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The co-activation of snapshot memories in wood ants

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Summary

Insects can guide themselves along a familiar route to a familiar place by retrieving and using visual snapshots that they have stored both along the route and at their destination and moving so that their current views match the target snapshots. To learn more about the matching process, we have investigated the interaction of snapshots by engineering a situation in which ants simultaneously retrieve two sets of memories.

Ants were trained from a fixed start position to feed in one site, after which the feeder was switched to a new one. It could take up to 30 trials after the switch before the ants headed directly to the new food site. We suppose that during this transition phase ants retrieve memories appropriate for both sites. We compared the ants' behaviour for two different sized separations between feeder sites. When the sites are relatively close together, the initial headings of the ants' paths rotated gradually from aiming directly at the first food site to aiming at the second food site, suggesting that ants' paths are controlled by the weighted average of two simultaneously activated snapshot attractors. By contrast, when the food sites were further apart, initial headings switched abruptly between the two sites – ants either headed for food site 1 or for food site 2. We show that these differences in transition behaviour can be simulated by the co-activation of snapshot attractors of restricted spatial extent, such that features encoded in a snapshot are only recognised if they occur within a limited retinal distance of the stored position of the feature.

Key words: Image matching, memory recall, navigation, visual landmarks, wood ant.

Introduction

Some insects remember a place with the aid of visual memories consisting of retinotopic views or snapshots, taken at vantage points close to that location (Cartwright and Collett, 1983; Durier et al., 2003; Junger, 1991; Wehner and Räber, 1979). These snapshots seem to be encoded in terms of the retinal positions of a collection of visual features, such as the edges of nearby landmarks (Cartwright and Collett, 1983; Harris et al., 2007; Judd and Collett, 1998). An insect, equipped with a snapshot, can return to where the snapshot was recorded by moving until the current view on its retina matches its stored view. Therefore, to be of use in guidance, a snapshot memory must be retrieved well before the insect reaches its goal and has achieved a close match between its current and stored views. Recent experiments by Kwon et al. (Kwon et al., 2004) on cockroaches and by Tang et al. (Tang et al., 2004) on fruit flies demonstrate that insects do show the necessary spatial generalisation when recognising visual stimuli and can identify stimuli that are presented at retinal positions distant from where the stimuli were learnt. We are concerned here with the retinal distance over which snapshot matching can occur, though we do not approach the problem until the Discussion.

Since insects can remember long visually guided routes (e.g. Kohler and Wehner, 2005) to several places (e.g. Menzel et al., 1996; Reinhard et al., 2004), it seems likely that they have the capacity to store multiple snapshot memories. Consequently, they require mechanisms to prevent confusion between memories and to aid the retrieval of the appropriate memory. Contextual cues, such as views of the more distant panorama (Collett et al., 1997), time of day (Gould, 1987) and motivational state (Harris et al., 2005) play an important role in priming the relevant visual memories. Under normal circumstances, such contextual influences will help prevent an insect's behaviour from being disrupted by the concurrent retrieval of two or more incompatible memories.

For understanding how memories are encoded and retrieved, it can be informative to disrupt such mechanisms. One such way is to engineer conditions in which two memories are activated at the same time and so may interfere with each other (e.g. Cheng, 2005). Co-activation can be achieved through reversal learning. An insect is first trained to select and approach one stimulus of a pair. Then, in a second training phase, it learns to approach the second stimulus. For a period after each switch in training conditions, the two memories may

be equally active and, since the memories share a common context, they may be co-activated leaving the insect confused about what it should do (Menzel, 1969). Uncertain performance caused by interference was, for instance, found when bumblebees were trained sequentially to turn either left or right in artificial flowers to reach sucrose (Chittka, 1998). Interference occurred although the flowers with their associated left or right turns were coloured differently.

Interference phenomena become particularly interesting if the behaviour generated by each memory closely reflects its contents, as happens when a snapshot memory leads an insect to a particular spatial location. Co-activated memories may then evoke purposive but novel behaviour due to mixing of the memories, and perhaps reveal new details about what the memories encode. Here we extend an earlier study on the mixing of snapshot memories in wood ants (Durier et al., 2004) in which we explored how ants behaved when two sets of snapshot memories were retrieved at the same time.

In the previous study (Durier et al., 2004), wood ants were trained in an indoor arena to find food, first at one location and then at another. The ants began their journey to the food from a fixed starting point in the room. After they were well trained to reach food at one location (F1), the food was switched to a second location (F2). The path of the ant over the floor of the arena was guided by snapshot memories related to F1 and F2, and the direction of the path indicated which set of memories exerted control. The initial direction of the ants' paths rotated gradually from aiming at F1 to aiming at F2. Immediately after the switch to F2, the initial segment of the path pointed at F1, over several trials it passed smoothly through intermediate directions before stabilising close to F2. One interpretation of the intermediate directions of this initial segment is that snapshot memories of F1 and F2 and the routes to these sites were retrieved simultaneously, and that their joint action generated an intermediate path with a direction that was determined by the relative strengths of the two sets of retrieved memories. When the memories exerted equal strength, the ant headed to a point half way between F1 and F2.

In the present paper we present further data from similar experiments to explore what happens with different separations between F1 and F2. An increase in separation turns out to have a powerful influence on the ants' behaviour, suggesting a model of how snapshot memories might combine. Our hypothesis assumes that ants are guided primarily by snapshots stored at F1 and F2 and perhaps on the direct route to these places. But there is an alternative possibility according to which the rotating vector results from a slow change in a learnt route. In the earlier experiments, ants were free to move wherever they wanted within the arena after the food had been switched from F1 to F2. Because the ants were unconstrained, they may have augmented their original F1 route with a new route segment from F1 to F2, before gradually learning to take a more direct path from the start to F2. In an attempt to distinguish experimentally between these possibilities, we also trained ants to F2 in a manner that restricted where they could acquire landmark information.

Materials and methods

Ants

Queen-right colonies of wood ants (*Formica rufa* L.) were housed in the laboratory and maintained on a diet of sucrose and crickets. For experiments, a small group of foragers was marked individually with coloured paint. These experimental ants were taken from the nest to the experimental arena where they could find sucrose solution. After their foraging run in the arena they were collected and returned to the nest. Within a few minutes, replete ants had passed on the contents of their crop to nest mates and were then ready for another foraging trip.

Apparatus

Experiments were performed within a rectangular arena (270 cm×480 cm) surrounded by floor to ceiling white curtains and illuminated by banks of high frequency fluorescent lights fixed above a false translucent plastic ceiling. Landmarks consisted of large black cylinders (15 cm diameter and 45 cm height or 20 cm diameter and 70 cm height) on the arena floor and large black shapes attached to the curtains that surrounded the arena. The landmarks were kept in the same position in the arena throughout the experiments so that we do not know what roles particular landmarks or other room cues played in guiding the ants.

The floor of the arena 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 paths. Ants frequently missed the feeder by a few centimetres and searched for it with no sign that they were attracted there by scent.

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) had movable optics allowing a high-resolution image of any part of the arena to be captured. Ant position and longitudinal orientation were recorded at 50 Hz (Fry et al., 2000; Graham and Collett, 2002). The ant's path was recorded for a maximum of 6 min. Occasionally, the ant approached so close to a cylinder in the arena that the tracking system 'lost' the ant.

Experimental procedures

Individuals were released at a fixed starting point (Fig. 1) and over a sequence of trials learnt to collect sucrose solution from a microscope slide at a site about 100 cm away (F1). To ensure that ants found the food, on early training runs Perspex barriers were placed to limit the area within which the ant could search. The area enclosed by the barriers was gradually increased and no barriers were required after approximately 10 runs. After about 30 visits to F1, the position of the feeder was switched. The line connecting the feeder and starting point was rotated through 45° or 90° so defining the position of a second food site (F2). The last three to five visits of each ant to F1 were recorded and these paths are referred to as 'runs to F1' in Figs 2, 4 and 6.

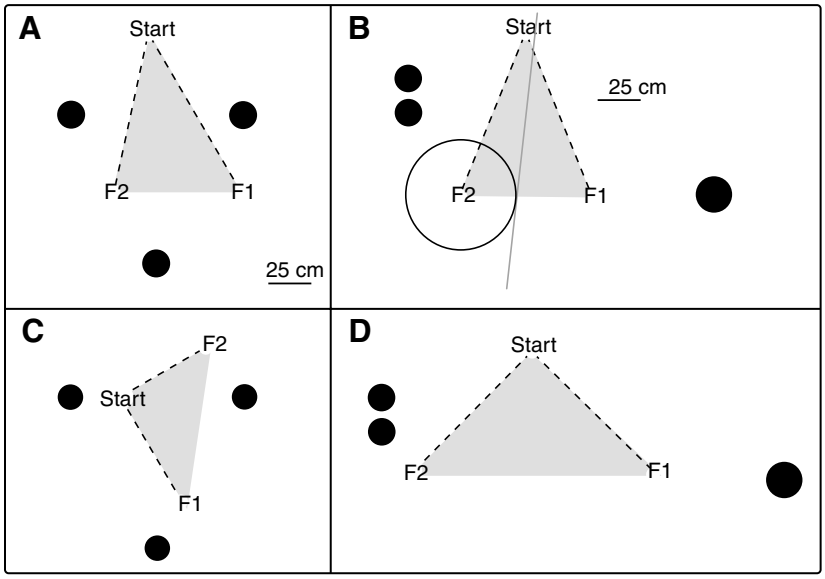


Fig. 1. Experimental arrangements. (A–D) The positions of food sources (F1, F2), the start and local landmarks are shown for the different experimental configurations. Landmarks were black cylinders approximately 45 cm in height. (A,B) The direct paths to F1 and F2 from the start are 45° apart. The configuration in B was used for two experiments: restricted and unrestricted training. The grey line and circle represent the barrier and metal ring used to prevent access to F1 during 'restricted training' to F2. (C,D) The direct paths to F1 and F2 from the start are 90° apart.

In a first experimental protocol ants continued to start from the same position after the food location had been switched from F1 to F2. On training runs immediately after the switch, ants searched near to F1 and sometimes found the feeder at F2 without help. But, if an ant failed to reach F2 after 6 min search, we encouraged the ant to walk towards F2 by tapping the floor in front of it. The progress of the ants' changing route was followed by recording as many as possible of the food-ward routes after the switch to F2. Further experimental details are given in Durier et al. (Durier et al., 2004).

In a second experimental protocol, the ants' movements were restricted after the feeder was switched to F2. After collection from the nest, ants were not released at the original start position. Instead, they were placed randomly at the edge of an 80 cm diameter metal ring (1.5 cm high), which surrounded F2. The ants' views while approaching F2 were limited to what they could see from positions within the enclosure. After ants had started to feed at F2, the enclosure was removed and then, after feeding, ants tended to return to the original start point, probably learning landmark views along the way. Ants were then replaced in the nest. Previous laboratory studies of route learning by wood ants during homeward routes suggest that views useful on food-ward routes are mostly acquired close to the feeding location (Graham and Collett, 2006; Nicholson et al., 1999). Additionally, the ants' path back to the start was constrained by a long low barrier (1.5 cm high) placed across the arena, which prevented ants from investigating the area between F1 and F2 (Fig. 1B). Ants trained this way could thus learn the location of F2 but had no opportunity to augment or change their original route from the start to F1. In occasional probe tests, ants were released at the original start position without the barrier or enclosure present. To reduce the opportunities for route learning, probe tests were separated by five or 10 training runs. In some experiments with restricted training, the positions of F1 and F2 were reversed. In the figures the trajectories of the reversed experiments have been mirrored so that the data from all the experiments can be pooled.

Results

Changing routes with unrestricted training

We began with a replication of the experiment reported in a previous study (Durier et al., 2004). We used a different landmark array to avoid placing landmarks either between F1 and F2 or close to the direct path from the start (S) to either F1 or F2 (Fig. 1B). Before the switch of the food position to F2, paths were straight to F1 (Fig. 2A). With increasing experience of F2, the initial direction of the paths rotated gradually towards F2. The direction of this initial segment of the trajectory was defined by the direction of a line between the start and a point on the path, 60 cm from the start. The headings were then categorised as falling within one of four sectors: towards F1, towards F2, intermediate between F1 and F2, or other. By about 20 trials after the switch most initial segments were intermediate (Fig. 2B). It then took about 30 trials before the majority of initial segments fell within the F2 category. The distribution of initial headings across all trials after the switch is shown in Fig. 2C.

The gradually rotating initial segment suggests that an attractor associated with F2 becomes stronger relative to that of F1. Further evidence for the strengthening of the F2 attractor is the finding that the initial segment was often followed by a distinct turn towards F2, and with increased experience of F2, the first section became shorter (Fig. 2C) (Durier et al., 2004), with ants turning towards F2 sooner. One methodological consequence of this trend is that, with increased experience, our measure of initial headings may include portions of the trajectory after the ant has turned towards F2.

The relative weakening of an F1 attractor with increasing experience relative of F2 is also suggested by a progressive drop in the amount of time spent searching close to F1 (Fig. 3A). After about 10 runs, ants that still arrived close to F1 no longer searched there, but instead headed directly towards F2. A re-analysis of the data from Durier et al. (Durier et al., 2004) reveals similar behaviour (Fig. 3B).

Routes after restricted training

Does the gradual rotation of the initial segment reflect a relative increase in the attraction of the F2 site or a gradually

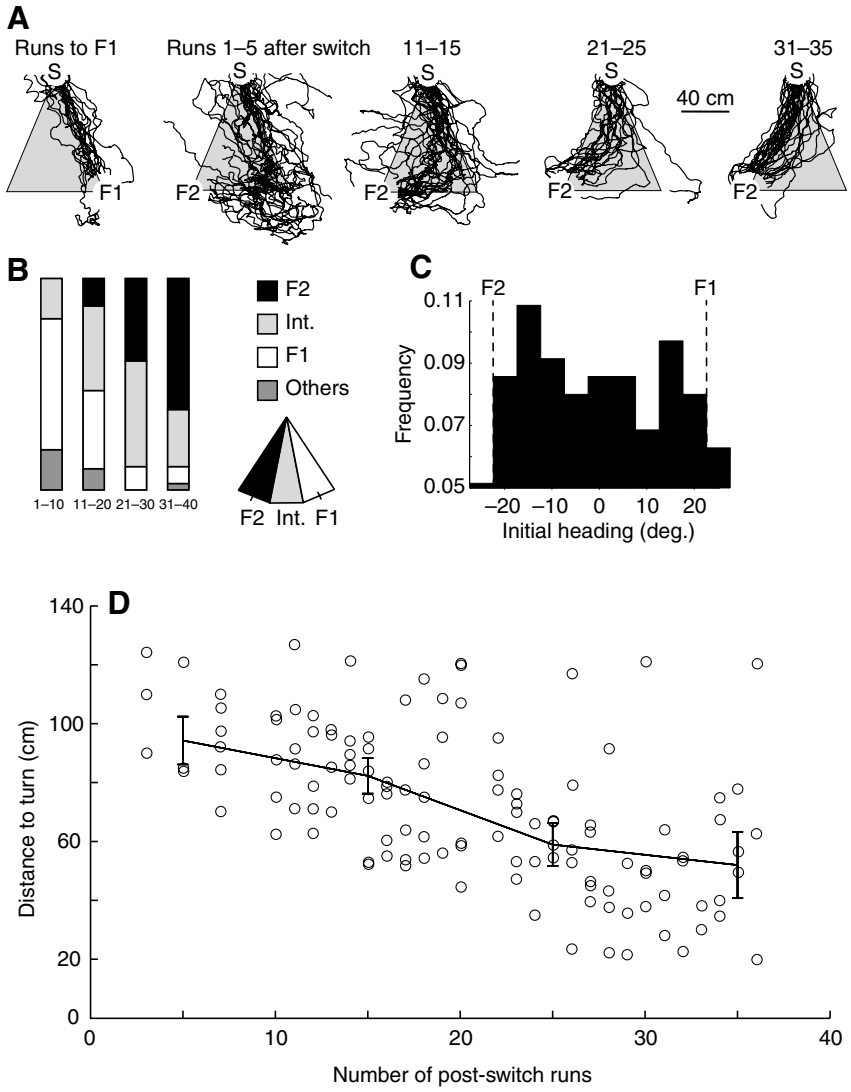


Fig. 2. Gradual change in trajectories with 45° separation between F1 and F2. (A) The trajectories of ants (N=6) after the feeding site was switched to F2. Paths are grouped by run number. The grey area is the triangle with vertices S, F1 and F2. (B) The initial direction of each path was categorised as F1, F2, intermediate or other. The first three categories are 22.5° wide as shown in the legend. The 'other' category represents trajectories that fall outside this range. Stacked bar charts show the change in proportions of each category with run number (N=6; n=32, 60, 46, 37). N, number of ants; n, number of trajectories. This convention is followed throughout. (C) Distribution of headings for all post-switch trajectories (N=6; n=175). (D) Scatter plot showing the change in length of the initial segment plotted against number of trials after the switch. The length of this initial segment was defined by the distance between the start and the location of the first obvious turn determined by eye. Independent observers agreed closely on the presence and location of the first obvious turn in a trajectory. Bars show means and 95% confidence intervals for bins of 10 runs, as in B. The ratio of trajectories containing distinct turns was 100%, 92%, 88% and 56%, respectively, for the four bins.

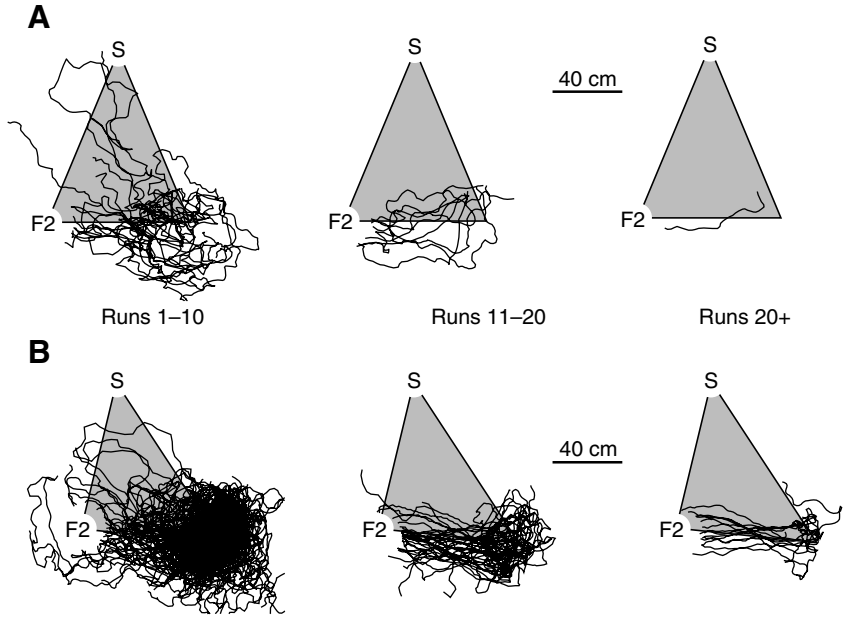


Fig. 3. Paths after reaching F1. Paths after the switch are shown from the point where ants have reached within 20 cm of F1 until the ants reach F2 or the end of the recording period. Trajectories are grouped according to the number of trials after the switch. (A) Experimental configuration as in Fig. 1B. Trajectories are from six ants and the proportion of trajectories that reached within 20 cm of F1 were 58% (runs 1–10), 17% (runs 11–20) and 3% (runs 20+). (B) Experimental configuration as in Fig. 1A. Trajectories are from 20 ants and the proportion of trajectories that reached within 20 cm of F1 were 81% (runs 1–10), 32% (runs 11–20) and 13% (runs 20+).

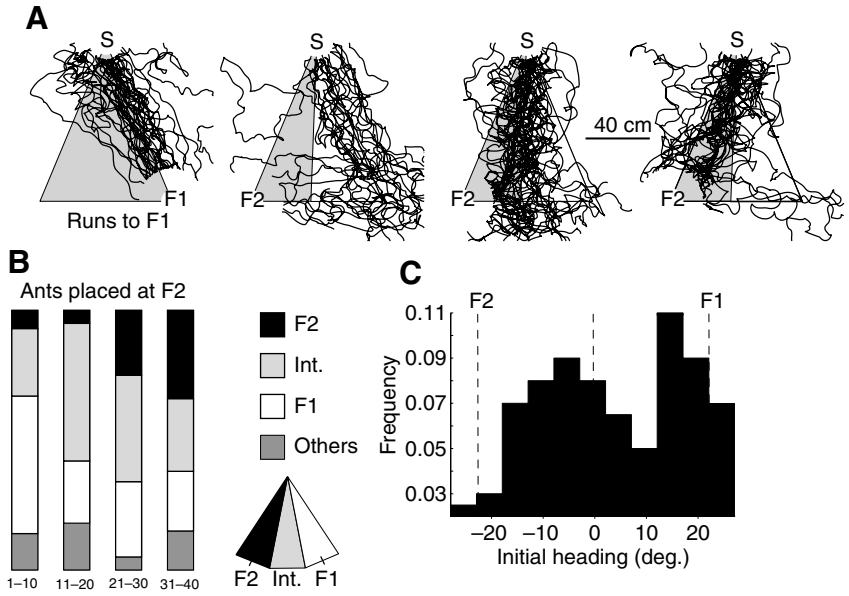


Fig. 4. Change in trajectories of ants with restricted training. (A) The trajectories of ants (N=30) during the final training run (left) and in probe trials after the food position has been switched to F2. Paths are grouped by initial heading (F1, intermediate and F2, respectively). A barrier (Fig. 1B) prevented access to the white region of the arena during post-switch training runs. (B) As in Fig. 2B, trajectories are categorised by their initial heading and grouped by run number. The groups contain 29, 40, 41 and 53 trajectories, respectively. (C) Distribution of initial headings for all probe trials after the switch (N=30; n=153).

evolving route? We approached this question by taking ants that had acquired a route to F1 and training them to F2 by releasing them in an enclosure surrounding the new feeder, so preventing any gradual evolution of a route to F1 into a route towards F2. After feeding, the enclosure was removed and ants could return to the start, with a low barrier placed to stop them approaching either F1 or their previous route to it (Fig. 1B). We performed occasional probe tests to examine how the existing F1 route interacted with the ants' growing knowledge of F2. Ants, in these tests, were released at S with no food in the arena. As the ants' experience of F2 increased, the directions of their initial segments still rotated towards F2 (Fig. 4A,B), suggesting again that gradual changes in the ants' initial headings may be due to a change in the weighted average of the F1 and F2 memories, rather than incremental changes to their route. There are, however, some differences between unrestricted and restricted training. With restricted training ants were more variable in their speed of acquisition of the new route (not shown), and there was also a tendency (Fig. 4C) for the directions of outward paths to be bunched just anticlockwise of the position of the barrier (central broken line).

By preventing ants from visiting certain areas of the arena during training we can also be sure that if they are attracted to

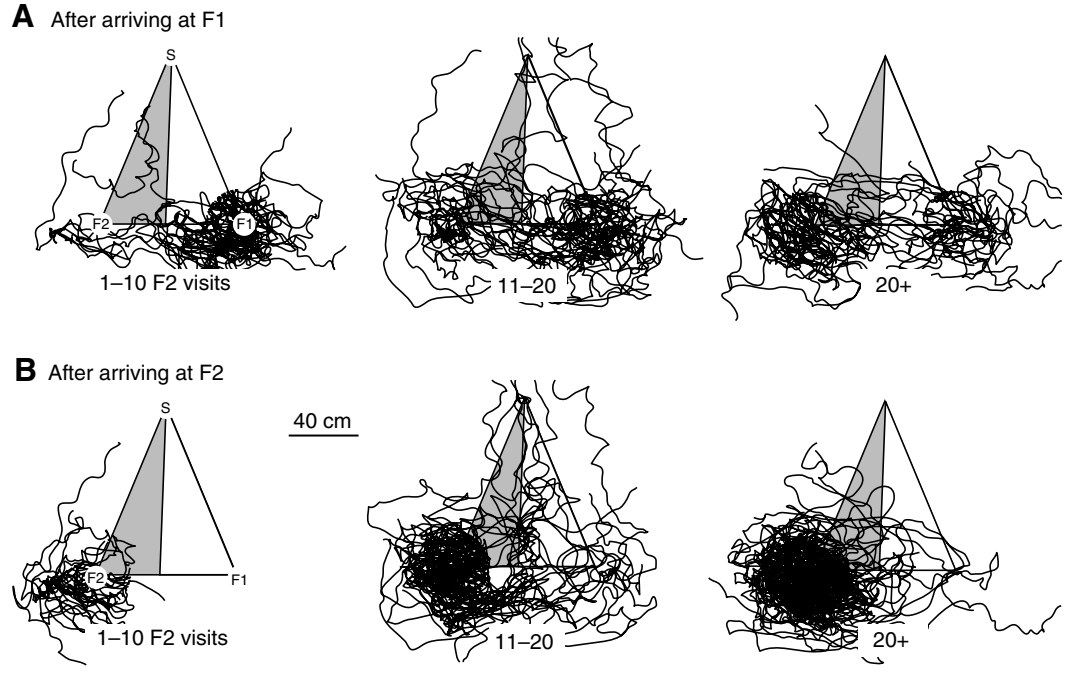


Fig. 5. Paths of ants with restricted training, after reaching F1 or F2. (A) Probe tests grouped according to the number of training trials after the switch to F2. Paths are shown from the point where ants reached within 20 cm from F1. Trajectories are from 30 ants and the proportions of trajectories that reached within 20 cm of F1 were 68% (runs 1–10), 47% (runs 11–20) and 40% (runs 20+). (B) As above, for test runs that reached within 20 cm of F2. The proportions of trajectories that reached within 20 cm of F2 were 34%, 86% and 81% for the three groups.

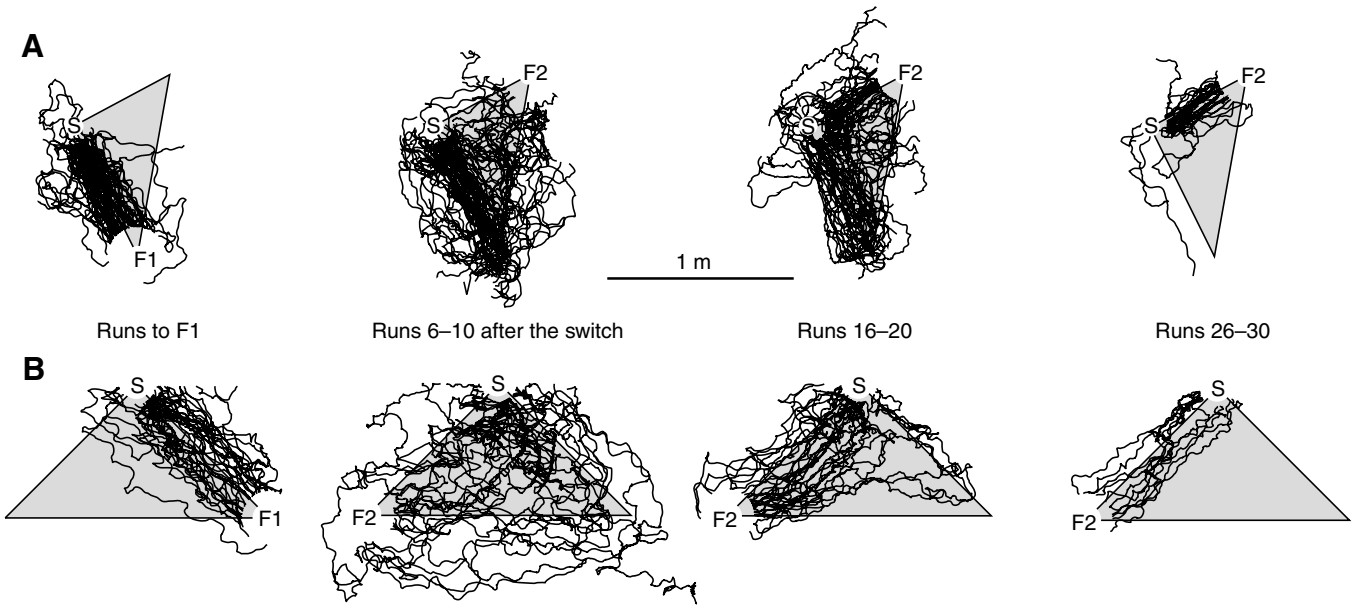


Fig. 6. Trajectory change with 90° separation between F1 and F2. Trajectories at the end of training to F1 and at different periods after the switch to F2 are shown for two groups of ants for which the direct path to F2 was rotated by 90° from the direct path to F1. (A) Experimental arrangement as in Fig. 1C. (B) Experimental arrangement as in Fig. 1D.

a food site across such a forbidden region, they cannot be following an acquired route to the site. Ants with restricted training, behaved like unrestricted ants in that after they reached a region close to F1, they turned towards F2, despite never having travelled that path before (Fig. 5).

Ants with restricted training also resembled normally trained ants in the way that their search at F1 or F2 changed with increased experience. The duration of their search at F1 became gradually shorter and at F2 longer (Fig. 5). As a measure of total search time we took the time spent within 20 cm of F1 and F2. With experience, the proportion of total search time spent at F2 relative to that at F1 increased significantly (runs 1–10: 29±43%; runs 11–20: 73±33%; runs 20+: 77±38%; Mann–Whitney (1–10 *versus* 11–20): U=603, Z=–4.8, $P \ll 0.005$; Mann–Whitney (11–20 *vs* 20+): U=1271, Z=–0.9, P=0.4). Since ants were prevented from visiting F1 during training to F2, and so could not have learnt to avoid F1, the effect is more likely to be attributable to an increasing attraction to F2 than to a reduction of their attraction to F1.

Routes with an increased distance between F1 and F2

With an increase in separation between F1 and F2, there was little sign of a smooth rotation in the direction of the initial segment between F1 and F2. We performed two experiments with a 90° angle between the straight routes to F1 and F2 (Fig. 1C,D). Ant trajectories with this training (Fig. 6) show two major differences from experiments with a 45° separation. First, ants switched more abruptly from heading to F1 to heading to F2, and secondly, the changeover occurred sooner.

These differences can be seen more clearly in Fig. 7, which shows separately for each ant the direction of its initial segment plotted against trial number after the switch between food sites. An ant's changeover point from going to F1 to going to F2 was taken as the first run with a trajectory towards F2. This changeover point occurred after 23±6 (mean ± s.d.) trials in ants trained with a 45° separation (Fig. 7A) and after 13±6 trials when the separation was 90° (Fig. 7B; *t*-test, d.f.=33, t=5.2, $P \ll 0.005$). The duration of the changeover was defined as the number of trials between the last run towards F1 and the changeover point. It was 14±6 (mean ± s.d.) trials when the separation was 45° and 4±4 trials when the separation was 90° (*t*-test, d.f.=33, t=5.7, $P \ll 0.005$).

Discussion

By studying the changing routes of wood ants as they switch from visiting one foraging site (F1) to visiting another (F2), we can see how the major properties of the changeover can be described in terms of a shifting balance of control by two sets of spatial memories, one which attracts an ant to F1 and a second which attracts it to F2. Experiments in which ants were prevented from learning a direct path between F1 and F2 show that an ant approaching F1 can be drawn from there to F2 in a novel direction across an area of the arena from which it had previously been excluded. These experiments suggest that when the ant switches direction and approaches F2, it has engaged attractors associated with F2.

The ants' paths reveal that they can switch both from F1 to F2 (e.g. Fig. 5A) and in the reverse direction from F2 to F1 (e.g. Fig. 5B). This switching implies that over the time course of these experiments the memories of both sets of attractors are retained and some selection or priming process determines which set of attractors is dominant. The intrinsic strength of a memory can therefore be divorced from whether that memory

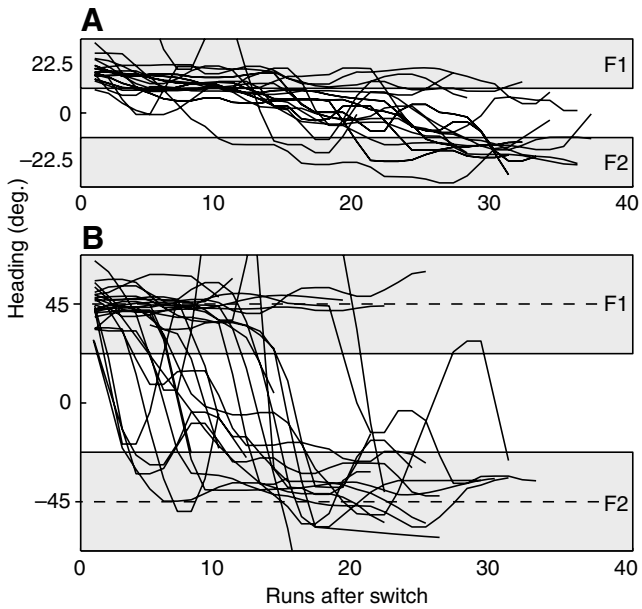


Fig. 7. Time course of changes in the direction of the initial segment. (A,B) The change of initial heading with experience is shown for individual ants after a 45° switch (A) or a 90° switch (B) between F1 and F2. The trace for each ant is a smoothed version of the raw headings using a median filter (window size, three runs). In A and B the upper and lower shaded areas represent the ranges over which headings are categorised as F1 and F2, respectively.

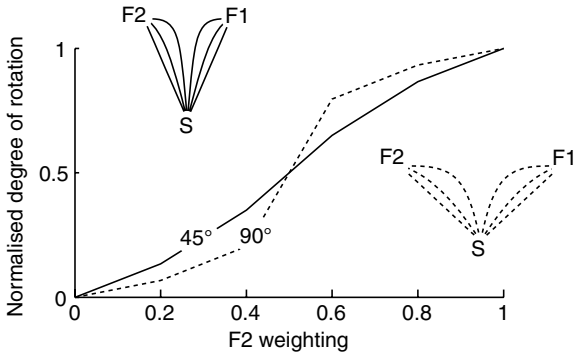


Fig. 8. Paths simulated by averaging weighted vectors. Insets show sets of simulated trajectories for food sites 45° apart (top left) and 90° apart (bottom right). The food was 100 cm from the start. Within each cluster, trajectories are shown for different weights of F2 (0 to 1 with increments of 0.2). The normalised headings of these trajectories after 80 cm are plotted. A normalised heading of 0 is directly toward F1 and a normalised heading of 1 is directly toward F2.

exerts control over the insect's behaviour, as is clearly the case for honeybees selecting between different familiar food sites (Greggers and Mauelshagen, 1997; Menzel et al., 1996). The duration of an ant's path to F1 or F2 and its search there indicate that neural states corresponding to activated attractors last for many 10s of seconds.

By adjusting which attractor currently controls their behaviour, ants can generate a large variety of routes. We focus here on the finding that, while ants learn to change from approaching F1 to approaching F2, the initial segments of their paths are directed between F1 and F2, provided that F1 and F2 are relatively close together. These intermediate headings suggest that the two sets of attractors are engaged at the same time and we would like to be able to explain in more detail how these intermediate trajectories might come about. Hints to possible explanations come from the very different time course of learning between the smaller and large spatial separations between F1 and F2. When the angle between F1, the start (S) and F2 was 45° the ants' initial heading gradually rotated, over about 25 trials, from pointing at F1 to pointing at F2. When the angle was increased to 90°, the switch was more abrupt with few if any intermediate trajectories (Fig. 7).

One way to think about this difference is in terms of vector addition (Collett et al., 1996). If ants are attracted at each point along their trajectory to both F1 and F2 and if their chosen direction is a weighted average of the pulls of the two attractors, then the resulting trajectories (Fig. 8) resemble, to some degree, the pattern of results seen in Figs 2 and 6. We simulate this process by supposing that at any point an ant has two unit vectors, mediated, for instance, by the co-activation of snapshot attractors. One vector points at F1 and the other at F2. The relative strengths of the two vectors co-vary such that their combined weights always sum to unity, and in the simulation (Fig. 8) the relative weights remain constant within a trajectory. The direction of movement of each step is determined by the average of these weighted vectors. The process is repeated step by step until the ant reaches F1 or F2.

If at the start F1 and F2 were in opposite directions, the average vector would always point at F1 or F2, whatever the relative weighting. The clustering towards F1 or F2 is less severe when the angle between the headings is less than 180°. In the 45° and 90° cases shown in Fig. 8, the clustering is slight at the start but increases as the trajectory progresses. Weighted vector addition accounts nicely for the initial intermediate headings followed by a turn towards the dominant attractor. However, it can only account for the ant turning to F2 after reaching F1 (Fig. 3), if one supposes that the relative weighting of the attractors changes during the trajectory. But vector addition is not an adequate explanation of all our results, because it fails to account for the lack of intermediate directions when F1 and F2 are 90° apart.

For a possible explanation of the lack of intermediate headings with 90° separation between F1 and F2, we consider in more detail how directional attractors may be implemented. We suppose that ants acquire directional views at various points along their route and when at, or close to, the feeding sites. In ants, stored directional views seem to consist of visual features, such as oriented edges (Judd and Collett, 1998), that are encoded retinotopically (Cartwright and Collett, 1983; Judd and Collett, 1998). To use such snapshots for guidance, it seems likely that features in the snapshot are paired with features in the current scene and that the positional discrepancy between paired features generates a movement signal that acts to reduce the discrepancy (e.g. Lambrinos et al., 2000).

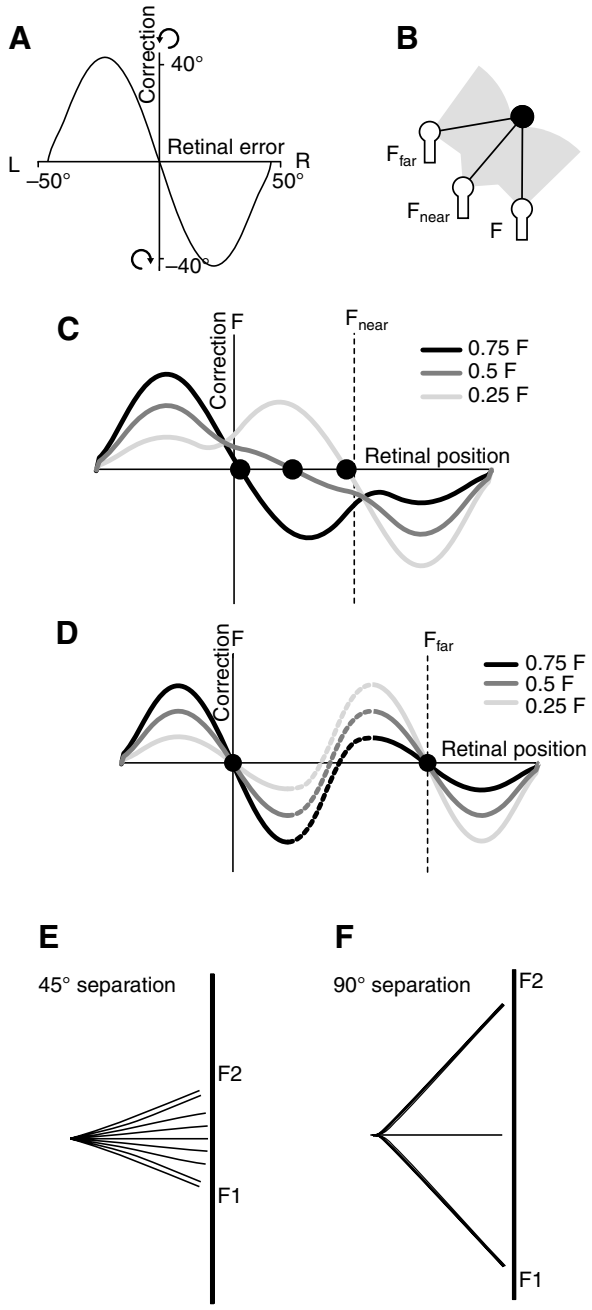


Fig. 9. The summation of feature attractors. (A) Hypothetical attractor in which retinal error is converted to a yaw force of the ant. (B) At three different goal locations (F, F_{near} and F_{far}) the stored retinal position of a local landmark, or, equivalently, equilibrium point of an associated attractor, will vary. (C,D) Weighted averages of attractors. If two attractors from snapshots taken close together (e.g. F and F_{near}) are averaged across retinal position (C) then the resulting combined attractor has a single equilibrium point that moves as the relative weightings change (solid circles). If the two attractors come from snapshots taken far apart (F and F_{far}) then the resulting combined attractor (D) has two stable equilibrium points (at F and F_{far}) that do not move as the weighting is changed. The zero crossings between the two equilibrium points (dashed portion of the attractor curve) are unstable as turns are away rather than towards the zero point. (E,F) Simulated routes to two feeders using spatially limited attractors of different weights. Further explanation is given in the text.

One problem in pairing an edge in a scene to the corresponding edge in a snapshot is that a cluttered scene may contain several edges that might potentially be matched to the same edge in the goal snapshot. A possible means of reducing the chances of mis-pairing edges is to limit the retinal distance over which pairing can occur, so that edges are only matched if the edge in a scene falls within a limited catchment area either side of a stored edge. The lack of interaction between widely separated goal snapshots becomes easy to appreciate, if one envisages the catchment area of each feature in the goal snapshots to be an attractor. Suppose that the retinal error (desired feature position – current feature position) produces an output that causes the ant to move so as to bring the feature towards the stored position. The output of the attractor is zero when the current feature is at the stored position, or equilibrium point, and increases with retinal error (Fig. 9A). Attractors from two snapshots that encode the same landmark feature will add in different ways according to the angular separation between them. If the separation is less than the distance between the peaks and troughs of the attractor, then the equilibrium point of the superimposed attractors shifts between the equilibrium points associated with each attractor, as their relative weightings change. This behaviour (Fig. 9C) fits with the gradual rotation of initial headings when ants are trained with a 45° separation between F1 and F2.

If the separation between the equilibrium points of the two attractors is greater than the distance between the peaks and troughs, superimposition of the attractors yields two stable equilibrium points which are fixed in position (Fig. 9D). Varying the relative weighting of the two attractors only alters the gradient of the composite attractor. The gradient is steepest at the equilibrium point associated with the more strongly weighted attractor curve. This equilibrium point is therefore more stable making the system more likely to move the feature to that point.

If the separation between the equilibrium points is roughly equal to the distance between peaks and troughs, the behaviour is similar, except that when the two attractors are activated in roughly equal proportions, the peaks and troughs cancel so that there is no obvious equilibrium point. This condition seems to fit the behaviour of ants trained with a 90° separation between F1 and F2. The exact form of the attractor does not alter the qualitative behaviour we have described. So long as attractors are of limited spatial extent, widely separated co-activated attractors, sensitive to the same feature, are independent and will not interact to generate intermediate equilibrium positions.

To test whether spatially limited snapshot attractors will generate the different patterns of initial segments found with the 45° and 90° separations between F1 and F2, we simulated routes in a simple visual environment. We have recently developed a model of memory retrieval and use to account for the routes that ants take to a feeder at the base of a single wall-

like landmark (Harris et al., 2007). According to this model, ants store the retinal positions of the vertical edges of the landmark at several points along their route to the feeder. At each acquisition point they link the stored retinal positions of the edges to the perceived angular width of the landmark. When ants later perform the route, they continuously measure the angular width of the landmark and retrieve the associated edge positions. They then move forward keeping the edges imaged on their retina as close as possible to the desired retinal positions. This model produces routes that match closely those of real ants in a variety of experimental tests.

For the simulations in Fig. 9E,F, such sequences of linked memories were stored for routes to two feeder positions at the base of the landmark that were either 45° or 90° apart. Each desired edge position was associated with an attractor of limited spatial extent, as illustrated in Fig. 9A. Routes are shown for different relative weightings of the attractors to F1 and F2. The routes match the experimental results (Fig. 7) in that when the separation between feeders is 90°, the paths switch abruptly between feeders for non-equal weightings. The trajectories change direction gradually when the separation between feeders is 45°.

This general style of modelling, with spatially limited interactions, has been used previously to explain saccadic eye-movements to simultaneously presented targets (Ottes et al., 1984). Human subjects tend to saccade to intermediate positions when two targets are close together, but to fix on one or other target when they are far apart. Clearly, more theoretical and experimental work is needed to determine whether this conceptual framework is appropriate for our results.

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