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ORIGINAL PAPER

Bumblebee flight performance in environments of different proximity

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Abstract Flying animals are capable of navigating through environments of different complexity with high precision. To control their flight when negotiating narrow tunnels, bees and birds use the magnitude of apparent image motion (known as optic flow) generated by the walls. In their natural habitat, however, these animals would encounter both cluttered and open environments. Here, we investigate how large changes in the proximity of nearby surfaces affect optic flow-based flight control strategies. We trained bumblebees to fly along a flight and recorded how the distance between the walls—from 60 cm to 240 cm—affected their flight control. Our results reveal that, as tunnel width increases, both lateral position and ground speed become increasingly variable. We also find that optic flow information from the ground has an increasing influence on flight control, suggesting that bumblebees measure optic flow flexibly over a large lateral and ventral field of view, depending on where the highest magnitude of optic flow occurs. A consequence of this strategy is that, when flying in narrow spaces, bumblebees use optic flow information from the nearby obstacles to control flight, while in more open spaces they rely primarily on optic flow cues from the ground.

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Abbreviations
TOF   Translational optic flow

Introduction

The habitats of flying animals often contain a mixture of cluttered and open spaces, which they must negotiate with high precision to avoid collisions with nearby obstacles or the ground. To be able to do this, they need to continuously monitor and adjust their position in space and their speed according to the proximity of these obstacles. Animals such as bees and birds control their flight by extracting information from the apparent image motion that is generated on the retina as they move through the world, known as optic flow. Because the optic flow arising from translation (translational optic flow, TOF) varies with the inverse of distance, it can provide information about relative distance to nearby surfaces, relative forward speed (Gibson 1950, 1979) as well as the spatial layout of the environment (Collett 2002; Koenderink 1986; Lappe 2000). Flying animals have been shown to exploit this property of TOF to control their lateral position in space (Baird et al. 2011; Bhagavatula et al. 2011; Dyhr and Higgins 2010; Kirchner and Srinivasan 1989; Linander et al. 2015; Serres et al. 2008a; Srinivasan et al. 1991), ground speed (Baird et al. 2005, 2006, 2010, 2011; Barron and Srinivasan 2006; Bhagavatula et al. 2011; David 1982; Fry et al. 2009; Kern et al. 2012; Linander et al. 2015; Portelli et al. 2010; Schiffer and Srinivasan 2014; Srinivasan et al. 1996), and height above ground (Baird et al. 2006; Portelli et al. 2011). TOF provides animals with a lightweight and energy efficient method for controlling flight, something that is particularly important for flying insects whose miniature size sets strict limitations on their sensory systems and brain.

When flying along narrow tunnels, bumblebees (Dhyr and Higgins 2010; Linander et al. 2015) and honeybees (Kirchner and Srinivasan 1989; Srinivasan et al. 1991) appear to balance the magnitude of the lateral optic flow experienced in each eye to control their position. This strategy allows them to maximise the distance to each wall, causing them to fly along the centre of the tunnel, a behaviour known as the centring response. Studies investigating centring behaviour in insects have been conducted almost exclusively in tunnels that are less than 40 cm wide. But how do they control their position when the distance to the nearby obstacles becomes much larger, such as when they are flying over meadows or grassland? Serres et al. (2008a) showed that, when flying along a 95 cm wide tunnel (the widest tunnel used to date for such studies), honeybees will tend to fly along the midline if both the feeder and the entrance are centred but will adopt a wall-following behaviour when both the feeder and the entrance to the tunnel are placed on one side. This finding suggests that it may not be necessary for bees to balance the TOF from each wall to control their position when flying along wider tunnels (Serres et al. 2008b), although it remains unclear how the bees would have controlled their position in the absence of a visible feeder as a target.

Ground speed is another aspect of insect flight that is controlled using TOF cues. When flying along a 30 cm wide tunnel, bumblebees fly nearly twice as fast as when they are flying along a 15 cm wide tunnel (Baird et al. 2010). This increase in ground speed in relation to the distance between the tunnel walls suggests that, like honeybees (Baird et al. 2005), bumblebees control their speed by holding constant the magnitude of TOF generated by the walls of the tunnel. This strategy automatically ensures that ground speed is reduced when the distance to nearby obstacles decreases because the magnitude of TOF varies inversely with the proximity to surfaces. In narrow spaces, relatively small changes in the distance to obstacles will generate relatively large changes in TOF and the bees will respond with large changes in speed and position. As the distance to obstacles increases, the same changes in proximity will generate much smaller differences in TOF making both position and speed control more challenging. Do optic flow-based flight control strategies become less accurate when the distance to the nearby obstacles is large?

Because very little is known about how insects and other animals control their flight in open spaces, the aim of this study is to investigate how large changes in the proximity of obstacles affect position and ground speed control in bumblebees. We trained buff-tailed bumblebees (*Bombus terrestris*) to fly through a 5 m long experimental tunnel and record the effect on flight control when the distance between the walls increases in 60 cm steps from 60 to 240 cm. Our results indicate that, as the distance to

the nearby surfaces increases, bumblebees rely increasingly upon TOF from the floor to control both their position and ground speed.

Materials and methods

Experimental setup

The experiments were conducted in a temperature-controlled greenhouse in Lund, Sweden. Light intensity and temperature in the greenhouse varied according to natural fluctuations in the weather (2309 ± 1495 lux, 22 ± 3 °C, mean $\pm$ SD).

Bumblebee hives (*Bombus terrestris* L., Koppert UK) were placed in a white tent (6 m long, 3 m wide, 2 m high) in the middle of the entrance (equidistant from each wall) to a 5 m long flight tunnel of flexible height (60–180 cm) and width (60–240 cm) mounted inside the tent. A total of three hives were used in the experiment, with each hive containing approximately 200 foragers. The bees were trained to fly along the tunnel by gradually moving a feeder towards the far end, where it was hidden from view in a white box. The feeder consisted of two U-shaped parallel channels—one containing sugar water and containing for pollen—that crossed the width of the tunnel from wall to wall. The top of the tunnel was covered with plastic insect netting and the only visible structures in the roof were three metal support bars. A camera (Mikrotron MotionBLITZ EoSens, Unterschleisheim, Germany) was mounted above the centre of the tunnel to record flights towards the feeder at 80 Hz. The bees were allowed to freely enter and exit the tunnel, which meant that sometimes several bees were foraging at the same time. Recordings that included more than one bee in the field of view of the camera were only included in the analysis if there was no interaction or obvious interference in the flight trajectory being analysed. In each experimental condition, the bees were given at least 1 h to adapt to their new environment before recording commenced. Technical constraints relating to the large tunnel size meant that the bees experienced each condition for several days before the tunnel configuration was changed. Due to the large width of the tunnel and the feeder, it was not possible to individually mark the bees but the possibility of pseudo-replication was minimised by recording over 80 flights for each condition.

Both walls and the floor of the flight tunnel were lined with a "dead leaves" pattern (Fig. 1a) with a 1/frequency^2 distribution that is designed specifically to make the distribution of spatial frequencies in the pattern—and therefore optic flow estimations—distance independent (for technical specifications see Lee et al. 2001). The pattern on the walls was black and white, while the pattern on the floor was red
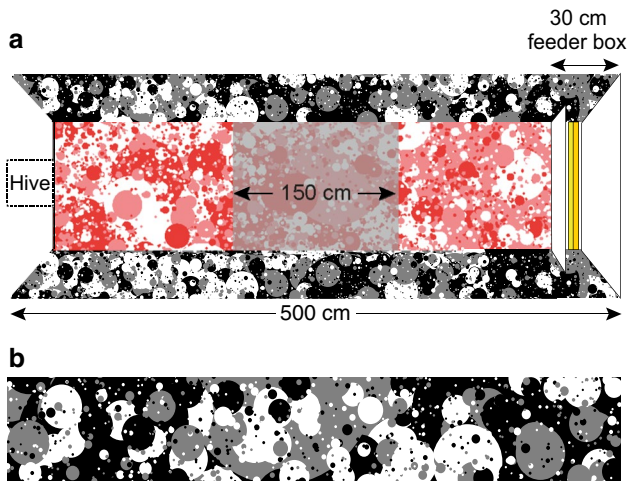
Fig. 1 The experimental setup. **a** Schematic diagram of the 5 m long flight tunnel. A high-speed camera recorded bees flying over the central (150 cm) section of the tunnel, indicated by the *grey* area. The hive was positioned at the tunnel's entrance at an equal distance from each wall. The floor was lined with a *red* dead leaves pattern. The feeder channels (marked in *yellow* for nectar and *orange* for pollen) were hidden from the view of the bees in a *white box* and extended across the width of the flight tunnel. **b** The dead leaves pattern that covered the walls and floor of the tunnel. This pattern contains all spatial frequencies with equal power, which makes optic flow estimations distance independent

and white to facilitate tracking the bees in the recorded sequences while maintaining a relatively high pattern contrast for the bees. The distance between the tunnel walls was set at 60, 120, 180 or 240 cm. In all conditions, the height of the walls was equal to the distance between them except for the 240 cm wide tunnel, which had a wall height of 180 cm due to space restrictions.

Recording and analysis of flight trajectories

The centre of mass of the bumblebee was determined (in *x*- and *y*-pixel coordinates) in each video frame using an automated tracking program (Lindemann 2005). The flight trajectories were analysed over a distance of 150 cm (75 cm before and 75 cm after the midsection of the tunnel). Data were converted from pixels to cm using a reference pattern placed 30 cm above the floor and flights where the bees flew more than 60 cm from the floor (as determined by the number of pixels they occupied in the recorded sequences) were excluded from further analysis to minimise calculation errors.

The density of lateral positions for all flights was calculated by dividing the tunnel's area into grid elements corresponding to 5 % of the tunnel width. For each frame of a recorded flight trajectory, the grid element that the bee was located in was determined. To create a histogram of the spatial distribution of the flight trajectories across the

width of the tunnel, the number of times a bee was located in a grid element was averaged over the tunnel length and normalised across the tunnel width. The lateral position for each flight trajectory was determined by finding the lateral distance from the midline of the tunnel (positive and negative values indicating flights to the left and right side of the midline, respectively) and then calculating the median of all such values for each flight. Variation in lateral position for each flight (used as a measure of how well the bees could control their position in one trajectory) was calculated from the 25 to 75 % interquartile range of these data.

Ground speed was determined by calculating the two-dimensional distance travelled between each frame and dividing this by the time step between the frames. The median and interquartile range were then calculated for each flight.

Flight height was estimated using the median number of pixels occupied by a bee in the recorded images of its flight trajectory. This number was converted into an estimate of the height that the bee flew above the ground by measuring the number of pixels occupied by a medium-sized bumblebee placed at known distances above the ground. The relationship between the number of pixels occupied by a bee and distance from the ground could be well described with a linear equation that was then used to convert all bee size values in pixels into height in cm. In addition, we calibrated the size of very small and very large bees at different distances from the ground and found that the error in our height estimates could reach 7 cm but was most likely smaller than this as very small and very large bees rarely flew to the feeder. These errors would have been consistent across all treatments.

In some cases, the data were not normally distributed; therefore, non-parametric Wilcoxon rank-sum and Kruskal-Wallis statistical tests at the 5 % significance level were used to test for the effect of tunnel width on the different flight control parameters.

Results

The effect of tunnel width on position control

In general, all flight trajectories were oriented parallel to the long axis of the tunnel but rather than being straight, they generally meandered about the overall direction of flight (Fig. 2a). The median lateral positions for the flight trajectories in each tunnel were distributed about the midline but the spread of these positions increased with the distance between the walls (Fig. 2b, Kruskal-Wallis, $\chi^2_{3/441} = 21$, $P < 0.0001$), as did the spread of lateral positions within each flight trajectory (Fig. 2c, Kruskal-Wallis, $\chi^2_{3/441} = 118$, $P < 0.0001$). Together, these results suggest
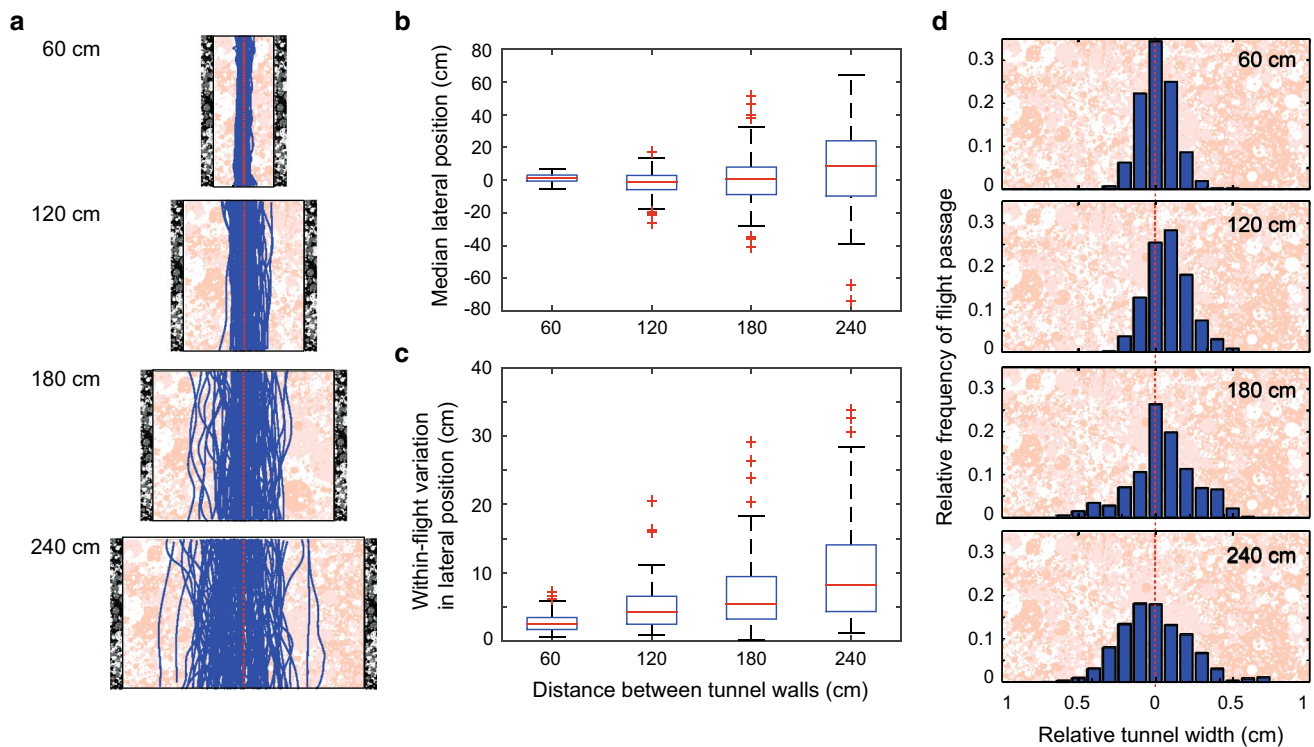
Fig. 2 The effect of tunnel width on lateral position. **a** Raw flight trajectories of bees flying in the 60, 120, 180 and 240 cm wide tunnels. **b** The median lateral position for each flight trajectory recorded in each tunnel width. *Boxes* indicate the extent of the 25–75 % interquartile range, the *red line* indicates the median, *whiskers* indicate the full extent of the data and *red crosses* represent outliers. **c** The variance (interquartile range) of lateral position for each flight trajectory (other details as in **b**). **d** The relative frequency of lateral flight positions in each tunnel. *Each bar* represents a longitudinal strip that has a relative width of 5 % of the tunnel diameter. The *red dotted line* represents the midline of the tunnel

that, as the distance between the tunnel walls increased, bumblebees were less likely to maintain an equal distance between the nearby surfaces and that their ability to control their within-flight lateral position decreased. These findings are further supported by an analysis of the relative distribution of lateral position normalised to tunnel width (Fig. 2d). While the positions were distributed over 50 % of the tunnel's width in the 60 and 120 cm wide tunnels, the bees flew over an increasingly larger proportion of the tunnel's width—65 and 70 %—in the 180 and 240 cm wide tunnels. As the distance between the walls increased, the relative and absolute lateral position of bees became less constrained but there was no evidence that they were either centring along the midline or flying consistently closer to one of the walls.

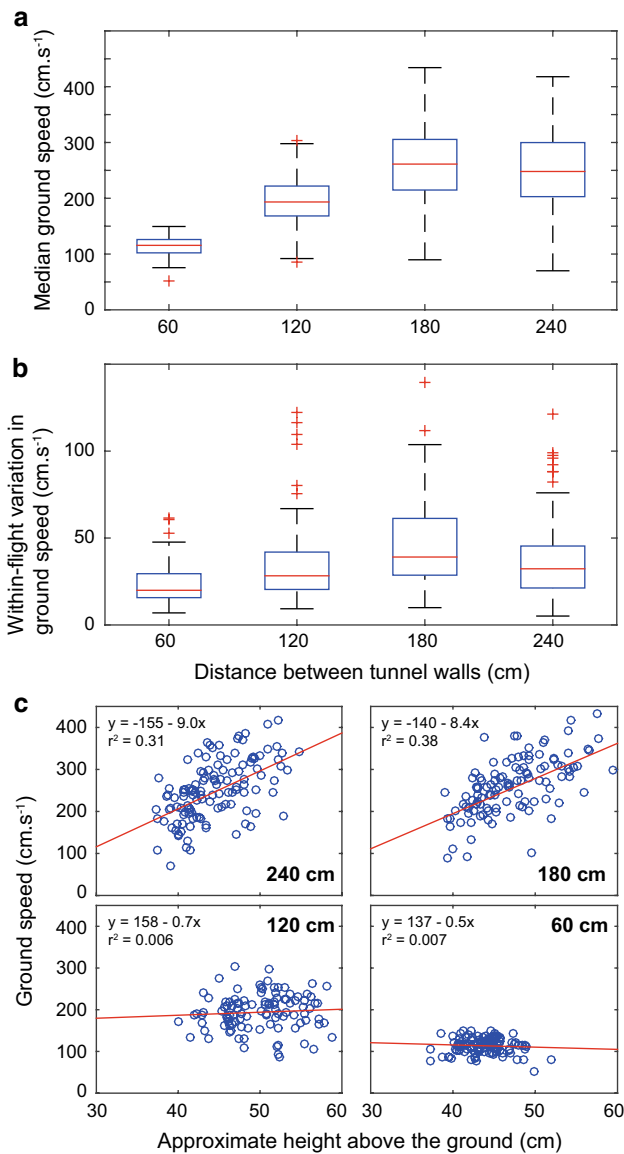## The effect of tunnel width on ground speed control

As the distance between the tunnel walls increased by a factor of 2 from 60 to 120 cm, the bumblebees responded by increasing their ground speed by a factor of approximately 1.7 from 115 [102 126] to 193 [168 222] cm s^{-1} (median [interquartile range], rank-sum: $Z = -11$, $P \ll 0.0001$; Fig. 3a). When the distance between the tunnel walls doubled from 120 to 240 cm, ground speed increased by a factor of 1.5 to 248 [203 300] cm s^{-1} (rank-sum: $Z = 6$, $P \ll 0.0001$). However, there was no significant change in ground speed between the 240 and the 180 cm wide tunnels (180 cm: 261 [215 306] cm s^{-1}, rank-sum: $Z = -1.18$, $P = 0.24$). The within-flight variation of ground speed followed a similar trend, with an increase between the 60 and 180 cm wide tunnels suggesting that the bees are less able to maintain a constant ground speed as the distance between the walls increases (Fig. 3b).

The effect of tunnel width on the relationship between height and ground speed

One possible explanation for the reduction in the effect of tunnel width on ground speed and the total absence of an effect between the 180 to 240 cm is that, as the distance between the walls increases, the bees rely increasingly on TOF from the pattern on the tunnel floor to control their flight. A Spearman's rank correlation analysis reveals

Fig. 3 The effect of tunnel width on ground speed control. The median two-dimensional ground speed (**a**) or within-flight ground speed variance (interquartile range) (**b**) of bees flying in tunnels of different widths (other details as in Fig. 1b). **c** Median ground speed as a function of the median height flown above the ground in tunnels of different widths (*bold text*). *Red lines* indicate a linear regression fit to the data; the equation and associated r^2 value are shown in the *top left* corner of each subplot

that there is a significant positive correlation between height and ground speed in the 180 and 240 cm wide tunnels (180 cm: $\rho = 0.63$, $P < 0.0001$; 240 cm: $\rho = 0.56$, $P < 0.0001$) but not in the 60 and 120 cm wide tunnels (60 cm: $\rho = -0.19$, $P = 0.06$; 120 cm; $\rho = 0.13$, $P = 0.17$). These results suggest that TOF from the tunnel floor influences flight control in the wider tunnels but not in the narrower ones.

Discussion

The variability of position and ground speed increases with tunnel width

Large increases in the distance between the tunnel walls affect both lateral position and ground speed control in bumblebees. Lateral position becomes more variable, both within and between flights (Fig. 2), and the bees fly at increasingly greater distances from the tunnel's midline. While the flight trajectories in the 60 and 120 cm wide tunnels are still relatively well-centred about the midline, as would be expected if position is being controlled using translational optic flow cues (TOF) from the walls (Dyhr and Higgins 2010; Kirchner and Srinivasan 1989; Linander et al. 2015; Serres et al. 2008a; Srinivasan et al. 1991), there is no clear evidence for either centring or wall-following behaviour (Serres et al. 2008a) in the 180 and 240 cm wide tunnels. In addition, we find that the effect of tunnel width on ground speed decreases as tunnel width increases (Fig. 3). While ground speed increases with the increase in tunnel width between the 60 and 120 cm wide tunnels—as would be predicted if the bees are holding the rate of TOF generated by the walls about a set-point (Baird et al. 2010)—this relationship becomes weaker between the 120 and 180 cm wide tunnels and is absent between the 180 and 240 cm wide tunnels. Overall, increases in the distance between obstacles in the environment affect the variability of both position and ground speed in bumblebees.

Why do lateral position and ground speed become more variable in less-cluttered environments? The change in behavioural response to the increasing distance between the tunnel walls that we observe in this study is most likely a reflection of how TOF changes with increasing distance. Because the magnitude of TOF varies inversely with distance, the absolute change in TOF generated by a given deviation in lateral position or speed will decrease as the distance to the surface generating the optic flow increases. For example, for a constant speed of 100 cm s^{-1}, a 10 cm decrease from 30 to 20 cm in the distance to a wall will result in a 95° s^{-1} increase in the maximum magnitude of TOF, whereas a 10 cm decrease in distance from 120 to 110 cm will generate only a 4° s^{-1} change in TOF. Similarly, a relatively large change in speed from 100 to 150 cm s^{-1} for a bee flying 30 cm away from the tunnel wall will generate a 95° s^{-1} change in the magnitude of TOF generated by that wall but at a distance of 120 cm, the same change in speed will cause only a 24° s^{-1} increase in the magnitude of TOF. As the distance between the walls increases, the change in the magnitude of TOF that they generate decreases and increasingly larger changes

in position or speed will need to occur before they are detected and a correction made (assuming that the visual system of the bumblebee has a fixed minimum threshold for detecting changes in the magnitude of TOF). Using TOF to control flight is, therefore, likely to result in a loss of precision and an increase in variability as the distance to the surfaces that are generating it increases, and this is precisely what we observe in our results.

Bumblebees measure translational optic flow for flight control in the ventral visual field

Although the increased variability in flight control observed here can be explained by the decreasing absolute change in the magnitude of TOF that occurs as the tunnels get wider, it does not fully explain why tunnel width has no appreciable effect on ground speed in the 180 and 240 cm wide tunnels. This result can be understood, however, if we consider firstly that the bees are measuring TOF not only in the lateral but also in the ventral field of view, as honeybees have been shown to do (Baird et al. 2006; Portelli et al. 2010, 2011) and, secondly, that the proportion of the visual field occupied by the walls and floor of the tunnel changes with increasing tunnel width. Evidence that bumblebees are not using only the TOF from the walls to control their ground speed comes from the non-proportional relationship between tunnel width and ground speed. As the tunnel doubles in width from 60 to 120 cm, bumblebees increase their ground speed by a factor of 1.7. Given that the lateral positions of bees in both tunnels are concentrated about the midline, we would expect ground speed to increase by a factor of 2 if the bees were only using TOF information from the walls. One explanation for the lack of a full proportional increase in speed with tunnel width is that the TOF from the floor is being used for speed control and that it has an increasing influence on flight control as the tunnels get wider. If this were the case, then we would expect ground speed to vary with height because, to hold the magnitude of TOF on the ground about a set-point, bumblebees that fly further from the ground should also fly faster. Indeed, we find a strong positive relationship between ground speed and height in the wider tunnels, but not in the narrower tunnels, where the influence of the tunnel walls is still large. Linear regressions of the relationship between height and ground speed in the 180 and 240 cm wide tunnels have similar slopes (8.4 and 9.0, respectively), suggesting that the bees are holding roughly constant the magnitude of ventral TOF in these two conditions (the slightly lower value in the 180 cm wide tunnel may be due to the narrower floor width). An increasing influence of the ground is also logical when we consider the proportion of the visual field that it occupies in the different tunnels. In the 60 cm wide tunnel, each of the walls and floor will subtend 90° on the visual field of a bee flying along the midline at a height of 30 cm. When the tunnel walls are 240 cm apart, the angular extent of the walls is reduced to 65°, while the tunnel floor covers 152° of the visual field. Thus, as the distance between the walls increases, they occupy a decreasing proportion of the visual field. Another important point to consider is that, even for the bees flying at the maximum height of 60 cm, the floor of the tunnel would generate a higher magnitude of TOF than the walls unless they flew closer than 60 cm to one of the walls, which was rarely the case in the 180 and 240 cm wide tunnels (Fig. 2b, d). Together, these results suggest that, as the distance between the walls increases, the TOF that is being used to control speed is being increasingly dominated by information from the ground.

Previously, we proposed the hypothesis that bumblebees measure optic flow for flight control flexibly in their visual field, depending on where the maximum magnitude of translational optic flow occurs (Linander et al. 2015). In this earlier study, however, the translational optic flow cues were restricted to the walls of flight tunnels that were only 15 or 30 cm wide, so the effect of ventral optic flow cues was not directly investigated. The findings of the present study lend further support to our hypothesis and add another dimension to it by suggesting that bumblebees can and do measure TOF in the ventral visual field if the magnitude is higher than that generated by obstacles in the lateral visual field.

If translational optic flow cues from the ground are being used to control speed, are they also being used to control position in the wider tunnels? It is not possible from the experiments performed in this present study to determine if the bees are relying on optic flow cues generated by the floor to control their position or whether they are using optic flow information from the walls of the tunnel. This is because, in both cases, we would expect lateral position control to become less precise as the distance between the tunnel walls increases, which is the case in our experiments. Although it would be problematic to try to maintain a straight line using only ventral optic flow cues, when bees are flying out in open environments they would normally have additional compass or landmark cues that would help them to maintain their course to a food source or to the hive. Although these cues might not necessarily enable the bees to have as precise control over their lateral position as they have when flying in narrow spaces, it would still be sufficient as the risk of collisions in these open environments is very low. As long as the bees have some external reference cue that allows them to maintain their heading, it would always be possible for them to safely control their flight and reach their goal using translational optic flow cues from the ground.

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