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Visual regulation of ground speed and headwind compensation in freely flying honey bees (*Apis mellifera* L.)

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Summary

There is now increasing evidence that honey bees regulate their ground speed in flight by holding constant the speed at which the image of the environment moves across the eye (optic flow). We have investigated the extent to which ground speed is affected by headwinds. Honey bees were trained to enter a tunnel to forage at a sucrose feeder placed at its far end. Ground speeds in the tunnel were recorded while systematically varying the visual texture of the tunnel, and the strength of headwinds experienced by the flying bees. We found that in a flight tunnel bees used visual cues to maintain their ground speed, and adjusted their air speed to maintain a constant rate of optic flow, even against headwinds which were, at their strongest, 50% of a bee's maximum recorded forward velocity. Manipulation of the visual texture revealed that headwind is compensated almost fully even when the optic flow cues are very sparse and subtle, demonstrating the robustness of this visual flight control system. We discuss these findings in the context of field observations of flying bees.

Key words: optic flow, wind tunnel, *Apis mellifera*, honey bee, ground speed

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Introduction

As a flying insect moves through space, the image of the visual panorama moves across the retina, creating a pattern of 'optic flow': the higher the ground speed, the greater the magnitude of the optic flow. There is now increasing evidence to suggest that the induced optic flow is used to regulate the speed of flight. David (David, 1982) observed that *Drosophila* flying in a tunnel regulate their ground speed by holding the induced optic flow constant. Srinivasan et al. (Srinivasan et al., 1996) and Baird et al. (Baird et al., 2005) obtained similar evidence for honey bees. How well is ground speed regulated in the presence of wind disturbances? David (David, 1982) found that *Drosophila* flying upwind in a wind tunnel compensate for the headwind by increasing their flight thrust to maintain the induced optic flow at its still-air value, for wind speeds of up to 1 m s^{-1}. Wenner (Wenner, 1963) timed the flights of honey bees flying outdoors from their hive to a feeder. He concluded that the cruising speed of unloaded honey bees in natural outdoor environments is ~7.5 m s^{-1}, and that this value changes very little even in the face of headwinds or tailwinds as large as 3 m s^{-1}. Riley and Osborne (Riley and Osborne, 2001) used sophisticated radar tracking methods to show that bumblebees only partially compensate their ground speed against headwinds and tailwinds, and possibly adjust altitude to maintain an innately preferred rate of optic flow during flights disturbed by winds (Riley and Osborne, 2001).

If compensation for wind is indeed achieved visually – by monitoring the optic flow – how sensitive is it to variations in the visual environment? Are bees better able to regulate ground speed when flying in a richly textured environment that provides strong optic flow signals, as opposed to a sparsely textured environment that offers impoverished optic flow information? We have investigated this question using honey bees.

We began by examining how bees control their flight speed in visual environments that produce strong or weak optic-flow cues. We then investigated the ability of bees to compensate for headwind in these two, rather diverse, optical environments.

Materials and methods

Bees

The honey bees used were a hybrid of various European subspecies of *Apis mellifera* L. that is commercially available in Australia. They were maintained according to standard beekeeping practices. Our experimental colony contained approximately 7000 workers and a queen, and was housed in a four-frame Perspex walled observation hive. The colony was installed in the All Weather Bee Flight Facility (beehouse) at the Australian National University's Research School of Biological Sciences. This is a modified glasshouse in which the internal temperature is regulated to maintain 24±5°C during the day and 17±3°C at night. The observation hive was mounted on the wall of the beehouse, and had two entrances that allowed bees to access both the inside of the facility, and outside to forage. All experiments were performed inside the beehouse between June and November 2004.

Bee training

In all of the experiments, bees were trained to enter and fly through a narrow wooden tunnel and forage at a feeder placed at its far end, which was sealed. The roof of the tunnel was covered with 1.5 m long strips of transparent Perspex, and the walls and floor were lined with visual patterns, described below. Training was commenced by placing a 2 mol l^{-1} sucrose feeder close to the entrance of the hive in the beehouse. Once the feeder had attracted a sufficient number of bees it was moved gradually, first to a position at the entrance of the tunnel, and then progressively further inside the tunnel to the final position, which was near the far end. Bees that continued to visit the feeder regularly after the feeder had been moved to its final position were marked with individually distinctive coloured dots of acrylic paint on the thorax and abdomen.

Visual stimuli

Depending upon the experiment, the walls and the floor of the tunnel were lined either with a checkerboard pattern (consisting of 3 cm×3 cm black and white checks) or a pattern composed of axially oriented stripes (each 2.2 cm wide, alternately black and white). The checkerboard pattern, by virtue of its geometry, produced strong optic flow cues as a bee flew along the tunnel. In contrast, the axial stripe pattern produced very weak optic flow, because flight was parallel to the direction of the stripes.

The patterns were generated on a computer, printed on a laser printer as a series of sheets of paper, and affixed to the walls using transparent mending tape, taking care to ensure that the junctions between adjacent sheets were true and as visually flawless as possible.

In experiment 4, ground speeds were measured under conditions in which the patterns on the walls were moved at various speeds, either in or against the direction of flight. In this case the bees were trained to fly into a tunnel 20 cm tall and 22 cm wide, with walls made of clear Perspex. This tunnel was placed between two motorized conveyor belts which could be moved at various speeds in either direction. The belts were 28 cm apart, and the tunnel was positioned centrally between them. The belts carried axial striped patterns, as described above. The object of this experiment was to examine whether axial stripes generated any residual optic-flow cues, as will become evident in the Results section. The distance from the tunnel entrance to the feeder was 3.23 m.

Tests in headwind

For experiment 2 a flow of air was generated through the tunnel by placing a fan 170 cm behind the feeder (Fig. 1). The air flow passed through an array of thin walled (0.5 mm) 30 cm long plastic tubes (internal diameter 3 cm), which were also placed behind the feeder. This honeycomb array reduced the vorticity and the turbulence of the air flow in the tunnel. The speed of the fan was adjusted using a variable voltage power supply. In this way we could alter the speed of the headwind experienced by bees flying toward the feeder in the tunnel. Fig. 1 illustrates the wind speeds generated at five different fan voltages: 0, 60, 100, 140 and 180 V. It shows that wind speed did not vary substantially along the length of the tunnel. At

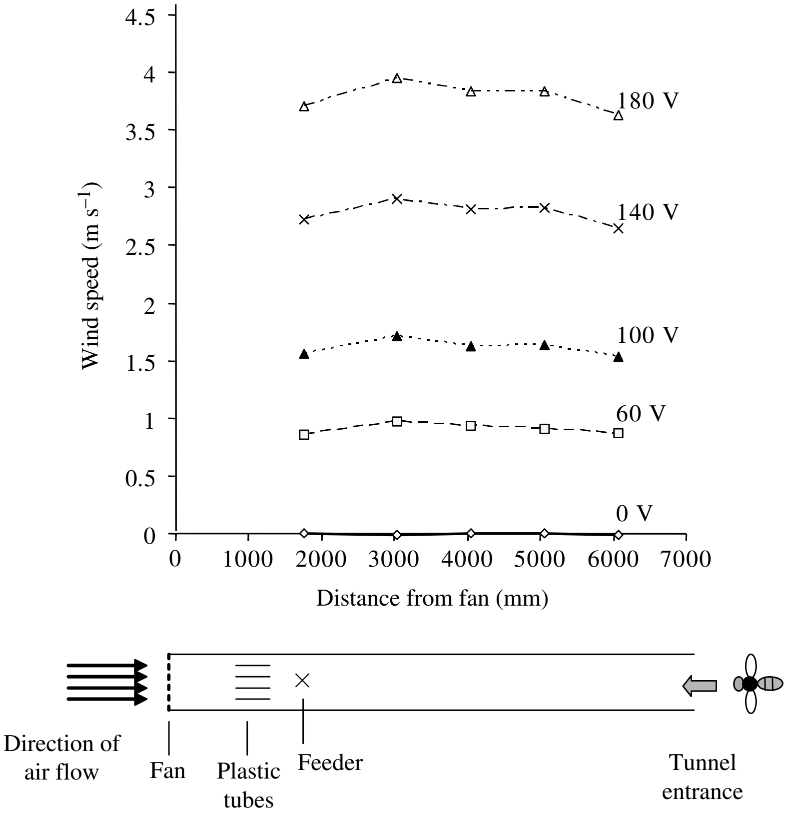

Fig. 1. Measurement and calibration of wind speed in the flight tunnel. Wind speed was varied by changing the voltage supplied to the fan. Wind speeds at the five different voltages used in experiment 2 are shown. Wind speed was measured using both a fan anemometer and a hot wire anemometer at five positions along the tunnel. At each position wind speed was measured with the hot wire anemometer at nine points arranged in a 3×3 array across the cross section of the tunnel. Additionally the fan anemometer was used to record wind speed in the centre of the tunnel. The plotted points are the averages of these 10 values, and thus represent the average wind speed encountered at that position in the tunnel. A diagram of the tunnel is shown, scaled to match the *x* axis of the graph.

maximum power, the fan created a headwind of 3.8 m s^{-1}. Estimates of honey bee ground speed in a natural, open environment vary from 7.0–7.5 m s^{-1} for unloaded bees to 5.3–6.5 m s^{-1} for bees carrying a load of nectar back to the hive (Wenner, 1963). Given these estimates, we believe that the fan generated a significant head wind for a flying bee.

Measurement of ground speed

Under each experimental condition, ground speeds were measured only after individual bees had visited the feeder at least 10 times (~1 h). Ground speeds were measured by recording the durations of the bees' flights in the tunnel when travelling toward the feeder. Using a manual stopwatch, bees were timed from the point at which they entered the tunnel until they passed a point 5 cm in front of the feeder. In effect, this procedure measured the cruising time of the bee in the tunnel, discounting the time required to finally alight at the feeder, which was variable. Very occasionally a bee landed on the wall or floor of the tunnel en route to the feeder, or made a U-turn and headed back toward the entrance. Such flights were not used in the analysis. Only continuous forward flights were recorded.

Data analysis

Bees were marked individually, and several flights were recorded for each bee. We first calculated the mean flight duration of each individual in a given experimental treatment, and performed statistical analyses on these means. Therefore each individual is considered only once per experimental treatment in our statistical tests, to avoid pseudo-replication.

Experimental conditions

Since each experimental condition lasted several days, it was difficult to use the same bees for each condition. However, the climate regulation of the beehouse ensured that temperature conditions were stable throughout the series of experiments that were run in this study.

Results

Experiment 1: ground speed in different optical environments

In this experiment we compared ground speeds in still air in environments which provided strong *vs* weak optic flow signals. Bees were trained to a feeder placed 10 cm from the closed end of a flight tunnel 5.48 m long, 14 cm wide and 20 cm high.

In one experimental condition, the walls and floor of the tunnel were lined with the checkerboard pattern, providing strong optic flow cues. The mean flight durations of trained bees in the tunnel were determined by recording at least five flights for each of 32 different bees. In another condition, the walls and floor of the tunnel were lined with the axial stripe pattern, which provided very weak or no optic flow. Ground speeds were recorded for a new set of 41 individual bees.

The results reveal that bees flew over three times faster in the axial striped tunnel, compared to the checkerboard tunnel (Fig. 2). This difference is highly significant (*t*-test, t=–19.5, d.f.=55, P<0.001).

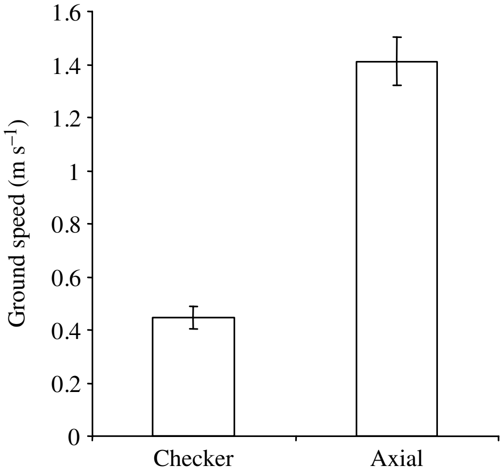

Fig. 2. Comparison of ground speeds in tunnels lined with checkerboard (left) and axial stripes (right). Values are means ±95% confidence intervals for 32 (checkerboard) and 41 (axial stripes) different bees.

Clearly, then, optic flow is important in the regulation of ground speed: reducing optic flow cues by changing the lining of the tunnel from checkerboards to axial stripes resulted in a threefold increase in ground speed. This finding is consistent with earlier, anecdotal observations that bees fly noticeably faster in axial-stripe tunnels (Srinivasan et al., 1996), and consistent with the hypothesis that bees maintain a preferred image speed across the eye during flight. If we imagine bees maintain a more or less constant response from the movement-detecting neurons in their visual system one might expect them to fly faster in the axial-stripe tunnel in order to generate the same level of response from the neurons in this visually impoverished environment. Further, the variation in ground speed observed in the axial stripe tunnel was not much greater than in the checkerboard environment (Fig. 2) suggesting that bees could regulate flight speed perfectly well in this optically impoverished environment.

Experiment 2: effect of headwind on ground speed in different optical environments

In this experiment bees were observed while they flew in the same two environments as above, but in the presence of a headwind. If bees relied on optic flow cues to compensate their ground speed against headwind, then one might expect that compensation would be better in the checkerboard environment (which produces strong optic flow cues) than in the axial stripe environment (which produces weak optic flow cues).

Individually marked bees were trained to visit a 2 mol l^{-1} sucrose feeder placed inside a flight tunnel, 5.48 m from the entrance. The tunnel was 7.18 m long, 14 cm wide and 20 cm high. Multiple flights for each bee were recorded for each of five different headwinds, generated by setting the voltage to the fan at five different levels: 0, 60, 100, 140 and 180 V, which generated the wind speeds shown in Fig. 1. Observations were made over four consecutive days and, if possible, flight times for each individual bee were recorded for each wind speed on each of the 4 days. The order of presentation of wind speeds was varied randomly across the 4 days.

The results for the checkerboard environment are shown in Fig. 3A. At each wind speed, data was recorded from at least 30 individual bees. The results show that, in this environment, the bees compensated extremely well for headwind speeds right up to the strongest headwind that could be produced in the tunnel, namely, 3.8 m s^{-1}. There was no significant effect of headwind on ground speed at any of the headwinds tested (ANOVA, F=1.97, d.f.=160, P=0.10). Bees maintained a mean ground speed of ~0.4 m s^{-1}, which is comparable to the value recorded in still air in experiment 1.

The results for the axial-stripe environment are shown in Fig. 3B. In still air, bees flew considerably faster in the axial striped tunnel (average ground speed=1.4 m s^{-1}) than in the checkerboard tunnel (average ground speed=0.4 m s^{-1}), as we have already shown in experiment 1. But, bees flying in the axial striped environment compensated for headwind just as effectively as in the checkerboard environment. Again, there was no significant effect of head wind on ground speed at any of the headwinds tested (ANOVA, F=1.24, d.f.=186, P=0.29).

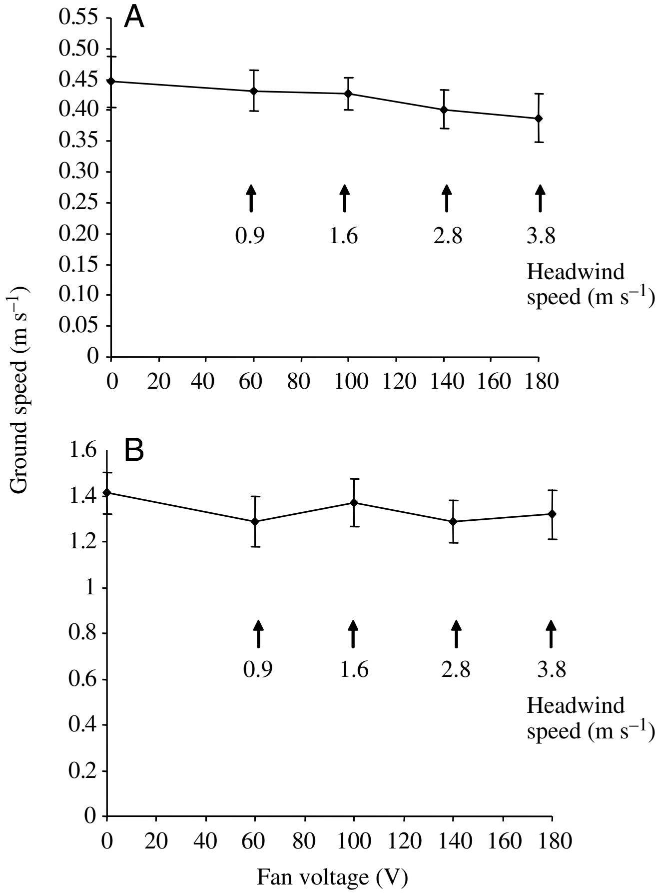

Fig. 3. Effect of headwind on ground speed. (A) In a tunnel lined with a checkerboard pattern. (B) In a tunnel lined with axial stripes. In both cases, the data show mean ground speeds ±95% confidence intervals. At each wind speed five flights were recorded for >30 different bees.

How were bees compensating for headwind in the axial-stripe tunnel, which offered very weak optic flow cues? One possibility is that the bees were able to extract enough image motion information even from the axial stripe patterns, to be able to regulate ground speed. Minor imperfections in the patterns, or visibility of the vertical joints between adjacent panels that carried the pattern, could have provided some optic flow cues. A second possibility is that the bees were able to use optic flow information from outside the tunnel. The ceiling structures of the beehouse were visible to the bees through the clear Perspex roof of the tunnel, and could have provided optic flow cues that were used by the bees to regulate ground speed. Since these structures were much further away than the walls and floor of the tunnel, one might expect the bees to fly at a higher speed to achieve the same rate of image motion across the eye, as they did. A third possibility is that bees possess an alternative, as yet unexplored mechanism for regulation of ground speed, which does not rely on visual information.

To distinguish between these possibilities, experiments 3 and 4 were designed to explore whether bees really use optic flow information from the axial stripes to regulate their ground speed.

Experiment 3: ground speed in axial-stripe tunnels of different widths

In this experiment, we compared ground speeds in axial stripe tunnels of two different widths, namely, 21 cm and 11.5 cm. If bees were able to detect optic flow information from the axial stripes in the walls and use it to regulate their ground speed, then halving the width of the tunnel should approximately halve the speed of flight. This is because, in a tunnel of half the original width, bees would have to fly at half the original speed in order to generate the same rate of image motion across the eye.

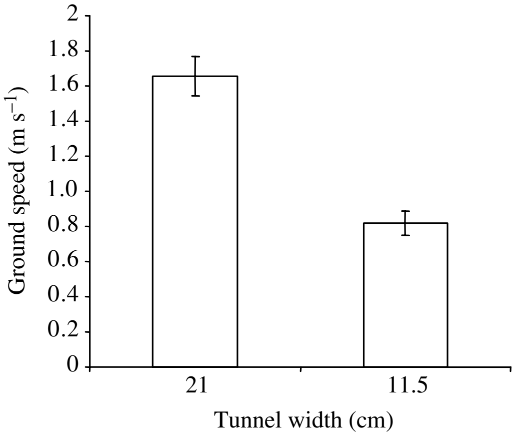

Fig. 4. Comparison of ground speeds in axial-striped tunnels of different widths. Values are means ±95% confidence interval: N=26 and 36 bees for the 21 cm and 11.5 cm wide tunnels, respectively.

Marked bees were trained to a feeder placed 10 cm from the end of a 5.48 m long, 20 cm high tunnel. The tunnel was lined with the axial stripe pattern used in experiment 2. Over 2 days, ground speeds were recorded in a tunnel of 21 cm width. The tunnel was then rebuilt to have a width of 11.5 cm and a new set of bees was trained to the tunnel and their ground speeds recorded. All observations were performed in still air.

The results (Fig. 4) reveal that halving the width of the tunnel does indeed reduce the average ground speed by almost exactly 50% (t=13.91, d.f.=60, P<0.001). This is consistent with the notion that the bees were indeed using optic flow information from the axial stripes on the walls, and not from the ceiling structures, to regulate their ground speed.

This possibility was tested more directly in the next experiment, where the axial stripes on the walls were moved to examine whether the motion affected the speed of flight.

Experiment 4: ground speed in axial striped tunnels with moving walls

Bees were trained to a feeder placed at the far end of a tunnel with transparent walls. The tunnel was placed between two conveyor belts which carried axial stripes that could be moved either in or against the direction of flight, as described in the Materials and methods. The effective width of the tunnel (the separation between the conveyor belts) was 28 cm. Flight speeds were recorded for five different pattern speeds, including zero. The entire experiment was conducted in still air, because the aim was no longer to examine the effect of headwind, but simply to ask whether the bees were using sparse optic flow information from the axial stripes to regulate their ground speed.

The results are shown in Fig. 5. Pattern speeds in and against the direction of flight are shown as positive and negative, respectively. Motion of the axial stripe pattern had a significant effect on ground speed (ANOVA, F=15.1, d.f.=115, P<0.001). Bees increased their ground speed when the pattern was moved in the direction of flight: higher pattern speeds elicited higher ground speeds. Conversely, bees decreased their ground speed when the pattern was moved against the flight direction, and higher pattern speeds elicited lower ground speeds. This provides clear evidence that the bees were able to extract optic flow cues even from the axial stripe patterns.

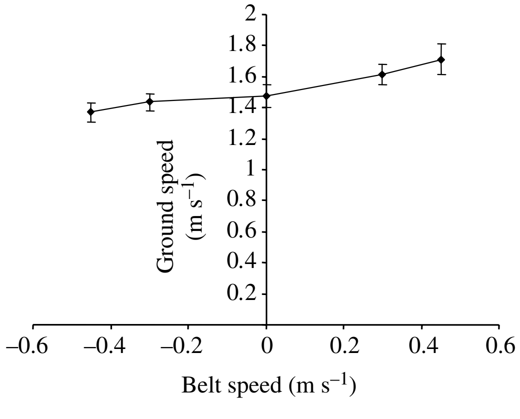

Fig. 5. Ground speed in a tunnel with moving axial stripe patterns. Bees flew through a transparent tunnel placed between two conveyor belts that moved the axial stripe pattern at various speeds in the direction of the bees' flight toward the feeder (positive values) or against it (negative values). The data show mean ground speeds ±95% confidence intervals. Five flights were recorded for >20 bees at each belt speed. Moving the axial stripe pattern significantly altered bee ground speeds (ANOVA, F=15.1, d.f.=115, P<0.001).

The changes in ground speed did not fully compensate for the movements of the pattern. Two possible reasons for this may be (i) the presence of the stationary Perspex walls between the bee and the pattern, which may not have been totally invisible; and (ii) the presence of a 'dead zone' in the regulation of ground speed at image speeds that are close to the target value (Baird et al., 2005).

Discussion

Our experiments demonstrate that honey bees use cues based on image motion to regulate ground speed, and that they maintain an innate preferred rate of image motion, even in the face of substantial headwind. Compensation for headwind is surprisingly robust, even when the visual environment offers optic flow cues that are very sparse and subtle. We have been able to duplicate these results in a different setting and in a different year, when bees were trained to fly into similar tunnels placed outdoors (data not shown).

The ground speeds we observed in these tunnel studies were all far lower than speeds observed for bees flying in the field. Even in the axial-stripe tunnel, bees flew at 1.4 m s^{-1} (experiments 1 and 2) compared to flight speeds greater than 7 m s^{-1} for bees in the field (Wenner, 1963). Very probably this is because in the flight tunnels bees are constrained to fly far closer to the source of optical cues than in the field [field bees typically fly at an altitude of 2 m (Riley and Osborne, 2001)]. Therefore bees experience a greater angular motion of the image when flying in the tunnel than when flying outdoors. If bees indeed have a preferred rate of image motion during flight, reducing ground speed in the tunnel would be a compensation for this magnified image motion.

Earlier work, investigating a different question, namely visually mediated odometry, reported that bees fly slower in headwinds, even when the headwinds are relatively weak (Srinivasan et al., 1997; Srinivasan et al., 1996). The present findings are clearly different from the earlier observations. Although the reasons for this discrepancy remain to be ascertained, it should be noted that in the earlier studies the bees were always trained in still air, and tested only occasionally and briefly in the presence of wind. Therefore, they had no opportunity to learn to compensate for the effects of wind in the tunnel.

Recent work in our laboratory suggests that, in still air, ground speed is quite invariant to changes in the contrast and the spatial frequency content of the patterns that line the walls and floor of the tunnel (Baird et al., 2005). This indicates that the neural mechanism that monitors the motion of the image in the eye is capable of registering the speed of the image rather faithfully, regardless of its visual texture. However, one can expect such robustness to prevail only as long as the geometry of the texture is capable of inducing horizontal optic flow in the eye. Examples of such textures are vertical stripes, checkerboards or random dot patterns. An axial-stripe texture, on the other hand, would theoretically induce no horizontal optic flow, because flight is parallel to the direction of the stripes. The only horizontal flow that such a texture could induce (if any) would arise from imperfections in the construction of the pattern. Experiment 1 shows that bees fly about three times as fast in an axial stripe environment, as in a checkerboard environment, but bees are still able to regulate their flight speed in this extreme condition of highly impoverished optic flow. Mean ground speeds in the axial stripe tunnels were significantly less than ground speeds recorded for bees in the field, and bees were able to regulate flight speed against headwinds in the axial stripe environment as well as in the checkerboard environment. These two observations indicate that flights were not uncontrolled in the axial stripe tunnel, rather bees regulated ground speed at a higher ‘set point’ than in the checkerboard tunnel.

Ibbotson (Ibbotson 1991; Ibbotson, 2001) has reported the existence of visual interneurons in the honey bee, which respond selectively to movements of patterns in the front to back direction on each eye. The strength of this response is approximately proportional to the velocity of the pattern, over a wide range of pattern velocities. They also display the robustness to changes in contrast and spatial frequency content, as discussed above. If bees adjusted their ground speed so as to maintain a constant response (e.g. a constant spike firing rate) in these neurons, then such neurons could be part of a neural circuit that regulates ground speed. Although such a system would perform well at regulating ground speed in a checkerboard environment rich in visual texture, in an axial stripe environment, the bees would have to fly considerably faster in order to generate the same firing rate from the neurons. Experiment 1 shows that bees indeed fly considerably faster in an axial stripe environment.

Experiment 2 shows that bees display excellent compensation for headwind when flying in a checkerboard tunnel, which provides strong optic flow signals. This is in accordance with what might be expected from the schema described above, if one assumes that the movement-detecting neurons are sensitive enough to detect small deviations from the desired (target) image speed. Headwind compensation continues to be excellent even when the bees are made to fly in an axial stripe tunnel, which provides very weak optic flow cues. Although the bees fly much faster in this environment, their ground speed continues to be largely unaffected by headwind. We suggest that, in the axial stripe tunnel, bees are able to extract the weak optic flow information from this environment. They fly at a higher speed, which evokes a similar firing rate in the movement-detecting neurons as that evoked by slower flight in the checkerboard environment. In the presence of headwind, bees increase their thrust to maintain the same level of neural response. Thus, although the bees fly faster in the axial stripe environment, compensation for headwind continues to be excellent. The percentage variability in flight speed is approximately the same, regardless of whether flight is in the checkered tunnel or in the axial stripe tunnel, as can be seen from Fig. 2. This suggests that the visual movement-detecting neurons that underlie the regulation of flight speed respond to changes in the speed of image motion in a Weber-fraction fashion.

These findings are congruent with earlier observations in our laboratory that bees are able to extract some optic flow information for the purpose of estimating distance flown even when they fly in axial stripe tunnels (Si et al., 2003). They are also consistent with the observation that the honey bee’s visually driven odometer continues to register distance flown – albeit at a reduced rate – even when flying over water surfaces, which provide only weak optic flow cues (Tautz et al., 2004).

In our flight tunnel studies honey bees responded to headwinds by increasing their thrust to maintain a constant level of image motion experienced during flight. However, observations of the flight paths of freely flying bumble bees in the field suggest that compensation of ground speed for headwinds is not perfect, and an additional response to wind is to change flight height (Riley and Osborne, 2001). Riley and Osborne suggested that reducing altitude in the face of headwind, and increasing altitude with tailwinds (Riley and Osborne, 2001) would be an energetically efficient way to maintain a preferred rate of optic flow during flight (Riley and Osborne, 2001). If the maximum thrust that a bee can produce is not sufficient to compensate fully for a headwind, flight at a lower height would restore the optic flow experienced by the eye to its original value. This response may have the added benefit of shielding the insect from the stronger winds that prevail at greater heights

In our experiments, we have not observed any consistent wind-induced changes of flight height, but the dimensions of the tunnel could have prevented this response, and we were not able to measure subtle changes in height. Further, our experiments were all performed at relatively low wind speeds, compared to winds that can be encountered by bees flying in a field environment. Even so, our observations of flights in tunnels show that bees maintain a remarkably constant rate of optic flow during flight, and bees will increase thrust to compensate for headwind in a situation where they cannot (or do not) significantly reduce altitude. The questions we must now ask are: do bees also maintain a preferred rate of optic flow during flight in the field, and, if so, is this achieved by modulating thrust or altitude? Further experiments, using a combination of controlled conditions of a larger flight tunnel with higher wind speeds, and precise measurements of ground speed and altitude of bees in the field are needed to address this.

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