

RESEARCH ARTICLE

When navigating wood ants use the centre of mass of a shape to extract directional information from a panoramic skyline

Joseph L. Woodgate^{1,*‡}, Cornelia Buehlmann^{1,‡} and Thomas S. Collett^{1,‡}

ABSTRACT

Bees and ants can control their direction of travel within a familiar landscape using the information available in the surrounding visual scene. To learn more about the visual cues that contribute to this directional control, we have examined how wood ants obtain direction from a single shape that is presented in an otherwise uniform panorama. Earlier experiments revealed that when an ant's goal is aligned with a point within a prominent shape, the ant is guided by a global property of the shape: it learns the relative areas of the shape that lie to its left and right when facing the goal and sets its path by keeping the proportions at the memorised value. This strategy cannot be applied when the direction of the goal lies outside the shape. To see whether a different global feature of the shape might guide ants under these conditions, we trained ants to follow a direction to a point outside a single shape and then analysed their direction of travel when they were presented with different shapes. The tests indicate that ants learn the retinal position of the centre of mass of the training shape when facing the goal and can then guide themselves by placing the centre of mass of training and test shapes in this learnt position.

KEY WORDS: Scene perception, View learning, Visual centre of mass, Visual features

INTRODUCTION

There is abundant evidence that honeybees (Dyer, 1987; Towne and Moscrip, 2008; von Frisch and Lindauer, 1954) and ants (Collett et al., 2001; Graham and Cheng, 2009; Wystrach et al., 2012; Narendra et al., 2013) foraging normally in familiar terrain can guide their direction of travel with visual information that they obtain from the surrounding panorama. More uncertain are the visual cues that these insects use for this directional guidance. We have examined this question in laboratory experiments in which wood ants (*Formica rufa*) reach a source of food guided by a single shape in an otherwise bare panorama.

Simple shapes that can be easily transformed are more tractable than natural scenes for identifying the guiding cues. The value of this approach is sometimes questioned because of doubts that mechanisms elucidated with simple shapes will apply to more complex natural scenes. We suggest instead that any robust perceptual mechanisms that ants are found to deploy in simple surroundings are more likely to be their evolved ways of coping with natural situations rather than *ad hoc* solutions to problems set by an

experimenter. Indeed, studies of visual pattern discrimination in honeybees and fruit flies reveal parallels between the cues by which shapes are distinguished and the cues used by a variety of insects in their natural behaviour when targeting objects or selecting between them.

Common to these two types of study is the conclusion that insects are particularly sensitive to the orientation of edges [shape discrimination (Ernst and Heisenberg, 1999; van Hateren et al., 1990), approach behaviour (Voss, 1967; Wallace, 1962)] and that they compute the centre of mass (CoM) of a shape [shape discrimination (Ernst and Heisenberg, 1999; Horridge, 2009), approach behaviour (Brackenbury, 1996; Voss, 1967)]. Whilst there is physiological evidence for visual interneurons sensitive to edge orientation (O'Carroll, 1993; Seelig and Jayaraman, 2013), there is so far no understanding of how the CoM of a shape might be encoded in the insect nervous system.

Similar visual features play a role in the directional control of wood ants. When an ant follows a habitual route in a familiar scene containing a single shape, it appears to learn the retinal positions of local and global features of the shape when it faces along the direct path to a goal (Judd and Collett, 1998; Lent et al., 2013). It can then control its direction of travel relative to the shape (Harris et al., 2007; Judd and Collett, 1998; Collett, 2010) by placing one or more features of the shape in the desired retinal position (Lent et al., 2013). If the shape is distant and the route short, as in the current experiments, then learning a single retinal position for each feature may suffice to direct the route.

We explored here how the visual features of a shape that an insect selects for guidance depend both on the scene itself and on the direction of the insect's goal within the scene. In a previous study (Lent et al., 2013), wood ants were trained to find food in a direction that was fixed relative to a simple panorama composed of a black rectangle or triangle, seen against a white background. The direction of the goal was aligned with a point that was within the base of the shape. Under these conditions, ants learnt and were guided by the proportions of the shape that lay to their left and right when they faced the goal – the fractional partition of mass (note change of terminology, FPM). The ants' use of this global cue was demonstrated by training insects with one shape and testing them with another. In such tests, ants kept the FPM of the guiding shape at the learnt FPM of the training shape (Fig. 1A) and their behaviour was incompatible with the use of the shape's CoM.

This result illustrates that one benefit of using global cues, computed across large segmentable areas of a scene, is that guidance by these cues is robust to some degradation of the image. Unwanted changes to the image can occur in a variety of ways. Shadows shift over the day or as the cloud cover changes. An ant's view of the scene can also change with small irregularities of the surface over which it walks. Moreover, in the one species in which it has been measured, ants appear not to attempt to keep the pitch angle of their head constant (Ardin et al., 2015). The use of global

¹School of Life Sciences, John Maynard Smith Building, University of Sussex, Brighton BN1 9QG, UK.

*Present address: School of Biological & Chemical Sciences, Queen Mary University of London, Mile End Campus, London E1 4NS, UK.

‡Authors for correspondence (j.woodgate@qmul.ac.uk; cornelia.buehlmann@gmail.com; t.s.collett@sussex.ac.uk)

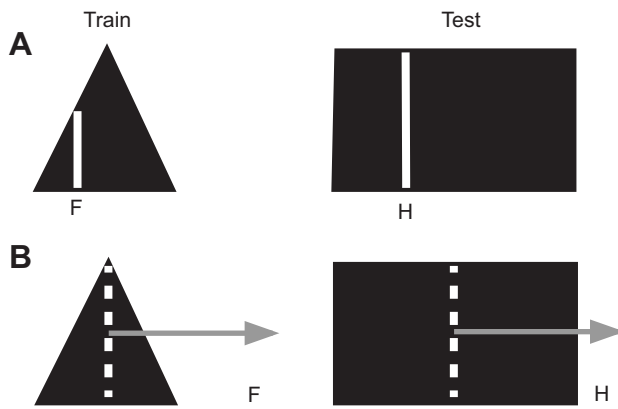


Fig. 1. Schematic diagram of two guidance strategies. (A) The fractional partition of mass (FPM). Left: ants compute the relative proportions of a shape that lie to the left and right (vertical line) of their desired heading and guide themselves to the food by keeping the proportions at the memorised value. Right: testing the use of a learnt FPM with a novel shape. (B) Centre of mass (CoM). Left: ants learn the retinal position of the CoM of a shape when they face the food and guide themselves by holding the CoM in that retinal position. Right: testing the use of CoM with a novel shape. Grey arrows indicate the direction that the ants are predicted to have computed after learning the retinal position of the CoM of the training shape. Dashed lines dividing the shapes illustrate the position of the horizontal component of the CoM. For both strategies, F marks the direction of the food in training and H shows the ants' predicted heading during tests.

cues in coping with such perturbations is aided by ants placing little reliance on the changing height of shapes when keeping to a route that is guided by a shape in their frontal visual field (Harris et al., 2007) and by employing proprioceptive cues and motor 'inertia' to help maintain a straight or a curved path (Lent et al., 2009).

By definition, an FPM strategy only applies to directions within a shape when its value can vary between 0 and 1. What do ants do when their goal is aligned with a position outside the shape and the FPM is not applicable? In this case, the value of the FPM will always be 0 or 1 whatever the direction outside the shape. Do ants use a different global cue? To answer this question, we have followed a similar experimental design to the earlier study (Lent et al., 2013). Ants were trained within a cylindrical arena to go from the centre of the arena to find a feeder. The direction of the feeder was specified by a black rectangle or isosceles triangle fixed to the white wall of the cylinder. We analysed the directional response of ants that were trained to a goal lying outside a shape, when they were presented with different test shapes. To anticipate the Results, ants behave as though guided by the retinal position of the CoM of the training shape (Fig. 1B). The data are consistent with the ants controlling their direction of travel by keeping the CoM of the test shape in the same position on the retina as they kept the CoM of the training shape when approaching the goal.

MATERIALS AND METHODS

Experiments were performed on individually marked wood ants from laboratory-maintained colonies collected from Broadstone Warren, East Sussex, UK. The colonies were kept under a 12 h:12 h light:dark cycle and the colony was sprayed with water daily. Water and sucrose dispensers were always available except during experiments. The colony then had limited access to sucrose to encourage enthusiastic foraging. Crickets were supplied several times a week.

The experimental procedures followed those described previously (Lent et al., 2013). Individually marked wood ants

were trained to go from the centre of a circular platform (120 cm in diameter) towards a drop of sucrose on a microscope slide at the periphery. The slide was positioned relative to a more distant 360 deg panorama that was fixed to the white inner wall of a rotatable cylinder (diameter 3 m, height 1.8 m).

The single shape comprising the panorama was constructed out of black cloth and fixed to white netting that covered the whole white painted inner wall of the cylinder. Two different training shapes were used – either a rectangle (20 deg wide by 29 deg high; experiment 1) or an isosceles triangle (experiments 2–5). Experiments, each with a new batch of ants, were conducted with a variety of training patterns and angular distances of the feeder from the training shape. In experiment 2, the triangle (30 deg high×51 deg wide) was placed level with the floor of the arena, with the feeder 54 deg from the triangle's CoM. Because the present study was designed as a companion to an examination of the ants' response to more complex panoramic scenes, in the other experiments the shape was placed on a uniform low black border 7 deg high that extended all around the bottom of the cylinder. In experiment 3, the triangle was 33 deg high×77 deg wide with the feeder 64 deg from the triangle's CoM; in experiment 4, the triangle was 33 deg high×77 deg wide with the feeder 59 deg from the triangle's CoM; and in experiment 5, the triangle was 33 deg high×40 deg wide with the feeder 40 deg from the triangle's CoM. The test patterns were rectangles of the same height as the triangles but of a variety of widths and in one case the test pattern was a wedge. All angles given here and elsewhere in the paper were calculated from the centre of the arena floor and heights were measured from the arena floor.

To compare the results of tests across experiments with different training conditions, we also normalised the width of the test rectangles. The normalised width was calculated as the angular difference between the CoM of the test rectangle and its edge divided by the angular difference between the CoM of the training shape and the feeder position. With a normalised width of 1, the travel direction predicted by a CoM strategy is then always in line with the edge of the rectangle, and for normalised widths of <1, the predicted direction lies outside the rectangle.

Ants were given about 30 trials of group training before being trained individually. For individual training, ants were put singly into a 6.5 cm diameter, cylindrical holding chamber in the centre of the platform. The chamber wall hid the shape from the ant's view. The ant was released from the holding chamber by remotely lowering the wall. Once the ant had reached the food reward and started to feed, the experimenter raised the wall of the holding chamber, entered the arena, transferred the ant to a feeding box and placed the next ant in the holding chamber. To avoid ants relying on cues other than those on the cylinder wall, the shapes and the slide with food were rotated together to a new position after the cohort of ants had completed a training trial.

Each ant's movements were recorded using a tracking video camera (Trackit, SciTrackS GmbH), which gave as output the ant's position on the platform and the orientation of its body axis every 20 ms. After about 30 group training trials and a further 5 individual training trials, over the course of about 3 days, the ant's path to the slide was fairly direct and a test was introduced after every 4–5 training trials. Before a test, the pattern on the arena wall was changed and the slide on the floor removed. Each ant was released from the holding chamber and its path recorded until it reached the edge of the platform, when it was placed in a feeding box. Each ant typically performed around 80 training trials and about 8 test trials during a ca. 8 day experiment.

Determining travel direction

Endpoints of saccade-like turns

In previous experiments with the food aligned with a point within the base of a shape, the ant's heading at the endpoints of saccade-like turns (SLTs) were mostly in the direction of the food site and served as a proxy for the ants' direction of travel (Lent et al., 2010). We began by examining whether SLTs would provide a good measure of travel direction in the present experiments. SLTs were picked out from plots of the ant's rotational speed during an approach. The start of a turn was identified as the moment when the ant's rotational speed was close to zero, just before a rapid acceleration that reached at least 2 s.d. above the mean rotational speed. The SLT endpoint was defined by a period of at least 60 ms during which body rotation was <1 deg. The horizontal orientation of the ant's longitudinal body axis at this endpoint gave its facing direction. Because of head-on-body movements, the angular difference between facing direction and the

eyes' forward viewing direction can be as much as 5 deg (Lent et al., 2010). Facing directions were measured over the ant's 'initial path'; that is, from when it left the area of the holding chamber until it was 30 cm distant from the centre of the holding chamber.

Path direction

Because the distribution of SLT endpoints was more scattered than in earlier studies (Lent et al., 2013), we also examined the actual direction of the ants' paths over the initial 30 cm of their trajectory towards the feeder. The direction over this segment was estimated in two stages. First, the directions of successive 1.5 cm segments were estimated from the regression coefficients of the lines passing through the ant's x - y positions recorded every 20 ms within each 1.5 cm segment. The overall direction of the 30 cm path was then taken to be the vector sum of the directions of all path segments until the ant's path took it 30 cm from the centre of the arena.

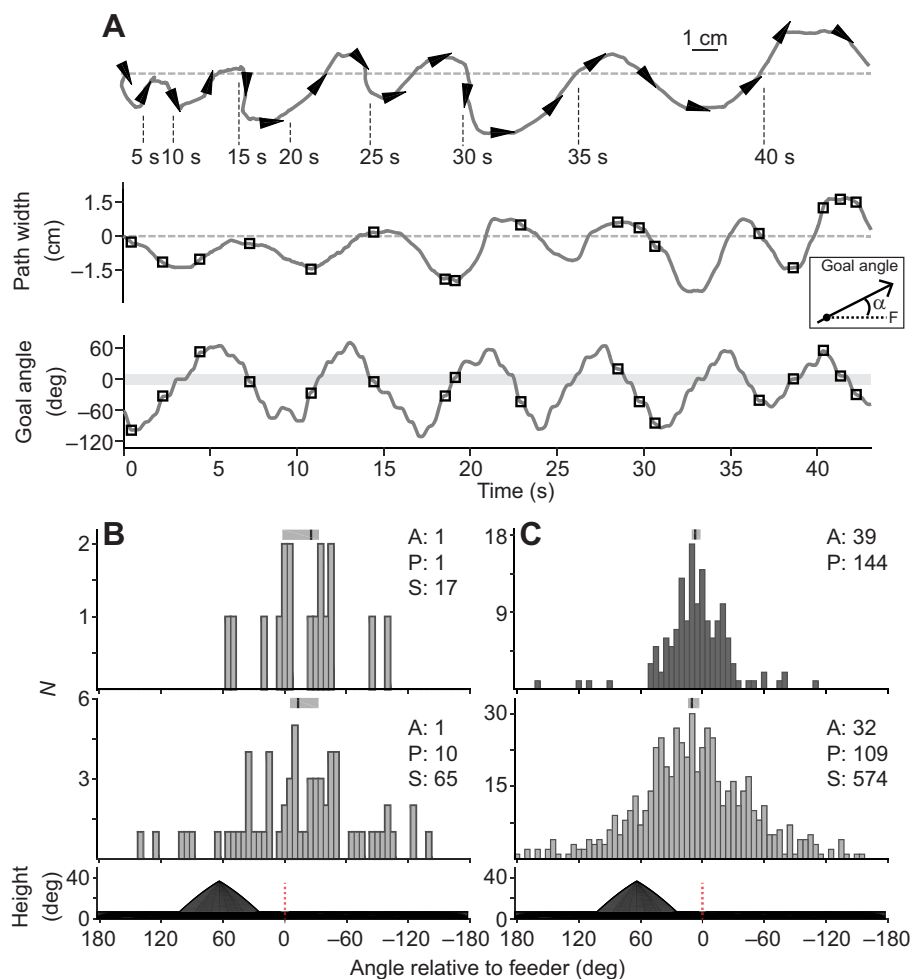


Fig. 2. Saccade-like turns (SLTs) and path directions of ants trained to a point outside a shape. (A) Three plots of the first 30 cm of the path of a single ant approaching the feeder. Top: trace of the ant's path. Arrows show body orientation every 2.5 cm. The ant travels from left to right, zigzagging close to the horizontal dashed line, which indicates the direct path to the feeder. Vertical dotted lines denote 5 s intervals from the start. Centre: the same path plotted against time with SLT endpoints marked by rectangles and the dashed line indicating the direction of the feeder. Bottom: the ant's body orientation plotted against time, with zero on the ordinate indicating when the ant faces the food. SLT endpoints are marked by rectangles. The grey bar highlights when the ant's body was oriented within 10 deg of the direction to the food. These facing points tend to occur at the peaks and troughs of the zigzags along the path. Inset: stick and ball showing the position and orientation of the ant relative to the food (F). α denotes the angle with respect to this goal. (B) Top: distribution of facing directions at SLT endpoints shown in A. In this and other figures, bin width is 5 deg and the vertical bar and grey rectangle indicate, respectively, the median of the distribution and its 95% confidence interval (CI). Bottom: facing directions at SLT endpoints extracted from other paths of this ant. (C) The distribution of path directions and of facing directions at SLT endpoints from ants in the same experimental cohort as the example ant. Top: path directions of training trials just preceding a test. Bottom: SLT endpoints during training. In B and C, a panorama is shown below the distributions, with the dotted red line at 0 deg indicating the direction of food. Sample size is shown here and in the remaining figures by A (number of ants), P (number of paths) and S (number of SLTs).

Histograms of facing directions and path directions

Facing directions

So that facing directions of SLT endpoints could be pooled over the initial path, the facing direction of each endpoint was converted into its projected position on the pattern. To do so, the pattern as viewed by the ant was first transformed into spherical coordinates and the facing direction was extrapolated into the plane of the pattern. The azimuth of the facing direction on the pattern was then translated into its angular distance along the width of the pattern, as measured from the centre of the arena. In the histogram, the facing directions along the initial path are pooled in 5 deg bins.

Path directions

Histograms of individual path directions show the overall path directions projected on to the pattern. Because some ants behaved erratically and gave no signs of route learning, we selected ants according to the consistency of their paths during training and did not analyse the training or test paths of ants with low consistency scores. To measure consistency, we calculated the resultant vector length of an ant's path direction by pooling the vectors from each of its recorded training trials. The ant was excluded if the length of this resultant vector was less than 0.4; 74 out of a total of 251 ants were discarded for this reason. Because paths were often erratic early in the day and immediately after tests, the training data that we analysed comprised all the training trials performed just before a test.

Position of the CoM

The CoM of the training and test patterns was determined from the spherical projection of the black area of the scene against a white background viewed from the centre of the arena through pixels 4 deg in diameter. The luminance (from black=1 to white=0) across the

pattern was integrated over the height of the pattern between the left and right ends of the shape.

Descriptive statistics

We present with each histogram the circular median of the distribution (Otieno and Anderson-Cook, 2003) and its 95% confidence interval (CI). We used bootstrapping to resample the data 10,000 times and calculated the CIs for the median using the likelihood-based arc method (Fisher and Hall, 1989). Rayleigh's tests for non-uniformity confirmed that, in every experiment, the ants' paths in training were not uniformly distributed but showed a tendency to head in one direction (all $P < 0.0001$).

Statistical tests

To test whether a CoM strategy gives a plausible account of an ant's choice of direction in each test, we used the Wilcoxon signed rank test (2-tail) to ascertain whether the ant's median heading during each test type differed significantly from the CoM prediction. For each type of test, we computed the median path direction of each ant across all the test trials that the ant performed and then used these individual medians as data for the Wilcoxon signed rank test.

RESULTS

Measurement of travel direction

Wood ants travelling towards a visually defined goal tend to take a sinuous path during which they make rapid turns (SLTs). In earlier experiments, when the desired direction of travel lay within the bounds of a single shape, the ants' facing direction at the endpoint of the SLTs was mostly in the goal direction (Lent et al., 2010, 2013). The narrow distribution of the direction of SLT endpoints meant that the endpoints provided a reliable proxy of the ants' travel direction

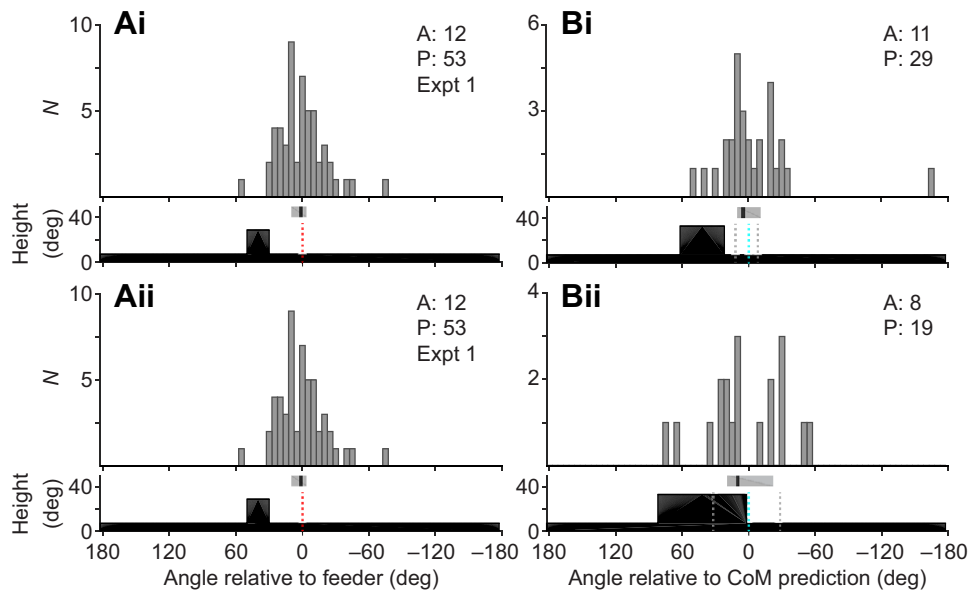


Fig. 3. Testing the use of the CoM on ants trained to head to the right of a rectangle. (Ai,ii) Training scene (bottom) as viewed from the centre of the arena (experiment 1). For consistency with later figures, the training data are shown twice, once with each of the two tests. Plotted above in 5 deg bins is the distribution of path directions relative to the pattern taken from all the training trials that precede a test. Zero on the abscissa of the training pattern and on the distribution of paths marks the position of the feeder, also shown by a dotted red line. Median and 95% CI of the median (bar and grey rectangle) are shown below the distributions. (B) Test rectangles (Bi: 40 deg, Bii: 80 deg wide) and associated distributions of overall path directions plotted as in A. Each data point in the distribution represents the mean direction of a single path. Both test distributions are significantly non-uniform (Rayleigh test: Bi: $Z=22$, $P < 0.0001$; Bii: $Z=13$, $P < 0.0001$). Blue dotted lines at 0 deg on the abscissa of test panels mark the predicted position of paths guided by CoM. Grey dotted lines give predicted heading directions, supposing that ants learnt the retinal positions of the vertical edge of the test rectangle. Headings do not differ significantly from CoM predictions (Bi: $N=11$, $Z=0.18$, $P=0.86$; Bii: $N=8$, $Z=-0.56$, $P=0.58$).

(Lent et al., 2013). When the learnt direction lay outside the shape or between two shapes (J.L.W., C.B. and T.S.C., unpublished data), we found that the distribution of facing directions at the SLT endpoints was more varied. We illustrate this pattern with an example path (Fig. 2A) of an ant's approach to the feeder during training in experiment 3. Body orientation with the SLT endpoints marked by rectangles (Fig. 2A, bottom plot) shows that some of the SLTs have endpoints with facing directions aligned within 10 deg of the goal (5/17 SLTs), but the facing directions of the majority of the endpoints are distributed widely on both sides of the goal. The

proportion of SLTs within 10 deg for the paths of all ants in the same experimental cohorts (Fig. 2C) is smaller (92/574).

Because 80% of the facing directions at SLT endpoints in this situation were not in the ants' major travel direction, we took as an alternative measure the overall direction of an ant's path (see Materials and methods) from the start until the ants' radial distance from the centre of the arena reached 30 cm. The distribution of the overall path directions of all ants (Fig. 2C, top) is more compact than the distribution of SLTs extracted from the same ants (Fig. 2C, bottom), but the median and 95% CI of the two distributions are

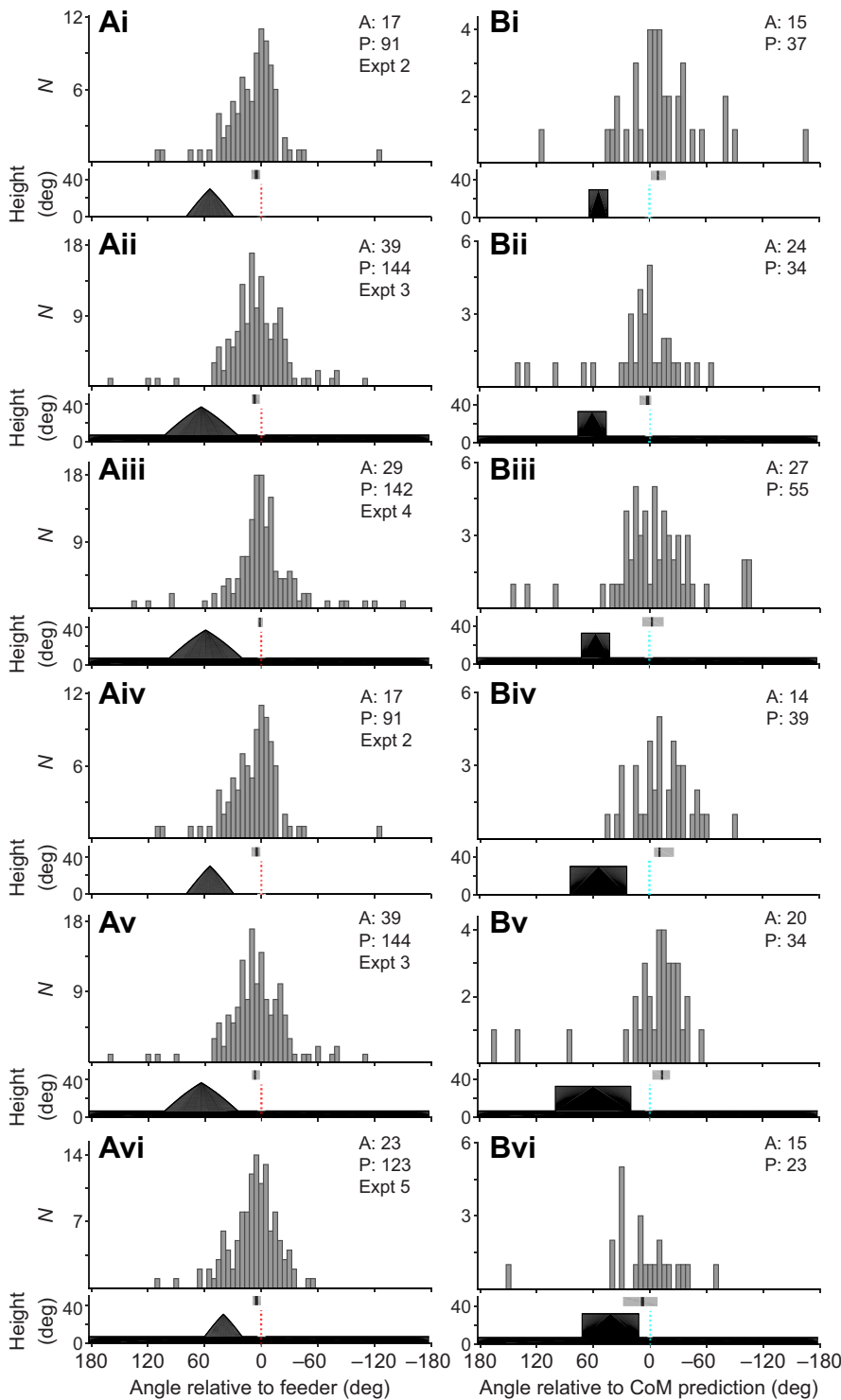


Fig. 4. Testing the use of CoM on ants trained to a goal outside a triangle. (A) Training arrangement with a triangle and the distribution of overall path directions during several training experiments (experiments 2–5; see Materials and methods). (B) Tests with rectangles with normalised width <1 (see Materials and methods). Details as in Fig. 3. Rows are ordered by the normalised width of the rectangles (widths in Bi–Bvi are 20, 30, 30, 60, 80 and 60 deg) with the corresponding training data for each test distribution shown in the same row. Distributions are all well oriented (Rayleigh test: Bi: $Z=22$, $P<0.0001$; Bii: $Z=20$, $P<0.0001$; Biii: $Z=31$; $P<0.0001$; Biv: $Z=30$, $P<0.0001$; Bv: $Z=22$, $P<0.0001$; Bvi: $Z=15$, $P<0.0001$). Headings do not differ significantly from CoM predictions (Bi: $N=15$, $Z=-0.80$, $P=0.43$; Bii: $N=24$, $Z=0.66$, $P=0.51$; Biii: $N=27$, $Z=-0.17$, $P=0.87$; Biv: $N=14$, $Z=-1.91$, $P=0.06$; Bv: $N=20$, $Z=-1.75$, $P=0.08$; Bvi: $N=15$, $Z=0.68$, $P=0.50$). Columns are aligned on the predicted direction of paths when guided by CoM.

similar. Overall path directions were less variable than SLTs for all the experiments reported here and were used throughout the paper to analyse the ants' behaviour.

The data in Fig. 2 come from training with the food outside the triangle and with the triangle on a border. Might the reason for the wide distribution of SLT endpoints be the presence of the border? To answer this question, we also extracted SLTs and examined their endpoints when the training was to food placed outside a triangle that was set level with the arena floor (experiment 2). The standard error of the mean of the distributions was 2.31 deg (574 SLTs) with a border and 3.39 deg (271 SLTs) with no border (data not illustrated), suggesting that the wide distribution of SLT endpoints cannot be

attributed to the border. We have not yet tackled the questions raised by the different distributions of SLTs or examined whether these distributions might be related to the computation of or guidance by a shape's CoM.

Direction of ants towards a goal lying outside a shape

Training with a rectangle

In a preliminary experiment, ants were trained to a goal that lay 40 deg to the right of the CoM of a rectangle (20 deg wide×29 deg high) and tested with two wider and slightly higher (33 deg) rectangles (Fig. 3). The medians of the directions of the paths in these tests were consistent with the use of a CoM strategy. These data cannot be explained by pixel by pixel image matching

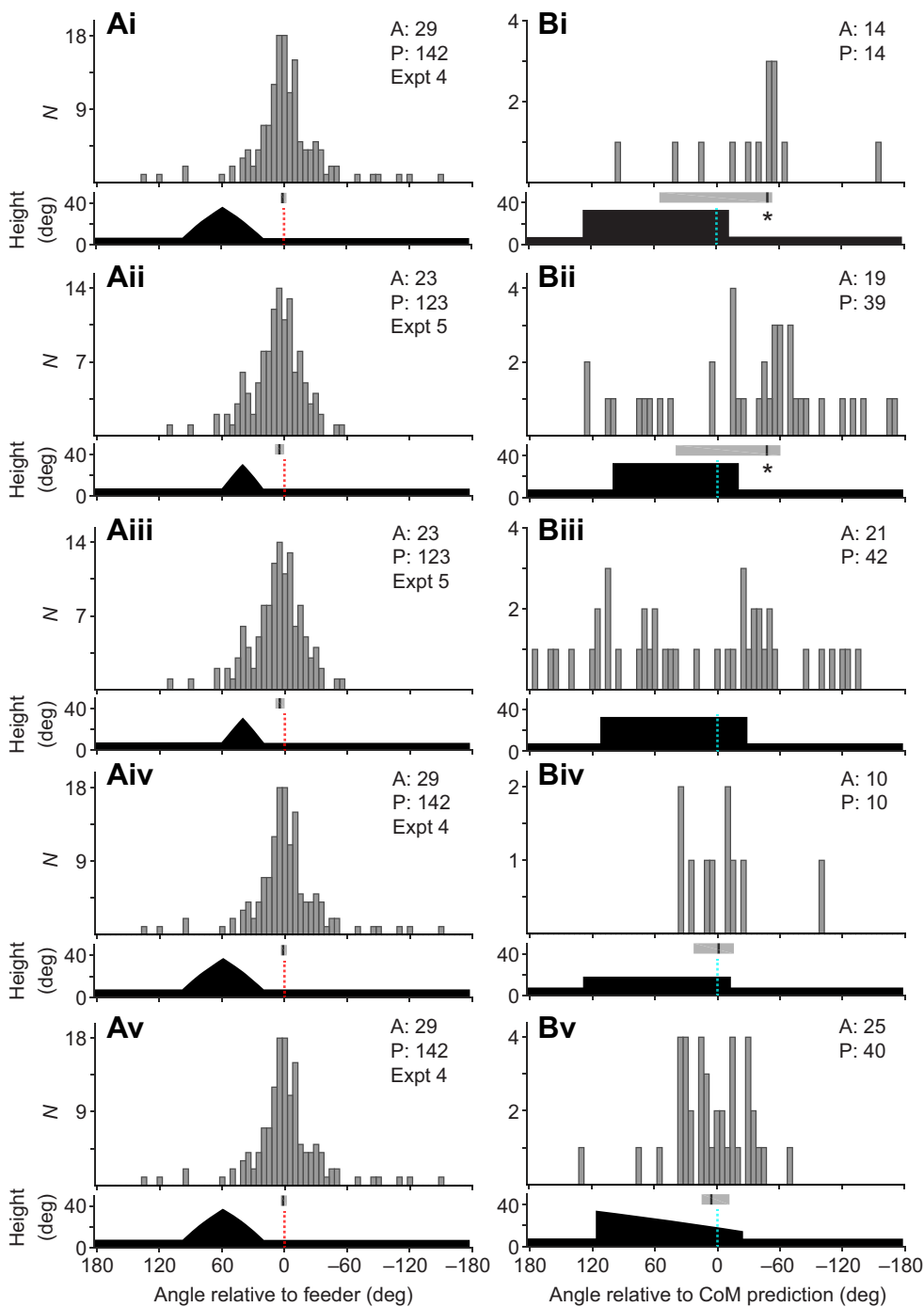


Fig. 5. Ants trained with a triangle and tested with wide rectangles. (A) Training arrangement and distribution of path direction with the training pattern. (B) Distribution of path directions for tests with wide rectangles, a wedge and a wide but low rectangle. Bi–Biii show rectangles ordered relative to their normalised width (in successive rows: 140, 120 and 140 deg). Distributions of Bi and Bii are well ordered; that of Biii is not (Rayleigh test: Bi: $Z=6.2$, $P<0.01$; Bii: $Z=6.7$, $P<0.001$; Biii: $Z=2.5$, $P<0.09$). The directions in Bi and Bii differ significantly from the CoM prediction as indicated by the asterisk (Bi: $N=14$, $Z=-2.2$, $P=0.03$; Bii: $N=19$, $Z=-2.1$, $P=0.04$). Biv and Bv show paths to a low rectangle and a wedge (details in Results). The directions are well ordered (Biv: $Z=6.8$, $P<0.001$; Bv: $Z=28$, $P<0.0001$). In both Biv and Bv, median path directions do not differ significantly from the CoM-predicted direction (Biv: $N=10$, $Z=-0.05$, $P=0.96$; Bv: $N=25$, $Z=0.77$, $P=0.44$). Other details are as in Figs 3 and 4.

(Zeil et al., 2003), in which ants turn to obtain the maximum overlap between the training and test patterns. The reason (see Lent et al., 2013, for a fuller account) is that with training and test rectangles of different widths, the same amount of overlap occurs for all positions in which the smaller rectangle is fully contained within the larger one, so preventing any precise prediction of an ant's direction of travel.

In addition to global features like CoM and FPM, wood ants can be guided by local features such as oriented edges (Judd and Collett, 1998). In this case, the ant learns the retinal position of an oriented edge when facing the goal and, as with CoM, controls its path by keeping that edge in its memorised position on the retina. Indeed, signals from an oriented edge can completely dominate the use of FPM (Lent et al., 2013). Because both training and test patterns had two vertical edges, we cannot discard the possibility that ants learnt the angular distance between each edge and the goal and used both edges to control their trajectory. In this event, the two edges would signal the same direction in training, but in tests with rectangles of different widths, each edge would signal a different direction (grey dotted lines in Fig. 3). Consequently, a weighted mean of the two signals might predict the direction to be taken. As ants distinguish between vertical and oblique edges (Lent et al., 2013), we hoped to avoid this potential problem by training ants to a goal specified by an isosceles triangle and then testing them with rectangles and other shapes.

Training ants with a triangle and testing them with rectangles

Four experiments were conducted on ants trained to a feeder placed to the right of a triangle and then tested with rectangles of different widths. The median path direction of the training data was in each case close to the direction of the feeder (Figs 4 and 5). The ants' behaviour during tests depended on the width of the rectangle. So long as the angular width of the test rectangle was less than double the learnt retinal eccentricity of the CoM, the path predicted by the use of the CoM was aligned with a point outside the rectangle. In such tests, the results of ants trained and tested with shapes on top of a border were similar to those of ants trained and tested when there was no border and the bottom of the shape was level with the arena floor. In Fig. 4, the different test rectangles were placed vertically, aligned on the predicted CoM direction and ordered by their normalised width (see below). In all cases in which the predicted CoM direction lay outside the test rectangle, the Wilcoxon test did not indicate a significant difference between the ants' median direction and that predicted by a CoM strategy (for details, see the legend to Fig. 4).

Tests with wide rectangles

When a test rectangle was so wide that the predicted path to the CoM-defined goal lay inside the rectangle, the path that the ants took did not follow the CoM prediction (see Fig. 5). Instead, the paths tended to be directed to a point outside the rectangle (Fig. 5Bi and Bii). Because the angular distance of the training shape's CoM from the goal varied across experiments, we normalised the width of the test rectangle (see Materials and methods) such that when the normalised width of a test rectangle is <1 , the ant's CoM-predicted direction lies outside the rectangle, and for values >1 , the predicted direction lies within the test rectangle. When the normalised width is <1 , the angular difference between the predicted CoM direction and the median direction taken by the ants is less than 15 deg; the difference is greater than 40 deg for normalised widths >1 (Fig. 6). There is one exception

(Fig. 5Biii) in which the Rayleigh test shows the headings to be too scattered to give a single reliable direction. At this widest value of normalised width, the headings seem to be clustered at each end of the rectangle.

The departure from the CoM-predicted direction can be remedied if the height of the test shape is changed. In one test, ants were presented with a 140 deg wedge with height dropping from 33 deg at the left edge to 14 deg at the right edge (Fig. 5Bv). The median direction of the ants' paths was then close to that of the CoM-defined goal inside the wedge. Agreement of the ants' median direction with a CoM prediction inside a 140 deg rectangle was also restored when the height of the rectangle was lowered from 33 deg to 17 deg above the arena floor (Fig. 5Biv). As discussed below, these data suggest that ants expect the height of the panorama in the CoM-defined goal direction in tests to be similar to the height experienced during training. If the height is very different, the ants modulate their direction of travel away from the CoM-defined direction towards a region of skyline that is closer to their expectations.

DISCUSSION

The use of multiple cues to direction

The results presented here suggest that when ants have learnt to move towards a point in a scene that lies outside a shape, they guide themselves by holding the CoM of the shape in the appropriate position on their retina. This use of the CoM is somewhat analogous to earlier findings on honeybees and fruit flies, which can distinguish different stimuli by the vertical position of their CoM. But we also found that ants supplement the CoM strategy and take note of other features in the scene. That guidance by the CoM is not the complete answer emerged from tests with wide rectangles in which the directions of the ants' paths were inconsistent with predictions from a CoM strategy (Fig. 5). What explains this failure? There are a number of possible answers to this question, some of which can be discarded. It is, for instance, unlikely that ants cannot compute the CoM of wide rectangles. Firstly, it was reported long ago (Voss, 1967) that naive ants emerging from the centre of an arena head spontaneously for the middle of a 180 deg black rectangle. Secondly, in our tests with a wide wedge or a wide low rectangle, ants were guided by the CoM

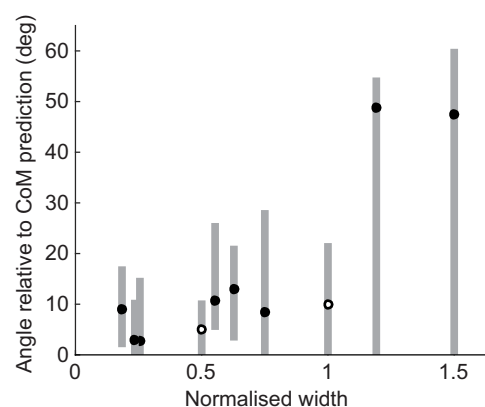


Fig. 6. Angular difference between CoM prediction and path direction versus normalised width of the test rectangle. For each test rectangle of standard height in Figs 3–5, the angular difference between the CoM-predicted direction and the median path direction is plotted against the normalised width of the rectangle. Open circles indicate that the training shape was a rectangle and filled circles that it was a triangle.

of the shape. A second possibility is that ants do not exhibit paths guided by CoM because the wide rectangle is so different from the triangle with which the ants were trained that they fail to retrieve their memory of the retinal position of the CoM. The results with the wedge and low rectangle also argue against this suggestion. A third possibility, which is consistent with our data, is that the CoM does not act in isolation and that the height of the skyline plays a supporting role. Should the desired path direction lie normally within a low region of the skyline and should the CoM-defined direction point at an unexpectedly high region of skyline, the ants' paths will be deflected towards a lower region. It seems that directional control by a panorama is interestingly complex, even when the panorama consists of just a single shape on an otherwise flat skyline.

Horizontal and vertical components of the CoM

The test with the wedge suggests that in addition to the horizontal component of shape's CoM, ants may also compute its vertical component, as do fruit flies (Ernst and Heisenberg, 1999) and leafhoppers (Brackenbury, 1996). Might ants use the vertical component when guiding their path? A possible example comes from ants that were trained to a route that lay parallel or oblique to a long vertical barrier (Collett et al., 2001; Graham and Collett, 2002). In this situation, the direction of their path was controlled by keeping some parameter related to the height of the barrier at a desired elevation (Graham and Collett, 2002). The current results suggest that the vertical CoM computed over some region of the barrier, rather than the elevation of the top of the barrier, could be the controlling parameter.

CoM and FPM

In principle, a shape's CoM can control direction whether the goal is aligned with a point within or outside the shape. However, FPM is only an applicable strategy for paths that are directed to a point within a shape. When this happens, FPM seems to dominate CoM (Lent et al., 2013). It is so far unclear why in these circumstances ants should bother to choose FPM in preference to the shape's CoM. One possibility elaborated previously (Lent et al., 2013) is that FPM provides a more robust directional cue than does CoM when the ant's distance to the guiding shape is short. It does so because the value of FPM then changes proportionally less during the approach than would the retinal position of the CoM. Once the mechanisms underlying the computation of these global cues are better understood, it could turn out that because FPM is derived from differences between the left and right visual fields, it is a more precise cue than the retinal position of the CoM or that the two strategies have more in common than our algorithmic descriptions suggest.

CoM- and FPM-based strategies share the characteristic that, in panoramas formed of a single shape, very different test shapes can substitute for the training shape without compromising the ant's ability to compute and be guided by the values of CoM and FPM that were learnt along the training route. This result seems to suggest that what the ant stores is the retinal position of the CoM or the FPM ratio relative to the front of the eyes. We must examine the ant's behaviour in more complex panoramas to understand how guidance by such global features is implemented in scenes containing several different shapes. In the meantime, the current results suggest that a feature-based account of directional control within panoramic scenes deserves to be explored further.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

J.L.W. wrote the Matlab scripts; all authors contributed to all other aspects of the research.

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References

- Ardin, P., Mangan, M., Wystrach, A. and Webb, B. (2015). How variation in head pitch could affect image matching algorithms for ant navigation. *J. Comp. Physiol. A* **201**, 585–597.
- Brackenbury, J. (1996). Targetting and optomotor space in the leaf-hopper *Empoasca vitis* (Gothe) (Hemiptera: Cicadellidae). *J. Exp. Biol.* **199**, 731–740.
- Collett, M. (2010). How desert ants use a visual landmark for guidance along a habitual route. *Proc. Natl. Acad. Sci. USA* **107**, 11638–11643.
- Collett, T. S., Collett, M. and Wehner, R. (2001). The guidance of desert ants by extended landmarks. *J. Exp. Biol.* **204**, 1635–1639.
- Dyer, F. C. (1987). Memory and sun compensation by honey bees. *J. Comp. Physiol. A* **160**, 621–633.
- Ernst, R. and Heisenberg, M. (1999). The memory template in *Drosophila* pattern vision at the flight simulator. *Vis. Res.* **39**, 3920–3933.
- Fisher, N. I. and Hall, P. (1989). Bootstrap confidence regions for directional data. *J. Am. Stat. Assoc.* **84**, 996–1002.
- Graham, P. and Cheng, K. (2009). Ants use the panoramic skyline as a visual cue during navigation. *Curr. Biol.* **19**, R935–R937.
- Graham, P. and Collett, T. S. (2002). View-based navigation in insects: how wood ants (*Formica rufa* L.) look at and are guided by extended landmarks. *J. Exp. Biol.* **205**, 2499–2509.
- Harris, R. A., Graham, P. and Collett, T. S. (2007). Visual cues for the retrieval of landmark memories by navigating wood ants. *Curr. Biol.* **17**, 93–102.
- Horridge, G. A. (2009). *What Does the Honeybee See and How Do We Know? A Critique of Scientific Reason*. Canberra: ANU E Press.
- Judd, S. P. D. and Collett, T. S. (1998). Multiple stored views and landmark guidance in ants. *Nature* **392**, 710–714.
- Lent, D. D., Graham, P. and Collett, T. S. (2009). A motor component to the memories of habitual foraging routes in wood ants? *Curr. Biol.* **19**, 115–121.
- Lent, D. D., Graham, P. and Collett, T. S. (2010). Image-matching during ant navigation occurs through saccade-like body turns controlled by learned visual features. *Proc. Natl. Acad. Sci. USA* **107**, 16348–16353.
- Lent, D. D., Graham, P. and Collett, T. S. (2013). Visual scene perception in navigating wood ants. *Curr. Biol.* **23**, 684–690.
- Narendra, A., Gourmaud, S. and Zeil, J. (2013). Mapping the navigational knowledge of individually foraging ants. *Myrmecia croslandi*. *Proc. R. Soc. Lond. B Biol.* **280**, 20130683.
- O'Carroll, D. (1993). Feature-detecting neurons in dragonflies. *Nature* **362**, 541–543.
- Otieno, B. and Anderson-Cook, C. M. (2003). A more efficient way of obtaining a unique median estimate for circular data. *J. Mod. Appl. Stat. Methods* **2**, 168–176.
- Seelig, J. D. and Jayaraman, V. (2013). Feature detection and orientation tuning in the *Drosophila* central complex. *Nature* **503**, 262–266.
- Towne, W. F. and Moscrip, H. (2008). The connection between landscapes and the solar ephemeris in honeybees. *J. Exp. Biol.* **211**, 3729–3736.
- van Hateren, J. H., Srinivasan, M. V. and Wait, P. B. (1990). Pattern recognition in bees: orientation discrimination. *J. Comp. Physiol. A* **167**, 649–654.
- von Frisch, K. and Lindauer, M. (1954). Himmel und Erde in Konkurrenz bei der Orientierung der Bienen. *Naturwissenschaften* **41**, 245–253.
- Voss, C. (1967). Über das Formensehen der roten Waldameise (*Formica rufa*-Gruppe). *Z. Vergl. Physiol.* **55**, 225–254.
- Wallace, G. K. (1962). Experiments on visually controlled orientation in the desert locust, *Schistocerca gregaria* (Forskål). *Anim. Behav.* **10**, 361–369.
- Wystrach, A., Beugnon, G. and Cheng, K. (2012). Ants might use different view-matching strategies on and off the route. *J. Exp. Biol.* **215**, 44–55.
- Zeil, J., Hofmann, M. I. and Chahl, J. S. (2003). Catchment areas of panoramic snapshots in outdoor scenes. *J. Opt. Soc. Am. A* **20**, 450–469.