flow from the ground and would therefore increase their height to decrease the perceived rate of optic flow. However, Riley et al. (Riley et al., 1999) were unable to test their hypothesis as the harmonic radar information they used did not provide accurate data about the height at which the observed bumblebees were flying.

We have explored the properties of visual ground speed control in the bumblebee. We began by investigating the importance of visual cues for ground speed control and tested the hypothesis that, like honeybees and *Drosophila*, bumblebees regulate their ground speed by holding the rate of axial optic flow constant. We then examined further the mechanisms of visually guided ground speed control by investigating the response to an abrupt change in optic flow. In particular, our aim was to identify the minimum visual angle and the extent of the visual field over which bumblebees measure optic flow for ground speed control.

MATERIALS AND METHODS

Experimental animals

Bumblebees (*Bombus terrestris* L.) from commercial bumblebee hives (Koppert, UK) were used in the experiments. Each hive, containing approximately 200 individuals, was placed in an aluminium netting cage (2.3 m long, 2 m high and 2 m wide) at least 4 days before the experiments commenced. Several different hives were used over the course of the experiments. The cage was situated inside a room with two large windows that provided natural sunlight. The temperature within the room remained relatively stable during the experimental period, with experiments being performed at temperatures between 19 and 26°C.

In the initial stage of training, a plastic feeder containing sugar solution was placed near the hive entrance. Once a number of bees were regularly visiting the feeder, it was moved gradually into the experimental tunnel. In this way, a number of bees learned to visit the feeder at the end of the tunnel. These trained bees were then colour-marked using acrylic water-soluble paint for identification of individuals in the experiments.

Flight tunnel

The tunnels used in the experiments consisted of two parallel 30 cm high vertical walls and a smooth flat floor; both the walls and floor were 2 m in length [this method has been modified from that of Srinivasan et al. (Srinivasan et al., 1991)]. The top of the tunnel was covered with insect netting. Four DC light sources were placed around the tunnel to provide additional light for the experiments.

Experiment 1: measurement of the effect of optic flow on ground speed

The flights of bees flying to the feeder were recorded when the distance between the tunnel walls was set at a constant width of either 15 or 30 cm. In each case, the tunnel walls and floor were lined with a randomised chequerboard pattern consisting of 1 cm × 1 cm black and white squares (Fig. 2A). The apparent rate of optic flow varies inversely with the distance to the visual environment. Thus, for a given ground speed, the apparent rate of optic flow perceived by a bumblebee flying in the centre of the tunnel will decrease as the distance between the tunnel walls increases.

To test the effect of visual cues (rather than other cues generated by changing the distance between the tunnel walls) on the regulation of ground speed, we minimised the axial optic flow cues in the tunnel by lining the tunnel walls and floor with an axial stripe pattern. This pattern consisted of alternating black and white, 3 cm wide stripes running the length of the tunnel (Fig. 2B). Although the axial optic flow cues generated by the random chequerboard pattern would be strong, flight in the direction of the stripes (along the long axis of the tunnel) would produce very little apparent axial optic flow on the retina. In this experiment, we tested the effect of minimising axial optic flow cues when the tunnel walls were either 15 or 30 cm apart.

Experiment 2: measurement of the effect of abrupt changes in tunnel width on ground speed

The distance between the walls was changed abruptly halfway along the tunnel, such that the distance between the walls in the first 1 m section of the tunnel was either larger or smaller than the distance between the walls in the second 1 m section. Flights of bees were recorded in two different tunnel configurations: 15 to 30 cm (Fig. 2C) and 30 to 15 cm (Fig. 2D). Two control experiments consisting of constant width 15 and 30 cm wide tunnels were also conducted and the results were compared with those obtained in the variable width tunnels. In this experiment, the texture on the floor of the tunnels was removed in order to simplify our estimations of the visual region that was being used to measure optic flow for ground speed regulation. Thus, in all of these experimental conditions, the walls of the tunnel were lined with a randomised chequerboard pattern whereas the floor was blank white, providing minimal visual features. In a further experimental condition, flights of bees were recorded when the distance between the walls remained constant at 15 cm but the pattern on the walls changed abruptly in the centre of the tunnel from the chequerboard to the axial stripe pattern.

Recording and analysis of flight trajectories

The bees were allowed to visit the feeder at the end of the experimental tunnel for at least 1 day before recording commenced. Trials for each experimental condition were conducted over 2–3 days. Flights of bees flying through the tunnel to the feeder were recorded at 60 Hz using a Mikrotron MotionBLITZ EoSens (Unterschleisheim, Germany) camera mounted above the centre of the tunnel. The position of the bee and the orientation of the long axis of the body were determined using an automated tracking program (Lindemann, 2005). The bee position data was calibrated using the output of the Camera Calibration Toolbox for Matlab (Bouguet, 1999) and converted to metres using known size reference patterns placed at different heights from the tunnel floor. The relationship between metre and pixel distances was such that it varied by less than 0.01 m per pixel between the floor and top of the tunnel. This meant that, by using an intermediate metre per pixel value, the distance error associated with bees flying at different heights in the tunnel would be minimised.

To avoid pseudo-replication, the data from repeated flights from individual bees were averaged so that each individual was considered only once per experimental treatment. Data from bees that flew a minimum of two times were included in the analysis. Non-parametric Wilcoxon rank sum tests at the 5% significance level were performed on the data.

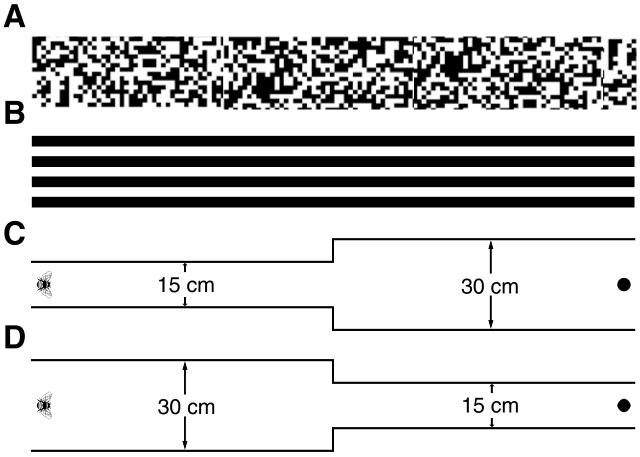

Fig. 2. Experimental patterns and setup. (A) The randomised chequerboard pattern used to generate strong axial optic flow cues and (B) the axial stripe pattern used to generate weak axial optic flow cues in experiment 1. (C) The 15 to 30 cm and (D) the 30 to 15 cm abrupt tunnel configurations used in experiment 2; black lines represent the tunnel walls. The feeder is indicated as a black circle.

Ground speed was calculated by finding the two-dimensional distance travelled between successive frames and dividing this value by the time step between the frames, 0.0167 s. Ground speed was calculated over a distance of 0.8 m in the central section of the tunnel. In experiment 2, ground speed data was averaged over 2 cm bins. The ground speed at each 2 cm step was then directly compared with the ground speed in the relevant control condition (15 cm constant width tunnel for the 15 to 30 cm abrupt change tunnel and 30 cm constant width tunnel for the 30 to 15 cm abrupt change tunnel – no texture on the floor) using Wilcoxon rank sum tests. A change in ground speed was deemed to occur when the difference between the ground speed in the abrupt tunnel and the ground speed in the control tunnel were significant (at the 5% level) and remained significant for the remaining distance of the tunnel. In the second half of the tunnel, ground speed was deemed to have reached the speed obtained in the control tunnel of the same width when there was no longer a significant difference between these values.

RESULTS

Experiment 1: effect of axial optic flow on ground speed control

In this experiment, we compared the ground speeds of bees flying in the experimental tunnel when the distance between the walls was either 15 or 30 cm. We recorded 34 flights from seven bees in the 15 cm tunnel and 40 flights from six bees in the 30 cm tunnel. Bumblebees fly significantly faster in the 30 cm tunnel, $0.46\pm0.09\,\mathrm{m\,s^{-1}}$ (mean ± s.d.), than in the narrower 15 cm tunnel, $0.29\pm0.05\,\mathrm{m\,s^{-1}}$ (Wilcoxon rank sum, N=13, P<0.001; Fig. 3). One possible explanation for the difference in ground speed between the two tunnels is that the bees were changing their ground speed in response to the different mechanosensory cues present in each tunnel. To test this possibility, we recorded the flights of bees flying in both the 15 and 30 cm wide tunnels when the pattern on the walls and floor provided very weak axial (front-to-back) optic flow cues. We recorded 26 flights from nine bees in the 15 cm tunnel and 30 flights from eight bees in the 30 cm tunnel. Bumblebees flew at $0.98\pm0.23\,\mathrm{m\,s^{-1}}$ in the 15 cm tunnel, and at $0.92\pm0.28\,\mathrm{m\,s^{-1}}$ in the 30 cm tunnel (Fig. 3). When the tunnel was lined with axial stripes,

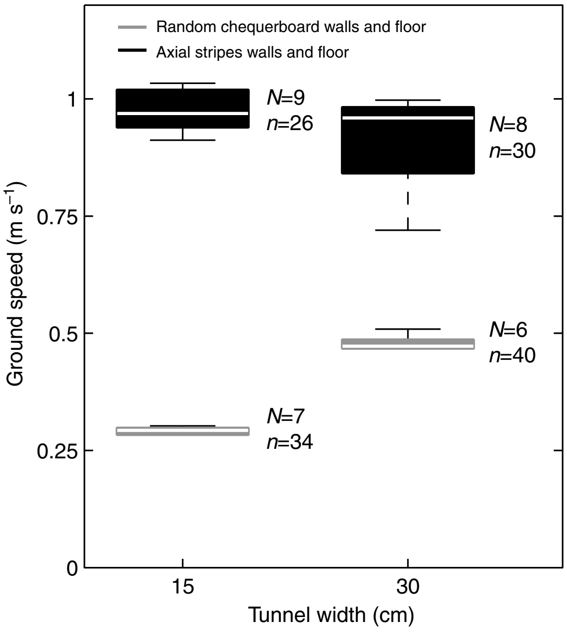

Fig. 3. Effect of axial optic flow on ground speed control. A box plot of the ground speed of bees flying in either a 15 or 30 cm wide tunnel when the walls and floor are lined with a random chequerboard pattern (grey boxes), or an axial stripe pattern (black boxes). Boxes indicate the distance between the lower and upper quartile values, white lines indicate the median values and whiskers indicate the entire spread of the data. *N* is the number of bees, *n* is the number of flights.

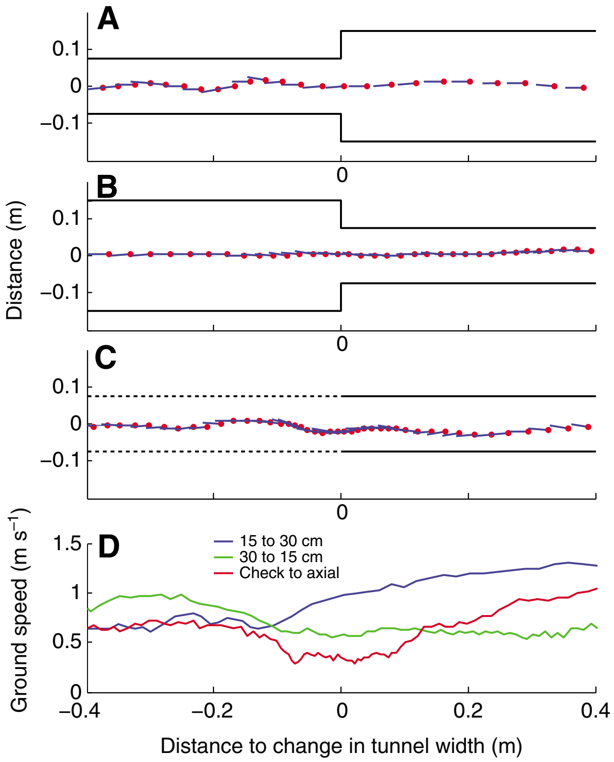

Fig. 4. Example of flight trajectories of bumblebees flying in the experimental tunnel when the width of the tunnel changed from 15 to 30 cm (A), 30 to 15 cm (B) or when the tunnel width remained constant but the pattern changed from chequerboard to axial stripes (C). Red circles represent the position of the bee every 0.033 s, blue lines indicate the orientation of the body long axis, black lines represent the tunnel walls. (D) The ground speed of the flight trajectories shown in A (blue line) B (green line) and C (red line).

there was no longer an effect of tunnel width on ground speed (Wilcoxon rank sum, *N*=17, *P*=0.606). The results of this experiment indicate that the bumblebees are relying primarily on axial optic flow cues to regulate ground speed. This theory is further supported by the two- to threefold increase in ground speed recorded in the axial stripe tunnels compared with that observed in the tunnels lined with chequerboard patterns. An increase in the ground speed is exactly what can be expected from a system that aims to hold constant the rate of translational optic flow between the two sets of tunnels.

Experiment 2: effect of abrupt changes in tunnel width on ground speed

In this experiment, we recorded the ground speed of bees flying in the experimental tunnel when the distance between the walls changed abruptly (from 15 to 30 cm or from 30 to 15 cm), 1 m along the length of the tunnel (example flight trajectories are shown in Fig. 4). These data were compared with data from two control conditions, a 15 cm wide constant width tunnel and a 30 cm wide constant width tunnel. We recorded 56 flights from nine bees in the 15 cm control condition, 45 flights from 11 bees in the 30 cm control condition, 57 flights from 19 bees in the 15 to 30 cm condition and 35 flights from eight bees in the 30 to 15 cm condition.

In the 15 to 30 cm tunnel, the ground speed of bees increased significantly from the ground speed in the 15 cm wide constant width tunnel at a distance of 0.14 m before the change in tunnel width (Wilcoxon rank sum, *N*=28, *P*=0.001; Fig. 5A). In the second half of the tunnel, ground speed reached the same level as in the 30 cm tunnel at a distance of 0.16 m after the change in tunnel width (Wilcoxon rank sum, *N*=28, *P*=0.16; Fig. 5A). In the 30 to 15 cm tunnel, the ground speed of bees decreased significantly from the ground speed in the 30 cm wide constant width tunnel at a distance of 0.26 m before the change in tunnel width (Fig. 5B; Wilcoxon rank sum, *N*=19, *P*=0.002). In the second half of the tunnel, ground speed reached the same level as the ground speed in the 15 cm tunnel at a distance of 0.18 m after the change in tunnel width (Wilcoxon rank sum, *N*=19, *P*=0.23; Fig. 5B). The results of this experiment again reveal that the bees do indeed change their ground speed in response to the change in tunnel width. More interestingly, in both conditions, the ground speed of the bees changed significantly from the control condition well before the bees had reached the change in tunnel width. The results also indicate that bumblebees do not reach the expected ground speed for the new tunnel width until some distance after the change.

Thirty flights from 11 bees were recorded in a tunnel of constant width, but the pattern changed abruptly from a chequerboard pattern to an axial stripe pattern halfway along its length. This experiment was designed to control for the possibility that the bees change their flight speed primarily as a response to the physical change in the distance between the tunnel walls – rather than to the change in the rate of axial optic flow. Again, ground speed changed significantly from the control condition, at –0.18 m, well *before* the bee has reached the change in patterns (Fig. 5C; Wilcoxon rank sum, *N*=20, *P*=0.01). This result supports the conclusion that the visual field over which bumblebees are measuring axial optic flow cues to regulate ground speed begins at a relatively low visual angle.

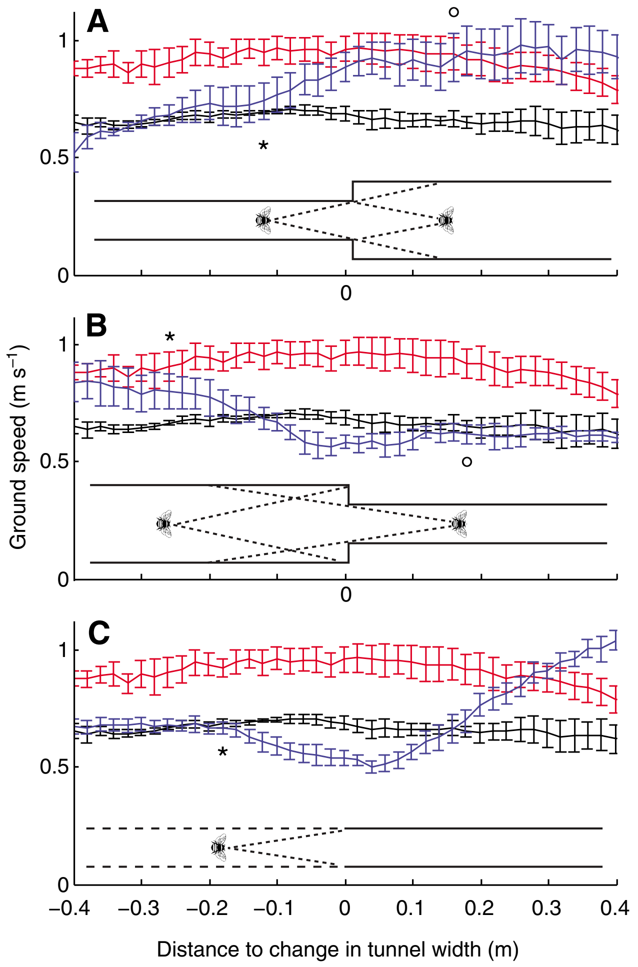

Fig. 5. Effect of abrupt changes in tunnel width on ground speed. Effect of abrupt changes in axial optic flow on ground speed (blue lines) when the width of the tunnel changes from 15 to 30 cm (A), from 30 to 15 cm (B) or when the pattern in a 15 cm wide constant width tunnel changes from random chequerboard to axial stripes (C). Black lines represent the mean ground speed of bumblebees flying in the 15 cm wide constant width tunnel, and red lines represent the mean ground speed of bumblebees flying in the 30 cm wide constant width tunnel. Means are calculated over 2 cm bins, error bars represent the standard deviation of data within each 2 cm bin (see Materials and methods). Asterisks indicate the position at which the test condition (blue lines) deviates significantly from the control condition (15 cm constant width for A and C; 30 cm constant width for B). Circles indicate the position at which the test condition first reaches the level of the control condition in the second half of the tunnel (30 cm constant width for A; 15 cm constant width for B). We recorded 45 flights from 11 bees in the 30 cm control condition, 56 flights from nine bees in the 15 cm control condition, 57 flights from 19 bees in the 15 to 30 cm condition (A), 35 flights from eight bees in the 30 to 15 cm condition (B) and 30 flights from 11 bees in the chequerboard to axial condition (C).

Based on our observations from experiment 1, we would expect the bees to speed up when they encounter the axial stripe pattern. However, the bees responded to the change in patterns by decreasing their ground speed and did not speed up until they had passed the change. This drop in speed is most likely a response to the sudden disappearance of axial optic flow cues. Once the bees had flown past this change, they did, however, increase their ground speed to a value that greatly exceeded the ground speed recorded in the first section of the tunnel.

Observations of flight trajectories

To be able to approximate the extent of the visual field over which bumblebees detect and respond to changes in optic flow, it is necessary to obtain information about the lateral position and orientation of the bees as they fly through the tunnel. The lateral distance from the midline of the tunnel of bees flying in the 15 to 30 cm tunnel is 0.01±0.005 m (mean ± s.d.) before the change in tunnel width. In the 30 to 15 cm tunnel, the mean lateral position before the change in tunnel width is 0.01±0.008 m. The orientation of the head, and therefore the visual field, is also crucial for understanding what visual information the bees receive as they approach the change in tunnel width. From the recordings taken in this experiment, it was not possible to resolve the head position. However, subsequent observations of close-up images taken of bumblebees flying in the tunnel reveal that the head is oriented in line with the long axis of the body for most of the time (data not shown). The orientation of the long axis of the body (which could be resolved in the recordings taken during this experiment) therefore appears to provide a reasonable indication of the orientation of the visual field. The mean body orientation (with zero representing orientation along the long axis of the tunnel in the direction of the feeder) is 2±9 deg. before the change in tunnel width in the 15 to 30 cm tunnel, and 4±9 deg. in the 30 to 15 cm tunnel. These results indicate that the position of the bumblebees as they approach the change in tunnel width can be approximated as being centred along the midline of the tunnel and oriented along its long axis.

DISCUSSION

The role of axial optic flow in ground speed control

The results presented above show that bumblebees rely primarily on visual cues to regulate ground speed. In the 30 cm wide tunnel, bumblebees fly significantly faster than in a tunnel that is half as wide (Fig. 3). The apparent rate of axial optic flow experienced by bumblebees flying in the tunnel is inversely proportional to the distance between the tunnel walls. As the distance between the walls increases, the apparent rate of axial optic flow decreases and, as a result, bumblebees increase their ground speed. The importance of axial optic flow cues for ground speed control in bumblebees is highlighted by the result that, when the axial optic flow cues are removed (such as when the pattern in the tunnel is composed of axial stripes), bumblebees fly significantly faster than when these cues are present (random chequerboard pattern; Fig. 3). Moreover, in the presence of axial stripes, the relationship between ground speed and tunnel width disappears. Instead, bumblebees now fly at a constant speed, even when the distance between the tunnel walls is doubled (Fig. 3).

Drosophila (David, 1982; Fry et al., 2009) and honeybees (Baird et al., 2005; Srinivasan et al., 1996) regulate ground speed by holding constant the rate of axial optic flow. A consequence of this strategy is that ground speed will increase proportionally with the distance to nearby surfaces. If bumblebees also control their ground speed in this way, we expect a factor of two increase in the width of the experimental tunnel to result in a factor of two increase in ground speed. However, in our experiments, ground speed increased by only a factor of 1.6 between the 15 cm and the 30 cm tunnels, resulting in only a partial compensation for the change in tunnel width. Nonetheless, this partial compensation was robust across many individuals and across different hives, suggesting that it is truly a consequence of the bumblebee's ground speed control strategy and that this strategy differs somewhat from that which is observed in *Drosophila* and honeybees. Additional information about ground speed could be derived from either visual or mechanosensory cues, or a combination of both (see below). A weighed sum of these cues and axial optic flow cues could then underlie the partial compensation in ground speed to the two-fold change in tunnel width.

Bumblebees also seem to use a different strategy to honeybees when tested in an environment with only very weak optic flow cues. Barron and Srinivasan (Barron and Srinivasan, 2006) showed that, when flying in an experimental tunnel lined with axial stripes, honeybees fly faster in a wide tunnel than they do in a narrower one. By contrast, bumblebees fly at a constant speed, irrespective of the width of the tunnel (Fig. 3). Whether this difference between honeybees and bumblebees is due to a difference in the sensitivity of the motion detection mechanisms of these insects, a fundamental difference in the ground speed control strategies or some other difference, remains to be tested.

What is the visual range over which axial optic flow for ground speed control is being measured?

Bumblebees begin to adjust their ground speed in response to an abrupt change in axial optic flow cues some distance *before* they pass the point at which these changes occur. This is clear from all of our experimental conditions that present the bumblebees with an abrupt change in the rate of axial optic flow (Experiment 2). If the lateral position and orientation of the bee with respect to the walls of the tunnel are known, it is possible to calculate the visual angle occupied by the change in tunnel width at the position where the change in ground speed occurs (Fig. 6A).

Our data indicate that the mean position and orientation of bumblebees is centred along the midline of the tunnel and oriented toward the feeder. Thus, according to our calculations, the change in ground speed takes place when the change in tunnel width occupies a visual angle of approximately 28 deg. in the 15 to 30 cm tunnel and 30 deg. in the 30 to 15 cm tunnel. Interestingly, when the tunnel walls remained at a constant width but the pattern changed from chequerboard to axial stripes, the change in ground speed took place when the change in pattern occupied a smaller visual angle of approximately 23 deg. This indicates that bumblebees are able to respond to changes in the rate of axial optic flow within a visual field whose minimum angle lies approximately between 23 and 30 deg. from the frontal direction of the midline. It is important to note that the calculation of the viewing angle at which bees first respond to changes in optic flow is derived from the point at which a change in flight speed occurs. Thus, these values do not take into account the processing delay between the detection of a change in optic flow and the change in ground speed. This processing delay has been estimated at 100 ms for *Drosophila* (Fry et al., 2009). If we use this as an approximate value for the processing delay in bumblebees, we estimate that the minimum viewing angle at which bumblebees first detect a change in optic flow is approximately 20 deg. in the 15 to 30 cm tunnel, 24 deg. in the 30 to 15 cm tunnel and 17 deg. in the axial stripe tunnel.

One obvious advantage of detecting changes in optic flow at low viewing angles is that changes in the density of the environment would be detected well before the bee enters the new surroundings. This would give the visual system time to detect the change in axial optic flow and the motor system time to adjust ground speed appropriately. By contrast, if changes in axial optic flow are first being detected at more lateral viewing angles, new environments may be encountered before the visual and flight motor systems have had time to detect and respond to it. Interestingly, both the centring response (Srinivasan et al., 1991) and short-range goal localisation (Lehrer, 1990) in honeybees are mediated by optic flow cues in the lateral visual field. Further investigations into the minimum viewing angles that different insects use for different behaviours are necessary to understand the full extent of the role that viewing angle has on the many components of flight control.

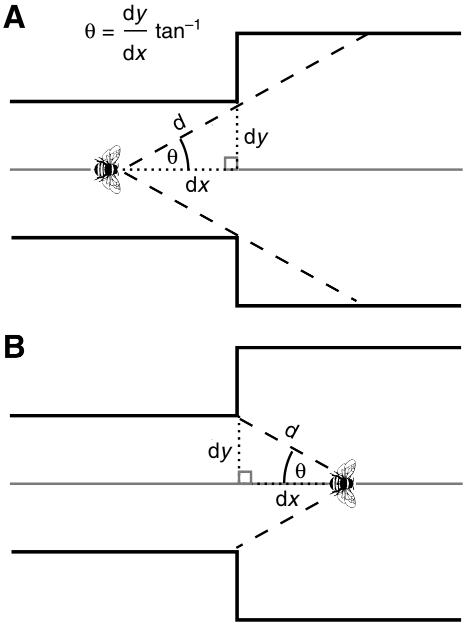

Fig. 6. Calculation of the angular range over which bumblebees measure axial optic flow for flight speed control. Illustration of the calculation of the viewing angle θ occupied by the change in tunnel width when ground speed initially changes in response to a change in tunnel width (A) or when reaches the same value as the control in the second half of the tunnel (B). Note that, in B, θ is subtracted from 180 deg. to obtain the maximum angle at which optic flow for ground speed control is being measured, with respect to the frontal direction of the midline of the bee. Black lines indicate the tunnel walls; the grey line indicates the midline of the tunnel.

It is possible to estimate the extent of the visual region over which optic flow for ground speed control is being measured by calculating the distance at which ground speed in the second half of the tunnel reaches the same value as the equivalent constant-width tunnel (Fig. 6B). In the 15 to 30 cm tunnel and the 30 to 15 cm tunnels, ground speed reaches its new value when the first half of the tunnel subtends a visual angle of 155 deg. and 140 deg., respectively. If we again factor in a processing delay of 100 ms, these viewing angles are reduced to 132 deg. and 129 deg. Our calculations thus suggest that the visual field over which bumblebees are measuring optic flow for ground speed control extends between approximately 17 deg. to 132 deg. It is important to note, however, that the rate at which a bumblebee can speed up or slow down in response to changes in optic flow is not known. As such, the maximal viewing angles calculated here are only approximate indicators of the true extent of the visual field that is used to measure optic flow for ground speed control. Nonetheless, our results do suggest that optic flow for ground speed control is being measured over an extensive visual range.

How do bumblebees detect changes in optic flow?

There are two distinct hypotheses to explain how bumblebees use optic flow for ground speed control. In the first hypotheses, visual information across the entire visual region is assigned equal weights, such that each area of the visual field has equal influence over the overall optic flow measurement. According to this model, a change

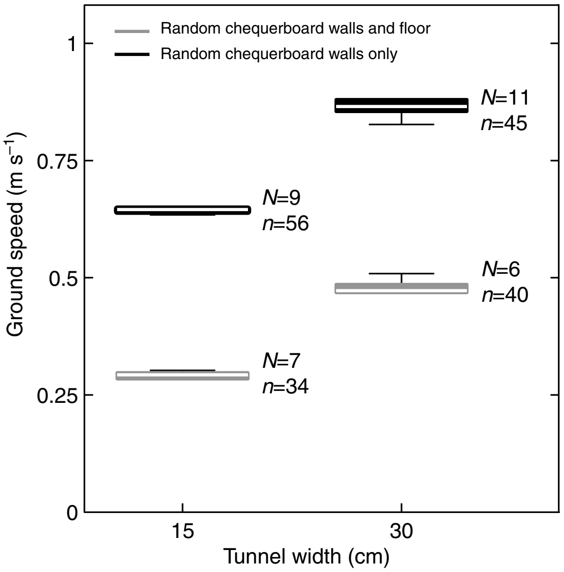

Fig. 7. Effect of ventral optic flow cues on ground speed in tunnels of different widths. The ground speed of bumblebees flying in either a 15 or 30 cm wide tunnel when either the walls and floor (grey boxes) or walls only (black boxes) are lined with a random chequerboard pattern. Details as in Fig. 3.

in ground speed would be initiated only when a change in optic flow subtends a large enough area of the visual field to influence the total output of motion-sensitive neurons. This model would predict that bumblebees respond equally to changes in optic flow, irrespective of where in the visual region they occur, provided that they are large enough to influence the overall output. In the second hypothesis, information from neurons across the visual field is weighted unevenly, such that information from a particular area has more influence over the total optic flow output. If, for example, neurons in the forward-looking sector of the visual region have a higher weighting, then changes in the upcoming visual scene will have a stronger influence over the overall optic flow output than changes that occur at larger visual angles. The plausibility of this hypothesis is supported by the discovery that wide-field-motion-sensitive neurons in the visual system of the fly exhibit increased sensitivity to motion in the frontal part of the visual field (Hausen, 1982). It is not possible from the present study to determine which model best describes visual processing in bumblebees. Further experiments investigating how bumblebees respond to changes in optic flow that occur in different parts of the visual field are necessary to better understand the mechanisms that underlie ground speed control.

The role of ventral optic flow in ground speed control

It is probable that the regions of the visual field that are used for measuring optic flow for ground speed control have a ventrally oriented component, particularly because they would provide useful information about ground speed in an open environment where lateral optic flow cues are sparse. Evidence for the importance of ventral optic flow cues for ground speed control is provided by the result that bumblebees fly at different ground speeds when optic flow in the ventral visual field is present or absent. When optic flow cues on the floor of a constant width tunnel are removed (experiment 1 and control conditions for experiment 2), bumblebees fly faster than when these cues are present (Fig. 7). The effect of removing ventral optic flow cues on ground speed control is consistent with the results from similar experiments in honeybees (Baird et al., 2006), highlighting the importance of these cues in ground speed control in these and possibly other flying insects.

Secondary cues for ground speed control

The elevated ground speed that was observed in the axial stripe tunnels (~0.9 m s^{-1}) is significantly slower than the speed at which bumblebees are capable of flying in an open environment (~7 m s^{-1}) (Riley et al., 1999). Thus, even in the absence of strong axial optic flow cues, bumblebees appear to be able to extract some information about the proximity of the environment and their ground speed within it, causing them to reduce their speed to a relatively low value. This is consistent with the results of Baird et al. (Baird et al., 2005) and Barron and Srinivasan (Barron and Srinivasan, 2006), which showed that, although honeybees fly nearly three times faster in a tunnel lined with axial stripes relative to one lined with a chequerboard pattern, this speed is still much slower than the speed at which honeybees are capable of flying outdoors. The downregulation of ground speed inside a narrow tunnel as compared with a flight outdoors suggests that bumblebees are able to obtain ground speed information from cues other than the axial optic flow cues present within the tunnel.

Examples of visual cues that could provide ground speed information are axial optic flow cues generated by structures above the experimental arena (such as the camera and light fittings), or expansion cues produced by flight at angles that are oblique to the longitudinal axis of the tunnel (in the case of the axial stripe tunnel, these would be limited to vertical expansion cues). Mechanosensory cues, such as airspeed information, could also provide the bees with important information about how fast they are flying relative to the air. In the relatively still air of the experimental tunnel, airspeed would provide a direct indication of ground speed. Evidence that bumblebees do not rely primarily on airspeed cues for ground speed control comes from the results of experiment 1, which showed that ground speed is significantly faster when the tunnel is lined with axial stripes than when it is lined with a chequerboard pattern. This makes sense because dependence on airspeed cues for determining ground speed would provide unreliable information in the natural habitat of the bumblebee, where the airflow patterns are turbulent and unpredictable. Future investigations are required to determine what additional visual and/or mechanosensory cues are involved in bumblebee ground speed control.

Conclusions

The results of the present study reveal that bumblebees regulate their ground speed using axial optic flow cues. Our investigation also shows that, although the rate axial optic flow is the primary cue used by bumblebees for ground speed control, information from other visual and/or mechanosensory sources is also used to mediate this behaviour. Nonetheless, our results indicate that changes in the rate of axial optic flow in the frontal visual field are sufficient to generate a change in ground speed. This strategy of regulating ground speed using optic flow cues from the frontal visual field enables bumblebees to detect and respond to changes in the density of the environment before the new environment is entered. This would be of particular importance when flying from a wide-open field into the cluttered environment around bushes and trees, where it is important to reduce ground speed in order to avoid obstacles. Our study also suggests that optic flow for ground speed control is being measured over a broad visual field, extending well beyond the lateral view of the insect.

The mechanisms of ground speed control investigated in this study focus on the effect of symmetrical changes in optic flow in a relatively cluttered visual environment. What remains unclear is how less cluttered and more natural environments influence ground speed control. Is the relationship between flight speed and proximity constant, or is there a maximum distance beyond which changes in ground speed are no longer observed? Of equal importance is understanding the effect of asymmetrical changes – such as those that may occur when an insect flies beside a hedge or a forest – on ground speed control in flying insects. Our results also raise interesting questions about the role of viewing angle in other visually guided flight control behaviours, in bumblebees as well as in other insects. Does the minimum viewing angle identified here represent the minimum point of the visual range over which other flight control behaviours are mediated, or are different visual regions specialised for mediating different flight control behaviours? Future investigations will be focussed on addressing these questions in both bumblebees and other flying insects.

ACKNOWLEDGEMENTS

The authors would like to acknowledge support from the AFOSR/EOARD (grant no. FA8655-08-C-4004), the Wenner Gren Foundation and the Swedish Research Council. We would also like to thank the reviewers for their helpful comments on the manuscript.

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