Visual Control of Flight Speed and Height in the Honeybee

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Abstract. The properties of visually guided flight speed and height control were investigated by training honeybees (*Apis mellifera* L.) to fly through a tunnel in which the visual cues in the lateral and ventral visual fields could be varied by changing the patterns on the walls and floor of the tunnel. The results show that honeybees regulate their flight speed by keeping the velocity of the image of the environment in their eye constant. The results also show that honeybees use visual information from the ground to control their height above the ground. The findings of this study reveal that the mechanisms of flight speed and height control in the honeybee are perfectly adapted for extracting information from a complex visual environment using simple sensors and computations. Consequently, the techniques of visual guidance that are reported here suggest insect-inspired strategies for the control of aircraft flight.

1 Introduction

Although the brain of a honeybee comprises less than one million neurons, it is able to process with extraordinary accuracy the complex sensory information necessary for a variety of orientation and navigation tasks. Honeybees employ a range of computationally simple techniques to aid flight control and navigation in order to overcome the limitations of their small brain.

Honeybees rely heavily on information from the visual system to navigate. However, information about the 3-D structure of the world is generally required for collision-free flight. Despite the perceptual limitations of immobile eyes, fixed focus optics, low spatial resolution and a lack of stereo vision, honeybees are able to acquire extract range information from cues based on image motion. During flight, the image of the environment moves across the retina, creating a pattern of apparent image motion called optic flow [1]. Properties of optic flow, such as the direction and velocity of certain objects in the visual scene, are useful cues for detecting course deviations or the proximity of objects in the environment. Honeybees are known to use information that has been extracted from optic flow to stabilize flight, estimate the range of objects, negotiate narrow gaps and estimate the distance flown to a food source [2], [3].

Previous studies have indicated that flying insects use visual cues to regulate flight speed (tethered bees: [4]; freely flying fruit flies, David [5]). A study by Srinivasan

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et al. [2] found that bees flying though a tapered tunnel slowed down as the distance between the walls narrowed, and sped up as it widened. This result suggested that the bees were adjusting their flight speed so as to hold constant the velocity of the image generated by the patterns on the walls of the tunnel on their eyes.

In the current study, we present, in part, findings from earlier experiments that tested directly and rigorously the hypothesis that honeybees control their flight speed by maintaining a constant rate of image motion (Baird et al. [6]). The purpose of presenting this data here (as Experiments 1 and 2) is to provide a context for novel data (Experiments 3 and 4) that investigate whether flying honeybees use visual cues to control both their flight speed and their height above the ground.

2 General Experimental Procedures

The experiments were carried out in an All Weather Bee Flight Facility at the Australian National University's Research School of Biological Sciences. The temperature inside the facility was maintained at 24 ± 5 °C during the day and 17 ± 3 °C at night. A beehive mounted on the wall of the facility supplied the bees (*Apis mellifera* L.) used in the experiments.

2.1 Experimental Setup

All of the experiments were conducted in a rectangular tunnel that had clear Perspex walls, which allowed bees flying through the tunnel to view a variety of stationary or moving visual patterns (see below). The tunnel was 320 cm long, 20 cm high and 22 cm wide. A clear Perspex ceiling permitted observation and filming of the bees as they flew in the tunnel (Fig. 1). For each experiment, up to 20 bees were individually marked and trained to fly through the tunnel to a feeder containing sugar solution placed at the far end of the tunnel. In Experiments 1 and 2, flights to the feeder were filmed at 25 frames per second in the central segment of the tunnel by a digital video camera positioned 2.5 m above the tunnel floor (Fig. 1). Due to the limitations of this camera set up, it was necessary to leave the floor of the tunnel blank in Experiments 1 and 2 so that the bees could be easily distinguished from the background.

In Experiments 3 and 4, two cameras were mounted 125 cm above the tunnel floor (Fig. 1.) and positioned such that they had parallel views of the tunnel. Flights of bees were captured directly into a computer from each camera simultaneously via a capture card at 30 frames per second. By tracking the position of the bee in both camera views it was possible, through triangulation, to calculate the three-dimensional position of a bee flying in the tunnel. All of the patterns that were used in these two experiments consisted of dark red-and-white elements because it was necessary to have patterns with a high contrast but it was not possible to track the positions of the bees against the black areas of a black-and-white pattern. The red color in the patterns was considered to be a suitable substitute for black as bees do not posses red color receptors and therefore, they would perceive the red parts of the patterns as a dark shade of grey.

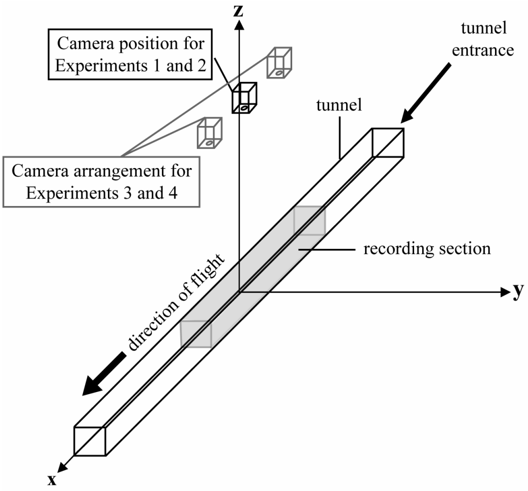

Fig. 1. Illustration of tunnel coordinates and camera position. Flight speed was calculated as the projection of the flight vector along the *x* axis. Height was measured along the *z* axis.

2.2 Analysis of Flight Trajectories

An automated tracking program was developed, using Matlab, to track individual bees and analyze the recordings of flights obtained in each experiment. For each flight, the program identified the position of the bee in consecutive frames. The position of the bee was defined in relation to the tunnel co-ordinates x, y and z, where x denotes axial direction, y the transverse direction and z the vertical direction (Fig. 1). In Experiments 1 and 2, only x and y could be measured, as the system used a single camera (rather than a stereo pair). In these experiments, z was assumed to be constant.

The camera configuration that was used in Experiments 3 and 4 allowed the measurement of the position of the bee in x, y and z coordinates. To do this, the position of the bees in x and y pixel coordinates from each camera view were entered into a database in which the three-dimensional coordinates of the bee's position were calculated using a triangulation algorithm.

To generate values of flight speed, the data was analyzed to calculate the component of the flight velocity in the axial (x) direction (V_x). Preliminary analysis revealed that the lateral component of flight velocity (V_y) was much smaller in magnitude compared to that of the axial component (V_x). Given this, it follows that V_x provides a good approximation of the actual magnitude of the flight speed. To generate values of height in Experiments 3 and 4, the average z position of each flight was calculated using the z coordinates of the bee's three-dimensional position.

2.3 Statistical Analysis

Statistical models accounting for multiple levels of variation were developed to assess whether covariates such as treatment (e.g. different patterns), time, temperature, light intensity or humidity affected bee flight speed, and to eliminate their effects. To account for the two principal levels of variation in the study -- variation between bees and variation within bees -- linear mixed models [7] were used, with bee identity as a random effect. For further details of the statistical analysis used see Baird et al. [6].

3 Optic Flow Cues in the Lateral Visual Field Affect Flight Speed

Experiment 1 was designed to examine the contribution of optic flow cues (i.e. cues that generate image motion in the eye of a honeybee) in the lateral visual field to the control of flight speed. The influence of optic flow cues was examined by recording flight speeds when the tunnel walls were lined with two different types of stationary pattern: chequerboard and axial stripes. The chequerboard pattern consisted of alternating black and white checks of 3 x 3 cm. The axial pattern consisted of alternating black and white, horizontally oriented stripes, each with a width of 4 cm. The chequerboard pattern was used in this experiment because the alternating black and white checks would provide strong image motion cues to a bee flying along the tunnel. The axial pattern, on the other hand, was used to create a condition in which the optic flow cues were very weak. This is because flight in the direction of the stripes would produce very little apparent motion of the images of the walls on the retina. In this experiment, the floor of the tunnel was blank white with no discernable optic flow cues.

The results of Experiment 1 are shown in Fig. 2. Interestingly, when optic flow cues are weak (when the tunnel is lined with axial stripes), bees fly considerably faster than when optic flow cues are strong (when the tunnel is lined with a chequerboard pattern). When the tunnel walls were lined with a chequerboard pattern, the mean flight speed was 54 cm s^{-1} but when the tunnel walls were lined with axial stripes, the bees flew significantly faster at a mean flight speed of 97 cm s^{-1} (two sided t-test, $t_{109} = 8.67$, $p < 0.0001$).

Experiment 2 was designed to examine the effect on flight speed of image motion in the lateral visual field. In this experiment, a motorized conveyor belt was placed along the length of the tunnel on each side. Each belt was white in color and carried a pattern of randomly positioned black dots, 2 cm in diameter, on its surface. The conveyor belt system allowed the pattern to be moved toward or away from the closed end of the tunnel, at a range of speeds. The influence of image motion was examined by recording flight speeds when the patterns on the walls of the tunnel were moving at six pattern velocities in each direction, and for one condition in which the pattern was static. When the pattern was moved in the direction of flight to the feeder, the highest pattern speed was limited by the maximum speed of the motor. The speeds used for pattern motion in this direction were 15, 22, 30, 37, 45 and 52 cm s^{-1} (these velocities were regarded as positive).When the pattern was moved against the direction of flight to the feeder, at high pattern speeds, the bees were unable to enter the tunnel. The maximum speed used in this condition was therefore limited to the highest speed at which the bees could enter the tunnel and fly to the feeder. The speeds tested in this condition were 6, 12, 18, 24, 30 and 36 cm s^{-1} (these velocities were regarded as negative).

The results of Experiment 2 showing the dependence of flight speed on pattern velocity are shown in Fig. 2. The results indicate that when the pattern is moved in the direction of flight (decreasing the velocity of the perceived image motion) flight speed increases (as indicated by the data points on the right hand side of the graph). When the pattern is moved against the direction of flight (increasing the velocity of the perceived image motion) flight speed decreases (as indicated by the data points on the left hand side of the graph.

If bees regulate their flight speed by keeping the rate of optic flow (i.e. the velocity of the image on the eye constant), flight speed should vary linearly with pattern velocity and the change of flight speed should be equal to the change of pattern velocity. Thus, the equation for the hypothesized flight speed adjustment takes the form:

$$y = mx + c \tag{1}$$

where c is the flight speed when the pattern is static, x is the pattern velocity and, if the bees maintain a constant rate of optic flow in the eye, $m = 1$. This calculation assumes that at zero pattern velocity, flight speed is set to achieve the desired optic flow.

An analysis of the data indicates that a model which includes three lines of different slopes provides a good approximation of the effect of large positive pattern velocities, large negative pattern velocities and small positive and negative pattern

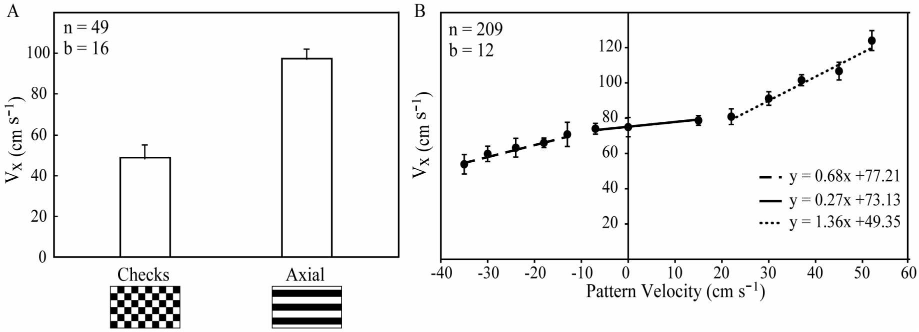

Fig. 2. (A) Experiment 1 – effect of optic flow cues in the lateral visual field on flight speed. Comparison of mean flight speeds when the walls of the tunnel are lined with a chequerboard pattern (producing strong optic flow cues) or axial stripes (producing weak optic flow cues). (B) Experiment 2 – effect of pattern motion on flight speed. The graph shows mean axial flight speed (V_x) when the pattern on the walls was static (0 pattern velocity), moved in the direction of flight (positive pattern velocity values) or against the direction of flight (negative pattern velocity values). The black circles represent V_x values for various pattern speeds. The dashed line represents a model of the flight speed data for large negative pattern velocities; the slope of this line is slightly smaller than 1. The solid line represents a model of the flight speed data for the positive and negative pattern velocities near zero. The slope of this line is not significantly different from zero. The dotted line represents a model of the flight speed data for large positive pattern velocities. For positive pattern velocities, the slope of the regression line was slightly greater than 1. The equations for each regression are shown. The error bars represent the standard error of the mean, n denotes the number of flights and b denotes the number of bees.

velocities (including zero pattern velocity) on flight speed. To fit this model, the pattern velocities were classified into three categories: high positive, near zero and high negative. A separate line was fitted within each class. For details of the development of the model, please see Baird et al. [6].

For large positive pattern velocities, the model revealed a slope of m = 1.36 (dotted line, Fig. 2). There is some evidence that this slope is significantly greater than 1 (two-sided t-test, $t_{189} = 1.86$, $p = 0.06$). This result suggests that when the pattern is moved in the direction of flight the bees respond by increasing their flight speed by slightly larger amount. Thus, when the pattern moved in the direction of flight, the bees were, to a small extent, over compensating for the changes in pattern speed and, as a result, experiencing a slightly decreased rate of optic flow.

For large negative pattern velocities, the slope of the model was m = 0.68 (dashed line, Fig. 2). There is some evidence that this slope is significantly different from 1 (two-sided t-test, $t_{189} = 1.78$, $p = 0.08$). Thus, when the pattern moved against the direction of flight, the bees were not making a complete adjustment of flight speed to counter the changes in pattern speed: they were experiencing a slightly increased rate of optic flow.

For small pattern velocities about zero, the slope of the model was m = 0.27 (solid line, Fig. 2). This slope is not significantly different from zero (two-sided t-test, $t_{189} = 0.63$, $p = 0.53$). Thus, at low pattern speeds, the bees were not adjusting their flight speed to compensate for the small changes in the rate of optic flow.

4 Optic Flow Cues in the Ventral Visual Field Affect Flight Speed and Height

Experiment 3 was designed to investigate the contribution of optic flow cues in the ventral visual field to the control of flight speed and height. The influence of optic flow cues was examined by recording the flight speed and height of bees when the tunnel floor was lined with two different types of pattern: chequerboard and axial stripes. The chequerboard pattern consisted of alternating red-and-white checks of 3 x 3 cm^2. The axial pattern consisted of alternating red-and-white stripes 4 cm in width, oriented along the longitudinal axis of the tunnel. In both Experiment 3 and 4, the walls of the tunnel were lined with a chequerboard pattern of 3 x 3 cm so that there would be strong optic flow cues in the lateral regions of the bee's visual filed The aim of this arrangement was to ensure that any changes in flight speed or height were a result of the changes in the patterns placed on the floor of the tunnel.

The results are shown in Fig. 3. When the tunnel floor was lined with an axial pattern, the bees flew at a mean flight speed of 60 cm s^{-1} and a mean height of 14 cm. When the tunnel floor was lined with a chequerboard pattern, the mean flight speed was 44 cm s^{-1} and the mean height was 19 cm. The data indicate that bees fly significantly faster ($t_{81} = 4.06$, $p < 0.001$) and lower ($t_{81} = 3.85$, $p < 0.001$) when the optic flow cues in the ventral visual field are weak (axial stripe patterns) than when the optic flow cues in the ventral visual field are strong (chequerboard pattern). This suggests that the mechanisms that mediate flight speed and height control in the honeybee are influenced by optic flow cues in the ventral region of the visual field

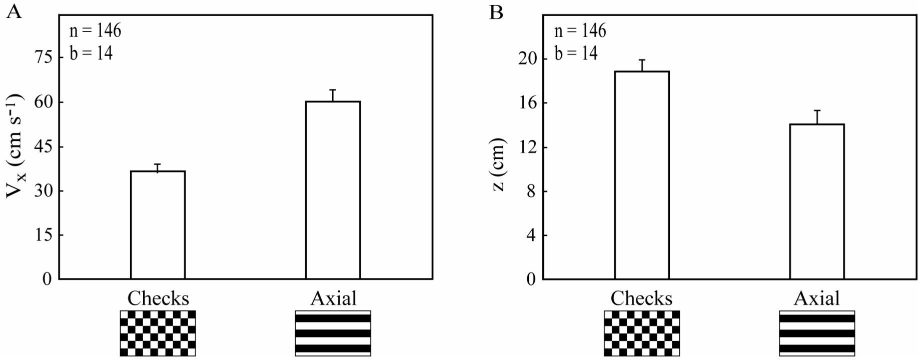

Fig. 3. Experiment 3 – effect of optic flow in the ventral visual field on flight speed and height. (A) Comparison of mean flight speeds when the floor of the tunnel is lined with either a chequerboard pattern (strong optic flow cues) or axial stripes (weak optic flow cues). (B) Comparison of height when the floor of the tunnel is lined with either a chequerboard pattern or axial stripes. Other details are as in Fig. 2.

even when the optic flow cues in the lateral region of the visual field are strong. Interestingly, flight speed is slightly lower when the floor is blank, than when it is lined with axial stripes. This could be an effect of the visual phenomenon known as "contrast adaptation", as discussed in [6].

Experiment 4 was designed to investigate whether the flight speed and height of bees is affected by changes in the spatial frequency (the number of changes in contrast over a given distance) of the pattern in the ventral visual field. Flight speed and height were measured when the tunnel floor was lined with chequerboard patterns of various check sizes: 1.5 x 1.5 cm, 3 x 3 cm and 6 x 6 cm. For a bee flying along the

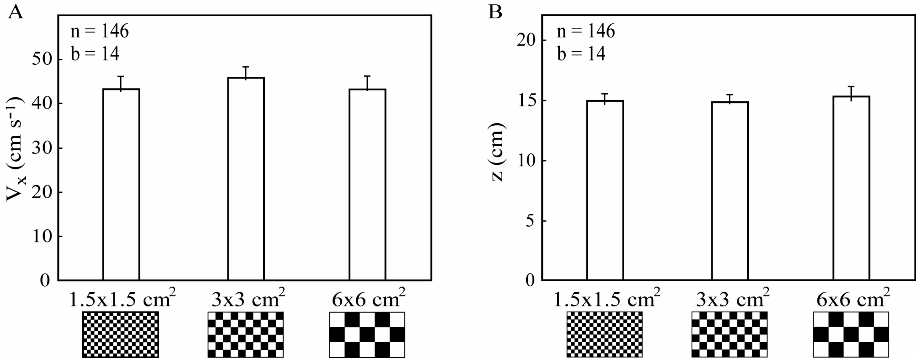

Fig. 4. Experiment 4 – effect of pattern texture in the ventral visual field on flight speed and height. Comparison of mean flight speed (A) and mean distance from the floor of the tunnel (B) when the floor of the tunnel is lined with chequerboard patterns with check sizes of 1.5 x 1.5 cm, 3 x 3 cm and 6 x 6 cm. Other details are as in Fig. 2.

midline of the tunnel, the dominant spatial frequency of the checks on the floor of the tunnel as seen by the ventral field of the eye would be 0.06 cycles deg^{-1}, 0.03 cycles deg^{-1} and 0.01 cycles deg^{-1}, respectively.

The results are shown in Fig. 4. The data indicate that neither the speed nor the height of flight is significantly influenced by changes in the spatial frequency of patterns in the ventral visual field. The average flight speed of bees was 45.5 cm s^{-1} with 3 x 3 cm checks, 43.5 cm s^{-1} with 1.5 x 1.5 cm checks ($t_{130} = 0.89$, $p = 0.37$ when compared with the 3 x 3 cm checks) and 43.8 cm s^{-1} with 6 x 6 cm checks ($t_{130} = 0.75$, $p = 0.46$ when compared with the 3 x 3 cm checks). The average flight height was 14.4 cm with 3 x 3 cm checks, 14.8 cm with 1.5 x 1.5 cm checks ($t_{130} = 0.58$, $p = 0.56$ when compared with the 3 x 3 cm checks) and 15.2 cm with 6 x 6 cm checks ($t_{130} = 1.26$, $p = 0.21$ when compared with the 3 x 3 cm checks). Therefore, the mechanisms that mediate control of flight speed control and height appear to be relatively robust to variations in the spatial frequency of patterns in the ventral visual field.

5 Discussion

The results shown here clearly demonstrate that flight speed and height control in the honeybee are regulated using optic flow. In different visual environments, flight speed is regulated so as to hold constant the speed of the image on the retina. This finding supports the hypothesis first proposed by Srinivasan et al. [2] that honeybees use the rate of optic flow to regulate their flight speed. In addition, this study has shown for the first time that height control in the honeybee is mediated by optic flow cues in the ventral region of the visual field. Earlier work in fruit flies [5], moths [8] and beetles [9] has shown that the flight speed of insects following odor plumes at different heights increases with their distance from the ground. From this work however, it is not possible to determine whether visual cues in the ventral region of the visual field influence the height at which an insect flies, as all of the insects in these experiments were following odor plumes at a set height. By using freely flying honeybees it was possible, in the present study, to test directly whether the properties of the optic flow on the ground influence height and flight speed. Until now, no study has demonstrated that flight height in insects can be influenced by the properties of visual features on the ground.

5.1 Flight Speed Control

Experiment 1 demonstrates that optic flow cues play an important role in the regulation of flight speed. When optic flow cues are weak, (when the walls are lined with an axial stripe pattern), bees fly much faster than when optic flow cues are strong (when the walls are lined with a chequerboard pattern). The reason for the difference in flight speed between these two conditions is likely to be related to the fact that, as the axial pattern carries no strong horizontal optic flow cues, it elicits weak image motion signals, thus causing the bees to fly faster. Interestingly, flight speed also increases when the optic flow cues on the floor of the tunnel are weak, even though the walls provide strong optic flow cues, as shown in Experiment 3. This indicates that the visual information in the ventral region of the bee’s eye is important for the regulation of flight speed. These results are consistent with those of Barron and

Srinivasan [10] who found that when the walls and floor of a tunnel are lined with axial stripes, bees fly three times faster than when the tunnel is lined with a chequerboard pattern.

Interestingly, flight speeds are lower (60 cm s^{-1}) when the floor of the tunnel carries an axial pattern and the walls a chequerboard pattern, than when the walls carry axial patterns and the floor is blank (97 cm s^{-1}). Similarly, bees fly slower (44 cm s^{-1}) when the chequerboard pattern covers all three surfaces of the tunnel, as compared to when it lines only the walls (54 cm s^{-1}). These observations suggest that the mechanism of flight speed control averages the perceived velocity of image motion from the lateral as well as the ventral regions of the visual field.

The hypothesis that flight speed in honeybees is regulated by optic flow was tested directly and rigorously in Experiment 2. Here we found that the bees adjusted their flight speed so as to hold the speed of the image on the retina constant. When the patterns on the walls of the tunnel were moved in the direction of flight, the bees increased their flight speed by an amount that was slightly greater than the speed of the pattern. When the patterns on the walls of the tunnel were moved against the direction of flight, the bees decreased their flight speed by an amount that is slightly lower than the speed of the pattern. When the patterns on the walls of the tunnel are moved at slow speeds either with, or against the direction of flight, there is no associated change in flight speed. This result indicates that the system that mediates flight speed control only responds to changes in the velocity of the image of the visual environment that exceed a certain threshold. This threshold is estimated to lie between 10 and 15 deg s^{-1}. Once the deviation in perceived image velocity exceeds this threshold, flight speed is adjusted so as to return the deviation to a level that is below threshold.

In Experiment 4 we showed that the flight speed of honeybees is not affected by changes in the spatial frequency of the image in the ventral visual field. This result is consistent with the findings of our earlier work [6] which showed that the flight speed of bees was not affected by changes in the spatial frequency pf patterns in the lateral visual field.

We have shown here that honeybees control their flight speed by holding the rate of image motion across their eyes constant. What are the consequences of maintaining a constant image velocity during flight? One outcome would be that, because perceived image velocity is related to the distance of the viewer from the substrate, flight speed is adjusted according to the proximity of objects and surfaces in the environment. For example, flight speed would tend to be high when flying in an open field and low during a flight through dense vegetation. Thus, maintaining a constant image velocity in the eye would ensure that the speed of flight is automatically adjusted to a level that is safe and appropriate to the environment. Our findings also suggest that the visual pathways that control flight speed are capable of measuring and regulating the velocity of the images of the walls, largely independently of the spatial structure of the environment.

5.2 Height Control

Maintaining a constant ground speed may affect the height at which bees fly, but it is not possible to extract absolute height information solely from the rate of optic flow. This is because the perceived velocity of motion of the image of the ground will depend on the speed, as well as the height, of flight. A given ground image velocity can be achieved by slow flight at a low altitude or faster flight at a higher altitude. So, what cues do honeybees use to control the height at which they fly above the ground? In this study we attempt to address this question by investigating whether honeybees rely on optic flow in the ventral region of the visual field to regulate their height, and whether flight height is influenced by the texture of the visual environment.

The data from Experiment 3 suggest that flight height is influenced by optic flow cues in the ventral region of the visual field. Bees fly at a lower height when the pattern on the floor of the tunnel carries weak optic flow cues (axial stripes), than when it provides strong optic flow cues (chequerboard pattern). This finding is interesting because it suggests that the system that mediates height control relies on optic flow cues in the ventral region of the visual field, even when there are strong vertical optic flow cues in the lateral region of the visual field (as provided by the chequerboard pattern on the walls of the tunnel). This result makes sense, because it is only optic flow cues in the ventral field of view that can provide useful information on flight height. Optic flow cues in the lateral visual fields will depend primarily on the distances to objects in the lateral field, which is irrelevant to the estimation of height above the ground.

The results of Experiment 4 indicate that the mechanisms that mediate height control are not sensitive to the spatial texture of the environment in the ventral field. This is consistent with the properties of the system that mediates flight control. This finding makes sense from a real world perspective where the texture of the ground can vary substantially, thus making it desirable to have a system for controlling flight height that is robust to variations in the visual texture of the ground.

The findings from this study, as well as those from our previous investigation [6] suggest that the mechanisms of flight speed and height control in the visual pathway of the honeybee measure and regulate the velocity of the images in both the lateral and ventral regions of the visual field and that these mechanisms are insensitive to the contrast or the spatial texture of the visual environment. The advantages of a system that relies on the measurement of image velocity to control flight speed and height are that these behaviors will be regulated according to the proximity of objects in the environment rather than their visual features. Similar properties have been observed in the visual pathways that mediate other flight behaviors such as the centering response [11] and the visual odometer [12]. The movement-detecting mechanisms that mediate the behaviors discussed above seem to have properties that are rather different from those of the well-studied optomotor response in insects. The optomotor response is a behavior in which a flying insect generates motions to compensate for unwanted body rotations by measuring the associated rotations of the image in the eye [13]. The movement-detecting mechanism that mediates the optomotor response appears to be sensitive to changes in the contrast, spatial frequency and temporal frequency of the moving image. As a result, this system does not seem to encode image velocity in a manner that is robust to variations in these parameters. The visual pathways that control flight speed and height, mediate the centering response and generate the odometric signal have properties that are different from the pathway that drives the optomotor response. There is extensive literature on the anatomy and physiology of movement-detecting neurons whose response properties reflect the characteristics of the optomotor response [reviewed by 14]. However, there is relatively little evidence for the existence of motion-sensitive neurons whose response properties reflect the properties of the system that mediates flight speed and height control, the centering response and the visual odometer. The movement-detecting mechanisms that underlie these behaviors must have the capacity to measure image velocity independently of contrast and spatial texture. There is some evidence that velocity-tuned neurons exist in the visual systems of insects but it is not clear whether these neurons participate in the behaviors discussed above [15].

5.3 Implications and Applications of the Present Findings

The groundspeed of a flying agent is determined by many parameters. Pilots of modern aircraft rely on the measurement of multiple parameters including thrust, local airspeed and global position, to calculate and regulate their groundspeed. The honeybee, on the other hand, appears to use only a single measurement from the external environment (namely the measurement of image velocity) to regulate groundspeed. Although this strategy will not achieve a constant groundspeed -- the groundspeed will depend upon the distances to objects and surfaces in the lateral fields of view -- it will ensure that the groundspeed is automatically adjusted to suit the environment through which the flight occurs. Thus, groundspeed will be high in an open environment and slow in a densely cluttered environment.

The present study was conducted in a controlled environment with no interference from air currents. How would this system of flight control respond in the natural environment, where winds are commonly prevalent? In a strong head wind, it would be difficult for bees to maintain a constant groundspeed and therefore, their preferred image velocity. To compensate, bees would have to fly closer to the ground, thus restoring the image speed to its original value. Interestingly, a reduction of altitude would be likely to reduce the velocity of the headwind that the bee experiences, thus enhancing the bee's ability to compensate for the headwind, decreasing the required thrust and reducing the energy expended for the flight [16], [17]. On the other hand, a strong tailwind would cause the bee to fly higher, in attempting to regulate the image velocity. This in turn would enable the bee to catch a stronger tailwind, thus increasing groundspeed, decreasing the required thrust and again reducing energy consumption.

Our findings in relation to the control of flight speed and height in honeybees suggest insect-inspired strategies for the control of aircraft flight. In the design of guidance systems for autonomous aerial vehicles, there is a growing need to avoid sensors that are heavy or expensive, and which use active devices such as radar, sonar or lasers [18], [19]. The techniques of visual guidance that are employed by flying insects, such as those reported here, suggest relatively light, inexpensive and computationally simple ways of achieving some of the desired functions like control of flight speed, and terrain following.

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