Obstacle avoidance in bumblebees is robust to changes in light intensity

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Abstract
Flying safely and avoiding obstacles in low light is crucial for the bumblebees that forage around dawn and dusk. Previous work has shown that bumblebees overcome the limitations of their visual system—typically adapted for bright sunlight—by increasing the time over which they sample photons. While this improves visual sensitivity, it decreases their capacity to resolve fast motion. This study investigates what effect this has on obstacle avoidance in flight, a task that requires the bees to reliably detect obstacles in the frontal visual field and to make a timely diversion to their flight path. In both bright and dim light, bumblebees avoided the 5 cm diameter obstacle at a consistent distance (22 cm) although in dim light they approached it more slowly from a distance of at least at least 80 cm. This suggests that bumblebees have an effective strategy for avoiding obstacles in all light conditions under which they are naturally active, and it is hypothesised that this is based on a time-to-contact prediction.

Keywords Insect · Flight · Obstacle avoidance · Light intensity · Bumblebee · Vision

Introduction
To move safely and efficiently through the world, animals must have the capacity to detect obstacles in their path and to do this with sufficient time to execute an avoidance manoeuvre. For visually-guided animals active in dim light, the difficulty of accurately detecting and avoiding obstacles is increased because the reduced number of available photons decreases the signal to noise ratio, making visual information less reliable (Land and Autrum 1981). Nonetheless, many visually-guided animals are active in dim light, including the bumblebee *Bombus terrestris* that, despite the limitations imposed by their apposition compound eyes that are adapted for bright daylight conditions (Nilsson and Land 2012), are capable of extending their foraging period into dawn and dusk (Steen 2017). *B. terrestris* improve their visual sensitivity in dim light, at least in part, by increasing the time over which their photoreceptors capture photons (Reber et al. 2015). This would have the effect of reducing their temporal resolution and limiting their ability to detect visual motion, a cue that is critical for controlling flight and detecting obstacles. Indeed, when landing in dim light, bumblebees extend their legs closer to the target (Baird et al. 2015) and their body posture is modified (Reber et al. 2016), suggesting that the decrease in temporal resolution does affect their behaviour. Does this also affect their ability to detect and avoid obstacles?

The aim of the present study is to answer this question by investigating how light intensity affects the ability of foraging bumblebees to detect and avoid a stationary obstacle. *B. terrestris* were trained to fly along an experimental tunnel to a feeder. An obstacle was then presented along their path and the resultant trajectories recorded.

Materials and methods
A bumblebee hive (*Bombus terrestris*; Koppert, The Netherlands) was placed at the entrance of a 200 cm long, 30 cm high and 30 cm wide tunnel covered with netting. The bees were kept in a 18 h:7 h light:dark cycle in a controlled
laboratory environment (24 °C, 32% humidity) and were
trained to fly to a sugar-water feeder hidden behind a white
panel at the end of the tunnel, where they were marked for
individual identification. The bees were allowed to forage
freely from this feeder (flying back and forth along the tun-
nel) for at least 2 days prior to the experiment and through-
out its duration. Dimmable fluorescent lamps (Biolux,
Osram GmbH, Germany) covered with white diffusion
filters (Lee 252 Eight White Diffusion) illuminated the tun-
nel from above.

The walls and floor of the tunnel were lined with uniform
50% grey. Bees flying to the feeder were presented with two
experimental conditions—(1) control and (2) obstacle—
under two light intensities, 500 lx and 19 lx, chosen because
they mimic the light intensities around dawn and dusk when
bumblebees naturally forage and because they were similar
to intensities used in similar studies with B. terrestris (Baird
et al. 2015; Reber et al. 2016, 2015). In the control condi-
tion, no obstacle was present in the tunnel. In the obstacle
condition, a 30 cm high, 5 cm diameter cylinder displaying
a grey-scale dead-leaves pattern (to provide the bees with
strong contrast cues and a naturalistic range of spatial fre-
quencies, (Lee et al. 2001) was placed in the tunnel. Before
each 30 min long trial commenced, the light intensity for
was set and the bees allowed to forage freely for at least
30 min to allow their visual systems time to adapt to the light
condition. To prevent habituation to the obstacle or its posi-
tion, it was only present during the experimental trials and
was placed midway between the walls at one of three loca-
tions (one location being used per trial)—25 cm before the
centre, at the centre or 25 cm after the centre. Only the first
three flights of an individual per trial were included in the
data (although most individuals performed only one flight
per trial). Each light intensity and obstacle position combi-
nation was presented in a pseudo random order. A camera
(MotionBLITZ EoSens mini, Miktron GmbH, Germany)
mounted above the tunnel recorded the 2 m long flights
towards the feeder at 100 Hz (Fig. S1). Upon arriving at the
feeder, the bee was identified by the observer and this infor-
mation was added to the saved video file. At 19 lx, an infra-
red illuminator (TV6700, Elfa Distralec AB, Sweden) was
used to improve the signal to noise ratio in the recordings
without modifying the intensity of light visible to the bees.

Data analysis and statistics

In each video frame, the centre of mass of the bumblebee
(in x- and y-coordinates) was determined using an automated
tracking program (Lindemann et al. 2005). The flight trajec-
tories were tracked over the tunnel’s 200 cm length and nor-
malised to the centre of the obstacle or the centre of the tun-
nel for the control condition. Only flights in which individual
bees flew alone in the tunnel to the feeder were included in
the analysis. Position data were converted from pixels to cm
using a check pattern placed 15 cm above the tunnel floor
(the approximate height of the flight trajectories). Ground
speed was calculated by dividing the two-dimensional
distance travelled between successive frames by the frame
duration (0.1 s). The speed and position data for each flight
were grouped in 2 cm distance bins from which a median
value was calculated. The position and ground speed values
at each distance step were averaged for each light intensity
and the data from the trials with an obstacle were compared
with the data calculated at the same relative distance for the
control condition using two-tailed Student’s t-tests in Matlab
(Mathworks, USA), as the data in each bin followed a nor-
mal distribution. A change in position or ground speed was
deemed to occur when the t-test between the obstacle and
control condition at the same distance resulted in p values
below 0.05. Values reported in the text are mean ± std. The
number of flights and individuals recorded for each condi-
tion are presented in Fig. 1. Repeated flights from the same
individuals were treated as individual data points because
intra- and inter-individual variation was similar (Fig. S2).

Results and discussion

Under both light intensities, the flights in the control condi-
tions and the obstacle were initially clustered close to but
slightly to the right of the midline (Control: −2.7 ± 4.3 cm
500 lx, −2.4 ± 6.0 cm 19 lx; Obstacle: −1.5 ± 4.1 500 lx,
−3.3 ± 4.1 cm 19 lx, Fig. 1a, b). When the obstacle was
present, bees deviated from the start of their original path
to avoid the obstacle by 9.1 ± 4.4 cm and 6.7 ± 3.9 cm in
500 lx and 19 lx, respectively. This was significantly dif-
ferent from the control conditions, where the deviation was
3.3 ± 3.3 cm and 4.4 ± 4.0 cm over the same distance in
500 lx and 19 lx, respectively (500 lx: n = 66, p < 0.001,
19 lx: n = 46, p = 0.007, insets Fig. 1e, g) and suggests that
the bees were actively adjusting their flight path to avoid the
obstacle. Interestingly, nearly all bees flew to the right of
the obstacle, except for six flights to the left (5 of 34 flights
in 500 lx, 1 of 34 flights in 19 lx). This may have been the
result of the slight right-side tendency the bees had at the
start of their trajectories. The result nonetheless raises the
possibility that, when negotiating obstacles, B. terrestris
may have a consistent side preference, which would repre-
sent an efficient strategy for minimising the risk of head-on
collisions with other individuals in areas with heavy traffic,
such as when they are approaching or leaving the hive or a
food source.

The average speed of the flights in the control conditions
was not affected by light intensity (500 lx: 50.9 ± 4.5 cm s−1,
n = 34; 19 lx: 50.6 ± 4.2 cm s−1, n = 12; p = 0.92), contra-
dicting the results of Reber et al. (2015), which found B.
Fig. 1 The effect of light intensity on obstacle avoidance in bumblebees. Trajectories of bees flying along a 30 cm wide experimental tunnel lined with uniform grey (control condition) at a 500 lx, b 19 lx, c 500 lx with an obstacle (black circle), d 19 lx with an obstacle (black circle). Note that the trajectories are normalised to the centre of the tunnel (a, b) or the centre of the obstacle (c, d), which varied in its location along the tunnel during the trials such that the normalised example flights shown are 160 cm long. e The mean lateral position or flight speed f of bees flying at 500 lx in either the control condition (grey data) or when the obstacle (represented by a grey shaded half-circle) was present in the tunnel (red data). g The mean lateral position or flight speed h of bees flying at 19 lx in either the control condition (grey data) or when the obstacle (represented by a grey shaded half-circle) was present in the tunnel (red data). In (g) and (h), data from the 500 lx condition with an obstacle (from (e) and (f), light red data) is included for comparison. The data in e–h represent mean values binned at 2 cm intervals, the error bars represent the standard error of the mean. Stars and values represent the distance at which the trajectories in the obstacle condition began and continued to deviate significantly from the control condition using a Student's t-test at the 5% significance level. N represents the number of individuals in each condition, n represents the number of flights. Insets in (e) and (g) show boxplots of the difference between the lateral position at the start and end (0 cm distance from the obstacle) of each trajectory for the 500 lx and 19 lx control and obstacle data. Boxes indicate the 25th–75th percentiles, whiskers show the extent of the data, blue lines indicate the median value and red crosses indicate outliers.
terrestris decreased their speed with light intensity. One major difference between these two studies is that, here, the tunnel walls did not provide strong contrast cues as they did in Reber et al. (2015). Thus, it appears as though the mechanism mediating the relationship between speed and light intensity in bumblebees is based on image motion cues because, when these cues are absent, this relationship is no longer observed.

At 500 lx, flights at the start of the tunnel were clustered close to the midline before deviating towards the right wall at a distance of 22 cm from the obstacle \((n = 66, p = 0.032, \text{ Fig. 1e}, \text{ Table S1})\). This lateral deviation also coincided with a reduction in speed \((n = 66, p = 0.021, \text{ Fig. 1f}, \text{ Table S1})\), suggesting that the bees were modifying their flight to avoid the obstacle when it subtended a visual angle of 13°. At 19 lx, the trajectories started at a similar position as those in the control, albeit slightly but not significantly tending to the right wall, before making a more distinct and consistently significant rightward deviation 22 cm from the obstacle \((n = 46, p = 0.046, \text{ Fig. 1g}, \text{ Table S1})\). Flight speed was initially slower than in the control condition and in the 500 lx obstacle condition but then made a consistent decrease at 22 cm \((n = 46, p = 0.002, \text{ Fig. 1h}, \text{ Table S1})\). As the only difference between these two conditions was the presence of the obstacle or the light intensity, these results suggest that, at 19 lx, the bees appeared to be detecting and responding to the obstacle by flying slower.

One mechanism by which \(B. \text{ terrestris}\) may be improving the reliability of vision in dim light, in addition to increasing the temporal integration time of their photoreceptors, is spatial summation (Reber et al. 2015; Warrant 1999). This is the neural pooling of photoreceptor signals across space, which could be used to improve sensitivity in dim light but would have the effect of reducing spatial resolution (Warrant 1999). At 19 lx were responding to the presence of the obstacle when it would have subtended a horizontal angle of only 3.6° on the frontal visual field. This value closely matches the minimum spatial resolutions previously reported for \(B. \text{ terrestris}\) (Chakravarthi et al. 2016: 2.4°; Dyer et al. 2008: 2.3°; Kapustiansky et al. 2010: 4°; Spaethe and Chittka 2003: 3.5°–7°; Wertlen et al. 2008: 2.5°–4°), suggesting that \(B. \text{ terrestris}\) do not appear to significantly compromise their spatial resolution to improve their visual sensitivity in dim light. It is also possible that instead of responding to the obstacle as an object, the bees were responding to the variation in contrast of the pattern covering it. Further investigations are needed to determine the visual cues that bees rely on to detect obstacles in dim light and the relative role that spatial resolution and contrast sensitivity may play.

The deviation in position and speed in response to the obstacle occurred at a remarkably consistent distance of 22 cm, even in dim light. What mechanism might be mediating this avoidance response? One possibility is that the bees respond once the obstacle reaches a certain angular threshold on the visual field, as do locusts (Robertson and Johnson 1993) and \(D. \text{ melanogaster}\) (van Breugel and Dickinson 2012). At 22 cm, the widest part of the obstacle would have subtended 13° on the frontal visual field of the bees, which is similar to the 10° threshold found for locusts but much lower than the 33° measured for \(D. \text{ melanogaster}\). One prediction of this strategy is that the size of the obstacle would affect the distance at which bees make an avoidance manoeuvre, something that remains to be tested in more detail using obstacles of different sizes.

Another possible mechanism that bumblebees may have used to determine when to initiate a deviation around the obstacle is a projected time-to-contact threshold—that is, they would respond when the time-to-contact projected from the speed of the bee and distance from the obstacle reaches a certain value. Flies use such a strategy to initiate a deceleration when landing (Wagner 1982). A time-to-contact strategy would enable the bees to respond efficiently and adaptively to obstacles even when they are flying at different speeds or when the obstacles have different widths (which would not be the case with the visual threshold hypothesis discussed above) and could ensure that there is always enough time for the visual system to detect the obstacle and to initiate a behavioural response to it. Is it possible that bumblebees use this strategy to avoid obstacles?

The data from this experiment alone are not sufficient to determine if the bees might be using a time-to-contact strategy because the object size, flight speeds and reaction distances were similar in all conditions. However, it is possible to compare the predicted time-to-contact values obtained here with those of previous studies—using a similar experimental setup—that recorded how \(B. \text{ terrestris}\) respond to changes in flight width (Baird et al. 2010) or in the optic flow presented in the lateral visual field (Linander et al. 2015). These calculations provide eight time-to-contact predictions that are remarkably similar (Table 1), with an average value of 0.33 ± 0.08 s. This value is also consistent with the time-to-contact prediction of 0.4 s, that could be made from the results of Ravi et al. (2019), which found \(B. \text{ terrestris}\) flying at ~ 50 cm s⁻¹ changed their flight at a distance of ~ 20 cm from a gap placed in their flight path (values given are approximate due to the binning method used to make these calculations). Altogether, these results provide evidence that bumblebees may indeed be using a time-to-contact strategy for obstacle avoidance. They also suggest, rather surprisingly, that the temporal summation that bees use to improve their visual sensitivity in dim light does not affect this calculation.
Overall, the findings of this study demonstrate that obstacle avoidance in Bombus terrestris is robust to changes in light intensity. The visual adaptation mechanisms that bumblebees have developed in order to forage in dim light thus appear to require little trade-off in terms of safe and efficient flight. This is also supported by an analysis of how far away from the obstacle the bees flew when they were passing by it (that is, at 0 cm from its centre), as the average lateral distance from the obstacle edge did not vary greatly between the two light intensities and was even marginally greater in dim light (500 lx: 9.4 ± 1.7 cm, n = 34; 19 lx: 10.3 ± 1.8 cm, n = 34; p = 0.050). Interestingly, the minimum lateral distances observed between a bee and the obstacle edge were also very similar (500 lx: 5.7 cm; 19 lx: 6.1 cm), again suggesting that B. terrestris can reliably determine the distance to objects under both light intensities. Considering that these bees have visual systems adapted for bright light, the findings of this study provide strong evidence that the neural mechanisms B. terrestris uses to improve sensitivity do not impair the precision with which they are able to detect and avoid obstacles in dim light.

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**Data availability** The data presented in this study are available in the Electronic Supplementary Material. Complete raw data are available on request.

**Compliance with ethical standards**

**Conflicts of interest** The author declares no conflicts of interest.

**Ethical approval** This work was carried out in accordance with the guidelines for the ethical use of animals in Sweden.

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