# THE GUIDANCE OF DESERT ANTS BY EXTENDED LANDMARKS

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## Summary

Desert ants (*Cataglyphis fortis*) were trained to follow a fixed route around a barrier to a feeder. Their homeward trajectories were recorded on a test field containing a similar barrier, oriented either as in training or rotated through 22 or 45°. Under one set of experimental conditions, the homeward trajectories rotated with the orientation of the barrier, implying that the visual features of this extended landmark can determine the route independently of compass cues: the barrier provided a 'visual scene' that controlled the trajectories of the ants. Under other conditions, the trajectories after rotation were a compromise between the habitual compass direction and the direction with respect to the rotated barrier.

Trajectories were determined primarily by the visual scene when ants were allowed to return close to the nest before being caught and tested. The compromise trajectories were observed when ants were taken from the feeder. It seems that ants exhibit at least two separate learnt responses to the barrier: (i) a habitual compass direction triggered by the sight of the barrier and (ii) a visual scene direction that is compass-independent. We suggest that the weighting accorded to these different learnt responses changes with the state of the path integration system.

Key words: desert ant, *Cataglyphis fortis*, guidance, navigation, landmark, path integration, compass, local vector.

## Introduction

Insects attach a variety of responses to landmarks. They use landmarks as beacons to aim at (von Frisch, 1967; Collett and Baron, 1994; Chittka et al., 1995). They link local vectors to them: flying or walking at a fixed compass direction and/or distance from a particular landmark (Collett et al., 1993; Collett et al., 1996; Srinivasan et al., 1997; Collett et al., 1998; Menzel et al., 1998). They learn to detour in specific ways around landmarks (Collett et al., 1992). They also place landmarks on learnt positions on the retina (Wehner and Räber, 1979; Cartwright and Collett, 1983; Junger, 1991). Some landmarks may have more than one type of response attached to them, and interactions may then occur between these different responses. In addition, there may be influences from other navigational systems, such as path integration. In this paper, we examine the use that desert ants make of a large, extended landmark in reaching their nest and the interactions between responses to this landmark and path integration.

It has long been known that honeybees will learn to fly along the edge of a wood or a lake from their hive to a feeder. They will continue to follow the forest margin or the shoreline in preference to the sky-compass when the hive is moved to a location where the edge of a different wood or lake has a compass direction that is orthogonal to the training situation. Extended landmarks thus seem to be a significant guidance cue that can override the remembered sky-compass direction (von

Frisch, 1967; Dyer, 1987). However, the exact path taken by flying honeybees is hard to monitor, and the details of their trajectories in this situation have not been reported. In this paper, we show the detailed trajectories of desert ants that are guided by an extended landmark.

A second type of landmark response that will be important to the argument we present here is the local vector, which may be attached to a familiar landmark and triggered when the landmark is encountered. Several pieces of evidence suggest that such local vectors are dominant over the global vectors computed on-the-fly using path integration. When a foraging bee encounters a familiar landmark that has been displaced, the attached local vector shifts by the same amount as the landmark displacement (Collett et al., 1996; Srinivasan et al., 1997), even if this leads to a shortening of the total length of the foraging path (Srinivasan et al., 1997). In homing desert ants, a remembered compass-guided local vector that is expressed on passing a landmark will often override (at least temporarily) the homeward global vector (Collett et al., 1998).

We focus here on the interactions between the use of continuous visual cues derived from an extended landmark, remembered compass-driven local vectors and path integration. Ants were trained to reach food placed behind a barrier 10 m long and 50 cm high. As von Frisch (von Frisch,

1967) did in his experiments with honeybees, we rotated the barrier to set up a conflict between visual and compass-based guidance cues. Homeward trajectories were recorded both from ants that were taken from the feeder and from ants that were allowed to return to the vicinity of the nest before being tested. We could thus examine the homeward paths of ants with their path integration system in two very different states. With ants caught at the feeder, the global vector at the release site has the compass bearing of the direction between the food site and the nest. With ants caught near the nest, the global vector due to path integration is close to zero on capture. It remains at zero at the release site and will point back towards the site when the ant walks away. We find that the way in which ants resolve the conflict between visual and compass cues depends upon the state of the global vector.

### Materials and methods

We worked with desert ants from a single nest of *Cataglyphis fortis* during June 1997 in Mahares, Tunisia. The experimental site was a large flat area of sand a few kilometres east of the town that has been used for similar work over the past 30 years (e.g. Wehner, 1970). A 50 cm high, 10 m long barrier made of dark cloth and supported by tent poles driven into the sand was erected 6 m east of the nest. This was the most prominent object in the field of view of the ants and it was larger than landmarks commonly encountered on that terrain. A feeding site, where watermelon could be collected, was established 6 m further east of the barrier (Fig. 1A). Ants were trained to the feeder around the south side of the barrier and they tended to follow the same homeward route, taking the shorter detour.

The homeward paths of individual ants were recorded as they returned to the nest from the feeder. We also caught ants either at the feeder while they were on the melon or on their return, when they were close to the nest, and released them with a biscuit crumb at one of two sites on the eastern side of the barrier. More extensive data were collected on a testing area 300 m to the south where a second 10 m barrier was erected. Ants were taken from the training area, either from the feeder or on their return when they were close to the nest, and released on the test ground near to the test barrier. The paths of the ants were recorded until they began to search (Wehner and Srinivasan, 1981). In some tests, this barrier was oriented north–south as in training. In other tests it was rotated clockwise by 22 or 45 ° from the training orientation (see Fig. 2).

We used the traditional method of recording trajectories (e.g. Wehner and Srinivasan, 1981): a grid of 1 m squares was painted on the sand, and the path of the ant over this grid was transcribed onto 1 cm squared paper. The paths were later digitised. The best-fitting line to a trajectory was computed by the method of principal axes (see page 586 in Sokal and Rolf, 1995). All the trajectories recorded on the test field are shown in the figures. However, the statistical analysis excludes trajectories that were shorter than 3 m. Circular statistics were
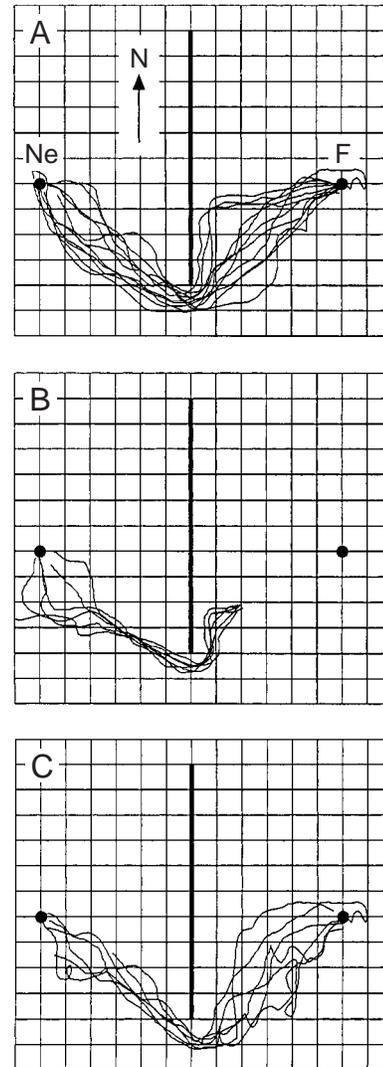


Fig. 1. Homeward paths of ants detouring around a familiar barrier to reach their nest. (A) Uninterrupted paths of ants from a familiar feeder to the nest. (B) Trajectories of ants taken from the feeder to a point 2 m to the east and 2 m to the north of the southern tip of the barrier. (C) Trajectories of ants allowed to return to within 1 m of the nest before being captured and replaced at the feeder. In this and subsequent figures, the barrier is shown by the thickened vertical line. Ne and F indicate nest and feeder respectively. The spacing between grid lines is 1 m. N, north.

used as prescribed by Batschelet (Batschelet, 1981). Directions are measured clockwise with respect to the line connecting the southern end of the barrier to the nest.

### Results

#### *Trajectories to the nest*

Fig. 1A shows sample trajectories, recorded on the training area, of ants returning from the feeder to the nest. In some cases, on leaving the feeder, the ant aimed for the end of the barrier and, after passing it, turned towards the nest. In other

cases, the ant appeared to be guided by path integration. It made for the middle of the barrier, then walked along it, and aimed for the nest when it reached the end. Some ants were less cooperative and climbed over the barrier instead of detouring round it (not shown). For those ants that returned around the barrier, the mean direction of their path over the first 3 m after the barrier was $-5.1\pm11.28\,^\circ$ (mean ± s.d., $N=11$) from the direction between the end of the barrier and the nest.

The initial direction of the path after the barrier was very similar in ants that were carried from the feeder and released at a point 2 m north and 2 m east of the southern end of the barrier ($-7.6\pm4.88\,^\circ$, mean ± s.d., $N=6$, Fig. 1B). When the ant reached the end of the barrier from this starting point, the direction of the vector derived from path integration (the global vector) was calculated to be approximately $12\,^\circ$ less than when starting from the feeder. This predicted difference in direction was not reflected in the trajectories of the ants, suggesting that this phase of their route is a learnt response to the barrier itself. It could be either a local vector that has been associated with the barrier or a direct response to visual features of the barrier.

The supposition that a learnt response is being observed gains support from the direction of the trajectories of ants that have been allowed to return almost to the nest. On their subsequent release at the feeding site, their global vector has the same value that it had at the nest. Nonetheless, the ants followed routes similar to those of ants caught at the feeder (Fig. 1C, c.f. Wehner et al., 1996). The mean direction of their paths after rounding the barrier was $9.5\pm4.98\,^\circ$ (mean ± s.d., $N=6$), whereas, had they followed instructions from path integration, they would have returned to the feeder. Firm conclusions about the controlling

action of the barrier itself cannot be drawn from such results because of the possible influence of other landmarks, and we turn to data collected on the test ground.

### *The trajectories of ants caught near the nest are driven by visual features of the barrier*

Ants returning home after feeding were caught near to the nest and released on the test ground close to a barrier of the same dimensions and orientation as that on the training ground. Fig. 2A shows the trajectories from the end of the barrier. The mean direction of the trajectories shown in the circular histogram below the tracks differs by $4.65\pm8.48\,^\circ$ (mean ± s.d., $N=11$) from the direction of the line connecting the end of the barrier to the nest.

With the barrier rotated either 22 or $45\,^\circ$ towards the feeder, the trajectories rotated by almost the same amount (Fig. 2B,C). Rotating the barrier through $22\,^\circ$ caused a $21\,^\circ$ rotation of the mean direction to $25.65\pm6.01\,^\circ$ (mean ± s.d., $N=9$). Rotating the barrier through $45\,^\circ$ caused a $37\,^\circ$ rotation to $41.67\pm10.03\,^\circ$ (mean ± s.d., $N=28$). These two rotated directions differ significantly from each other (Watson–Williams test, $P<0.001$, $F_{1,35}=20.05$) and from the mean direction without rotation (0 *versus* $22\,^\circ$, Watson–Williams test, $P<0.001$, $F_{1,18}=36.1$).

If the trajectories from the three conditions are superimposed, they are widely dispersed, with a mean direction that differs by $30.29\pm17.51\,^\circ$ (mean ± s.d., $N=48$) from the trained compass direction between the barrier and nest (Fig. 3A). If, however, the trajectories are aligned so as to superimpose the rotated barriers, the trajectories form a single narrow cluster with a mean direction of $-0.81\pm9.76\,^\circ$



Fig. 2. Homeward paths of ants caught near the nest (as in Fig. 1C) and then carried to a point on the test field close to the end of the barrier. Paths are shown beginning where the ants are in line with barrier. (A) Barrier oriented as in training; (B) barrier rotated clockwise through $22\,^\circ$; (C) barrier rotated clockwise through $45\,^\circ$. In this and the remaining figures, the circular histogram below each set of trajectories shows the direction of each trajectory that was 3 m or longer, with the mean direction of the trajectories being drawn as a radius. Here, and in Fig. 4, the filled triangles show the direction of the nest from the end of the barrier and the open triangle shows the bearing of that direction plus the angle through which the barrier was rotated. N, north.
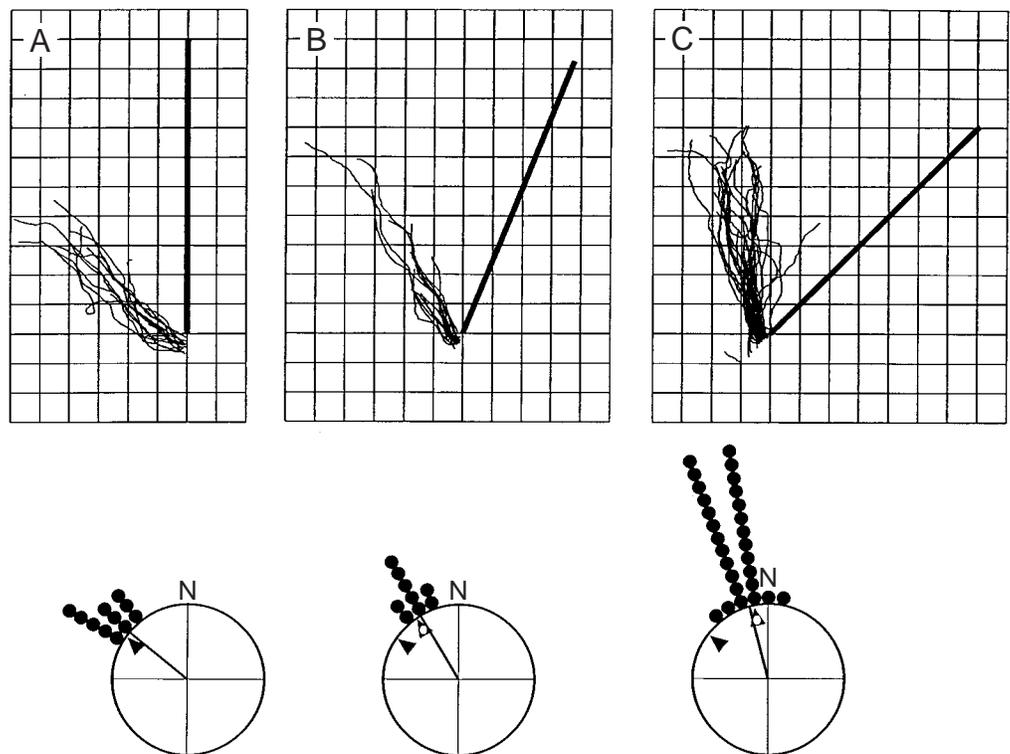
(mean ± S.D., *N*=48) from the trained angle between the barrier and nest (Fig. 3B). The dispersion of these trajectories is significantly less than when the same trajectories are superimposed without rotation (*P*<0.01, $F_{47,47}$=5). The conclusion from these tests is that trajectory direction depends principally on the orientation of the visual scene provided by the barrier and is little influenced by the sky-compass.

### The directions of trajectories of ants caught at the feeder are controlled both by compass information and by visual features of the barrier

Ants taken from the feeder to the test ground behaved differently from those taken near the nest. Their trajectories followed the rotation of the barrier less closely. With the barrier rotated through 22° (Fig. 4A), the mean trajectory direction was 8.01±6.71° (mean ± S.D., *N*=21). With a 45° rotation of the barrier (Fig. 4B), the mean trajectory direction was only rotated to 16.58±12.07° (mean ± S.D., *N*=24). Although the direction of the trajectories with a 45° rotation was greater than those with a 22° rotation (Watson–Williams test, *P*<0.01, $F_{1,43}$=8.15), the difference between the two sets of trajectories (8.57°) was significantly less than the 23° difference in barrier positions (*t*=5.035, d.f.=43, *P*<0.001). We conclude that the paths of ants taken from the feeder are governed by two competing sets of control signals: one stemming from the remembered visual scene provided by the barrier and the other from compass cues.

### Discussion

The major finding of this paper is that, under certain conditions, the visual scene that is provided by an extended landmark controls the direction of the trajectory of the ant with little or no contribution from the sky-compass. Under other conditions, the direction appears to be a compromise between the directions specified by the visual scene and by the sky-compass. Two questions arise from these findings. First, what is the navigational strategy using compass cues that competes with guidance by the visual scene? Second, why should this second strategy be suppressed by the visual scene in one situation, but play a major role in another?

Two navigational systems operate using compass cues and both could influence the path of ants displaced from the feeder. A defined compass direction would be seen either if the ant were to follow commands from its path integration system or if the ant were to perform a local vector that is triggered by the sight of the barrier. Earlier evidence that local vectors often suppress the output of the path integration system suggests that
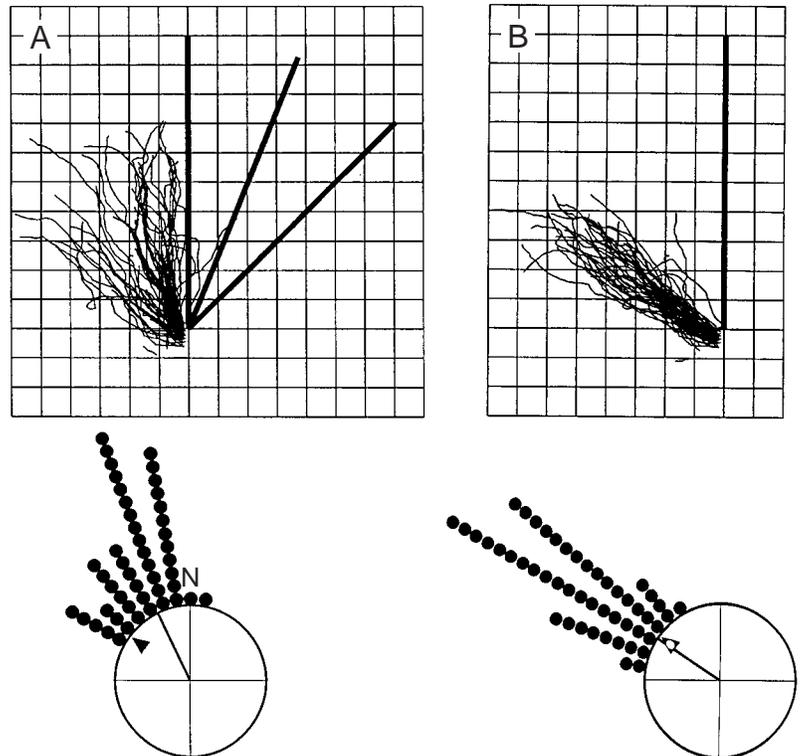


Fig. 3. Trajectories from Fig. 2 superimposed. (A) Superimposition without rotation. The filled triangle shows the direction of the nest from the end of the barrier. (B) Trajectories rotated by 0, 22 or 45° so as to align the barriers. The open triangle shows the predicted direction assuming that the trajectories are controlled by visual cues from the barrier. N, north.
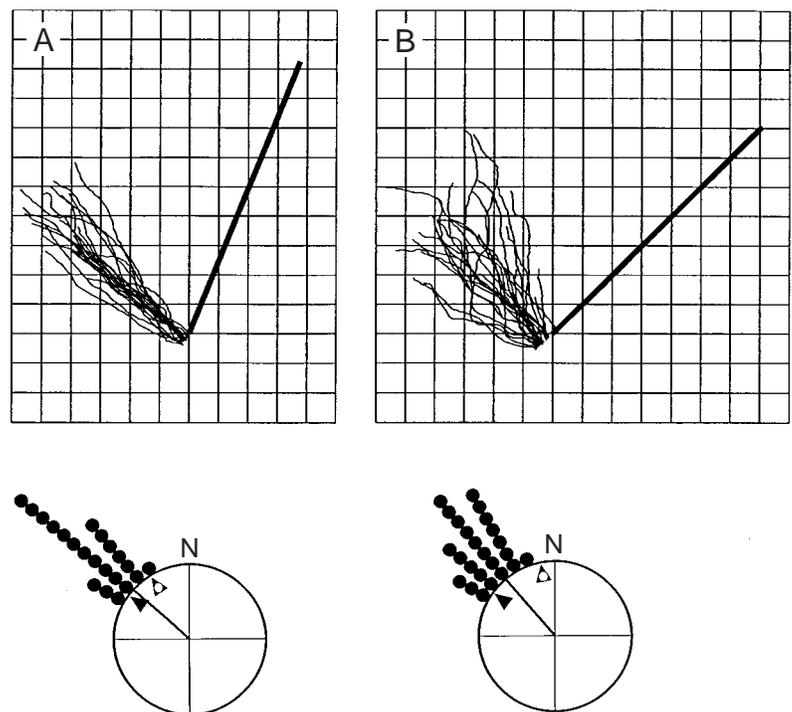


Fig. 4. Homeward paths of ants caught at the feeder and taken to a point on the test field close to the end of the barrier. (A) Barrier rotated clockwise through 22°; (B) barrier rotated through clockwise 45°. For further details, see Fig. 3. N, north.

the second of these alternatives is more likely (Collett et al., 1998). The present results also support this hypothesis: on the training ground, we saw no difference between the trajectories of ants that returned from the feeder and ants that were displaced from the feeder to the barrier. If it is indeed a local vector that we observe, then the compromise must be between these two different landmark navigational strategies.

The present results, with a highly visible extended landmark, suggest a less prominent role for local vectors, and a role that varies with context. We suggest that this context derives from path integration. The trajectories were determined primarily by the visual scene when ants were allowed to return close to the nest before being caught and tested. In this case, the output of the path integration system, the global vector (Collett et al., 1998), points at the release site, and is very different from the local vector associated with the barrier. In contrast, the local vector does appear to influence the ants' trajectories, when the directions of the global and local vectors are more in agreement, as happens with ants taken from the feeder. In other words, a visible landmark will cause a local vector to be ignored, unless the local vector is at least approximately in accord with the global vector. Thus, local vectors are weighted more strongly when the context for their performance is correct (e.g. Bisch and Wehner, 1999). Direct visual responses to landmarks are less critically dependent on the correct contextual cues. The functional argument might be made that the conditions for performing local vectors need to be stringent, because movements attached to landmarks that occur in the wrong context may lead ants away from familiar territory, whereas direct responses to landmarks are less risky because they do not take the insect far from the landmark.

We have shown that desert ants will follow a straight trajectory at an angle to a barrier and that, under certain conditions, when the barrier is rotated, the direction of the trajectory rotates through almost the same angle. Visual features of the barrier can thus control the direction of the ant's trajectory through a process that appears to be independent of path integration. These visual control mechanisms (discussed by P. Graham and T. S. Collett, in preparation), thus appear to lie at the top of a three-layer hierarchy of navigational strategies. The learnt visual response overrides the learnt compass response, the local vector, which in turn overrides the global vector due to path integration. Only when the latter two approximately coincide does the hierarchy partially break down, so that the ant performs a compromise between two types of learnt responses to a landmark. Under normal conditions, the two classes of learnt responses will work synergistically to keep an ant to its preferred route.

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