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Local and global vectors in desert ant navigation

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Desert ants returning from a foraging trip to their nest navigate both by path integration and by visual landmarks[1–3]. In path integration, ants compute their net distance and direction from the nest throughout their outward[1] and return[4] journeys, and so can always return directly home from their current location[1]. 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[2,3,5]. Here we show that, as in honeybees[6–8], such multi-segment 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[9], using a variety of guidance strategies[3]. Indeed, the complex homeward paths of desert ants navigating through scrub are almost identical under these two conditions[3], 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[10]. 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 centimetres 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
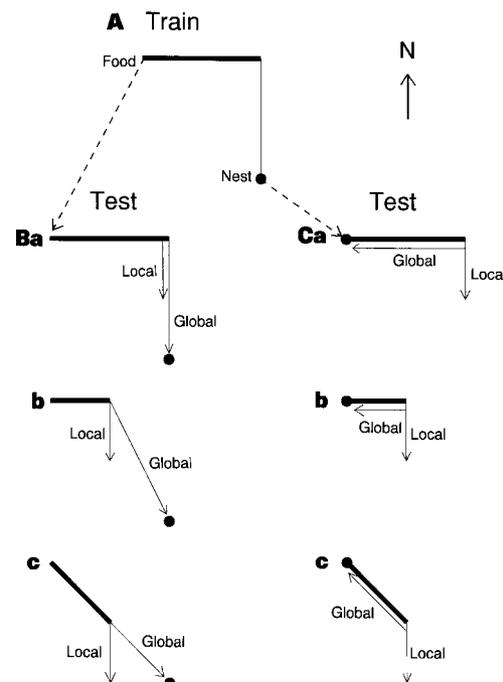

Figure 1 Rationale of experiments. **A**, Training arrangement. Dot indicates nest. Thick line shows the channel which forced the ants to travel west to reach food at the end of the channel and to return east on the first leg of their homeward journey. Thin line shows directed path over open ground. **B**, **C**, Dot illustrates position of the fictive nest, where the predicted value of the global vector is zero. Thin arrows show the directions of the predicted global and local vectors at the exit to the channel. **B** (left), ants are taken from the training feeder (left dotted arrow from **A**). **a**, Test condition reproducing training, when directions of local and global vectors coincide. **b**, **c**, A short and/or rotated test channel was used; global and local vectors point in different directions. **C**, Ants are captured at the nest and taken to the test channel (right dotted arrow from **A**). Predicted directions of vectors in tests performed when ants are placed at the end of the channel after capture at the nest. The fictive nest is then at the release site in the channel so that global vectors point towards the release site, whereas local vectors point south.

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) ($P < 0.05$, 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 ($P < 0.01$), but were not different from the local vector ($P > 0.05$, 2-m southeast and 4-m northeast channels; $P > 0.01$, 8-m southeast channel). The direction of the local vector was thus determined by compass (probably skylight[3]) information. However, local vectors can 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
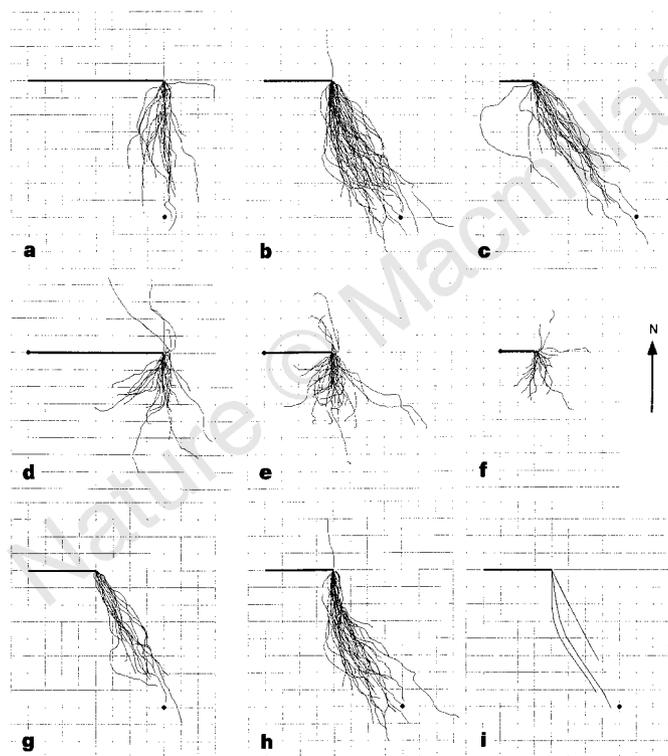
and released on open ground (Fig. 3h). It seems that ants have associated a compass-bound, local vector with a familiar channel, and that they retrieved the local vector when walking along and exiting that channel.

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 cm diameter, 80.5 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
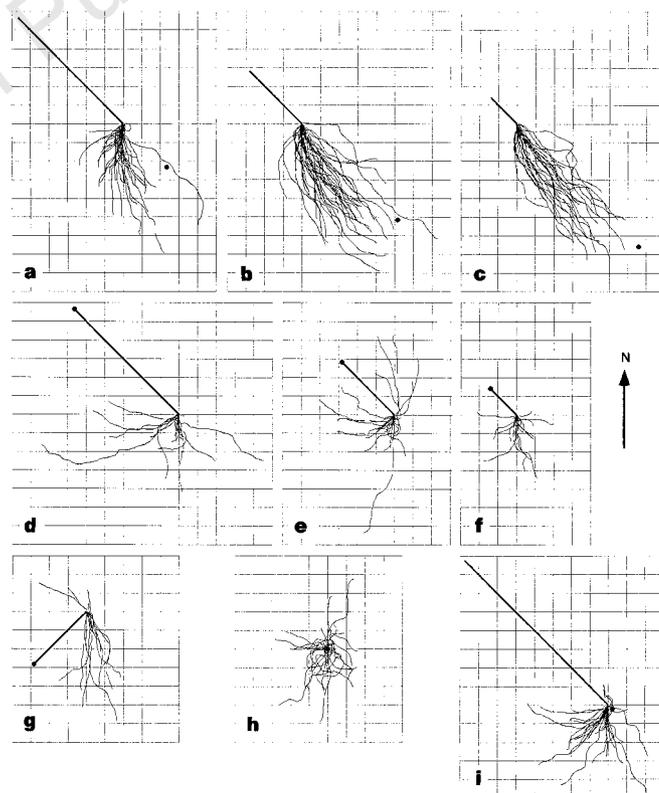

Figure 2 Trajectories of ants 'homing' on the test area after their release at the end of a 2-, 4- or 8-m east-pointing channel. The ants' paths were recorded from leaving the channel until they had changed direction several times, indicating searching behaviour[12]. Analysis and figures include trajectories until the initiation of search behaviour. **a–c**, Data from ants collected at feeder. **d–f**, Data from ants collected at nest. **g, h**, Trajectories in **b** are segregated according to whether ants went to the left (**g**) or to the right (**h**) of a point 2 m south and 0.5 m east of the channel exit. **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°) (mean = 3° E, s.d. = 6.8°, $n = 37$) is significantly different from that of the same trajectories between 4 m and 6 m from the channel exit (mean = 30° E, s.d. = 13.0°, $n = 27$) ($P < 0.001$, 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.

Table 1 Directions and distances of trajectories

Corresponding figure	Capture site	Channel	Direction with respect to south (°)		Distance (m)		Number of observations
			Predicted global	Observed	Predicted global	Observed	
2a	Feeder	E 8 m	0	1W ± 11	8.0	5.77 ± 0.33	20
2b	Feeder	E 4 m	27E	21E ± 8	8.94	7.48 ± 0.30	57
2c	Feeder	E 2 m	37E	31E ± 7	10.0	8.58 ± 0.33	30
2d	Nest	E 8 m	90W	2W ± 45**	8.0	2.18 ± 0.21	34
2e	Nest	E 4 m	90W	6 E ± 36**	4.0	1.91 ± 0.15	57
2f	Nest	E 2 m	90W	27E ± 43	2.0	1.55 ± 0.14	30
3a	Feeder	SE 8 m	45E	8W ± 21*	3.31	2.06 ± 0.21	35
3b	Feeder	SE 4 m	45E	26E ± 14	7.31	5.87 ± 0.31	42
3c	Feeder	SE 2 m	45E	35E ± 10	9.31	7.32 ± 0.32	30
3d	Nest	SE 8 m	135W	35W ± 40	8.0	1.67 ± 0.37	17
3e	Nest	SE 4 m	135W	23W ± 56**	4.0	1.39 ± 0.21	28
3f	Nest	SE 2 m	135W	4E ± 32***	2.0	1.18 ± 0.14	25
3g	Nest	NE 4 m	45W	8E ± 7***	4.0	2.49 ± 0.34	15
3i	Feeder	SE 11 m	45E	20W ± 39	0.31	2.21 ± 0.27	38
Text	Nest	E 4 m with cylinder	90W	19W ± 46*	4.0	2.39 ± 0.24	36

'Predicted global' columns show calculated values of the global vector at the exit to the test channel. 'Observed' columns show means and standard deviations of the vector between the channel exit and the trajectory endpoint (where the ant begins search behaviour[11]). Single, double and triple asterisks indicate cases in which ants used local vectors. The means of the observed directions do not differ from that of the local vector (*$P > 0.01$; **, *** $P > 0.05$), but do differ from the direction of the global vector ($P < 0.01$) and also, when applicable, from the perpendicular to the channel (*** $P < 0.01$).

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[11].

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 a row of three black cylinders (Fig. 4a). Trained ants were caught

Figure 4 Trajectories of ants trained to a feeder at the end of a corridor of black cylinders (20 cm in diameter and of different heights ranging from 20 cm to 53 cm). **a**, **b**, Tests with landmarks arranged in training situation. Ants were caught either at the feeding site (**a**) or at the nest (**b**). Mean distance of vector from release site to beginning of search is 12.47 m (s.d. = 0.92 m, $n = 14$) for ants caught at the feeder, and 11.82 m (s.d. = 0.59 m, $n = 22$) for ants caught at the nest. The initial search path of ants with zero global vector is not shown; a cross marks the release site to the south; a box marks the position of fictive next relative to the corridor of cylinders. **c**, Tests with landmarks rotated through 45° for ants caught at the nest. The direction of the ants just before leaving the corridor of landmarks (means = 44° W, s.d. = 4.3°, $n = 9$). **d**, Circular histogram of the directions of the last 3 m of all 17 trajectories shown in **c**. Using the 3-m circle centred at the endpoint of the trajectory, direction is defined as the inward radial that starts at the intersection of the trajectory with the circle.

either at the feeder or after reaching their nest, and taken to a test area where there was another corridor of cylinders. Ants collected at 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[12] 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[4].

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
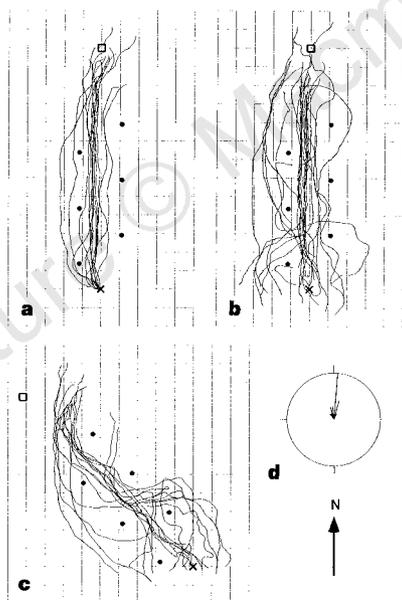
exiting the 8-m or 4-m southeast-pointing test channels (Fig. 3d, e). The direction of turning back was not random but was biased to the right ($P < 0.001$, binomial test), indicating that, even here, the local vector influences the initial direction that the ant takes when it follows the global vector.

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[3]. Our results indicate that the ant's path is then governed predominantly by a mixture of landmark-based 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 provocative 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[3]. □

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[10] 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 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.

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Species extinction and the relationship between distribution and abundance

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Within taxonomic groups, there is almost always a positive relationship between the size of geographic range and the local abundance of species[1–4]. This pattern has attracted much interest, and several ecological mechanisms have been proposed as causes of it[5]. However, these hypotheses do not consider the effect of the extinction of rare species on range-abundance relationships. If both range size and local abundance influence the risk of extinction, species with small ranges might avoid extinction if they have high local abundance, whereas species with low local abundance might avoid extinction if they are widespread; species with both small range and low local abundance should be at high risk. This interaction between range, abundance and extinction should produce negative correlations between range and abundance in groups that have experienced many extinctions. Here I test this idea using Australian marsupials, and I show that although the relationship between range size and local abundance is positive for recently evolved species, it is negative for ancient species. This indicates that positive relationships between range size and abundance may be generated during adaptive radiation, but are then gradually reversed as a result of differential extinction.

I defined recently evolved species as those known to have radiated from a common ancestor within the last 4 million years, and ancient species as those that diverged from their closest extant relative more than 4 million years ago. Analysis of the relationship between range
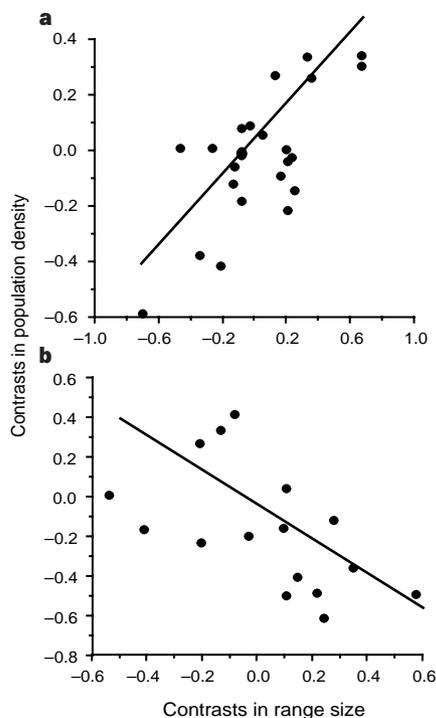

Figure 1 Relationships between phylogenetically independent contrasts[27] in geographic range size and population density for **a**, recently evolved marsupials ($r = 0.72, n = 23, P < 0.001$), and **b**, ancient species ($r = -0.56, n = 16, P < 0.05$).