Commentary

Novel landmark-guided routes in ants

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Summary

We review studies in which ants familiar with fixed routes between their nest and a feeding site are displaced from one of these destinations to an unfamiliar site away from the route. Ants can reach their goal from such novel release sites guided by distant landmarks. We suggest that an ant's ability to take such novel landmark-guided routes after displacement is a by-product of the robustness of normal route-following and is unlikely to reflect the ant's use of a map-like knowledge of its surroundings.

Key words: ant navigation, landmarks, novel routes.

Introduction

Some animals, like chimpanzees, explore widely within a large home range and form a rich spatial representation of this territory that allows them to take novel routes to destinations within it (Menzel, 1973; Menzel et al., 2002). Here, we are concerned with ants that are more limited in what they learn about their surroundings. Ants in general are central place foragers that bring resources back to their nest and so must be able to navigate home after locating food. Foragers of the species that we consider here tend to adhere to fixed visually guided routes, which they follow repeatedly between their nest and a profitable foraging area (e.g. Wehner et al., 1983; Fresneau, 1985; Collett et al., 1992; Wehner et al., 1996; Kohler and Wehner, 2005; Wehner et al., 2006). It seems that the landmark information of these ants is limited to what they have acquired along a route and near their nest. Can they still reach their goal when they are displaced to sites well beyond the paths that they normally travel?

While route-following can be enough for efficient foraging, accidents happen. If ants are to recover from them, they need some capacity to navigate when they have left their usual path. Ants are sometimes blown off their route by sudden gusts of wind, an event that for the Australian desert ant *Melophorus bagoti*, is not uncommon (Narendra, 2007a). A rarer mishap observed by Fourcassié was for wood ants with a nest near a stream to fall into the water when crossing it along a fallen branch (Fourcassié, 1991). The ants managed to regain the bank after drifting a little downstream and then return home (Fourcassié, 1991). Ants in these two examples are carried passively. Active movement away from a familiar route may also occur when, for instance, avoiding a predator. If the ant manages to escape, it may find itself in an unfamiliar place, but this time with the advantage of having reached it through active locomotion.

We review here current evidence that ants can take direct routes towards their goal after experimental displacements, both in a small-scale laboratory environment and in realistic field conditions. Most likely, the ability to take novel routes after large displacements is no more than a by-product of the robustness of normal route-following. We describe some of the mechanisms that may be involved in the performance of novel routes and discuss how analysis of such routes may improve our understanding of guidance along habitual routes.

Path integration

Ants that are displaced passively or move actively to unknown places are in different states. Desert ants, and probably many other ant species as well, perform path integration. This process involves an ant, on leaving its nest, monitoring the directions and distances of the various segments of its path and integrating this information so that it always knows its current distance and direction from its starting point (for a review, see Wehner and Srinivasan, 2003). Because the ant knows its location relative to the nest, it can return straight home after being chased over unfamiliar ground, performing what has come to be known as a home-vector. But, if the ant is displaced passively, path integration is less useful. The home-vector, which relies on information actively acquired prior to displacement, will then lead the ant along a trajectory that is parallel to the path that would normally have taken it from the point of capture to its nest.

In such displacement tests, the distance that an ant follows along this parallel path varies with species and landscape. The

desert ant *Cataglyphis fortis*, which inhabits relatively barren terrain, runs the approximate distance encoded in its home-vector after it has been displaced to another open area (Merkl et al., 2006). *Formica japonica* and *Melophorus bagoti* live in richer habitat with many natural landmarks. When these ants are displaced to a new area and perform a home-vector, the distance that they travel across strange habitat before searching is much shorter than expected [*F. japonica* (Fukushi, 2001); *M. bagoti* (Narendra, 2007a)]. The extent to which an ant is guided by its home-vector may, thus, depend on whether the ant is in a familiar spatial context. Support for this suggestion comes from *M. bagoti* foragers made to travel between their nest and a feeder in an open-topped channel, which occludes most external landmarks but still allows a view of the sky. In contrast to their behaviour on unfamiliar open ground, the ants run complete home-vectors when taken from the feeder and placed in a similar-looking test channel (Narendra, 2007a).

Given that the ant is ignorant of the direction or distance of passive displacement and that chance displacements are likely to be smaller than the home-vector, executing a home-vector after displacement remains the ant's best guess for returning home. There seems to be no evidence that an ant, after completing its home-vector, continues with an upwind search to counter the chance of having been blown downwind, or that it casts across wind to pick up familiar scents. Indeed, *C. fortis* searches symmetrically around the end point of its home-vector (Wehner and Srinivasan, 1981).

Regardless of whether the displacement is active or passive, ants do better if there are familiar landmarks to guide them towards their goal. The examples, which we review, are mostly cases in which displaced ants headed roughly towards their goal from close to the release point and so must be guided by large landmarks that are visible from both the novel start point and their usual route. The paths taken seem to be driven by mechanisms that act primarily to guide ants along familiar routes but that can also steer them after displacement.

Small-scale displacements

Wood ants that are trained in a laboratory arena over a short route from a start point to a feeder will aim directly at the feeder after being released at a novel start point (Durier et al., 2004) (Fig. 1). In this case, the complexity of the environment with multiple landmarks and room cues makes it difficult to work out how the novel routes are guided. A simpler example to analyse is one with ants trained to a route along which they were guided by just a single vertical edge (Harris et al., 2007). The edge was constructed by papering a vertical wall with a brightness gradient that faded across the wall from black at one end to the same white as the background at the other (Fig. 2). To ensure that this gradient landmark was the major source of visual information, the landmark was rotated about a fixed start position between training trials. The ants learnt to run 80 cm directly towards a drop of sucrose that was placed at the base of the gradient landmark, inset 10 cm from its edge. If the ants were displaced to another starting point relative to the gradient
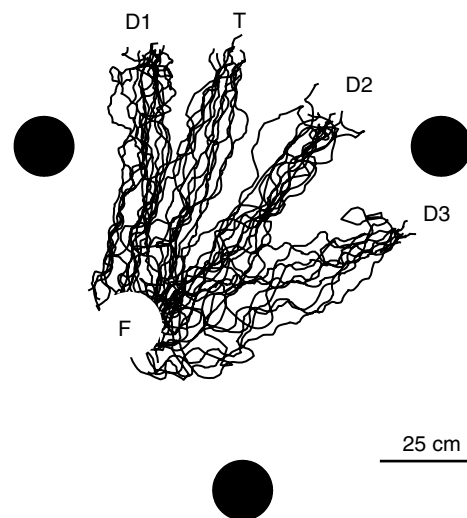

Fig 1. Novel routes of wood ants (*Formica rufa*) to a food site. Ant trajectories are shown from displaced (D1, D2, D3) and training (T) start points. Solid black circles indicate cylinders, and F indicates the food site. Food was removed during these tests [adapted from Durier et al. (Durier et al., 2004)].

landmark, and viewed it from an unusual angle, their route was still aimed approximately at the food (Fig. 2).

From both start points, the edge of the landmark shifts to increasingly eccentric retinal positions as the ants approach the food. Ants' paths in a variety of experimental conditions, including when displaced, can be modelled by supposing that the ant steers its route by keeping the edge at one of a series of desired retinal positions, each of which is associated with the currently perceived width of the gradient landmark (Harris et al., 2007). According to this model, when the ant learns its route, it stores a sequence of memories. Each memory consists of the desired position of the edge linked to the angular width of the landmark at its acquisition point. On later trips, the width of the landmark provides a cue for retrieving the appropriate desired edge position. The ant then moves forwards, with the edge held in that desired position, until it retrieves the next memory associated with a slightly greater apparent width and shifts the edge further into the periphery.

That this same 'look-up' model works to some degree for normal and displaced routes indicates that the guidance mechanism is robust and can still bring the ant close to the goal when errors have been made. It also emphasizes that routes from unfamiliar start positions to a goal can be accomplished using landmark information that an ant acquired while travelling a distinctly different route to that goal.

Large-scale displacements

If a goal is close to a large object, such as a tree, ants have a simple way of guiding themselves to the goal from any direction. They can treat the object as a beacon at which they aim. Santschi displaced ants from a nest close to an isolated

A

120 cm

F

B

F

20 cm

○   ○
Train   Test
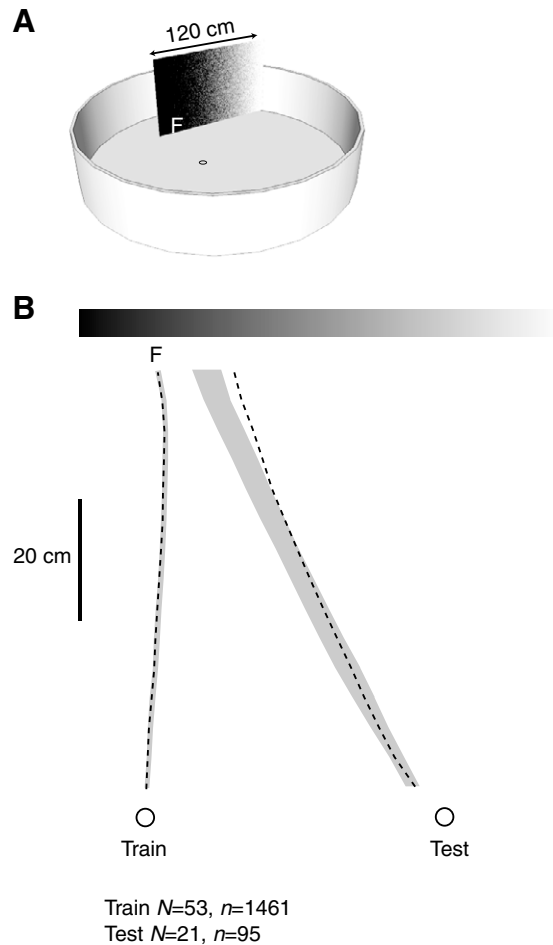
Train *N*=53, *n*=1461
Test *N*=21, *n*=95

Fig. 2. Novel route of wood ants (*Formica rufa*) to a food site. (A) Food was placed at the base of a gradient landmark. (B) The mean path along the habitual route and the mean path from a displaced start point are shown as a grey ribbon whose width represents the 95% confidence interval of the mean path. *N* is the number of ants trained and tested, and *n* is the number of recorded trajectories (T.S.C., P.G. and R.A.H., unpublished data). Line superimposed on the grey ribbon shows the path predicted by the 'look-up' model described in the text and in more detail in Harris et al. (Harris et al., 2007). The paths of the displaced ants and the model do not quite reach the goal. This error is probably caused by the foreshortening of the wall, when seen from an acute angle. Discrepancies between data and model are partly because the ant may switch to a second strategy when it is close to the landmark and becomes unable to assess the overall width of the gradient and partly because of inaccuracies in the model's simulation of the gradient width perceived by the ant.

palm tree and found that the ants headed for the tree from a variety of release points (Santschi, 1913). Similarly, Fourcassié took wood ants (*Formica lugubris*) from a nest-mound adjacent to trees and found that from several release sites ants tended to head in the direction of trees with the highest retinal elevation viewed from the release site, whether or not they were the appropriate trees (Fourcassié, 1991). The radial symmetry of such dominant landmarks makes them recognizable from all directions, and the landmark cues seem to override the use of

any compass-based information associated with the ant's normal route.

In most other cases, the complexity of the environments in which large-scale displacement studies have been conducted makes it difficult to be certain how novel routes are guided. These studies have, however, given impressive examples of novel routes and suggest unexpected interactions between navigational strategies.

Fukushi recorded the homeward paths of another species of wood ant (*F. japonica*) after displacing them away from their familiar route (Fukushi, 2001; Fukushi and Wehner, 2004). The ants' nest was situated conveniently at the edge of a flat-tiled terrace, beyond which was a row of trees (Fig. 3A). Ants were trained to a sucrose feeder on the terrace and they followed an almost straight route over the terrace between their nest and food. Fukushi caught experienced foragers at the feeder and then released them elsewhere on the terrace. The displaced ants had two potential guidance strategies at their disposal. The first was a home-vector driven by path integration, which would lead the ants in a direction parallel to their normal route. The second was guidance by visual landmarks, principally the trees in their frontal visual field. Ants headed neither parallel to the bearing from feeder to nest nor did they aim accurately at the nest site. The errors in the ants' direction had an interesting pattern. The paths converged on a point beyond the nest itself, as though the displaced ants were aiming at some visual feature of the tree line directly behind the nest (Fig. 3A). This conclusion was supported by the directional change caused by obscuring the ants' view of the tree line. According to this interpretation, the ants' novel routes after displacement were guided by a view of the skyline that normally helped direct their accustomed route and suppressed commands from path integration.

What is the role of path integration in routes taken after displacement?

A follow-up study (Fukushi and Wehner, 2004), only part of which we consider here, indicated that the interactions between path integration and landmark guidance may be more complex than simple inhibition of the performance of a home-vector. The ants' homing behaviour when they had a normal home-vector was compared with their behaviour when there was none. As before, ants were taken from the feeder to one of several release sites. Two examples are shown in Fig. 3B. The normal route from the feeder (solid lines) is a straight trajectory as far as the edge of the terrace. The dotted lines are trajectories with a displaced start. The displaced trajectories begin straight but become convoluted towards the edge of the terrace – perhaps because the local view then looked wrong to the ants.

Additionally, on some trials, ants were put in a zero home-vector state by allowing them to follow their normal route home and then catching them just before they reached the nest. When these ants are released, their path integration system indicates that they are already close to the nest. These 'zero-vector' ants also found their way to the nest, but with two intriguing
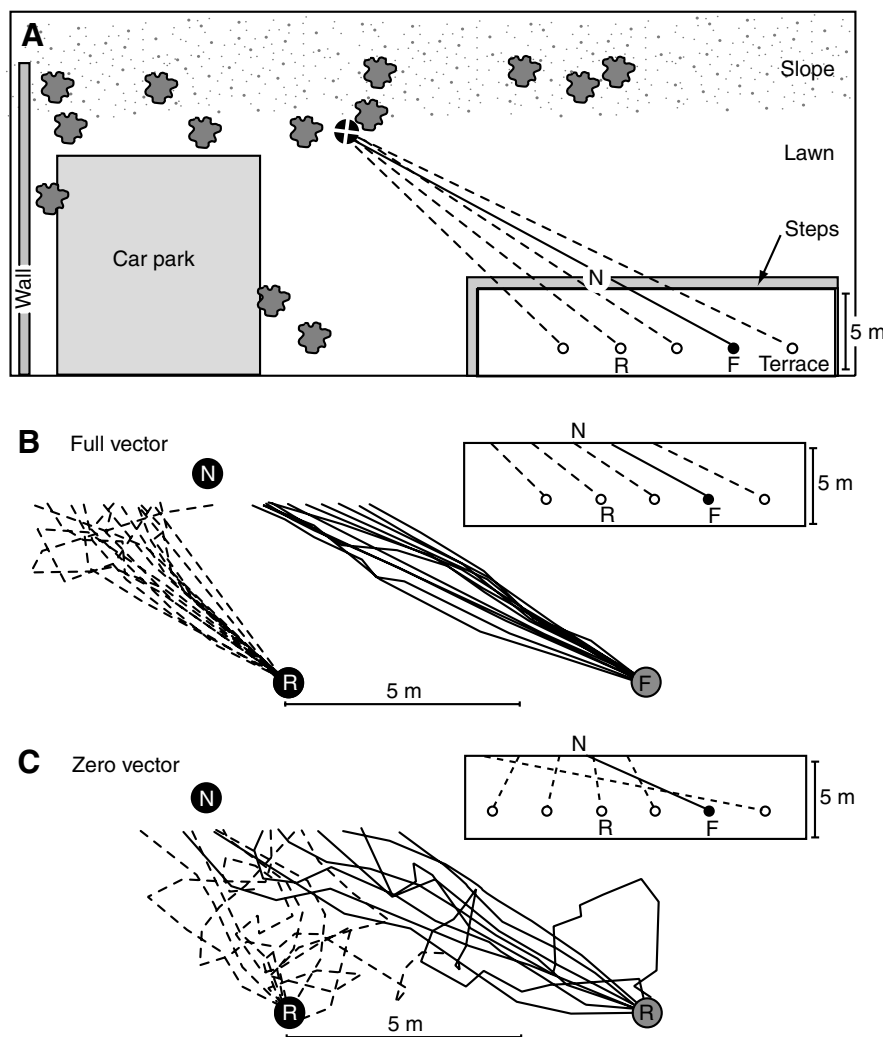
Fig. 3. Homeward routes of wood ants (*Formica japonica*) from a feeder and after displacement. (A) Map of site showing positions of trees behind the nest relative to the terrace. N marks the nest, F the food site and R one of the displaced release sites. B and C show the routes of full- and zero-vector ants, respectively. Inset shows mean directions of the initial part of the trajectories, with B extended in A to indicate the point of convergence. Trajectories from the food site (B) and close to the food site (C) are shown as solid lines. Trajectories from the displaced sites are shown as broken lines [adapted from Fukushi and Wehner (Fukushi and Wehner, 2004)].

differences: first, their paths were more convoluted (Fig. 3C) than when they navigated with a home-vector (see below) and, second, their paths were somewhat better directed at the nest site (inset to Fig. 3C).

Thus, home vectors, when present, seem to influence the direction of novel routes. They could contribute to the ants' choice of direction in several ways. An ant's path could be driven by an additive interaction between a path integration home-vector and attraction by landmarks. The two navigational systems will give conflicting information and so point ants in different directions. If the relevant landmark is a nearby beacon, the resulting path would be curved. The path would first be aimed between the directions of the home-vector and the beacon and would bend increasingly towards the beacon as

the ant approached it and the angle between the home-vector and the landmark's compass bearing grew. Evidence favouring this type of interaction comes from displacement tests in which the directions of the ants with home-vectors differed strongly from zero-vector ants.

A different possibility is that path integration state acts more as a contextual cue and focuses the ant's attention on relevant landmarks along the home vector.

The zero-vector ants in Fukushi and Wehner's tests generated less erratic paths when they were released close to their usual feeding site than when they were displaced to other points on the terrace (Fig. 3C), as though guidance cues were available to them along their normal route but were absent or conflicting elsewhere. These cues could be local visual landmarks, odour cues or directionally dependent views of more distant landmarks. Local vectors that carry ants in a defined direction along their route can be linked to remembered views and triggered when ants recognize those views (Collett et al., 1998). The operation of such local vectors is likely to be disrupted if ants are displaced from their normal route. At unfamiliar release sites, the cues triggering local vectors will often be absent, and, if local vectors are evoked, their direction may be inappropriate.

Whatever the stored information that ants use along their normal route, it enables them to follow that route even when their home-vector points in the opposite direction (Wehner et al., 1996; Andel and Wehner, 2004; Kohler and Wehner, 2005). The rich set of memories available on the habitual route seems to suppress completely the performance of home-vectors. The more convoluted paths of zero-vector ants, when taking novel routes, might in part occur because the available route and landmark memories are sparser. The performance of path integration might then fail to be inhibited completely and ants would be pulled back towards the release site. In summary, path integration state does influence the route that ants take after displacement but it has little direct effect on their normal foraging routes.

Further clues to the interaction between path integration and landmark guidance come from somewhat similar experiments performed on the Australian desert ant *Melophorus bagoti* (Narendra, 2007b). Again, we only consider a small part of this study. *M. bagoti* inhabits a semi-arid terrain with clumps of grass and scattered trees, giving an abundance of small and large landmarks. Ants were trained over about 300 trials along a foraging route, which consisted
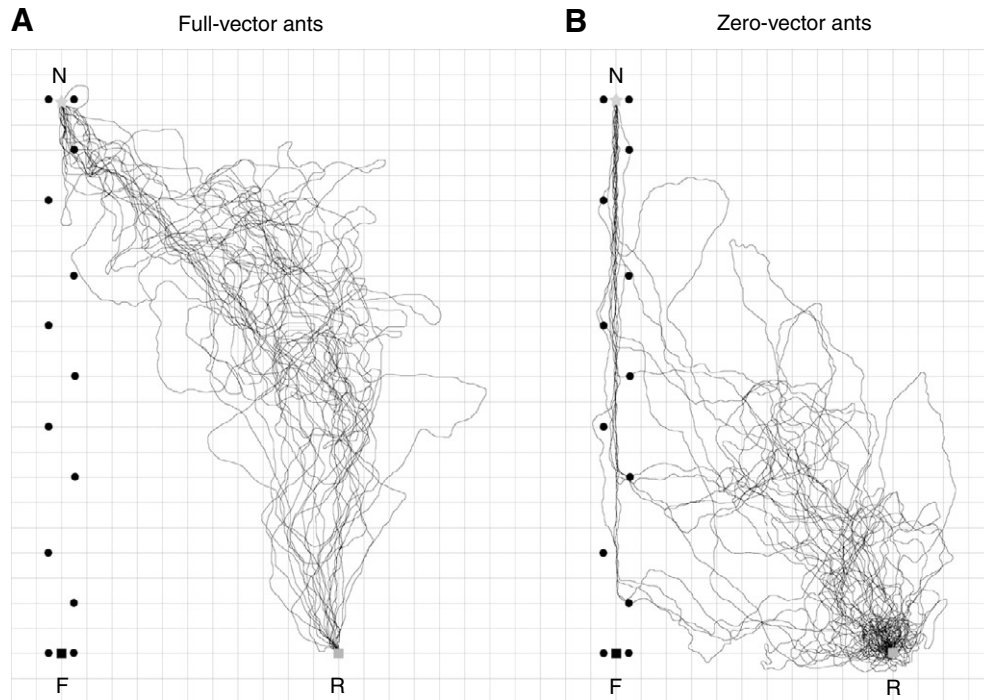
Fig. 4. Homing routes in *Melophorus bagoti* after displacement. A and B show the routes of full- and zero-vector ants, respectively, that have been displaced 10 m from the food site. Ants reach the nest in both cases but they take different routes, and the paths of zero-vector ants tend to be more convoluted. N marks the nest, F the food site and R the release site [adapted from Narendra (Narendra, 2007b)].

of an avenue of cylindrical landmarks connecting the nest to the feeder. After training, ants were displaced with or without a home-vector.

Ants displaced 1.5 or 3 m from the feeder tended to return to the trained route, presumably attracted by the route landmarks. Ants displaced 10 m from the feeder behaved differently (Fig. 4). Over the first 5 m, their paths were roughly parallel to the column of landmarks, although slightly deviated to the nest. The paths then turned in the direction of the nest. To interpret these findings, it helps to know that when these ants are taken from a feeding site to an unfamiliar test area, their home-vectors tend to be half the expected length (Narendra, 2007a). In the 10 m displacement test, the first section of the route seems to be driven predominantly by the home-vector and the second segment by visual landmarks, which are situated at some distance from the turning point and which guide ants to the nest. Although it is very unlikely, it cannot yet be excluded that this second segment of the trajectory is a compromise between ants aiming directly at the nearest route landmark and the direction indicated by the residual home-vector, rather than using distant landmarks to reach the nest site.

Narendra also caught and displaced ants once they had almost reached the nest after feeding and so had little or no home-vector to guide their return (Narendra, 2007b). These ants found their way to the nest, but, like the paths of *F. japonica* with zero vectors, their paths were more tortuous (Fig. 4B), except when they were on their normal route within

the corridor of landmarks. The displaced zero-vector ants searched for a while around the release site and then some ants made for route landmarks, whereas others moved towards the nest. The relatively straight second segments of the full-vector ants, as they head towards the nest (Fig. 4A), are consistent with the residual home-vector aiding landmark guidance. A homeward path integration state could contribute to overt behaviour by focussing the ant's path in a direction that is not too far from the ant's usual homeward route, so that the relevant landmarks will be on the appropriate part of the retina. It could also act internally as a contextual signal that makes the ants attend more strongly to the relevant landmark cues.

Thus, while path integration state manifestly does not have a large influence on the performance of habitual routes, the paths in Fig. 4 hint that contextual effects associated with path integration might nonetheless assist normal landmark guidance in subtle ways. Still, the major and certain conclusions from the novel routes of both *F. japonica* and *M. bagoti* are straightforward. They are that the landmark information guiding ants is detectable at several metres and that landmarks are identifiable from unaccustomed vantage points.

Does large-scale image matching play a role in homing routes after displacement?

In homing by image matching, an ant moves so as to transform the image on its retina to match an image or snapshot

that it has previously stored along its route or at its destination. By decreasing the discrepancy between its current and stored image, the ant travels closer to its goal. Most of the evidence supporting the use of this strategy comes from ants and bees pinpointing the exact position of a goal, guided by landmarks that are close to it (Wehner and Räber, 1979; Cartwright and Collett, 1983; Åkesson and Wehner, 2002; Durier et al., 2003; Graham et al., 2004). But image matching can, in principle, guide insects to a goal over a much larger range of distances. It works robustly with a set of snapshots at different scales, all of which are taken close to the nest (Cartwright and Collett, 1987). A snapshot that encodes distant landmarks, particularly those viewed against the sky (Möller, 2002), can lead an ant over a long distance to the rough neighbourhood of the nest (Cartwright and Collett, 1987; Zeil et al., 2003; Stürzl and Zeil, 2007), from where snapshots emphasizing landmarks close to the nest can take over and bring the ant precisely to the goal.

The results of displacement experiments on the Mediterranean desert ant *Cataglyphis fortis* have been explained in terms of image matching (Wehner et al., 1996). Ants trained to forage at a feeding site 30 m from their nest were caught on their return to the nest and displaced 30 m to one of four sites around the nest (Fig. 5). When the release site was on the normal homeward route, ants searched briefly around the release point, and, once they had found their way out of the bushes, returned straight home. They did much the same, after a longer search, when displaced to a site in the opposite direction, from where they had to travel through terrain that they were unlikely to have explored before. It is impressive that ants continued to find their way home, although by more circuitous paths, when they had to approach the nest from directions perpendicular to their accustomed direction of travel (Fig. 5).

At the start of its foraging career, a desert ant makes a small number of short exploratory trips from its nest in different directions that take it, at most, about 10 m from the nest (Wehner et al., 2004) – a much shorter distance than the displacements in Fig. 5. During these trips, the ant seems to be uninterested in finding food, but perhaps more interested in learning the surroundings of the nest, as in honeybee orientation flights (Becker, 1958; Capaldi and Dyer, 1999; Capaldi et al., 2000). The ant often turns back to look at the nest, perhaps acquiring snapshots at different vantage points while facing in different directions. Since ants mostly walk forwards and emphasize frontal views (Nicholson et al., 1999; Graham et al., 2004), it would assist snapshot matching for ants to take a number of different directional views when near the nest. Ants might also use information derived from path integration to attach local homeward vectors to these snapshots. When an ant later encounters a familiar view during foraging, because for instance it overshoots the nest, it can retrieve the associated local vector.

Once *C. fortis* starts foraging and finds food, it tends to forage in the same direction on subsequent trips (Wehner et al., 1983; Schmid-Hempel, 1984; Wehner et al., 2004), only switching direction if it fails to find food on several trips. Thus, by and large, each ant comes to have a preferred foraging route (Wehner
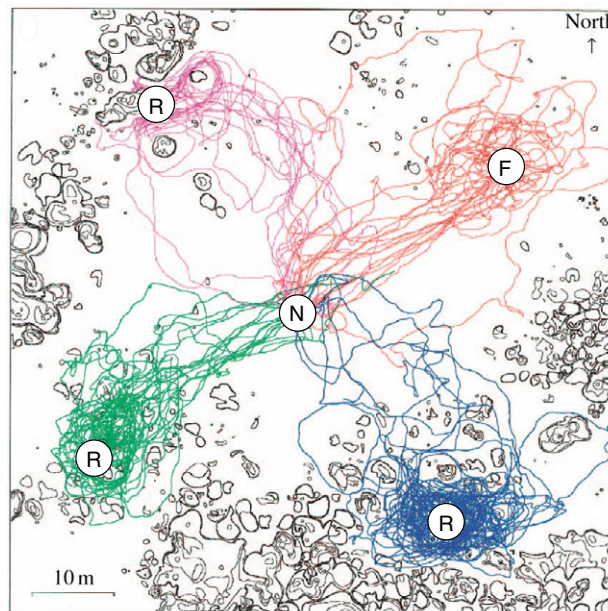

Fig. 5. Homing in *Cataglyphis fortis*. Location of nest (N), feeding site (F) and release points (R) within bushy, desert terrain. Ants that had returned from F to N were displaced from N and released at sites R and F and their paths recorded for 15 min or until they reached within 2 m of N [adapted from Wehner et al. (Wehner et al., 1996)].

et al., 1996) and to learn the appearance of landmarks along it (Collett et al., 1992). In terms of the experiment of Fig. 5, it means that views learnt on the route are likely to be acquired when ants face within a limited range of directions and to be of little help if ants are displaced to sites 30 m perpendicular to the route. The trajectories in Fig. 5 from the three novel release sites are likely to rely on information that was acquired close to the nest, either during initial exploration, when ants stored views while facing in several directions, or later, while the ant was searching for its nest.

Which of the two possible homing mechanisms that we have mentioned, image matching or stored local vectors, do ants employ? The power of image matching lies in extrapolation. Provided that snapshots emphasize relatively salient and distant landmarks, the ant can compute differences between its current and stored images when it is far away from the point of snapshot acquisition. The power of local vectors, on the other hand, lies in their precision and so requires snapshots that can only be retrieved within a small area. It is feasible that displaced *C. fortis* could employ both strategies to home from distances well beyond the nest, starting with the rough directional commands computed from panoramic image matching and, when near to the nest, supplementing them with the more precise local vectors that are attached to more local snapshots.

Conclusions

These few examples show that guidance by large-scale landmarks can occur after displacement over sizeable

distances. Although conclusive evidence is missing, ants probably acquire most of their landmark knowledge while relatively close to the nest or on fixed routes, rather than during wide exploration. Wood ants show long-term fidelity to specific routes (Rosengren, 1971), and Mediterranean desert ants that scavenge for dead insects tend to explore outwards from the tip of a growing route (Schmid-Hempel, 1984; Wehner et al., 2004).

Large-scale landmark information enhances normal route performance in several ways. Distant landmarks can provide directional cues and rough positional information. They can also set the context for the correct retrieval of local landmarks such as tufts of grass (for a review, see Collett et al., 2003). Although such small, local landmarks are easy to confuse, when *M. bagoti* is displaced forwards or backwards on its tussocked route, it continues normally (Kohler and Wehner, 2005), showing that it has little difficulty in identifying where it is released. In addition, panoramic image matching along a regular route could assist path integration in giving a rough directional drive to bridge any hiatus, should local landmarks or local vectors fail to provide continuous guidance.

The study of novel routes in ants has suggested several things about landmark guidance along normal foraging routes. First, it emphasises the importance of relatively distant landmarks in route guidance. Second, it suggests that path integration may play a role during route following. Although visual information and local vectors are sufficient to guide ants normally along their habitual route in the absence of concordant cues from path integration (Kohler and Wehner, 2005), there are hints that an appropriate path integration state makes it easier for ants to recognise or respond to landmarks seen from unusual places. But the details of any synergy between landmark guidance and path integration are sitll to be worked out.

The ant's ability to perform novel routes may be no more than a by-product of the complex guidance mechanisms that allow ants to be robust in following their habitual path and to regain it should they accidentally deviate from it. Recently, there has been renewed interest (Menzel et al., 2005) in the question of whether honeybees might have a richer representation of their environment (Gould, 1986; Wehner and Menzel, 1990) than seems to be the case for the ants discussed here. The studies we have reviewed do not bear directly on this question. But they do sound a note of caution when interpreting results derived from displacement experiments. Novel routes to a feeder or nest need not reflect the possession of 'map-like' spatial knowledge obtained during wide exploration of a home range.

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