Local and global vectors in desert ant navigation

M. Collett*, T. S. Collett†, S. Bisch‡ & R. Wehner§

* BBSRC-NERC Ecology and Behaviour Group, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK
† Sussex Centre for Neuroscience, School of Biological Sciences, University of Sussex, Brighton BN1 9QG, UK
‡ Zoologisches Institut, Universität Bonn, Kirchallee 1, 53115 Bonn, Germany
§ Department of Zoology, University of Zurich, Winterthurerstrasse 190, CH 8057 Zurich, Switzerland

Desert ants returning from a foraging trip to their nest navigate both by path integration and by visual landmarks. In path integration, ants compute their net distance and direction from the nest throughout their outward and return journeys, and so can always return directly home from their current location. As the path-integration vector is updated over the entire journey, we call it a global vector. On a familiar route, when ants can steer by visual landmarks, they adopt a fixed and often circuitous path consisting of several separate segments that point in different directions. Here we show that, as in honeybees, such multisegment journeys are composed partly of stored local movement vectors, which are associated with landmarks and are recalled at the appropriate place. We also show that a local vector learnt at one value of the global vector can be recalled at many values, and that expression of the global vector is temporarily inhibited while the local vector is used. These results indicate that the global vector is ignored during navigation through familiar, cluttered territory, but that it re-emerges to take the ant home once the insect leaves the clutter and other guidance strategies cease to operate.

Insects steer by familiar landmarks both when homing normally from a feeding site and if transported there from their nest, using a variety of guidance strategies. Indeed, the complex homeward paths of desert ants navigating through scrub are almost identical under these two conditions, even though the predicted values of the global vector differ greatly. This similarity in homeward routes raises the question of what happens to the global vector during landmark navigation. To find out, we have examined interactions between global and local vectors by presenting ants with experimental situations in which the two predicted vectors point in different directions (Fig. 1).

Desert ants (Cataglyphis fortis) were trained on a flat, sandy area along a two-leg route to and from a feeder (Fig. 1A). The first leg from the nest was over 8 m of open ground. The second leg was perpendicular to the first along a narrow channel 8 m in length that allowed a view of the sky but not of the surrounding landscape. To avoid complications that might be introduced if the channel itself were to be used as a landmark by approaching or departing ants, we hid the channel in a trench, making it invisible to ants more than a few centimeters away. Ants collected food in a compartment at the end of the channel and then returned east along the channel to its exit, from which they walked south to reach their nest.

Trained ants were caught either at the feeding box, where their global vector was directed 11.3 m southeast towards the next (Fig. 1B), or at the end of the return trip to the nest, where the global vector was zero (Fig. 1C). Each ant was then carried to a test area, and released into a feeding box at the end of another channel which was 2, 4, 8 or 11 m long. Here it found a biscuit crumb which it carried along the channel and then homewards across open ground. The value of the global vector on exiting the test channel depends on where the ant was caught and on the length and orientation of the channel (Fig. 1 and Table 1). The postulated local vector, on the other hand, always points south (Fig. 1).

Ants taken at the nest and placed in an east-pointing channel tended to walk in their accustomed southerly direction on reaching open ground (Fig. 2d–f and Table 1). This southward path was not driven by the global vector, for the vector was zero at the release site and increased in a westerly direction as the ant walked east along the channel (Fig. 1C). Once out of the channel, there were no local visual landmarks to guide the ants. We suggest that their path was...
dictated by a local south-pointing vector, which ants had associated with the channel and retrieved on leaving it. The prominence of the local vector depended on the length of the channel. Trajectories on exiting the 2-m channel (Fig. 2f) were shorter than those on leaving the 8-m channel (Fig. 2d) \( (P < 0.05, \text{Mann–Whitney test}) \) and were less well directed.

Is the local vector controlled by compass cues, or did ants simply make a 90° turn to the right on leaving the channel? We tested ants in southeast- and northeast-pointing channels (Fig. 3). Ants that had short global vectors when they left the channel tended to walk southward (Table 1). Thus, the trajectory directions of ants caught at the nest and released into the 2-m southeast-pointing channel (Fig. 3f) or the 4-m northeast-pointing channel (Fig. 3g), or taken from the feeder to the 8-m southeast-pointing channel (Fig. 3a), were significantly different from the global vector and the 90° turn \( (P < 0.01, \text{Mann–Whitney test}) \), but were not different from the local vector \( (P > 0.05, 2\text{-m southeast and 4-m northeast channels}; P > 0.01, 8\text{-m southeast channel}) \). The direction of the local vector was thus determined by compass (probably skylight) information. However, local vectors could be less salient if the global vector is longer and the direction of the test channel differs from that in which ants were trained (compare Fig. 2d and Fig. 3d). In a control test, no directional preferences were seen in the trajectories of ants caught at the nest and released on open ground (Fig. 3h). It seems that ants have associated a compass-bound, local vector with a familiar channel, and that they retrieved the local vector when walking along and exiting that channel.

Whenever local vectors were performed, they were substantially shorter than the distance covered by ants homing in the training configuration (Table 1). Was the local vector short because it carried the ant to small, local features on the training ground that the ant uses as landmarks? To minimize the use of such features, we placed a large \( (44.5 \text{ cm diameter, } 80.5 \text{ cm high}) \) black cylinder just south of the nest. The ants used the cylinder immediately after they left the channel, zigzagging towards it. After 5 days foraging with this cylinder in place, ants were taken at their return to the nest and released in the end of the 4-m east-pointing channel on the test ground where there was no cylinder. Trajectories were neither detectably shorter nor longer than before (Table 1). The lack of any shortening indicates that the vector probably does not encode the distance between the ant’s leaving the channel and its coming under the influence of the cylinder. On the other hand, the absence of an increase in length suggests that the local vector does not encode the distance between leaving the channel and reaching the cylinder (assuming that the subsequent lack of a cylinder on the test ground does not shorten the vector). Instead, the role of the local

**Figure 2** Trajectories of ants 'homing' on the test area after their release at the end of a 2-, 4- or 8-m east-pointing channel. The ants’ paths were recorded from leaving the channel until they had changed direction several times, indicating searching behaviour. a–c, Data from ants collected at feeder. d–f, Data from ants collected at nest. g–i, Means of the trajectories of b, g and h computed by a ‘wave-front’ method. The mean direction of the first 2 m of the trajectories shown in h relative to south \( (0°) \) \( (n = 38, \bar{d} = 6.8°, n = 37) \) is significantly different from that of the same trajectories between 4 m and 6 m from the channel exit \( (n = 30°, s.d. = 13.0°, n = 27) \) \( (P < 0.001, \text{Watson–Williams test}) \). The origin of the global vector (position of fictive nest) is marked with a black circle. Grid lines are 1 m apart.

**Figure 3** Trajectories of ants on the test area after their release at the end of a southeast- or northeast-pointing channel or on open ground. a–f, As for Fig. 2 but with channel orientated southeast. g, Trajectories from ants collected at nest and released into a 4-m northeast-pointing channel. h, Trajectories of ants collected at nest and released on melon on open ground. i, Trajectories of ants collected at feeder after their release into an 11-m southeast-pointing channel.
vector may be to ensure that the ant sets off in the correct direction along a path segment, allowing the ant to view the next set of landmarks from a standard vantage point and orientation. Are local vectors found only in ants that have been confined to channels or are they also associated with other location-specific cues? We trained ants from a second nest to feed at a site 13 m south of their nest along a straight route that was flanked on either side by the feeder and released at the corridor entrance walked down the corridor and continued in the same direction for a few metres after passing the last cylinder. Ants with zero global vector followed a search path before discovering the corridor. They then walked through the corridor and their trajectories also continued beyond its end (Fig. 4b).

The crucial test to detect a compass-based local vector was to shift the orientation of the corridor through 45° (Fig. 4c). Ants caught at the nest were released with zero global vector in a northwest-pointing corridor. After an initial search, most ants (10 out of 17) travelled northwest along the corridor and, on leaving it, turned consistently north. The remainder turned north earlier as though they had retrieved their local vector after passing only one or two of the landmarks. Thus, despite the reorientation of the landmarks, the paths of all the ants eventually pointed north (Fig. 4d). In contrast, ants collected at the nest and released on open ground, clear of cylinders, searched for a long period with no directional preference (data not shown). The ants must have associated a northerly directed local vector with the landmarks.

How do global and local vectors interact? For ants accustomed to the two-leg route, global and local vectors on exiting the test channel always pointed in different directions from each other, apart from in the test condition reproducing training (Fig. 2a). In many cases ants resolved this conflict by transiently inhibiting the expression of the global vector (Table 1). This suppression is best seen with ants taken at the feeder and released in the 4-m east-pointing channel (Fig. 2b). Some trajectories (33%) were directed entirely southeast along the global vector (Fig. 2g), but most trajectories (66%) first pointed south along the local vector and then turned into the direction of the global vector (Fig. 2h, i); the global vector emerges only after the local vector has been performed. Some ants caught at the feeder and released in 2-m east-pointing, 4-m southeast-pointing, or 2-m southeast-pointing channels behaved similarly (Figs 2c and 3b, c), but the proportion doing so was smaller (30%, 47% and 30%, respectively). Local and global vectors are thus not simply combined; instead, expression of the global vector can be inhibited while the local vector is performed. The global vector is probably continually updated while it is suppressed, so that its value is always appropriate for guiding the ant home.

A variant of the interaction between local and global vectors is sometimes found in ants released with zero global vector. For ants taken after their return to the nest, the release site at the end of the channel became the origin of the global vector, and ants often tended to return there. This tendency was very marked in ants...
exiting the 8-m or 4-m southeast-pointing test channels (Fig. 3d, e).
The direction of turning back was not random but was biased to the right ($P < 0.001$, binomial test), indicating that, even here, the local vector influences the initial direction that the ant takes when it follows the global vector.

Inhibiting the expression of global vectors allows local vectors to be executed without interference. The advantage this brings can be seen when desert ants take complex, fixed routes through familiar scrub, where there can be sizeable discrepancies between the optimal path between bushes and the direction indicated by the global vector. Our results indicate that the ant’s path is then governed predominantly by a mixture of landmark-guidance mechanisms and stored local vectors, with little contribution from the global vector. This suppression of the global vector by local vectors helps to explain the provacative results with which we began: that an ant’s normal homeward path, as it weaves through familiar scrub, is identical to the path it takes when it is displaced to the same feeding site with zero global vector.

Methods
Training and testing procedure. Ants were free to collect watermelon and sometimes biscuit crumbs in a feeding compartment at the end of the 6-cm-wide training channel during testing and for 2 days before. Ants were tested singly at an open test area ~100 m west of the training ground. A 1-m grid was painted on the ground so the ant’s path could be recorded by an observer drawing on squared paper. Three separate trenches were dug into the test field and channels placed in them: one pointed east, as did the training channel, and the two others pointed southeast and northeast. The lengths of the test channels within the trenches could be varied. A trained ant was caught either at the feeder in the channel or at the end of its return trip within 50 cm of the nest entrance. It was carried in a darkened container to the test area where it was placed onto a piece of melon in a feeding box at the end of a channel, and provided with a biscuit crumb which it picked up and carried homewards.

Computing mean trajectories. Mean trajectories (Fig. 2i) were computed in 1-m steps. For the first step we computed for each trajectory the mean direction of the vector connecting the channel exit to the intersection of each trajectory with a circle of 1 m radius centred on the exit. The position of the mean direction on the circle became the origin of step 2. The mean vector from the channel exit to the circle was projected 1 m beyond the origin of step 2. We then computed for each trajectory the vector from the origin of step 2 to where the trajectory crossed the normal to the tip of the projected mean vector. The intersection of the mean direction of these vectors with the normal defined the origin of step 3. This process was repeated until fewer than ten trajectories contributed to the mean.

Figure 1 Relationships between phylogenetically independent contrasts in geographic range size and population density for a, recently evolved marsupials ($r = 0.72, n = 23, P < 0.001$), and b, ancient species ($r = -0.56, n = 16, P < 0.05$).