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Switching destinations: memory change in wood ants

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Summary

We have studied the changing use of spatial memories in wood ants by charting how the ants' paths transform when ants are first trained to feed at one site and must then switch to another site. Because ants, which are trained to approach a single feeding site from a single starting point, are attracted directly to that goal when started from unfamiliar positions, we describe the ants' paths in terms of the use of two stored snapshots. Each snapshot consists of retinotopic views of the ants' surroundings acquired at one of the two feeding sites. When a snapshot is activated, it draws an ant to the related site from a wide range of directions. Here, we focus on routes that occur before ants have learnt to go directly from the start to the second site. The initial

direction of the ant's path is then mostly aimed either at the first site or between the two sites. On 62.2% of all recorded paths, this segment is followed by an abrupt turn, after which the ant often aims directly at the second feeding site. The details of this behaviour suggest that, after the turn, control of the path switches from the snapshot recorded at the first feeding site (or some combination of the two snapshots) to the snapshot recorded at the second feeding site. We discuss different ways in which control might be transferred from one snapshot to the other.

Key words: wood ant, *Formica rufa*, route, snapshot memory, re-learning.

Introduction

As new resources become available and old ones disappear, a foraging insect adjusts its route to exploit the new resources. The insect's evolving route in such circumstances provides a natural situation for exploring the way in which new memories are incorporated into existing spatial knowledge and how the new memories might reshape the route. A wood ant, walking a short distance to a familiar food site, in an indoor laboratory, is largely guided to the site by its memory of what its surroundings look like from the vantage point of that site (Durier et al., 2003; Graham et al., 2004). This memory is encoded in retinotopic coordinates and the ant moves until the image on its retina resembles its memory, or acquired snapshot, of the view from the goal. Snapshot matching, as a means of visual guidance to a place, has been studied in several insects (ants – Wehner and R ber, 1979; Wehner et al., 1996; Judd and Collett, 1998;  kesson and Wehner, 2002; Durier et al., 2003; honeybees – Cartwright and Collett, 1983; solitary wasps – Zeil, 1993; social wasps – Collett and Rees, 1997; flies – Collett and Land, 1975; waterstriders – Junger, 1991) and its operation analysed in simulation (Cartwright and Collett, 1983, 1987; Lambrinos et al., 2000; M ller, 2000; Zeil et al., 2003). But there remain many unanswered questions.

In the present paper, we start by examining the directionality of snapshots. Do snapshots recorded at a goal

only attract ants over a small range of directions? We approach the question by testing the ants' ability to reach a goal from different starting points. We then analyse a wood ant's changing paths, as it switches from feeding at a familiar site to feeding at a new one. How does an ant adjust the use of its visual memories of the two sites as it gains experience of the second site? What can an ant's path reveal about the dynamics of memory recall during a route and to what extent does an ant emphasise different snapshot memories at different stages of its route?

Materials and methods

Ants

Queen-right colonies of wood ants (*Formica rufa* L.) were housed and maintained in 670 litre plastic tanks. For experiments, a large group of foragers (~50 ants) was placed in the test arena. The fastest ants to reach the feeder (10–20 ants) were caught and marked individually with enamel paint. Training was continued with this smaller group. After a few trials, the group was divided into several smaller groups of 2–3 foragers in order to reduce interactions between ants. After the foragers had fed, they usually returned to the starting point, from where we returned them to the colony. They gave sucrose to their nestmates by trophallaxis and were

soon ready for another trip. Ants made about three foraging trips per hour.

Apparatus

Experiments were performed within a rectangular arena (2.7 m×4.8 m) surrounded by floor-to-ceiling white curtains and illuminated by banks of high-frequency fluorescent lights fixed above a false translucent plastic ceiling. The ants' trajectories were tracked with a fixed video camera hidden in the false ceiling 3 m above the centre of the test arena. The camera (Sony EVI-D30) has movable optics, allowing a high-resolution image to be captured of any part of the arena. The camera is controlled by a PC (Pentium II 233 MHz) running custom software (Fry et al., 2000). The system extracts the ant's position and longitudinal orientation at 50 Hz. Before analysis, the output was smoothed by taking a moving average with a window size of nine frames. The ant's path was recorded for 6 min, or until the ant approached so close to a cylinder in the arena that the tracking system 'lost' the ant.

Experimental procedures

Foragers were normally released at a fixed starting point (Fig. 1) close to a triangular arrangement of cylinders (45 cm high × 15 cm in diameter). Since the triangles were kept in the same position in the arena throughout the experiments, we cannot say which landmarks guided the ants' paths. The surrounding curtains, the overhead lights and the cylinders could all have played a role. Over a sequence of trials, ants learnt to collect sucrose solution from a microscope slide at a site ~100 cm away (F1). After ~30 visits to this site, the position of the feeder was switched. The line connecting the feeder and starting point was rotated through 45°, so defining the position of a second food site (F2). The last 3–5 visits to F1 and most of the 30 subsequent visits to F2 were recorded. In some cases, the experiment was speeded up by recording every other path for the first 10 runs after the switch. For a few trials after the switch to F2, ants were helped in their search for the new food site. Once the recording session was finished, we tapped the floor with our fingers a few cm in front of the ant and it would usually follow our fingers to the food. Also to shorten the experiment, ants were taken from the sucrose before they had finished feeding, were placed in a container and the next ant started. After a group of about five ants had been collected from the feeder, the group was replaced on the sucrose and allowed to return to the starting position, from where the ants were taken to the nest.

The floor was washed periodically with water and alcohol to reduce odour cues. We could see no signs that our results are biased by chemical cues. Ants did not take the same route from one trial to the next or follow each other's routes. Ants frequently missed the feeder by a few cm and searched for it with no sign that they were attracted there by scent.

Analysis

The starting direction of each path (the first segment, b in Fig. 1) was determined by the direction of the line between the

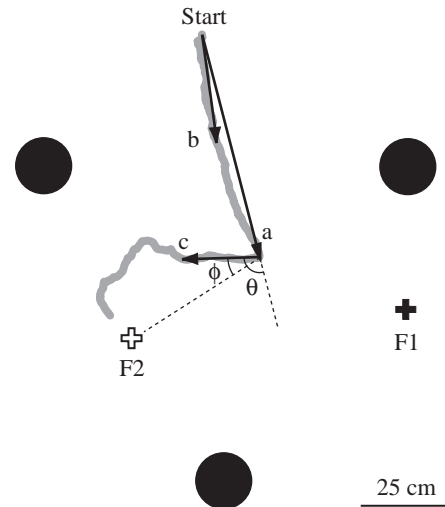


Fig. 1. Diagram showing the relative positions of the start of the trajectory, the cylinders (black circles) and the two feeding sites (F1 and F2). The directions of the first (b) and second (c) segments of a path and the direction of the path until the turn (a) are shown superimposed upon a trajectory recorded during training to F2. The turn is where the trajectory abruptly changes direction towards F2. The turn's magnitude is shown by the angle θ and its direction relative to F2 by the angle ϕ .

start and a point on the path, 30 cm from the start. Many paths had a similar overall shape (e.g. Fig. 3) in which a roughly straight initial part was followed by a sharp turn, after which the second part of the path was again roughly straight. The position of the turn was determined by eye. The direction of the path after the turn (the second segment, c in Fig. 1) was determined in the same way as the direction of the first segment. The principal axes of the ellipses in Fig. 6 were computed as described by Sokal and Rohlf (1995, p. 586).

Results

A goal can be reached from novel starting points

Our interpretation of the ants' changing routes relies on the assumption that ants, in these experiments, were, for the most part, moving so as to match snapshots taken at one or more goals, rather than being directed by route-specific memories or by path integration. One test of this assumption is to see whether ants can reach a goal from novel release points. Ants, which had been trained to go to a single feeder from a fixed starting position (Fig. 2), were therefore given occasional tests, with no feeder present, in which they were released at one of three unfamiliar positions. The direct path to the feeder location from these positions was 20° to the left or right, or 50° to the left, of the familiar training trajectory. The apparent curvature of the paths from D1 may be caused by ants swerving to avoid coming close to a landmark, or the distribution of paths could be biased by the loss of those paths that were too close to the cylinder to be recorded. The paths from the other displaced release sites were, like the trained trajectories,

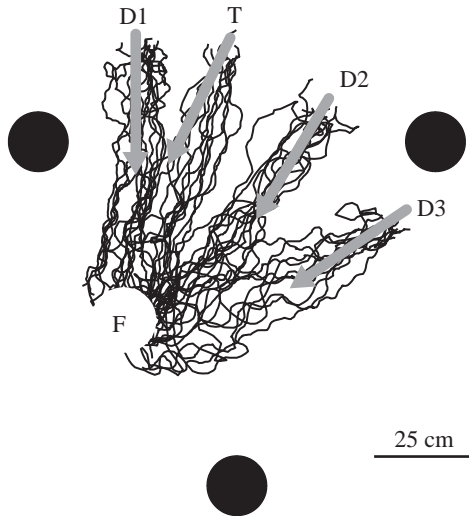


Fig. 2. Trajectories to a food site from displaced (D1, D2, D3) and training (T) start points. For clarity, not all the recorded trajectories are plotted. We show 13, 13, 10 and 13 releases from sites D1–D3 and T, respectively, and the mean vectors of all the first segments (grey arrows). Mean vectors are measured with respect to the direct line between each starting point and the food site. The direction and 95% confidence interval of each mean vector are D1: $4.76 \pm 6.61^\circ$, $r=0.95$, $N=30$; T: $-2.20 \pm 6.62^\circ$, $r=0.94$, $N=34$; D2: $11.9 \pm 7.82^\circ$, $r=0.93$, $N=29$; D3: $14.4 \pm 18.4^\circ$, $r=0.87$, $N=13$. Data come from 12 ants. Solid black circles indicate cylinders, and F indicates the food site. Food was removed during these tests.

directed straight at the goal (Fig. 2). In this situation, ants take novel paths to their destination, rather than being attracted towards their accustomed route (cf. Graham et al., 2003).

Ants (*Cataglyphis* sp.) are known to use path integration to perform novel routes (e.g. Müller and Wehner, 1988; Schmidt et al., 1992; Collett et al., 1999). They probably do so by subtracting the coordinates of their current position, which they have obtained through path integration, from those of the goal, which they have learnt on an earlier occasion (Collett and Collett, 2000). The results of Fig. 2, in which wood ants are displaced to a new site and so are deprived of accurate knowledge of their current position, cannot be explained by path integration. The ants' behaviour suggests instead that they were guided to the goal by snapshot memories stored there. This behaviour reinforces the argument presented in an earlier paper (Durier et al., 2003) that wood ants recall snapshots stored at the goal well before reaching it. In interpreting the experiments that follow, we assume that a direct path segment to the first (F1) or to the second feeding site (F2) indicates that the ant is using a snapshot memory stored at F1 or F2, respectively.

Ways of reaching the second feeder (F2)

Ants were given 30 trials with the food at F1, the food was then switched to F2 and a further 30 trials were given. As the training to F2 progressed, ants took a variety of routes to reach the new site. Fig. 3 shows examples of the changing paths of

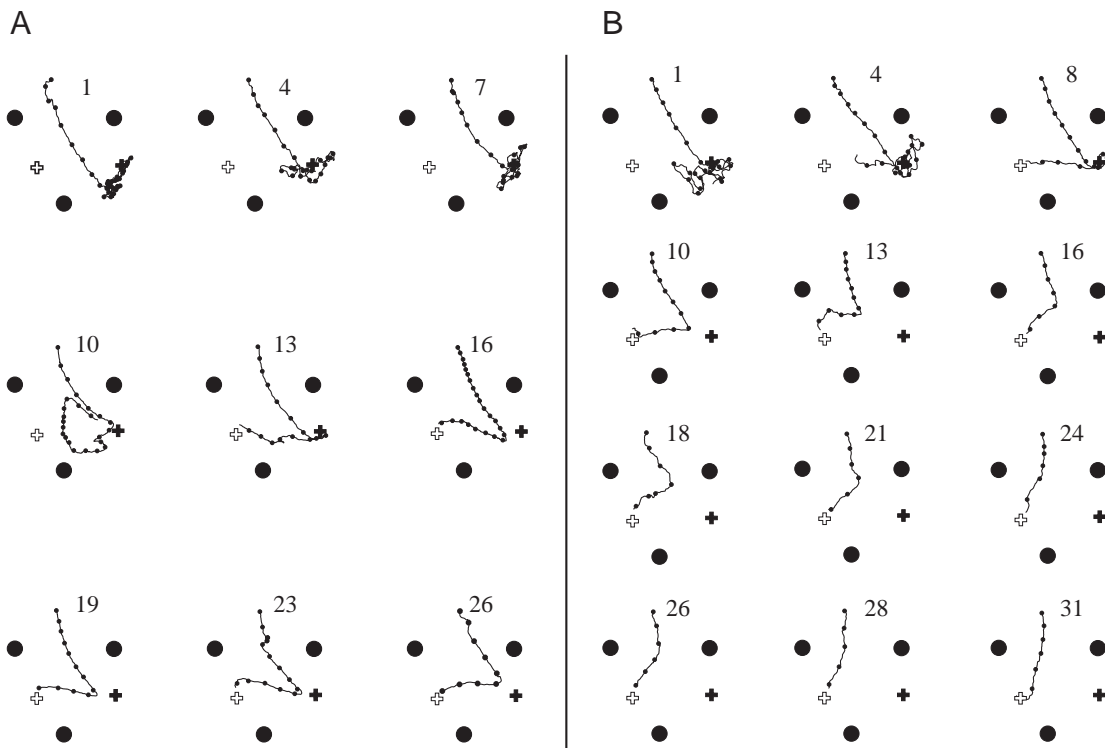
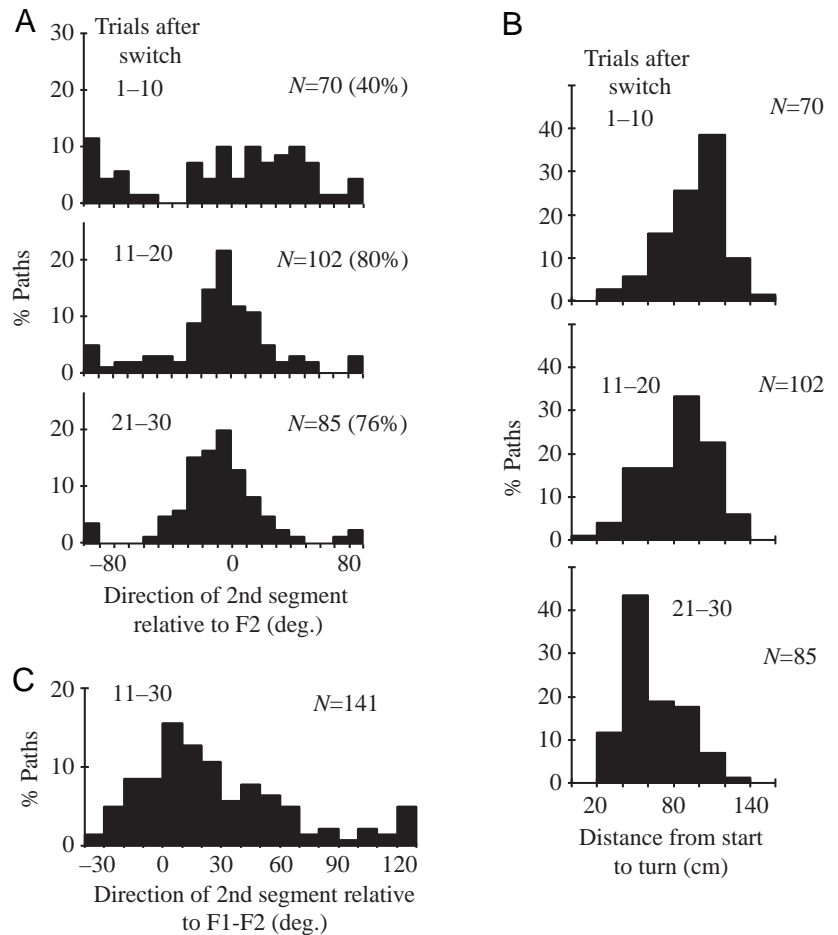


Fig. 3. Trajectories of two ants (A and B) after the sucrose has been switched from F1 to F2. Each trajectory is labelled with its trial number relative to the switch from F1 to F2. F1 is denoted by the filled cross and F2 by the open cross. Dots on each trajectory are placed 10 s apart.

Fig. 4. Characteristics of the second segment. (A) Direction of second segment measured with respect to the direct path from the turn to F2 (angle ϕ in Fig. 1). Histograms plot the direction of the second segment in 5° bins for successive blocks of 10 trials after the switch. 0° on the abscissa marks the direct path to F2. N gives the number of data points in each histogram with data pooled across ants and trials. Paths are only included when there is a turn. % shows the proportion of trials with a turn. The direction of the second segment changed over training (Kruskal–Wallis test: $\chi^2=22.9$, d.f.=2, $P<0.001$). Accuracy improved between the first and the second blocks of trials but not afterwards (Mann–Whitney test: first block vs second block, $z=-3.965$, $P<0.001$; second block vs third block, $z=-0.437$, $P=0.662$). (B) Similar histograms showing changes in the distance of the turn from the ant's starting position. The distance between the start and the turn decreased as training progressed (Kruskal–Wallis test: $\chi^2=58.3$, d.f.=2, $P<0.001$; Mann–Whitney test: first block vs second block, $z=-2.861$, $P=0.004$; second block vs third block, $z=-5.587$, $P<0.001$). (C) Histogram showing the direction of the second segment measured with respect to the direct path between F1 and F2, for all those segments from trial 11–30 that were aimed within $\pm 20^\circ$ of F2. 0° on the abscissa is the direction from F1 to F2. Here and elsewhere, positive angles are counterclockwise.



two ants. The first segment of one ant's path was directed roughly at F1 throughout training (Fig. 3A). At some point on the way to F1, the ant turned sharply and aimed at F2. These paths suggest that the start of the ant's trajectory was set by a snapshot associated with F1 and that the trajectory later switched to being driven by a snapshot associated with F2. This ant seemed to acquire a two-stage route to F2 that may have been controlled by the sequential activation of two snapshots.

The other ant illustrates a more commonly found pattern, in which the direction of the first segment of the trajectory rotated as learning progressed (Fig. 3B). For the first few trials, the first segment pointed at F1. It then gradually rotated to point more in the direction of F2. The initial segment was again often followed by an obvious turn towards F2. Turns were identified in 62.2% of the recorded paths of all ants. Analysis of walking speed before, during and after these turns indicates that ants did not slow down at the turn but that they transiently speeded up immediately afterwards.

The second segment

In the present paper, we focus on the portion of the path following the turn (second segment). As training progressed, trajectories after the turn were aimed more accurately at F2. Histograms of the directions of the second segment are shown in Fig. 4A over successive blocks of 10 trials. Directions are

plotted as the angular difference between the ant's heading and the direction of F2 from the turning point. The accuracy with which the segments were aimed at F2 improved significantly over the three blocks of trials, and the distance from the start to the turn dropped (Fig. 4B).

The second segment pointed directly at F2 at a stage in training in which the direction of the first segment was still rotating, with the consequence that the position of the turn varied. This variability allowed us to infer whether during the second segment the ants were attracted to F2, headed in a fixed direction or turned through a fixed angle. The best-controlled parameter should be associated with the smallest standard deviation. We therefore computed for each ant, over trials 5–25, the standard deviations of (1) the angular difference between the direction of the second segment and the direct path to F2 from the turn (angle ϕ in Fig. 1), (2) the absolute heading of the second segment and (3) the turn size as given by the angular difference between the ant's overall direction from start to turn and the direction of the second segment (angle θ in Fig. 1). The standard deviation of (1), i.e. the precision of aiming at F2, was smaller than that of both (2) and (3) for 12 out of 13 ants ($\chi^2=9.31$, $P=0.002$), supporting the conclusion that the controlled parameter is attraction to F2.

A related question is whether those second segments that are aimed towards F2 tend to lie along the direct route between F1

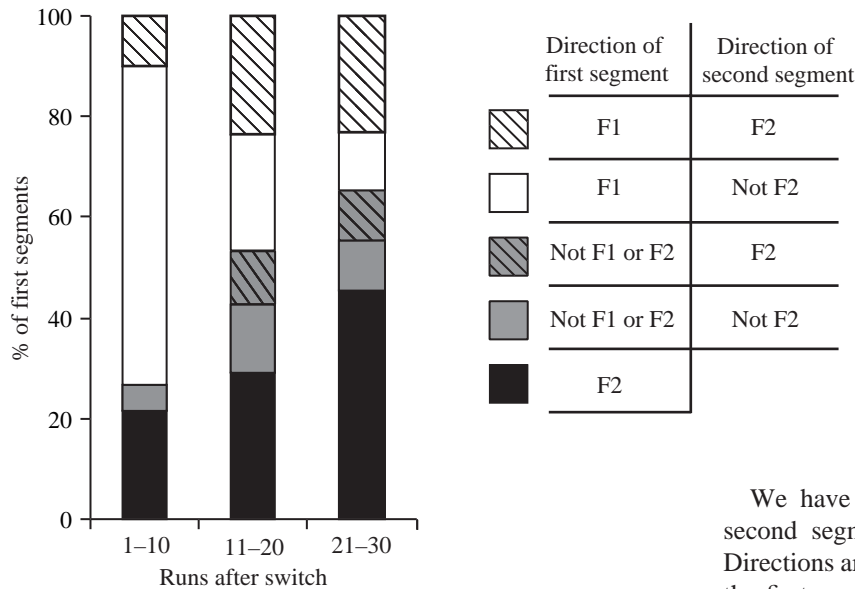


Fig. 5. Coarse categorisation of all recorded trajectories after the switch. The three columns show the first, second and third blocks of 10 trials. Each column is divided into the percentage of first segments that are aimed (1) within 20° either side of F1, (2) aimed neither at F1 nor at F2 – a category that is only 5° wide and (3) aimed within 20° of F2. The first two categories are further subdivided into those trajectories in which the second segment is aimed at F2 and those in which it is not.

and F2. To obtain an answer, we measured, relative to the direct path from F1 to F2, the directions of all those second segments, in trials 11 to 30, which were within 20° of F2. The observed distribution (Fig. 4C) has a mode at zero indicating that some paths do indeed lie along the F1 to F2 route. However, the distribution is not normal (Kolmogorov–Smirnov test, $z=1.471, P=0.026$) and the directions of 48% of the segments differed by more than 30° from the direct route between F1 and F2. Thus, the ants were not simply performing a fixed route between F1 and F2, but they could be attracted to F2 from different directions.

Interactions between first and second segments

The changing direction of the first segment (e.g. Fig. 3B) may suggest that there is increasing control of that segment by F2 as training progresses. Similarly, the second segment is aimed more precisely at F2 with increasing number of trials. Is there a trial-by-trial variation in the strength of control by F2 that is expressed jointly in the first and second segments? Our first step in answering this question was to classify the trajectories in the following way. The first segments were placed into one of three categories: directed at F1, directed neither at F1 nor at F2, and directed at F2. The first two of these categories were then sub-divided into whether or not a second segment was aimed within ±20° of F2. In Fig. 5, this classification is shown separately for successive blocks of 10 trials.

The proportion of trials in which the first segment was aimed at F2 increased with training. By the last block of trials, ~45% of first segments were directed at F2. The proportion of trials in which the second segment was directed at F2 also rose with training. The proportion did not depend on whether or not the first segment was aimed at F1 or neither at F1 nor at F2. Over the three blocks of trials, the percentage aimed at F2 was, respectively, 13.4%, 50.8% and 66.7%, when the first segment was directed at F1, and 0%, 45.2% and 50%, when the first

segment pointed neither at F1 nor at F2. Thus, the accuracy of aiming the second segment at F2 is not obviously related to the direction of the first segment.

We have also plotted for each trial the direction of the second segment against the direction of the first segment. Directions are given in terms of the angular difference between the first or second segment and the direction of F2 from the start or the turn, respectively (α and β in the inset to Fig. 6). Plots are shown separately for each block of 10 trials. The conclusion from this graphical analysis is also that there is no trial-by-trial correlation in the magnitude of control that F2 exerts in the first and second segments. Thus, the development of accurate control of the second segment by F2 seems to be independent of the details of the first segment.

Displacement during training to F2

We know from Fig. 2 that ants can reach a goal directly by a novel route. Since they do so after displacement, their novel routes cannot be explained through path integration but must involve the use of visual cues, and most likely snapshots stored at the goal. The same argument cannot be extended automatically to cases of retraining. Ants could, in principle, recall the path integration coordinates of F2 relative to their fixed starting point and use this information to help determine their route after the turn. We therefore performed displacement experiments on ants during retraining. Although such experiments can show that visual cues are sufficient to guide an ant to F2, they cannot, of course, show that path integration makes no contribution to the ant’s normal trajectories.

Ants were trained for ~30 trials to F1 and then retrained to F2 for a further 10 trials, starting as usual from the same place on each trial (T in Fig. 7A). Each ant was then given six tests, starting alternately 15° anticlockwise (D1 in Fig. 7A) or 30° clockwise from the training position (D2 in Fig. 7A), with F2 as the centre of rotation. A few test trials were aborted because ants were attracted to the cylinder nearest the release point.

In test trajectories with a sharp turn, the direction of the second segment often pointed roughly at F2. If ants were to rely primarily on path integration to plan a trajectory to F2 and assumed that they were starting from their accustomed position, the second segment of their trajectories would not point in the direction that the ants intended (Fig. 7C). Their intention could then be made apparent by shifting the trajectories through the vector that connects the actual release

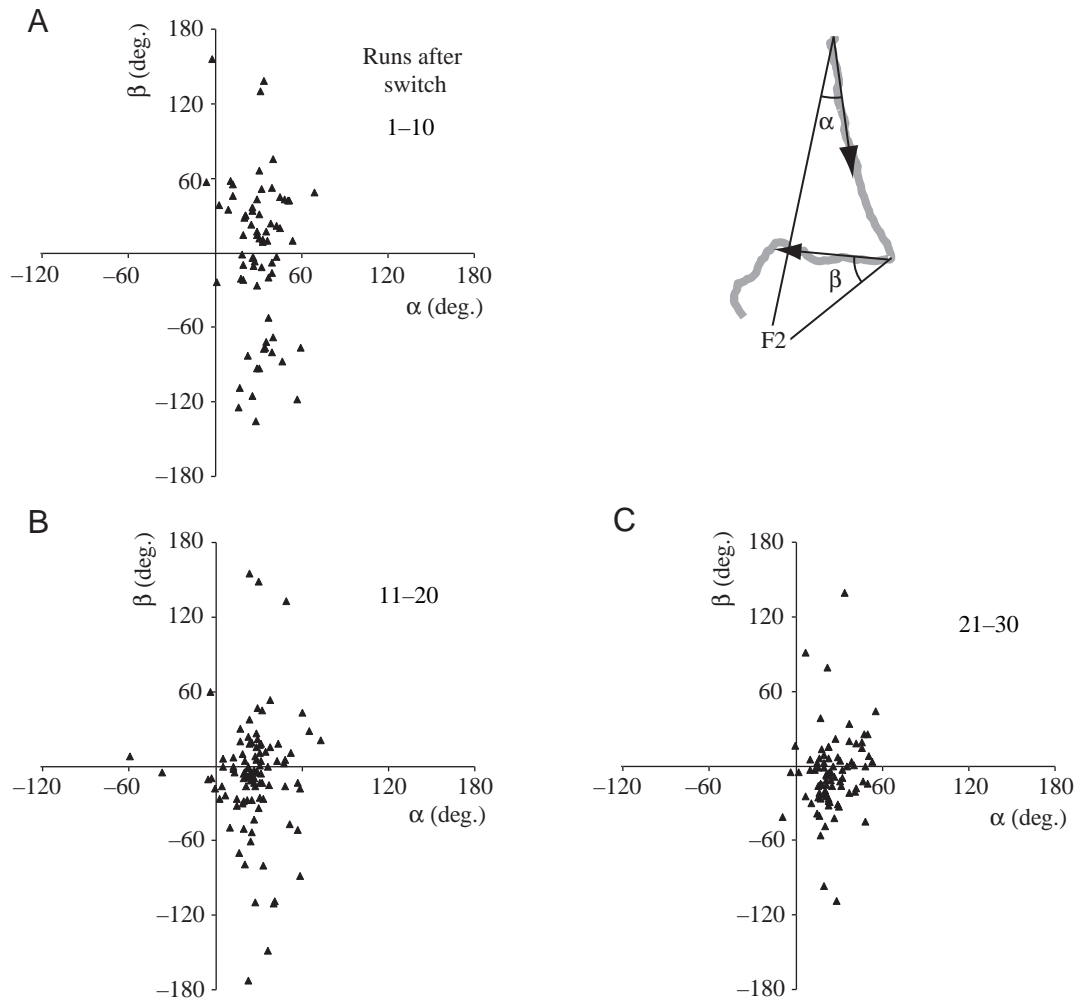


Fig. 6. Lack of correlation between the directions of the first and second segments. The directions of the first and second segments with respect to the direction of F2 from the start and from the turn, respectively (α and β in inset), are plotted against each other for successive blocks of 10 trials after the switch. (A) Paths 1–10: $N=70$, mean $X=30.47\pm 3.26^\circ$, mean $Y=3.71\pm 15.62^\circ$, direction of principal axis= 92.08° . (B) Paths 11–20: $N=102$, mean $X=26.47\pm 3.435^\circ$, mean $Y=-7.79\pm 14.355^\circ$, direction of principal axis= 89.98° . (C) Paths 21–30: $N=86$, mean $X=25.38\pm 2.78^\circ$, mean $Y=-7.62\pm 6.9^\circ$, direction of principal axis= 80.23° . The closeness of the principal axis to 90° indicates a lack of correlation between the directions of the two segments.

site (D1 or D2) to the ants' normal starting point (T). Fig. 7D shows, for each trajectory, the angular difference between the direction of the second segment and the direction of F2 plotted against the same angular difference computed after the start of the trajectory has been shifted to T. The data points will lie below or above the diagonal, depending on whether the paths are determined primarily by a snapshot or by path integration, respectively. The data points fell significantly below the diagonal, supporting the hypothesis that ants aimed at a snapshot-defined goal (20 out of 29, $\chi^2=4.172$, $P=0.041$).

Five ants were each given two final tests from a third start position (D3) that was rotated 100° from the normal start (Fig. 7B). Although the sample is too small for statistics, it is clear that more than half of the trajectories from D3 were directed at F2, indicating that the ants were guided directly to F2 by visual landmarks specifying that site.

Discussion

We began by showing that wood ants are attracted directly to a visually defined feeding site when started from novel locations. The most likely explanation of these novel routes is that an ant begins its trajectory having already engaged a stored snapshot that it previously recorded at the feeding site. The snapshot is presumably recalled through a combination of associated contextual cues and the ant's view of visual features of the arena from the starting point. Such early recall, before there is a close match between the currently viewed scene and the ant's snapshot of the scene taken at the feeder, sets up an attractor landscape, which can draw the ant to its goal from a range of starting points. Although this behaviour has been shown earlier in simulation (Cartwright and Collett, 1983; Lambrinos et al., 2000), this is its first demonstration in a real insect. When ants approach a goal located at the bottom of a landmark, they seem to learn views of these landmarks from

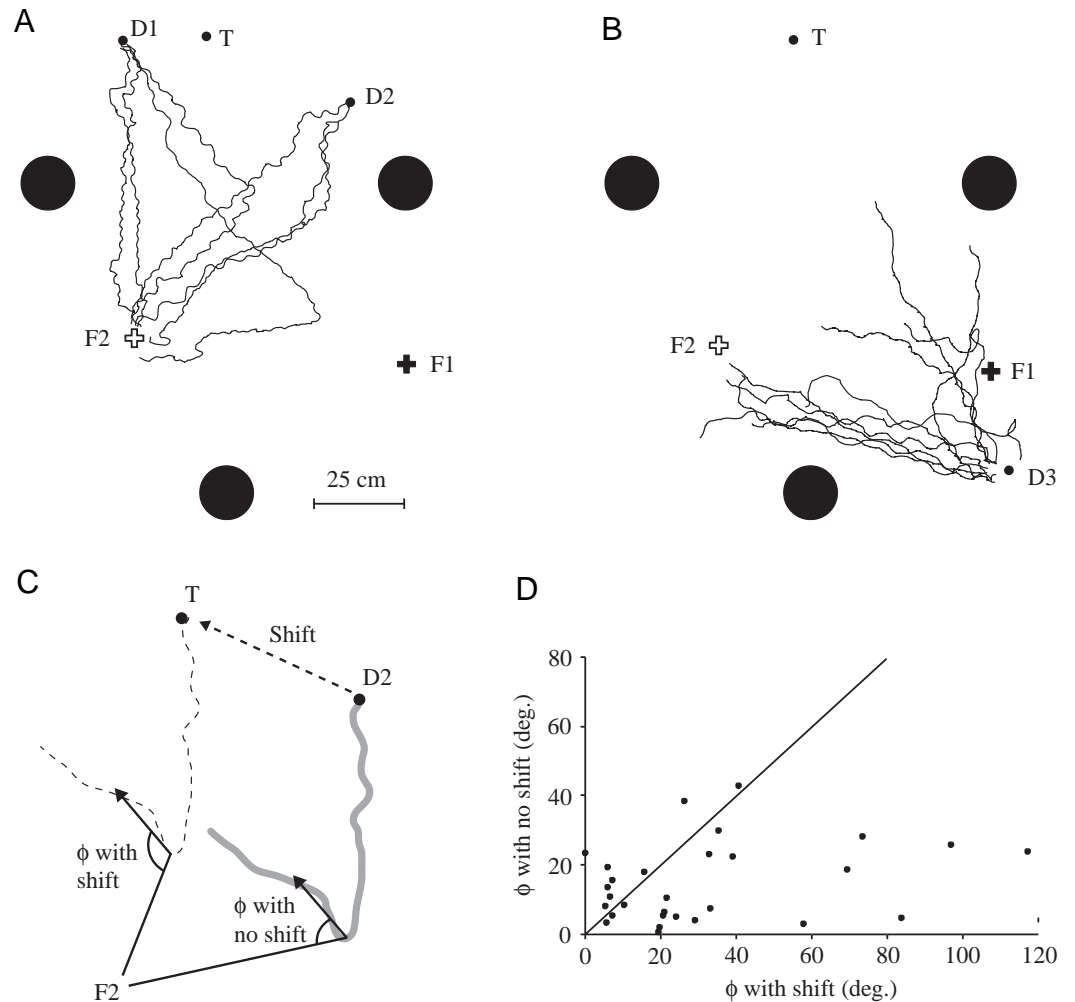


Fig. 7. Routes performed from novel starting points. (A) Examples of routes with ants started at positions D1 and D2 rather than from their usual start position at T. (B) Routes with ants started at D3. (C) Diagram to show the angular difference between the direction of the second segment and the direction from the turn to F2 (the angle ϕ in Fig. 1) with the trajectory either shifted as though the ant had started at T or with no shift of the trajectory. (D) For each trial with a turn, ϕ with no shift is plotted against ϕ with shift. This plot pools data from ants started at D1 and D2.

several distances and to be guided by these *en route* snapshots on the way to the goal. It is not yet clear how *en route* snapshots interact with snapshots taken at the goal. It seems that in the present experiments, the goal snapshots attract the ants more powerfully than any *en route* snapshots.

The data of Fig. 7B show ants approaching a goal from a broad range of directions ($>100^\circ$). How do ants accomplish this feat if, as increasing evidence suggests (Judd and Collett, 1998; Nicholson et al., 1999; Durier et al., 2003; Graham et al., 2004), they record snapshots when facing conspicuous landmarks and their direction of travel is predominantly forwards? A single snapshot stored at the bottom of a circularly symmetric object, such as a cylinder or cone (Judd and Collett, 1998), can attract an ant from many directions, but more typically a single snapshot will only be matchable to a scene when the ant faces and moves in roughly the same direction in which the snapshot was stored. One solution to this problem is to store several snapshots at a single location, each taken when facing in a different direction (Cartwright and Collett, 1983). There is evidence from ants trained to a feeding site between two cylinders of unequal sizes that the ants store two snapshots at the site, one when facing each cylinder (Graham et al., 2004). We suggest that ants may equip themselves with

multiple goal-related snapshots recorded at one site, which together provide a more or less omni-directional snapshot.

When ants gradually abandon one feeding site in favour of another, they often aim first towards the old feeding site (F1), or at some point between the two sites, and then turn abruptly to head towards the new site (F2). On their return from F2, they often head directly to the start. Three major changes occur as the ants gain experience of F2. The first segment of the route rotates away from F1, a finding that we will discuss in more detail elsewhere. Second, the initial vector becomes shorter so that the turn is closer to the start. Third, the segment of the route after the turn, which we have termed the second segment, is aimed more accurately at F2. The ant's ability to aim first at F1 and then at F2 within a single route (e.g. Fig. 3A) stresses that separate snapshots of the same scene taken from slightly different positions in space can act independently without mutual interference (although the rotating first segment suggests that sometimes the two snapshots are co-activated and that the ants are guided by a mixture of the two).

We wish to explain how, first, one snapshot and then another manages to capture full control of the ant's trajectory at different stages of the route. One class of model is that both the F1 and F2 snapshots are recalled at the start of each route and that,

during training, the relative strengths of the two recalled memories gradually change in favour of the F2 snapshot. This model could be called static because for any single trip the attractor landscape set up by the two more or less omnidirectional goal snapshots is fixed at the start. On early trials, the ant is first drawn by the F1 snapshot towards F1. At F1, the attractive force of the F1 snapshot is minimal and the ant is drawn to F2. When, with increased training, the unrewarded F1 snapshot becomes weaker and the rewarded F2 snapshot becomes stronger, the ant becomes attracted to F2 earlier in the route. One problem with this static model is to explain why, particularly in the early stages of training to F2, when the ant goes from F1 to F2, the ant is not then trapped by F1. Thus, on reaching F1, the ant may start moving towards F2, but its omnidirectional F1 snapshot would act to draw the ant back to F1. A possible solution to this difficulty is to suppose that, despite the ant's ability to reach both F1 and F2 from different directions, their omnidirectional goal snapshots retain a strong directional bias along the ant's normal route. For instance, snapshots taken at F2 when arriving on a direct path from F1 could be relatively stronger than those taken from other directions.

A second possibility is that ants recall snapshots sequentially. At the start, they recall the F1 snapshot (or, when the first segment rotates away from F1, a weighted combination of the F1 and F2 snapshots). At the turn, they recall the F2 snapshot and de-activate the F1 snapshot. The migration of the turn towards the start would then suggest that F2 is recalled earlier as training progresses. Initially, recall of the F2 snapshot may be triggered by the view from F1, but, with increased training, it may be activated from a wider range of locations. The essential feature of this model is that ants are guided by snapshots that are recalled at different stages along the route, with recall driven either by what the ant sees or by more internally derived signals. The attractor landscape set up by snapshots may then evolve during a single trajectory. This model accounts naturally for the 'trap-lining' that has been reported in orchid bees (Janzen, 1971) and bumblebees (Heinrich, 1979; Thomson et al., 1997) as they follow a fixed route from one flowering plant to another. So far, our data do not allow us to decide definitively between the two models. But a rotating initial vector that is followed by an abrupt turn towards F2 does perhaps argue in favour of a dynamic model in which snapshot memories are switched on and off during the course of a route.

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