Calibration of vector navigation in desert ants

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Desert ants (*Cataglyphis* sp.) monitor their position relative to the nest using a form of dead reckoning [1–3] known as path integration (PI) [4]. They do this with a sun compass and an odometer to update an accumulator that records their current position [1]. Ants can use PI to return to the nest [2,3]. Here, we report that desert ants, like honeybees [5] and hamsters [6], can also use PI to approach a previously visited food source. To navigate to a goal using only PI information, a forager must recall a previous state of the accumulator specifying the goal, and compare it with the accumulator's current state [4]. The comparison – essentially vector subtraction – gives the direction to the goal. This whole process, which we call vector navigation, was found to be calibrated at recognised sites, such as the nest and a familiar feeder, throughout the life of a forager. If a forager was trained around a one-way circuit in which the result of PI on the return route did not match the result on the outward route, calibration caused the ant's trajectories to be misdirected. We propose a model of vector navigation to suggest how calibration could produce such trajectories.

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Results and discussion

Vector navigation

Evidence that an ant's homeward trajectories can be guided by vector navigation comes from displacement experiments [1,7], an example of which is given in Figure 1. Ants (*Cataglyphis fortis*) were trained from the nest to reach food at the end of a 15 m channel (Figure 1a). When displaced from the feeder and released individually on a test ground, ants followed homeward trajectories whose direction, parallel to the channel, showed no sign of the displacement (Figure 1b). It is difficult to use displacement experiments to demonstrate that vector navigation can also guide outward trajectories to a feeder because foraging ants, when

disturbed, tend to return to their nest rather than continue foraging. We therefore trained ants along the enclosed route shown in Figure 1a, and subsequently observed their trajectories over open ground. Ants were confined to the channel linking the nest to the feeder for the whole foraging trip so that, although they could see the sky and determine their direction of travel, the surrounding landscape was always hidden from view. Ants were trained for 6 days and, from day 4, we occasionally interrupted training to observe the trajectories of individual ants released singly from the enclosure into a shortened channel, which either pointed in the same direction as in training or was rotated through 38°.

After leaving the channel, ants ran over open ground in the approximate direction of the food site (Figure 1c,d). Unlike the homeward trajectories (Figure 1b), which ended in

Figure 1

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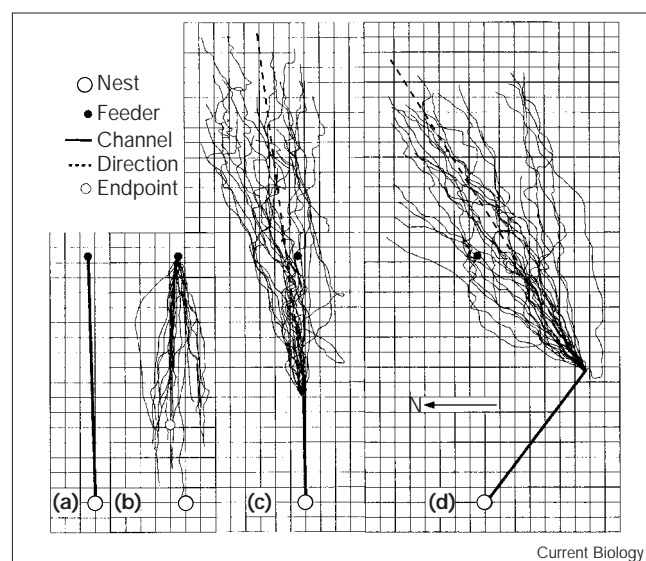
Vector navigation to a feeder. **(a)** Training route. Circular enclosure of diameter 1.2 m was placed around the nest, restricting the ants' exit from the enclosure to a single tube that led to a channel with a feeding box at the end. The tube was open only during training (8am–5pm daily). **(b)** Homing trajectories of ants taken from the feeder. Large open circle shows position of fictive nest. Trajectory direction is the best fitting line computed by the method of principal axes (see [11]). Mean direction was computed using circular statistics [12] and is 273.05°, SD ± 5.97° (clockwise from north). Trajectory length is the distance between the start of the trajectory and the beginning of search behaviour. Mean length is 11.10 ± 2.40 m, $n = 21$. **(c)** Foraging trajectories on open ground after leaving a shortened channel which pointed in the same direction as the training channel. Mean direction 83.95°, SD ± 6.53°, $n = 21$. **(d)** Foraging trajectories on leaving a channel pointing 38° to the east of the training channel. Mean direction (58.28°, SD ± 12.15°, $n = 28$) was significantly ($p < 0.01$) to the east of the direct path from the end of the channel to the feeder. Grid lines are spaced at 1 m.

Figure 2
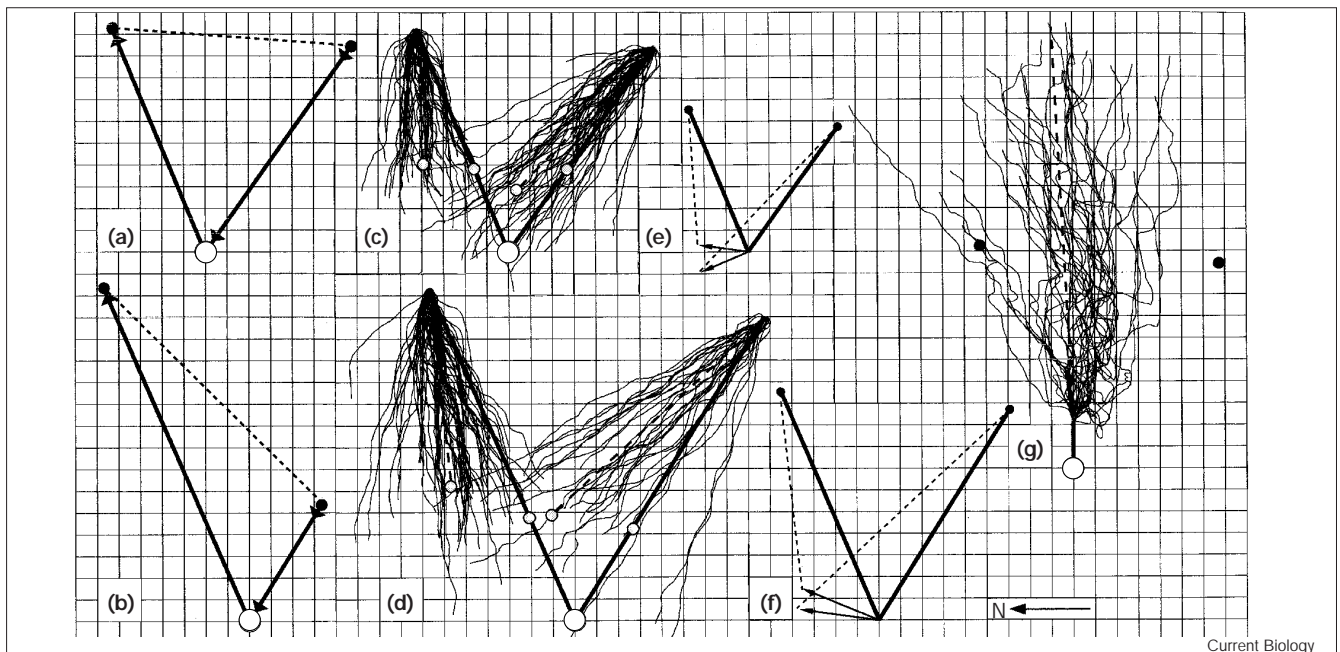
A foraging route that transforms trajectories. **(a,b)** Training arrangement. Ants were carried southwards along the dashed line between the northeasterly pointing outward and the northwest return channels. Arrows show position and direction of one-way valves. **(c,d)** Homeward trajectories of ants taken from the training or test feeder to an empty test ground are shown as though originating from the feeders where the ants were collected. Dashed lines leading to small open circles show the mean directions and lengths of the trajectories relative to the feeder. (c) From training feeder, mean direction is 267.10°, SD ± 12.10°, length 5.93 m, SD ± 1.64 m, $n = 57$; from test feeder, mean direction is 313.83°, SD ± 11.65°, length 9.04 m, SD ± 2.53, $n = 54$. (d) From training feeder, mean direction is 263.88°, SD ± 11.19°, length 9.08 m, SD ± 1.17 m,

$n = 73$; from test feeder, mean direction is 317.21°, S.D ± 11.32°, length 13.18 m, SD ± 1.56, $n = 28$. The directions of mean trajectories all differed significantly from that of the associated training channel. Open circles on solid lines give mean lengths of homing trajectories obtained in separate experiments after travelling along (c) 10 m or (d) 15 m channels to a feeder (mean 6.87 m, SD ± 1.39 m, $n = 32$ for 10 m channel; mean 11.34 m, SD ± 1.42 m, $n = 67$ for 15 m channel). **(e,f)** Transformation (arrows) as calculated from difference between mean transformed trajectories (dashed lines) and expected untransformed homeward trajectories (solid lines). **(g)** Outward trajectories of ants trained on the route in (a); mean direction 93.10°, SD ± 12.65°, $n = 39$. Solid circles indicate normal positions of the ends of the two channels.

spiral search paths [3] (data not shown), foraging ants continued indefinitely in an approximately steady direction. Although the paths of ants leaving the 38° channel had a small directional error (Figure 1d), the ants could approach the approximate location of the feeder from two directions without the aid of familiar landmarks. This ability indicates that they had recorded the coordinates of the feeder and could reach it by vector navigation. The immediate redirection of the trajectory at the end of the 38° channel shows that the comparison to determine direction can occur anywhere on the trajectory (see also [8]).

Relationship between outward and homeward trajectories
We modified the training arrangement to discover whether ants store the location of the feeder using PI information from their outward or homeward path. The results suggest that the ant's memory, like the location indicated by the waggle dance in honeybees [9], is derived from the state of the accumulator at the feeder. We imposed a one-way system so that, instead of going

out and back along the same channel (as in Figure 1a), ants reaching the feeder were transported to the end of a second channel which led back to the nest (Figure 2a). After ants had experienced several days' training, we recorded both the unconstrained homeward trajectories of single ants taken from the 'training' feeder (Figure 2c, left side) and the outward trajectories of ants leaving the nest singly (Figure 2g). Both types of trajectories have directions intermediate between the directions of the two channels. The outward trajectories might be interpreted as showing that foragers record the position of the feeder by averaging the states of the accumulator at the ends of the outward and return trajectories. This explanation was proposed for a corresponding observation in honeybees [10], but it would not account for the accompanying transformation of the homeward trajectories. Our interpretation of the results is that the direction of the homeward trajectories is the inverse of the outward trajectories, and we propose a model of how a single accumulator can produce such a result.

It is commonly supposed that the accumulator is reset to an initial state before a forager leaves the nest [4]. We propose that, in addition, before a forager starts its homeward trajectory, the accumulator state is stored in memory and the accumulator is again reset to its initial state. The stored accumulator state then serves as the goal for both the homeward trajectory and a subsequent return to the feeder. For the same state to act as a goal in both directions, the sun compass must be rotated through 180° each time the accumulator is reset. Unconstrained trajectories from the nest and from the training feeder will then remain in opposite directions, even after the navigation process has been transformed by our training.

Transformation of homeward trajectories

To study the transformation of the homeward trajectories further, we recorded unconstrained homeward trajectories from an additional point. We briefly interrupted training, twice towards the end of the experiment, to allow about 25 ants to travel outwards to a 'test' feeder at the same distance, but along the direction of what was normally the return channel. In this case too, the individual homeward trajectories of ants taken at the test feeder were rotated with respect to their immediately preceding outward path (Figure 2c, right side). We also repeated the same training using a circuit with two channels of differing lengths (Figure 2b). The homeward trajectories from the training and test feeders in the second circuit showed similar transformations (Figure 2d). Normal homeward trajectories after a straight outward path along a channel are along the direction of the channel [2], but their length is shortened (length shown by open circles on the solid lines in Figure 2c,d). Training around the one-way circuits transforms the relationship between the outward path and unconstrained homeward trajectories. In both one-way circuits, the 'transformed' homeward trajectories were rotated similarly from the 'normal' trajectories, but the mean length of homeward trajectories from the test feeder was greater than that from the training feeder ($p < 0.01$ in both circuits; Mann–Whitney U-test, 2-tail). The vector difference between the mean transformed and the mean normal trajectories from both feeders was roughly similar (Figure 2e,f), so we describe the transformations as a shift of the endpoint of the homeward trajectories by a 'correction' vector.

The relationship between the normal and the transformed homeward trajectories can be expressed as follows. If g is the vector between the start and end of the normal homeward trajectory, x the position of a forager with respect to the start of the homeward trajectory (also a vector), and d the correction vector, then the direction of movement of the forager at x is given by the function f,

$$f(x,g) = g - x + d \qquad (1)$$

In line with the observations, this function describes a straight homeward trajectory to the point $x = g + d$. In normal trajectories $d = 0$, and f is simply vector subtraction.

Calibrating vector navigation

Because the unconstrained homeward trajectories from the training feeder are intermediate in direction between the two channels, we believe that the observed transformations are the result of a recalibration of the vector navigation system to reduce differences between the constraints of the return channel and the output of the system. As the ants behaved similarly despite different ages and experience, calibration must continue throughout an ant's foraging career. We now use our model of vector navigation to explain how such calibration could produce the trajectories in Figure 2.

An unconstrained ant with normal vector navigation (Figure 1) follows trajectories, from both the nest and the feeder, that bring the state of the accumulator towards the state at the feeder. The one-way training circuits (Figure 2a,b) produce a consistent difference between the state of the accumulator at the feeder and the state at the nest after returning from the feeder. After training, there was also a difference between the state at the end of the unconstrained homeward trajectories and the state at the feeder (Figure 2c,d). This latter difference cannot be explained by a change in the accumulator. The change must occur at a later stage in the vector navigation process. Two possibilities are the processes of storing accumulator states in memory, or comparing the memory and the present state to give the direction of desired movement. Whatever process is calibrated, the calibration is likely to occur at locations that can be recognised independently of PI, and where the process can be adjusted to bring the output towards an expectation. These conditions are most obviously met at the nest and at the feeder. Both places can be recognised by visual landmarks or odours. At these places, the current accumulator state should correspond to the memory, serving as a goal, and the output of the comparison should specify a zero movement. Connections can then be adjusted to make the memory reflect the actual accumulator state, or to make these inputs to a comparator produce zero output.

Calibration at the nest, while reducing the differences between the output of the navigation system and the constraints of the return channel, produces differences along the outward channel (Figure 2g). Calibration at the feeder would therefore act in opposition to calibration at the nest. A gradual process of calibration at both points would result in the unconstrained trajectories intermediate in direction between the two channels (Figure 2a,b; left sides). We illustrate this with an equation to describe vector navigation within the training circuit in terms of the states of the accumulator. To correspond with the form of the trajectories

Figure 3
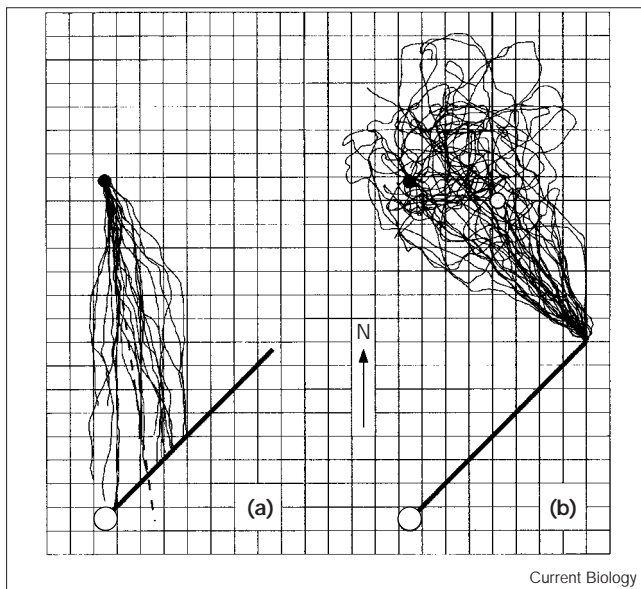
Trajectories recorded on the training field of ants following another one-way circuit. **(a)** Homeward trajectories from when ants left the feeder until they began searching or reached the channel. Mean direction is 172.40°, SD ± 5.66°, *n* = 20. The mean trajectory is rotated significantly eastward from the direct route home (*p* < 0.01). **(b)** Outward trajectories until the ant reached the feeder or was lost from sight. Open circle indicates mean endpoint at which the ant starts search behaviour (mean direction 327.95°, SD ± 13.07°; mean length 6.90 m, SD ± 2.48 m, *n* = 40). The direction differed significantly from the direct path from the end of the channel to the feeder (*p* < 0.01).

described by equation 1, X is the current state of the accumulator, G the state of the accumulator at the training feeder, and D the adjustment due to calibration. The output of the vector navigation system is given by F, where

$$F(X,G) = G - X + D \qquad (2)$$

Calibration at a goal adjusts D to reduce the difference between G + D and the accumulator state X at that goal. If on returning to the nest X = G − L, then the difference there is D − L. At the feeder X = G, and the difference is D. So while calibration at the nest reduces D − L by increasing D, it is counteracted by calibration at the feeder which reduces D.

A semi-natural example

Transformed trajectories can also be produced in a way that does not involve passive displacement (Figure 3). Ants from a second enclosed nest were trained to collect food at the end of a two-leg route. The exit tube from the enclosure surrounding the nest led to a 10 m northeast channel sunk into the ground. From there, ants travelled 10 m northwest across open ground to the food and were free to return directly to the nest (Figure 3). This lopsided route induces errors in PI on the outward trip [2]. We

could thus observe the unrestricted homeward and food trajectories of ants that have experienced consistent discrepancies between the results of PI on their outward and inward paths. As is typical after L-shaped routes, errors in PI result in homeward trajectories that are not directed towards the nest [2] (Figure 3a). Because the results of PI are different for the outward and return trajectories, calibration will occur at the nest, reducing the error in the homeward trajectories. From the arguments above, the error eliminated at the nest is transferred to the feeder, introducing opposing errors in the outward trajectories. These errors are evident in the observed outward trajectories which are rotated clockwise from the food source and are a little shorter than expected (Figure 3b). In contrast to the previous experiment (Figure 2g), the trajectories to the feeder end in a search pattern [3], perhaps because in this case the landscape is familiar. The directional error in the trajectories and the subsequent search indicate that, even on familiar ground, the ants used vector navigation.

Our study suggests a new function for landmarks. Although, in the short term, vector navigation can operate without landmarks, over a longer time scale landmarks help keep vector navigation accurate.

Supplementary material
Supplementary material including additional methodological detail is available at http://current-biology.com/supmat/supmatin.htm.

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Supplementary material

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Supplementary materials and methods

Training ants

We studied *C. fortis* on flat, sandy ground near Mahares, Tunisia in June–July 1998. Circular enclosures of diameter 1.2 m were placed around the nests, restricting the ants' exit from the enclosure to a single tube which led to a channel with a feeding box at the end. The tube was open only during training (8am–5pm daily). The channel was flat-bottomed with sloping sides and a lip at the top to prevent escape. From the middle, ants had a 90° view of the sky [S1]. Ants were trained to a feeder on the first day by moving a small piece of melon stepwise from the nest along the channel (and, in the case of Figure 3, over-ground). For Figure 2, two channels were attached to the exit tube and the ant's route was determined by a system of one-way valves. Each valve consisted of a 20 cm tube between two containers. The tube left the first container at ground level and entered the second 15 cm higher, so that ants were unable to climb up again. Valves were closed by corking the tube. Ants travelled along the outward channel to reach the watermelon inside a container where they were trapped. Approxi-mately every 15 min, we moved the container with the trapped ants and opened a valve to allow the ants to enter the return channel. A third valve led from the channel to the nest. We marked approximately 60 foragers on the first day of each training, and tested the marked ants after 5–8 consecutive days of training in the first configuration and after 2–4 days in the second.

Testing ants

Homeward trajectories of ants taken from the feeder were recorded at a flat, featureless area 70 m to the southwest on which a 1 m grid had been painted. Each ant was released individually with a biscuit crumb, and its path across the grid recorded until it started searching [S2]. For recording outward trajectories, a 1 m grid was painted around the nest. The exit tube from the enclosure was blocked, the feeder removed and the channel shortened. The tube was then briefly unblocked to release ants individually into the channel so that their trajectories could be recorded singly.

Trajectory analysis

The best-fitting line to a trajectory was computed by the method of principal axes (see page 586 in [S3]). Circular statistics were used as prescribed by Batschelet [S4]. Trajectory lengths were taken as the distance between the start of the trajectory and the beginning of search behaviour.

Supplementary references

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