

Visual flight control in naturalistic and artificial environments

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Received: 25 March 2011 / Revised: 3 September 2012 / Accepted: 3 September 2012 / Published online: 16 September 2012
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Abstract Although the visual flight control strategies of flying insects have evolved to cope with the complexity of the natural world, studies investigating this behaviour have typically been performed indoors using simplified two-dimensional artificial visual stimuli. How well do the results from these studies reflect the natural behaviour of flying insects considering the radical differences in contrast, spatial composition, colour and dimensionality between these visual environments? Here, we aim to answer this question by investigating the effect of three- and two-dimensional naturalistic and artificial scenes on bumblebee flight control in an outdoor setting and compare the results with those of similar experiments performed in an indoor setting. In particular, we focus on investigating the effect of axial (front-to-back) visual motion cues on ground speed and centring behaviour. Our results suggest that, in general, ground speed control and centring behaviour in bumblebees is not affected by whether the visual scene is two- or three dimensional, naturalistic or artificial, or whether the experiment is conducted indoors or outdoors. The only effect that we observe between naturalistic and artificial scenes on flight control is that when the visual scene is three-dimensional and the visual information on the floor is minimised, bumblebees fly further from the midline of the tunnel. The findings presented here have implications not only for understanding the mechanisms of visual flight control in bumblebees, but also for the results of past and future investigations into visually guided flight control in other insects.

Keywords Bumblebee · Vision · Flight control · Ground speed · Centring

Introduction

Over the past few decades, much attention has been focussed on how insects extract information from the pattern of visual motion generated on the retina during flight (known as optic flow) and how they use this information to control flight (for recent reviews, see Taylor and Krapp 2007 and Krapp et al. 2012). These studies have mostly been conducted under relatively controlled indoor conditions, and the visual environment of the insects has been composed primarily of artificial stimuli such as computer-generated graphics shown on a display, or two-dimensional images printed on paper (for example: David 1982; Kirchner and Srinivasan 1989; Srinivasan et al. 1991; Tammero and Dickinson 2002; Baird et al. 2005, 2010; Dyhr and Higgins 2010). This approach is effective because it enables experimenters to precisely control properties of the environment (such as temperature and light intensity), to manipulate different features of the visual scene (such as contrast and spatial frequency), and to easily record the behavioural or neural response. While artificial stimuli are a useful tool for investigating visual flight control strategies in insects, recent studies have highlighted the importance of using natural scenes to understand how visual motion is processed (Lewen et al. 2001; Reinagel 2001; Straw et al. 2008).

Flying insects as diverse as honeybees (Srinivasan et al. 1991, 1996; Baird et al. 2005; Serres et al. 2008), flies (David 1982; Fry et al. 2009), bumblebees (Baird et al. 2010) and the nocturnal sweat bee, *Megalopta genalis* (Baird et al. 2011) use the rate of optic flow to control

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ground speed and to maintain an equal distance to nearby obstacles when flying through narrow spaces (the centring response). However, Straw et al. (2008) showed that the responses of motion-sensitive neurons to moving visual stimuli differ depending on whether these neurons are presented with natural scenes or artificially generated patterns. When shown moving natural scenes, these neurons respond to the rate of optic flow *independent* of the spatio-temporal or contrast properties of the scene. When the same neurons are stimulated with sinusoidal gratings, their response is *dependent* on these properties. This appears to be because motion-sensitive neurons in the visual system of the fly are finely tuned to the complex spatio-temporal and contrast properties of natural visual scenes, rather than to the simplified spatio-temporal and contrast properties of artificially generated patterns (Straw et al. 2008). Findings such as these, which have also been supported theoretically (Dror et al. 2001), demonstrate that the results obtained using simplified artificial stimuli are insufficient for understanding how these neurons respond to visual information in the natural environment of the animal.

While it has been shown that the neuronal response to optic flow varies between natural and artificial scenes, little is known about how these differences affect the behavioural response to these different stimuli. In one of the only experiments of its kind, Fry et al. (2009) examined the ground speed of fruit flies when they were presented with natural and artificial images. Interestingly, the authors found that the ground speed response to motion in the visual scene was the same for both types of visual stimuli. One limitation of this study is that it was conducted in an indoor laboratory setting using two-dimensional visual stimuli. It therefore still remains unclear how more naturalistic, three-dimensional scenes in an outdoor environment affect the mechanisms of visual flight control in insects.

Here, we investigate if the differences in visual properties between naturalistic and artificial three- and two-dimensional visual scenes generate observable differences in optic flow-based flight control behaviours. In particular, we test the effect of different visual environments on ground speed and centring behaviour in bumblebees in both indoor and outdoor environments with a focus on investigating the effect of axial (front-to-back) optic flow cues in the lateral visual field.

Methods

Commercial *Bombus terrestris* hives (Koppert, UK) were placed either indoors in a netted cage (2-m wide, 2-m high, 3-m long) or outdoors in a circular tent (3 m in diameter and 2.5-m high) in a garden in southern Sweden. The roof

of the tent was made of white cloth and the walls were made of fine black mesh through which the external environment could be observed. For the outdoor experiments, the average temperature was 21 ± 3 °C (mean \pm SD) and the light intensity ranged from 12,000 to 20,000 lux in all experiments except for the control experiment using a blank white floor. For these experiments, the light intensity varied from 1,500 to 3,000 lux. For the indoor experiments, the average temperature was 20 ± 1 °C and the light intensity was 100 lux. The trials of each experimental condition, 1 h in length, were conducted three to four times throughout the day.

The bees were individually marked and trained to visit a plastic sugar water feeder placed at the end of a 2-m long experimental tunnel consisting of two parallel vertical walls (30-cm high, 15 or 30-cm apart) and a flat floor. The floor was covered with green plastic grass in all experiments except for the control experiment investigating the effect of floor texture on the bumblebees' response to the different visual stimuli used on the walls. In this experiment, the floor was covered with blank white matte-laminated paper.

To investigate the effect of axial optic flow cues on flight control, we used visual stimuli that generated strong axial optic flow cues on the eyes of bees flying along the tunnel. Depending on the experimental condition, the walls of the tunnel were lined either with printed two-dimensional artificial and naturalistic scenes or composed of three-dimensional naturalistic stimuli. The two artificial patterns were a randomised chequerboard pattern composed of 2-cm \times 2-cm black-and-white squares (Fig. 1a) and a greyscale sinusoidal vertical stripe pattern with a spatial frequency of 0.033 cycles deg^{-1} (calculated from the midline of the 30-cm-wide tunnel). The spatial frequency of the sinusoidal pattern was closely matched to that of the naturalistic 3D visual scene to test primarily for the effect of other visual differences (such as the colour or dimensionality) on flight control behaviour. To generate a three-dimensional naturalistic visual scene, the walls of the tunnel were constructed of plastic 30-cm long tulips placed at regular intervals (either 8 cm or 16 cm along the length of the tunnel) ('naturalistic scene', Fig. 1b, c). The space between the tulips was left clear so that a view of the surrounding garden provided the background (Fig. 1c). Images taken along the length of the tulip-lined tunnel (8-cm inter-tulip interval) were used to create a two-dimensional version of the three-dimensional naturalistic scene ('naturalistic picture', Fig. 1c). The two-dimensional visual stimuli were printed on paper (in greyscale for the artificial patterns and in colour for the naturalistic scene) and attached to sheet plastic that lined the walls of the tunnel.

The spatial frequency of the tulips at 8-cm intervals and the picture of the tulips was 0.033 cycles deg^{-1} as



Fig. 1 Examples of the scenes used to investigate the effect of natural visual stimuli on flight control in bumblebees. **a** An image taken looking along the length of the experimental tunnel from the feeder (marked with *blue paper*) to the entrance, when the walls are lined with a two-dimensional artificial stimulus (random chequerboard pattern). **b** A view along the experimental tunnel from the entrance to the feeder when the tunnel walls were made up of plastic tulips ('naturalistic scene'). **c** An image of the 'naturalistic scene' taken from the midline of the tunnel. This is also an example of the images that were used to make up the 'naturalistic picture' visual stimulus (see "Methods" for details)

calculated from the midline of the 30-cm-wide tunnel. In the 15-cm-wide tunnel, the tulips spaced at 8-cm intervals and the picture of the tulips had a spatial frequency of $0.016 \text{ cycles deg}^{-1}$. In the 30-cm tunnel, we also used an inter-tulip interval of 16 cm. This stimulus had the same spatial frequency as the tulips at 8-cm intervals in the 15-cm tunnel, i.e. $0.016 \text{ cycles deg}^{-1}$.

The visual properties of natural and artificial visual scenes have distinct differences that are also represented in the artificial and naturalistic stimuli used in this study. The artificial and naturalistic stimuli used here vary not only in their dimensionality, colour and contrast properties, but also, and perhaps most importantly from a motion processing perspective, in their spatial properties. To examine the spatial differences between the visual scenes used in

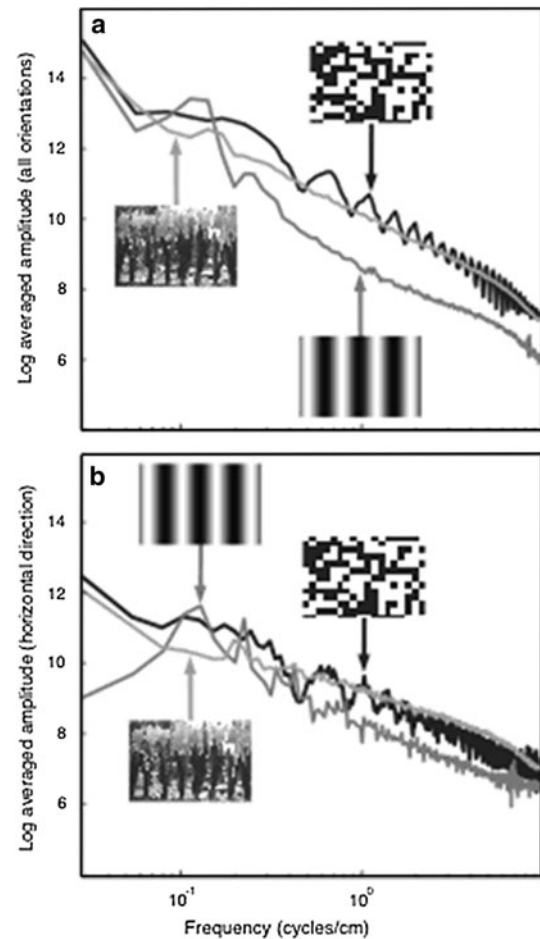


Fig. 2 The spatial properties of the visual scenes used in this study; randomised chequerboard pattern (*black line*), the sinusoidal vertical stripe pattern (*dark grey line*) and the naturalistic picture (*light grey line*). The amplitude of each spatial frequency coefficient in the Fourier spectrum averaged across orientation (**a**) or across just the horizontal direction (**b**)

this study, the amplitude spectra of each spatial frequency coefficient in the Fourier spectrum were calculated across all orientations (Fig. 2a), or just the horizontal orientation (corresponding to the axial optic flow generated by these images, Fig. 2b), according to the method of Tolhurst et al. (1992). One of the main differences between the spatial properties of artificial patterns and natural scenes is that the amplitude spectra of each spatial frequency coefficient do not decrease monotonically with spatial frequency (Tolhurst et al. 1992). This is also evident in our analysis of the artificial and naturalistic scenes used here, particularly in the comparison between the randomised chequerboard and the naturalistic picture in Fig. 2a. Another stark difference between the patterns used here can be seen at low frequencies. For example, the amplitude spectra of the naturalistic scene and the vertical stripe pattern differ by more than one order of magnitude in the horizontal direction (Fig. 2b).

Flights to the feeder were recorded at 50 Hz (indoor experiments) or 60 Hz (outdoor experiments) using a camera mounted above the centre of the tunnel. Ground speed was calculated by digitising the position of the bee in each video frame and finding the two-dimensional (forward and lateral) distance travelled between successive frames. To investigate whether the different visual scenes affect the natural centring behaviour of bumblebees (that is, the tendency to centre the flight trajectory along the midline of the tunnel), we calculated the average lateral distance from the midline for each flight and used one-sample *t* tests to compare this with the midline's value of 0. Thus, a value of 0 would indicate that, on average, the flight was centred about the midline of the tunnel, and positive or negative values would indicate that the flight was centred around a lateral position that was either to the left or right of the midline, respectively. All calculations were made over a distance of 50 cm in the central section of the tunnel.

Although our experimental set-up did not permit us to calculate the height at which the bees flew in the tunnel, changes in the lateral visual scene had no obvious effect on this parameter. This is most likely due to the fact that the texture on the floor of the tunnel, which can affect ground speed and height control behaviour in honeybees (Baird et al. 2006), was held constant throughout each experiment.

Linear mixed model analyses (McCulloch and Searle 2001), with individual identity as a random effect were used to account for the two principal levels of variation that are introduced by including repeated observations from individuals—variation within individuals and variation between individuals. The effect of different experimental treatments was compared using one-way ANOVAs (calculating *F* values) and *t* tests (calculating *T* values) at the 5 % significance level. Analyses were performed using the 'lme' function in R (release: GUI 1.26, the R Foundation for Statistical Computing).

Results

The effect of visual scene on flight control

Five different visual stimuli were used to investigate the effect of naturalistic and artificial visual scenes on flight control: two two-dimensional artificial patterns (randomised chequerboard and sinusoidal vertical stripe), a two-dimensional naturalistic scene (a colour picture of tulips spaced 8-cm apart) and two three-dimensional naturalistic scenes (tulips spaced either 8- or 16-cm apart). In all conditions, the distance between the tunnel walls was 30 cm and the floor was lined with plastic grass. Despite the differences between the visual properties of the stimuli, ground speed remained constant across all conditions

(Fig. 3; $F_{4,163} = 1.64$, $P = 0.17$). Likewise, the centring behaviour of the bees (Fig. 4) was not affected by the different visual scenes. The average lateral distance from the midline of bees flying in the tunnel did not differ significantly from 0 in any of the conditions (chequerboard, $T_{44} = -0.4$, $P = 0.68$; stripes, $T_{41} = -0.1$, $P = 0.95$; tulips 16-cm gap, $T_{33} = 1.5$, $P = 0.15$; tulips 8-cm gap, $T_{49} = -1.0$, $P = 0.30$; tulips picture, $T_{38} = 0.03$, $P = 0.97$). This first result suggests that the mechanisms that mediate ground speed control in the bumblebee are not acutely sensitive to the differences between the visual properties of the naturalistic and artificial two- and three-dimensional stimuli.

To investigate if, instead of responding to the changes in the lateral visual field in the previous experiment, the bees were relying primarily on the texture in the ventral visual field to regulate their flight, we repeated the experiments described above when the floor of the tunnel was a white featureless floor (instead of being covered with plastic grass). In this experiment, we included an additional control in which one wall of the tunnel displayed the chequerboard pattern, whilst the other was composed of tulips spaced at 8-cm intervals. As with the previous experiment, we find that ground speed is not affected by the differences in the visual scenes (Fig. 5; $F_{5,194} = 0.43$, $P = 0.83$), although the average ground speed in all of these conditions is higher than when the tunnel floor is lined with plastic grass.

Again, the average lateral distance from the midline of bees flying in the tunnel (Fig. 6) did not differ from 0 in the chequerboard ($T_{44} = -0.4$, $P = 0.66$), stripe ($T_{26} = -1.5$, $P = 0.14$) and tulip picture ($T_{41} = -0.6$, $P = 0.57$) conditions. However, the flights were *not* centred along the midline of the tunnel when the walls were made of three-dimensional tulip stimuli (8-cm gap, $T_{34} = -3.8$, $P < 0.001$; 16-cm gap, $T_{26} = -7.4$, $P < 0.001$). This result suggests that, in a three-dimensional visual scene, bumblebees are no longer able to centre their flights between the nearby obstacles (i.e. the tulips) when the visual texture from the floor is removed. This effect of the three-dimensional stimuli on centring is *not* evident, however, when only one wall displays tulips (8-cm gap) and the other the chequerboard pattern. In this case, the bees centred their flights, once again, along the midline of the tunnel ($T_{64} = -0.5$, $P = 0.60$). Thus, the centring behaviour of the bumblebees was affected only when the tunnel floor was featureless and both walls were composed of widely spaced three-dimensional stimuli. This indicates that, in addition to lateral visual information, the bees may also rely on visual information on the floor to guide their centring behaviour, at least when the distance between nearby obstacles is large.

Overall, the results from these experiments suggest that the mechanisms that mediate centring behaviour and

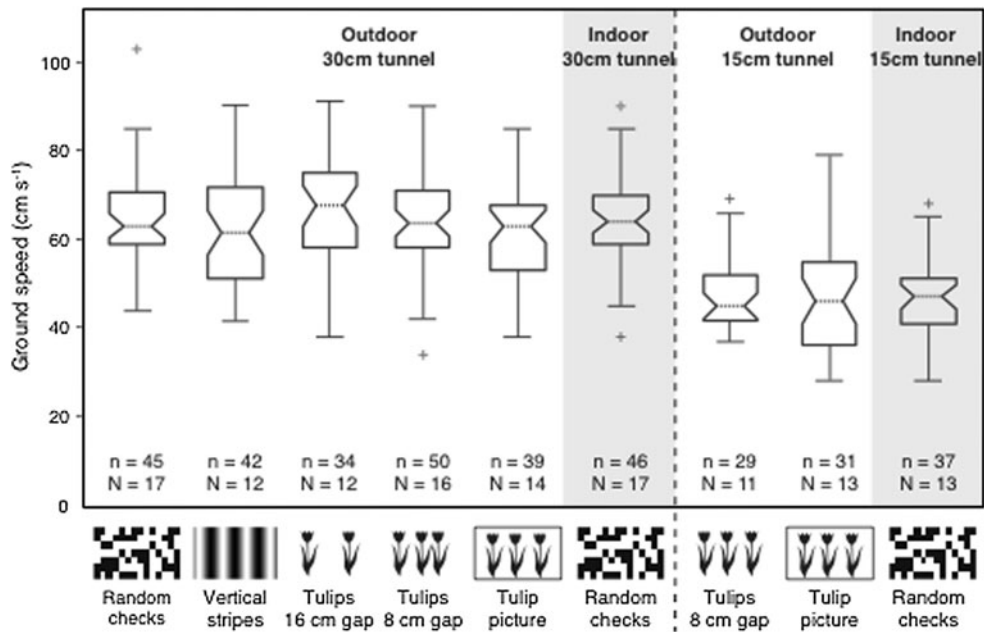


Fig. 3 The average ground speed of bumblebees flying along experimental tunnels with walls made up of different naturalistic and artificial three- and two-dimensional visual stimuli. The floor of the tunnel was covered with green plastic grass. The distance between the walls was either 30 or 15 cm and the experiments were conducted either outdoors or indoors, as indicated by the headings. The number

of flights and the number of different individual bees are given by *n* and *N*, respectively. The *dotted* line marks the median of the data, the boxes extend between the 25th and 75th percentiles, *notches* indicate the 95 % confidence interval, whiskers indicate the rest of the non-outlier data and *crosses* indicate outliers

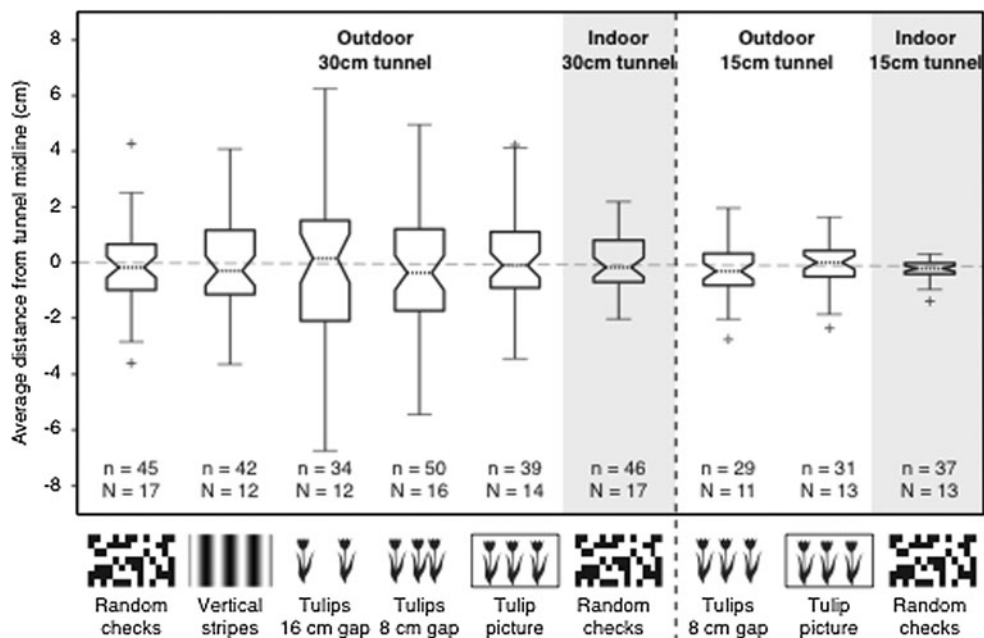


Fig. 4 The average lateral distance from the midline of bumblebees flying along experimental tunnels with walls made up of different naturalistic and artificial three- and two-dimensional visual stimuli. The floor of the tunnel was covered with green plastic grass. The distance from the midline (*grey dashed line*) to the *left* (positive values) or *right* (negative values) wall was either 15 cm (in the 30-cm-wide tunnels) or 7.5 cm (in the 15-cm-wide tunnels). The

experiments were conducted either outdoors or indoors, as indicated by the headings. The number of flights and the number of different individual bees are given by *n* and *N*, respectively. The *dotted* line marks the median of the data, the boxes extend between the 25th and 75th percentiles, *notches* indicate the 95 % confidence interval, whiskers indicate the rest of the non-outlier data and *crosses* indicate outliers

Fig. 5 The average ground speed of bumblebees flying along an experimental tunnel with walls made up of naturalistic and artificial three- and two-dimensional visual stimuli and a featureless white floor. The number of flights and the number of different individual bees are given by n and N , respectively. The dotted line marks the median of the data, the boxes extend between the 25th and 75th percentiles, notches indicate the 95 % confidence interval, whiskers indicate the rest of the non-outlier data and crosses indicate outliers

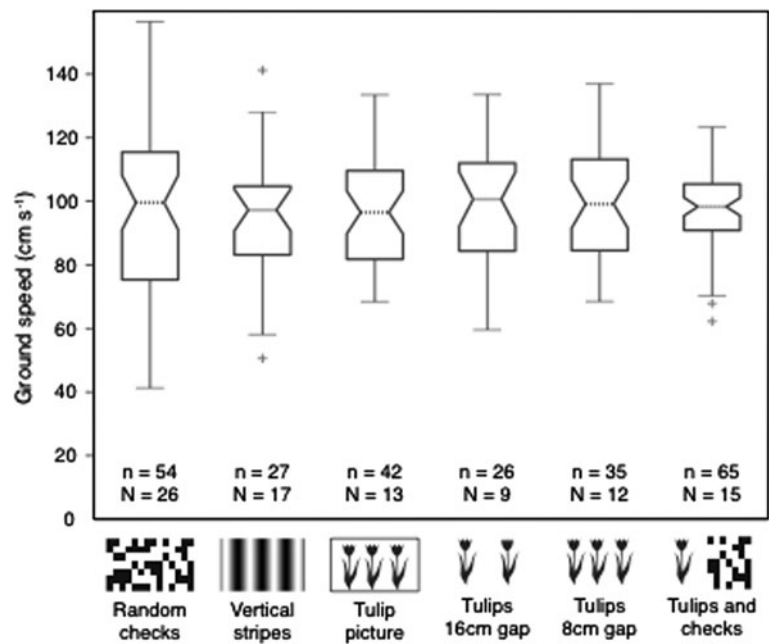
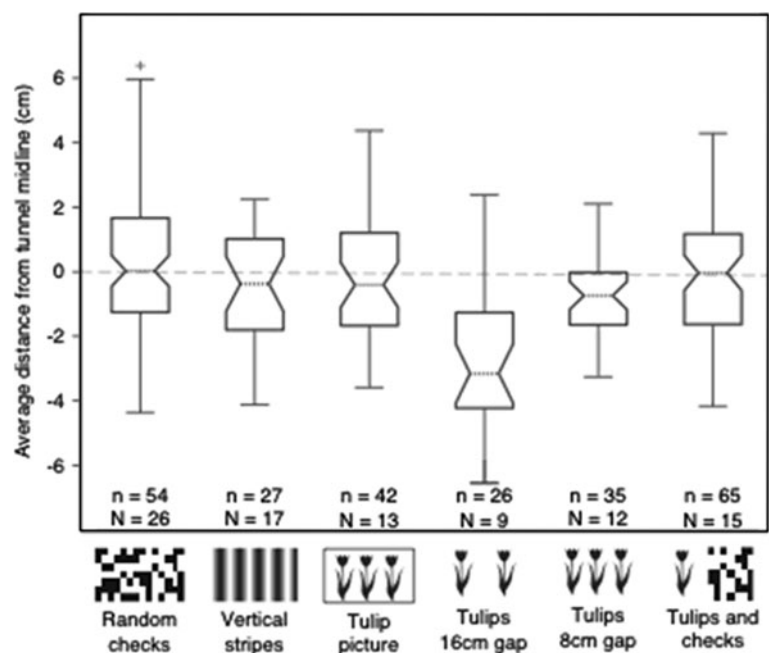


Fig. 6 The average lateral distance from the midline of bumblebees flying along experimental tunnels with walls made up of different naturalistic and artificial three- and two-dimensional visual stimuli and a featureless white floor. The distance from the midline (grey dashed line) to the left (positive values) or right (negative values) wall was 15 cm. The number of flights and the number of different individual bees are given by n and N , respectively. The dotted line marks the median of the data, the boxes extend between the 25th and 75th percentiles, notches indicate the 95 % confidence interval, whiskers indicate the rest of the non-outlier data and crosses indicate outliers



ground speed control in bumblebees are largely robust to differences between naturalistic and artificial visual scenes. This holds true even when one wall of the flight tunnel is composed of a two-dimensional black-and-white artificial pattern and the other of a three-dimensional naturalistic scene.

The effect of tunnel width on flight control

In the next experiment, we investigated the effect of naturalistic and artificial stimuli on ground speed and centring

behaviour when the proximity to nearby obstacles is reduced. To do this, we recorded flights in the outdoor tunnel when the walls were made up of either a three-dimensional naturalistic scene (8-cm inter-tulip interval) or a two-dimensional image of the same scene. In both conditions, the ground speed of bumblebees in the 15-cm-wide tunnel was reduced in comparison to the 30-cm tunnel. (Fig. 3; $F_{1,125} = 98$, $P < 0.0001$). As in the 30-cm tunnel, the flight trajectories were centred around the midline (tulips 8-cm gap, $T_{28} = 0.46$, $P = 0.65$; naturalistic picture, $T_{30} = -0.89$, $P = 0.38$). Interestingly, when the

tunnel walls displayed the naturalistic picture, the bumblebees flew closer to the midline (i.e. the average absolute distance from the midline) in the 15-cm-wide tunnel than in the 30-cm-wide tunnel (Fig. 4; $T_{54} = 5.00$, $P < 0.0001$), but there was no difference in how close the bees flew to the midline of the 15- and 30-cm-wide tunnels when the walls comprised a naturalistic three-dimensional scene (8-cm inter-tulip interval; $T_{52} = 1.64$, $P = 0.21$).

The effect of setting (indoors or outdoors) on flight control

Finally, we compared the results from the outdoor experiments (30- and 15-cm-wide tunnels; 8-cm inter-tulip interval naturalistic scene, naturalistic picture) with those from experiments conducted in an indoor laboratory environment using the ‘artificial’ randomised chequerboard stimulus in tunnels that were either 30- or 15-cm wide.

The results reveal that in both the 30- and 15-cm-wide tunnels, ground speed is unaffected by the setting (indoors or outdoors) or by the type of visual stimulus (Fig. 3; 30 cm: $F_{1,90} = 0.46$, $P = 0.49$; 15 cm: $F_{1,61} = 1.04$, $P = 0.31$). This result suggests that the differences in light intensity and surrounding visual environment between the outdoor and indoor experimental settings do not affect ground speed control in bumblebees. Furthermore, these findings indicate that the ground speed response to artificial two-dimensional stimuli in an indoor setting is not different from the ground speed response to naturalistic stimuli in an outdoor setting.

As with the outdoor conditions (see above), the flight trajectories of bees flying indoors in the 15- and 30-cm-wide tunnels were centred about the midline (15 cm, $T_{35} = -0.09$, $P = 0.93$; 30 cm, $T_{45} = 0.03$, $P = 0.97$). Overall, these results seem to suggest that the experimental setting, indoors in a laboratory, or outdoors in a more natural visual environment, does not strongly affect the centring response in bumblebees.

Discussion

In the visual system of the fly, the response to the rate of optic flow depends on whether motion-sensitive neurons are presented with natural or artificial stimuli (Lewen et al. 2001; Reinagel 2001; Straw et al. 2008). This is because these scenes vary markedly in their visual properties (Ruderman 1994). The naturalistic three-dimensional outdoor scene and the two-dimensional artificial indoor scene used here differ not only in their spatio-temporal and contrast features, but also in the light intensity, colour and structure of the visual environment. We find that ground speed remains unaffected by these differences and that centring behaviour (i.e. the average lateral distance from

the midline) becomes worse only when the bees are presented with three-dimensional lateral stimuli in combination with a featureless floor.

The effect of naturalistic and artificial visual scenes on ground speed control

Despite the large variation in the properties of the visual scenes used in this study, the different features of these scenes do not have any observable effect on ground speed control. This may be because the differences in neuronal response that are observed in the early stages of visual processing to moving naturalistic and artificial scenes are reconciled, at some later point in the neural pathway, to produce a behavioural output that is independent of the properties of the visual scene. It is possible, of course, that the naturalistic stimuli used here were not sufficiently different from the artificial stimuli to cause differences in the neuronal response and therefore the behavioural output. However, considering the large differences in dimensionality, colour, contrast and spatial properties between the visual stimuli included in this study, our results nonetheless suggest that the mechanism that mediates flight control is highly robust to changes in visual scenes.

It is interesting to note that, even when the spatial structure of the naturalistic scene and the proportion of visible background are modified (by increasing the distance between the tulips from 8 to 16 cm), there is no obvious effect on ground speed. This leads to the intriguing possibility that only the motion of nearby obstacles is being used to measure the rate of optic flow in the visual scene, although more detailed behavioural and neuronal investigations are necessary for understanding this result.

The effect of naturalistic and artificial visual scenes on centring

The accuracy of centring in bumblebees, in almost all cases, is not affected by the different visual properties of the naturalistic picture and the artificial pattern, or by the experimental setting (indoors or outdoors). This holds true even when one wall of the tunnel displays an artificial two-dimensional pattern, while the other is composed of a three-dimensional naturalistic scene (tulips spaced 8-cm apart). This suggests that the centring response, like ground speed control, is robust to the large differences in visual properties between naturalistic and artificial scenes.

Centring behaviour is somewhat less precise when the walls of the tunnel are constructed of a naturalistic three-dimensional scene. A likely explanation for this loss of precision is that the increased proportion of distant background information affects centring behaviour. This hypothesis is supported by the observation that centring is

worse when the tulips are spaced 16-cm apart than when spaced 8-cm apart. It is worth noting that the average lateral position of bumblebees flying in the tunnels with the naturalistic three-dimensional scenes is clustered along one particular side of the tunnel (Fig. 6). A possible explanation for this is that the distance to visual features in the background that can be seen between the tulips (such as trees and bushes) is not equal on both sides. Although the relative importance of background distance for centring in bumblebees cannot be determined from the data presented here, our results do suggest that it may play a role.

Conclusions

Here, the presented results suggest that ground speed control in bumblebees is not strongly affected by the differences between artificial and naturalistic two- and three-dimensional visual stimuli. Centring behaviour, like ground speed control, also appears to be robust to the differences between naturalistic and artificial two-dimensional stimuli in both indoor and outdoor environments. Our findings suggest that, in general, the flight control behaviours observed in the typical laboratory setting—in which the visual scene comprises nearby artificially generated two-dimensional visual patterns—are indeed a reasonable representation of these behaviours in a cluttered natural setting. Due to the generality of ground speed control mechanisms across different insect species, such as flies (David 1982; Fry et al. 2009) and honeybees (Srinivasan et al. 1991, 1996; Baird et al. 2005; Serres et al. 2008), it is likely that the results of the present study apply not only to bumblebees, but also to other flying insects that rely on vision for flight control.

Acknowledgments This work was supported by the Air Force Office of Scientific Research/European Office Aerospace Research and Development (grant no. FA8655-08-C-4004), the Wenner Gren Foundation and the Swedish Research Council. We would also like to thank Shikhar Mann for assistance with the image analysis and Lana Khaldy for assistance with the experiments and analysis.

Ethical standard The experiments were carried out according to the current laws on animal experimentation in Sweden.

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