

The influence of beacon-aiming on the routes of wood ants

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Summary

Many insects have an innate propensity to approach conspicuous objects. We explore how such beacon aiming determines the shape of a wood ant's habitual route. We find that a single large black cylinder within an arena biases the route taken by ants as they run from a start position at one end of the arena to reach a feeder at the other. Ants learn a stable route with the first segment of their trajectory aimed at the cylinder, which becomes an intermediate goal on the way to the feeder. When in occasional tests the cylinder is removed or displaced, ants head for the usual site of the cylinder. They also aim for the same site when the cylinder is removed and the ant's normal start position is changed. This behaviour suggests that visual features of the arena are learnt from the

vantage point of the cylinder and that this stored snapshot guides the ant to that site. Ants thus reinforce their ability to reach the cylinder by learning other visual features in their surroundings that can also steer them to its location. The use of beacon aiming in fixing routes has several benefits. Because the same path will be traversed on every trial, beacon aiming facilitates the acquisition of routes. Beacon aiming also increases the robustness of learnt routes: ants straying from the route will be attracted to the closest beacon and so regain their habitual paths.

Key words: wood ant, *Formica rufa*, beacon aiming, landmark, navigation, route learning, visual cue.

Introduction

Both wood and cataglyphid ants follow fixed routes from their nest to a feeding site and back again guided by visual landmarks (Santschi, 1913; Rosengren, 1971; Collett et al., 1992; Wehner et al., 1996). Doing so increases the precision of their navigation and so reduces the time that they need to spend searching for a goal. Wood ants, like honeybees (von Frisch, 1967; Collett and Baron, 1994; Chittka et al., 1995; Fry and Wehner, 2002), tend to treat discrete landmarks along the route as beacons at which they aim (Nicholson et al., 1999), making each landmark an intermediate goal, so partitioning the route into segments. Many insects approach conspicuous stationary objects under a variety of circumstances (fruit flies: Wehner, 1972; Götz, 1994; Strauss and Pichler, 1998; locusts: Wallace, 1962; ladybirds: Collett, 1988; mantids: Poteser and Kral, 1995) and it seems likely that in ants and bees beacon aiming is an intrinsic visuo-motor response that has been co-opted as a part of route following. The incorporation of beacon aiming into routes brings several benefits. For ants learning a route, it means that the same path will be repeated from trial to trial, giving ants consistent views, thereby speeding up the acquisition of a route. For ants familiar with a route, it makes route following more robust. For instance, if an ant loses its way, it will automatically be attracted to a prominent beacon and so back to the route, even if the beacon's appearance is unfamiliar when viewed away from the ant's usual route.

Additionally, the use of discrete landmarks to segment the route, placing segment boundaries at the landmarks, allows defined local vectors to be associated with each landmark (Collett et al., 1998), so that errors of path integration in specifying the goal are restricted to those of the final local vector (Srinivasan et al., 1997). In the present study, we test explicitly the hypothesis that an ant's tendency to aim at beacons is an important factor in determining the shape of its route. We then go on to show that the shape of a route, as fixed by a landmark, is reinforced by the learning of other more distant visual cues additional to those provided by the beacon. These additional cues can then help channel the ant along the route.

Materials and methods

The ants

Experiments were performed on foragers from queen-right wood ant (*Formica rufa* L.) colonies, housed in large plastic tanks within the laboratory. The temperature was a constant 21°C and the laboratory was on a 12h:12h light:dark cycle. When the colony was not being used for experiments, it was allowed constant access to sucrose solution and water, with protein (frozen crickets) provided every 2–3 days. At the start of training, the colony's only access to sucrose was through the individuals performing the experiment. After a cohort of

foragers had been selected for an experiment, the colony was given a reduced ration of sucrose during the 10 days (approximately) that the experiment lasted.

The arena

Experiments were performed in a 220 cm×300 cm arena that was lit by four fluorescent strip lights. The arena was surfaced with roughened white Perspex. Visual cues external to the arena were reduced by a 280 cm-high curtain that surrounded the arena. One landmark, a black cylinder, 25 cm×50 cm (diameter×height), was placed in the arena. Ants were carried from the nest on a drinking straw to a small raised starting platform in the arena, from which they descended by a small ramp to reach the floor. A feeder (a drop of sucrose solution on a microscope slide) was placed approximately 300 cm from the starting point. Ants were trained with the cylinder either to the left or to the right of the direct path from start to feeder (Fig. 1).

Training

At the beginning of training, 20–30 active ants from the colony were placed on top of the start ramp and the feeder placed at the finish. The first 15 ants to reach the feeder were caught and individually marked with enamel paint. These ants were then allowed to feed and to return to the start, where they were caught again and returned to the nest. Ants typically emerged from the nest mound after a few minutes and were given another training trial. Tests were introduced after 15 training trials. During the testing phase, ants were given three rewarded training runs between non-rewarded tests. Between runs, the arena

surface was wiped down with ethanol to remove possible pheromone cues.

Tracking

The ants' trajectories were tracked with a camera placed 3 m above the centre of the arena. The camera (Sony EVI-D30) has movable optics, allowing a high-resolution image of any part of the arena to be captured. The camera is controlled by a PC (Pentium II 233 MHz) running custom software (Fry et al., 2000) that maintains the ant at the centre of the camera's visual field and stores the pan and tilt values of the camera at 50 frames s⁻¹. The orientation of the long axis of the ant is calculated in real time. The 180° ambiguity is solved by assuming that the ant always walks forwards. Before analysis, the output was converted to arena coordinates and smoothed by taking a moving average with a window size of 9 frames. The recordings of trajectories were cut short when, as often happened, the ant walked close to the cylinder. The directions of trajectories are measured anti-clockwise relative to the straight line between the start position and the feeder.

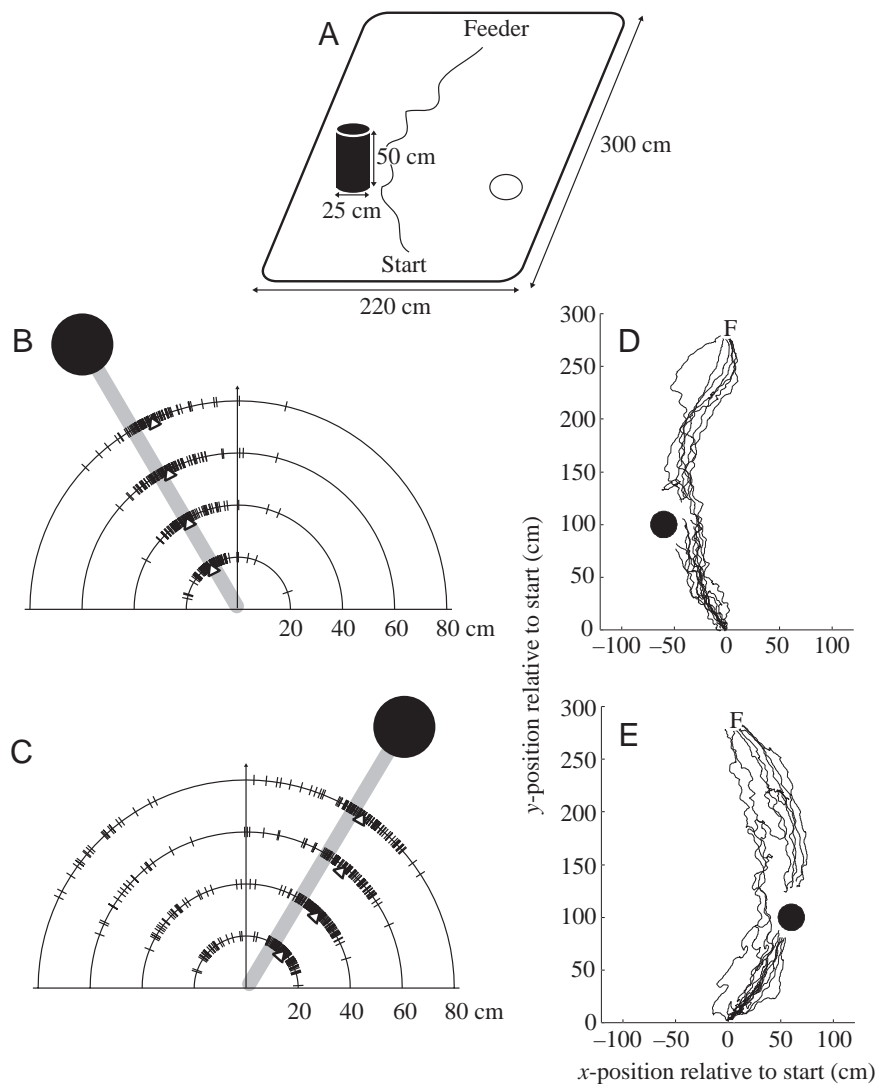


Fig. 1. Route shapes are influenced by landmark position. (A) Ants were trained to go from a start position at one end of a large indoor arena to a feeder 3 m away at the other end. A black cylinder was placed either to the left or to the right of the direct path. (B) Ants headed to the left of the direct path (grey band) when the cylinder (filled circle) was on the left. Each dash marks the point of intersection of one trajectory with a semi-circle centred on the start with a radius of 20 cm, 40 cm, 60 cm or 80 cm [n (number of trajectories)=101, N (number of ants)=10]. Open triangles show the mean heading at each distance. (C) Ants tended to head to the right when the cylinder was on the right ($n=136$, $N=14$). Two ants were atypical and headed away from the cylinder; their trajectories were excluded from subsequent analysis. The grey band indicates the direct path from start to cylinder. (D) Trajectories of one ant trained with the cylinder on the left and (E) trajectories of one ant trained with the cylinder on the right.

Measuring straightness

The straightness of each trajectory was computed over the first 80 cm of the route, a distance over which the trajectory could be recorded without mishap. The method for calculating straightness follows that suggested by Batschelet (1981). Paths are broken into small sections recorded at equal time intervals of 1 s. The path is therefore reduced to a series of unit vectors. The length of the mean direction of the unit vectors provides a measure of the coherence of their directions and thus the straightness of the path: the closer the mean vector (\mathbf{r}) is to 1, the straighter is the path.

Results

Cylinder position influences trajectory shape

In one set of experiments, ants were trained to find a food source 3 m from the start point with a single cylindrical landmark placed 1 m from the start line and 60 cm either to the left or to the right of the direct route (Fig. 1). On the first training run, many of the ants headed for the landmark. Ants then often took a long time (approximately 5 min) to discover the feeder, approaching it from a variety of directions.

The first 10 or so trials were not recorded. Trajectories thereafter changed little. Their straightness (see Materials and methods) improved slightly over another 50 trials (regression: $r^2=0.30$, $\beta=0.175$, $P<0.01$) but there was no change in the overall time taken to reach the food (regression: $r^2=0.001$, $\beta=-0.026$, $P=0.8$).

The shape of mature trajectories is strongly determined by the position of the cylinder (Fig. 1). When the cylinder was on the left, nine out of 10 ants always headed towards it on leaving the starting position (binomial test, $P\approx 0.01$). The tenth ant headed slightly right on three occasions but the rest of its 18 trajectories were all oriented left of centre. When the cylinder was on the right, 10 out of 14 ants headed right towards the cylinder on every trajectory, two ants headed towards the cylinder on $\geq 75\%$ of their trajectories (binomial test, $P\approx 0.01$). The remaining two ants always headed left. These atypical ants are excluded from subsequent analysis.

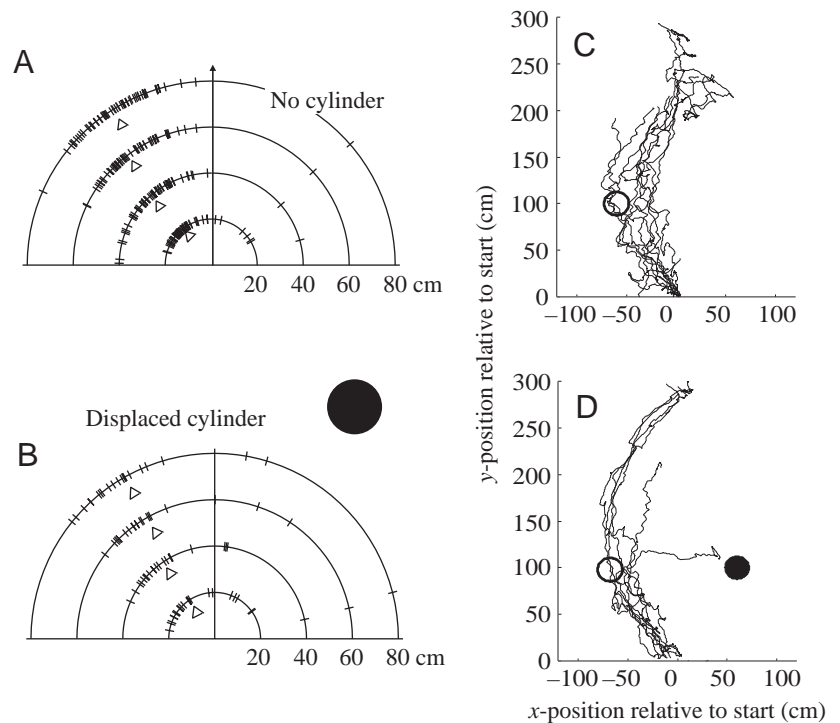
Fig. 2. Route shapes survive the removal or displacement of the cylinder. (A) Headings of trained ants when no landmark was present and (B) when the landmark was shifted to the opposite side from that in training. Data from ants trained with the landmark to the right of their route are mirrored to generate a single data set (no landmark: $n=66$, $N=14$; landmark opposite: $n=23$, $N=8$). Each dash marks the point of intersection of one trajectory with a semi-circle centred on the start with a radius of 20 cm, 40 cm, 60 cm or 80 cm. Open triangles show the mean heading at each distance. (C,D) Sample trajectories from one ant in each test condition. Open circles represent the position of the landmark during training, and the filled circle in D represents the position of the landmark in test runs.

Trajectories with the cylinder removed or displaced

After 15 training trials, ants were occasionally tested either with the cylinder removed or with the cylinder shifted to the equivalent position on the opposite side of the arena to that used in training. In both conditions, ants headed roughly in the same direction as they had in training (Fig. 2). With no cylinder present, the first 40 cm of the trajectory differed significantly from the training conditions, with the direction of trajectories rotated a little further from the direct line from start to feeder than it was in training (mean heading \pm circular s.d., number of trajectories: training: $26.86\pm 10.9^\circ$, $n=194$; no cylinder: $39.5\pm 23^\circ$, $n=64$; Watson Williams F -test: $F_{256}=31.9$, $P<0.01$). At 80 cm, the heading directions of ants with no cylinder present were similar to those of ants during training (training: $28.5\pm 12.3^\circ$; no cylinder: $30.7\pm 15^\circ$; $F_{256}=1.48$, $P=0.23$). However, the differences earlier in the trajectory mean that, with no cylinder present, ants at 80 cm continued to head towards the usual position of the cylinder, rather than turning towards the food, as they did in training.

When the cylinder was shifted to the equivalent position on the other side of the arena, ants also headed towards the training position of the cylinder (Fig. 2B). Trajectory headings after 40 cm and 80 cm did not differ significantly from those performed during training (after 40 cm: training: $26.86\pm 10.9^\circ$, $n=194$; cylinder in opposite position: $32.4\pm 29^\circ$, $n=21$; Watson Williams F -test: $F_{213}=2.7$, $P=0.1$; after 80 cm: training: $28.5\pm 12.4^\circ$; cylinder in opposite position: $27.4\pm 26^\circ$; Watson Williams F -test: $F_{213}=0.1$, $P=0.8$).

Although the direction of mature trajectories was not much influenced by removing or displacing the cylinder, both the speed and the straightness of the trajectories were reduced. Ants took significantly longer to reach 80 cm when there was



no cylinder in the arena. (mean \pm s.d., number of trajectories: training: 54 ± 32 s, $n=194$; no cylinder: 74.4 ± 42 s, $n=71$; Mann–Whitney test: $U=5379$, $Z=-4.5$, $P \ll 0.01$) or when the landmark was displaced (training: 54 ± 32 s, $n=194$; displaced cylinder: 89.0 ± 62 s, $n=22$; Mann–Whitney test: $U=1403$, $Z=-3.5$, $P \ll 0.01$). The mean walking speed of ants in the two test conditions was slightly but significantly lower than it was in training (training: 2.8 ± 0.89 cm s $^{-1}$; no cylinder: 2.48 ± 0.58 cm s $^{-1}$; displaced cylinder: 2.49 ± 0.69 cm s $^{-1}$; t -test pooled across test types, d.f.=263, $t=-3.1$, $P < 0.01$). The trajectories during these tests were significantly less straight than in training (training: 0.71 ± 0.17 ; no cylinder: 0.52 ± 0.16 ; displaced cylinder: 0.43 ± 0.18 ; one-way ANOVA: $F_{2,294}=4.7$, $P \ll 0.005$; *post-hoc* comparisons: training vs no cylinder and training vs displaced cylinder, $P \ll 0.005$).

What maintains trajectory shape when the cylinder is missing?

To understand better what preserves the shape of the ant's route when the cylinder is removed, ants were tested with no cylinder present and with the start position displaced by 30 cm to the left or to the right of the usual start position. The ants' trajectories in these conditions were compared with those in tests with no cylinder when started from their normal position. Data from ants trained with the cylinder on the left or the right were combined and the two test conditions are referred to as 'near start' and 'far start', referring to the distance of the start position from the cylinder (Fig. 3).

The trajectory headings of ants started from the near and far positions differ significantly from those with normal starts at 40 cm, 60 cm and 80 cm from the start (see Table 1). The mean headings in the far condition are rotated further away from the direct line from start to feeder than with normal starts, and the headings in the near condition do not rotate as far. At all three distances from the start, the directions of the normal, near and far trajectories tend to converge towards the usual position of the cylinder (Fig. 3). The areas of convergence are represented by the open triangles on Fig. 3.

The data are consistent with the ant moving towards a point in the arena that is familiar to them from their training runs. Two possibilities can be rejected. The data are not consistent with ants having learnt to take a particular direction from the start, as given, for instance, by a constant angle relative to the strip lights on the ceiling (cf. Hölldobler, 1980). Nor do the data suggest that ants first head towards their normal start position. We suggest that the ant has stored a view of the room from the position of the landmark. As the arena floor is featureless, this view is most probably based on more-distant landmarks such as the lighting array, folds in the curtain and contrast boundaries where the curtains meet the ceiling.

Retinal position of the cylinder during the ants' approach

An analysis of where the cylinder was placed on the ant's retina during the trajectories, as estimated from the orientation

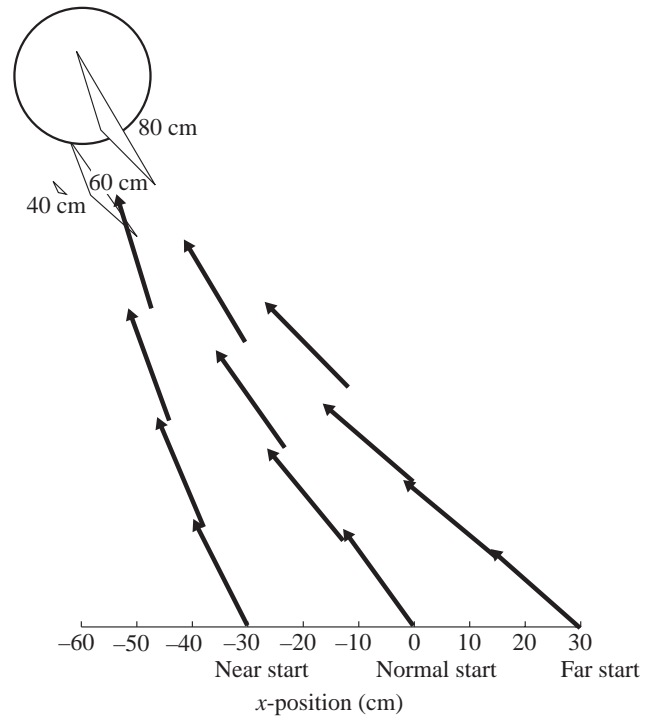


Fig. 3. Trajectories with displaced start position. Ants with no cylinder present were started from the normal position or 30 cm to its left (near) or to its right (far). Arrows show mean trajectory directions measured at 20 cm, 40 cm, 60 cm and 80 cm from the start. Trajectories within a start condition are sufficiently similar that r , the mean vector length, is greater than 0.9 at 20 cm, 40 cm, 60 cm and 80 cm from the start. The open circle indicates the normal position of the absent cylinder. The three triangles represent the areas enclosed by extending the three headings at 40 cm, 60 cm and 80 cm.

Table 1. Headings with displaced start conditions

Distance	Start position	Mean heading (\pm s.d.)	Watson's F -test
20 cm	Normal	$35.9 \pm 14.9^\circ$	
	Far	$49.7 \pm 20.8^\circ$	$F_{85}=4.76$, $P=0.03$
	Near	$26.9 \pm 15.3^\circ$	$F_{89}=2.54$, $P=0.11$
40 cm	Normal	$39.5 \pm 12.5^\circ$	
	Far	$50.4 \pm 15.2^\circ$	$F_{85}=3.98$, $P=0.05$
	Near	$23.6 \pm 7.6^\circ$	$F_{89}=11.3$, $P \ll 0.01$
60 cm	Normal	$35.7 \pm 10.8^\circ$	
	Far	$49.2 \pm 17.0^\circ$	$F_{85}=11.0$, $P \ll 0.01$
	Near	$20.6 \pm 11.0^\circ$	$F_{89}=19.5$, $P \ll 0.01$
80 cm	Normal	$30.8 \pm 8.6^\circ$	
	Far	$44.3 \pm 11.3^\circ$	$F_{85}=15.5$, $P \ll 0.01$
	Near	$16.9 \pm 9.4^\circ$	$F_{89}=19.3$, $P \ll 0.01$

Mean headings of the trajectories for the three start conditions are measured at 20 cm, 40 cm, 60 cm and 80 cm from the start. 'Far start' trajectories and 'near start' trajectories are tested for differences against the normal start trajectories using Watson's F -test. Both the far start and the near start differ significantly from the normal start at 40 cm, 60 cm and 80 cm.

of the ant's longitudinal axis, is shown in Fig. 4A. The mean retinal positions of the centre and of the 'left' and 'right' edges of the cylinder, from the ant's viewpoint, are plotted for the first 80 cm of the trajectories. Over the first 45 cm, the cylinder shifts from 'right' frontal retina to the centre of the eye (Fig. 4C), where it appears to be fixated for a short spell (approximately 10 cm). The cylinder then shifts further to the left and the 'right' edge is held stably on frontal retina (Fig. 4D). After about 65 cm, the ant turns towards the feeder.

The same analysis can be performed on trajectories from the tests in which the cylinder was removed or displaced. In this case, one calculates the retinal position of an imaginary cylinder placed in the usual position of the real one. There are two major differences between the paths of imaginary and real cylinders over the retina (Fig. 4B). First, the spread of retinal positions is much narrower when a real cylinder is present than in its absence. Second, ants head towards the imaginary cylinder for longer before turning towards the food than they do when the cylinder is present. These differences suggest that the sight of the cylinder fine-tunes the ant's trajectory in two ways. It first acts as a beacon that the ant fixates in different ways (cf. Nicholson et al., 1999) and it then signals that the ant should turn in the direction of the feeder (cf. Collett et al., 1992).

Training with more-distant cylinders

Two additional groups of ants were trained with the same sized cylinder placed 2 m from the start line and 60 cm from the direct line from start to food (Fig. 5). Despite its increased distance from the start, the cylinder continued to attract ants. The

trajectories of 10 out of 11 ants were biased towards the side of the arena containing the cylinder (binomial test $P \leq 0.01$). But the trajectories were less tightly clustered than they were when the cylinder was closer. Individual ants developed idiosyncratic routes that were consistent across trials (Fig. 5A–C). With the cylinder less prominent, it seems likely that, during learning, ants were also attracted by other visual features of the arena. The paths of the ant in Fig. 5A, for instance, suggest that this ant has learnt to aim at some feature of the side wall before turning towards the cylinder. That different ants appear to be channelled by different, rather unobtrusive, visual features suggests that when an ant's attention is momentarily captured by a particular feature at the start of route acquisition, that

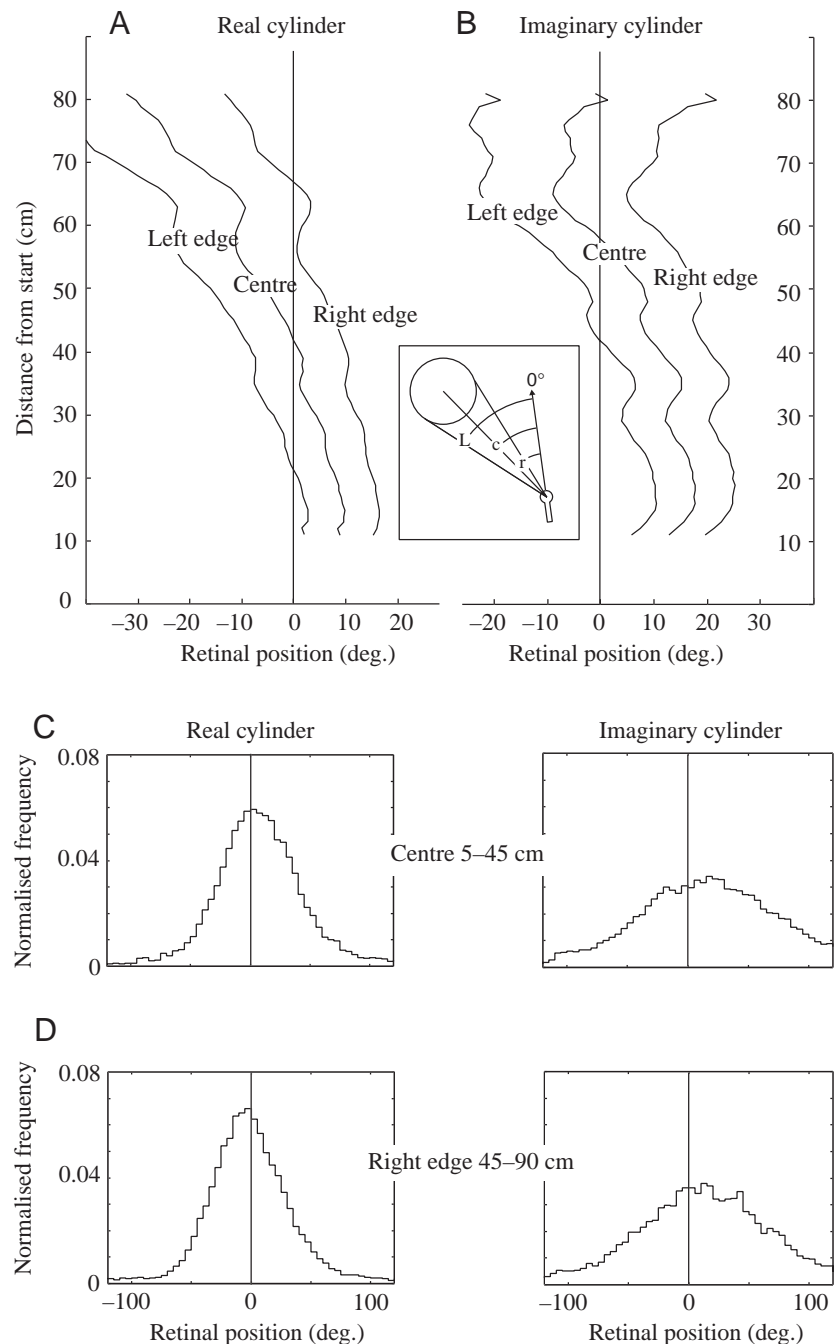


Fig. 4. Retinal position of real and imaginary cylinder during a trajectory. (A) The horizontal path of the centre and of the left and right edges of the bottom of the cylinder across the retina is shown as the ant moves from the start to a point 80 cm away. Estimated horizontal, retinal position for a stated distance comes from the mean retinal position of all data (194 trajectories from 20 ants) within the interval 4 cm either side of the stated distance. (B) Imaginary retinal positions for tests with no cylinder present (71 trajectories from eight ants). (C) The distribution of retinal positions of the centre of the cylinder accumulated over the first 45 cm of the route. Left panel: trajectories with cylinder present (194 trajectories from 20 ants). Right panel: imaginary retinal positions in tests without a cylinder (71 trajectories from eight ants). (D) Distribution of retinal positions of the right edge of the landmark over the second 45 cm of the route. Left panel: trajectories with cylinder present. Right panel: imaginary retinal positions in tests without a cylinder. Data from ants trained with the cylinder on the left or right are combined and represented as though the cylinder is on the left.

feature is rapidly learnt and continues to guide the ant on subsequent trips. Like those of ants trained with the landmark in the closer position, the ants' paths had roughly the same shape when the cylinder was removed (Fig. 5D–F). The difference in clustering between the closer and more-distant cylinder is shown in Fig. 5G–J, which plots the mean trajectory of each ant trained with the cylinder at 1 m or 2 m from the start. We calculated the distances between mean directions for individual ants after 80 cm and the mean direction of all trajectories within that condition. The paths of ants trained with the cylinder at 2 m are significantly more dispersed than those of ants trained with the cylinder at 1 m (mean \pm 95% confidence, number of ants: 1 m: $4.9 \pm 2^\circ$, $n=15$; 2 m: $11.2 \pm 6^\circ$, $n=10$; Watson's F -test: $F_{23}=5.92$, $P=0.02$).

Discussion

The shape of a wood ant's route to a feeder is fixed by the position of a single cylinder placed to the side of the direct path. Instead of taking the shortest path, ants are attracted by the cylinder and follow this longer route stably over many trials (Fig. 1). Perhaps the most interesting result of this paper is the richness of the ant's visual learning. Ants not only learn the appearance of objects at which they aim (Judd and Collett, 1998), but the route that has been fixed by approaching these objects encourages the learning of additional visual cues, such as features of the lighting array or the curtains. Consequently, when a beacon is removed, ants continue to be drawn down the same route (Fig. 2). The power of these additional learnt visual cues is seen when the cylinder is shifted. The ants usually ignore the cylinder in its unusual position and instead direct their path to its accustomed site.

Of particular significance is the finding that if ants are displaced away from the route, in the absence of the cylinder, they are not attracted to the closest point along the route but rather to where the cylinder is normally found (Fig. 3). This position seems to have been learnt as an intermediate goal. Perhaps the extra visual cues that are learnt comprise a snapshot taken at the site of the cylinder. This finding adds significantly to the body of evidence suggesting that insects are pre-disposed to partition routes into segments, using landmarks to define the boundaries between segments (e.g. Collett et al., 2002). It suggests further that memory acquisition is particularly abundant at segment boundaries.

In addition to supporting the ant's navigation to the beacon, it is likely that the putative snapshot taken at the site of the cylinder provides a contextual cue that can prime an ant's memory of the cylinder and so increase the reliability of its recognition (cf. Collett and Kelber, 1988; Collett et al., 1997).

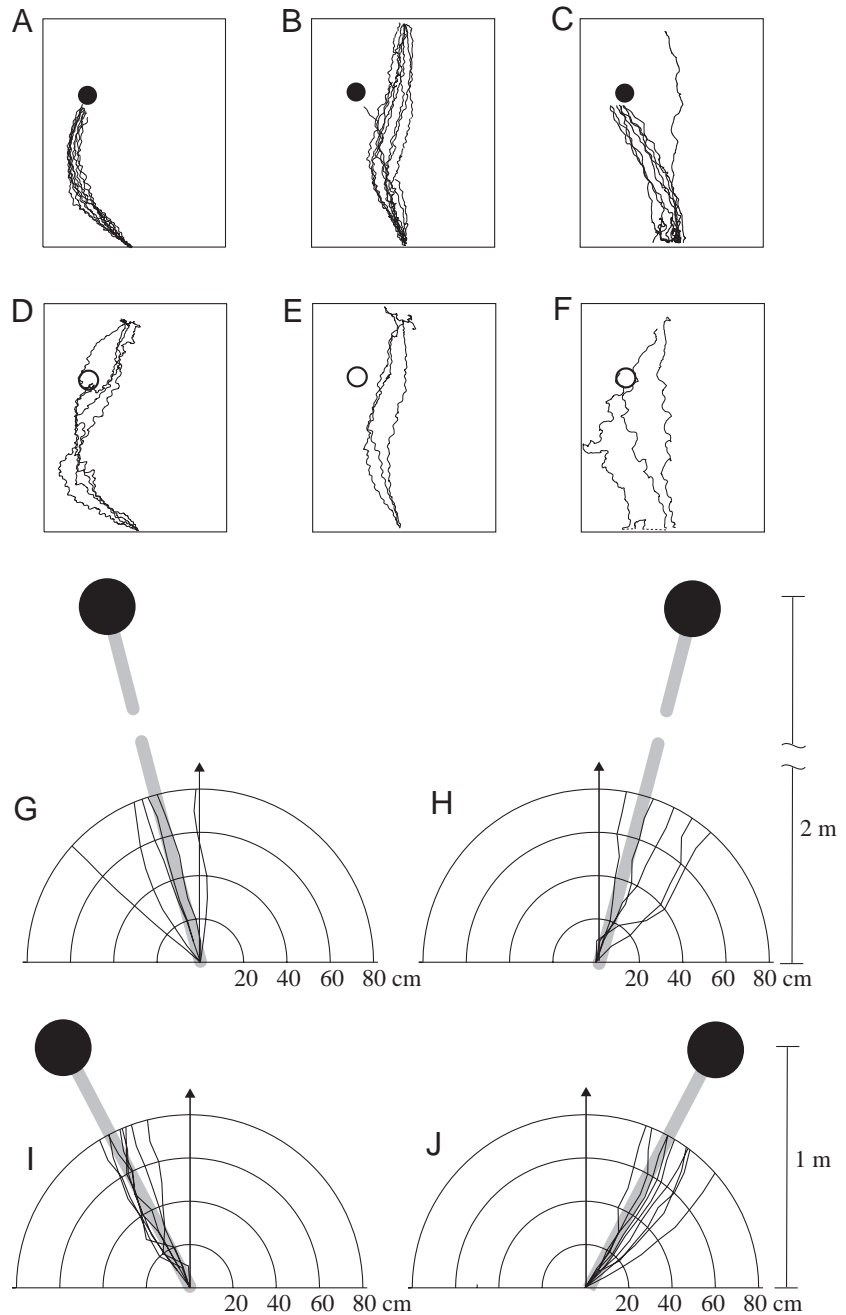


Fig. 5. Routes of ants trained with the cylinder at 2 m from the start. (A–C) Paths of three ants with the cylinder (filled circle) in place. Each ant followed a different route that was consistent from trial to trial. (D–F) Paths from the same three ants in tests with the cylinder removed (the open circle indicates the normal position of the absent cylinder). (G–J) Mean trajectories of individual ants trained with the cylinder 2 m from the start (G,H) are compared with a similar plot for ants trained with the cylinder 1 m from the start (I,J). Eight or more trajectories contribute to each mean. Trajectories are significantly more dispersed in G and H than they are in I and J. The grey bar shows the direct path from start to landmark.

In general, accurate recognition of a beacon is important because particular actions are associated with particular beacons – turning towards the feeder in this case. Contextual support for accurate recognition may well be essential along more natural, longer routes, if several rather similar discrete beacons must be distinguished or if the ant's path is noisy and it approaches a beacon from an unusual direction. Its atypical context may explain why the ants tended to ignore the cylinder when it was moved to an unusual position.

It is instructive to compare the present results with the way that desert ants and wood ants treat extended landmarks (Collett et al., 2001; Graham and Collett, 2002). If ants can obtain continuous landmark information along the route from an extended landmark, like a wall or a dense row of plants, their path is less constrained by the landmark and they can learn a variety of paths relative to this landmark. They learn the appearance of a wall along their chosen route in terms of the retinal elevation of the top of the barrier at different points along it (Pratt et al., 2001, Graham and Collett, 2002) and they then adjust their path to keep the barrier at the learnt elevation(s).

In the case of desert ants, ants homed from a feeder around a 10 m barrier that was positioned perpendicularly to the direct route. On rounding the barrier, the ant's path was initially driven by the global homewards vector that directed the ant from the end of the barrier straight to the nest site along a path at an angle of approximately 34° to the barrier. Once the appearance of the barrier along the route had been learnt, ants followed the same route relative to the barrier, when the barrier had been rotated through 45°, and the ants were placed at the end of the barrier after nearly reaching the nest entrance on their return. Ants will thus follow a consistent path relative to a barrier, despite the absence of useful information from path integration or the sky compass (Collett et al., 2001; Graham and Collett, 2002). Information that was essential to learning the path can thus be dispensed with once the route is familiar. We have shown here that beacons, like path integration, can act as a scaffold during route learning. The beacon must be present for ants to learn a particular route. But, once the route has been acquired, this scaffold can be omitted without seriously degrading the shape of the route.

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