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Egocentric information helps desert ants to navigate around familiar obstacles

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Summary

Homing ants have been shown to associate directional information with familiar landmarks. The sight of these local cues might either directly guide the path of the ant or it might activate a landmark-based vector that points towards the goal position. In either case, the ants define their courses within allocentric systems of reference. Here, we show that desert ants, *Cataglyphis fortis*, forced to run along a devious path can use egocentric information as well. The ants were trained to deviate from their straight homebound course by a wide inconspicuous barrier that was placed between the feeding and nesting sites. At a distant test area, the ants were confronted with an identical barrier rotated through 45°. After passing the edge of the obstacle, the ants did not proceed in the trained direction, defined by the skylight compass, but rotated their courses to match the rotation of the barrier. Visual guidance could be excluded because, as soon as the ants turned around the end of the barrier, the visual cue it provided vanished from their field of view. Instead, the ants must have maintained a constant angle relative to their previous walking trajectory along the obstacle and, hence, must have determined their new vector course in an egocentric way.

Key words: homing, landmark guidance, landmark obstacle, detour, vector navigation, motor learning, idiothetic orientation, desert ant, *Cataglyphis fortis*.

Introduction

Individually foraging workers of the desert ant *Cataglyphis fortis* navigate in their flat and mainly homogeneous environment by path integration: during a foraging trip, the distances covered and all angles steered are integrated and provide the ant with a continuously updated vector that points to the nest (Wehner, 1982; Schmidt et al., 1992). As this kind of navigation is a self-centred system, computational errors inevitably accumulate [for an experimental demonstration, see Wehner and Wehner (1986)]. Such errors can be reduced by using additional external cues such as landmarks. Indeed, when *C. fortis* forages within desert areas covered with low shrubs, it is able to acquire and use landmark-based routes for negotiating its way through its foraging area (Wehner et al., 1996). While the home vector derived from path integration is represented as a single compass bearing leading the ant directly to its nest, directional information in a cluttered environment might consist of a series of local vectors pointing in different directions. What information is used while the ant travels along such multi-leg (tortuous) courses?

For the sake of argument, let us consider that ants returning to the nest had to detour around an obstacle. What information do they acquire and use once they have reached the edge of the obstacle and must decide upon the course to be taken next? There seem to be at least three possibilities. The animals could use a local vector that is given by an external system of reference such as skylight coordinates (hypothesis 1). Alternatively, they could define the course to be taken with respect to the visual cue provided by the landmark obstacle (hypothesis 2) or with respect to the locomotor course taken prior to reaching the edge of the obstacle (hypothesis 3).

It is possible to discriminate between these three hypotheses by experimentally rotating the obstacle by α degrees. In this case, hypothesis 1 would predict that the animal would maintain its previous compass course irrespective of the angle α about which the obstacle had been rotated. If the course of the animal also rotated by angle α, either hypothesis 2 or hypothesis 3 could hold. To discriminate between the two, it was necessary to design an experimental situation in which the obstacle disappeared from the field of view of the ant once the ant reached the edge of the obstacle. If the course taken by the ant followed the rotation of the (now invisible) obstacle, then the animal must have relied on egocentric (hypothesis 3) rather than allocentric (hypotheses 1 and 2) information.

Previous experiments have shown that ants of the genus *Cataglyphis* can behave according to hypothesis 1 and 2. For example, if the ants were presented with an array of landmarks (small black cylinders) flanking a frequently travelled route, they were able to associate so-called local vectors with the landmarks. These local vectors pointed in the compass direction the animal has previously chosen irrespective of

whether the landmark array had been rotated (Collett et al., 1998). This is in accordance with hypothesis 1. However, if an extended landmark (a large black wall) obstructed their straight homebound path, ants arriving at the end of the wall chose a constant angle relative to the wall. When the obstacle was rotated by 45 °, their courses were rotated by almost the same angular amount relative to the direction chosen by the ants during training (Collett et al., 2001). This result leads to a rejection of hypothesis 1 because the ants did not follow the trained compass direction after turning around the edge of the wall. One cannot distinguish, however, between hypotheses 2 and 3, because the landmark obstacle in this experiment was so conspicuous.

In the present study, we set out to test whether egocentric information (hypothesis 3) can be used to determine the course taken by the ants after turning around an obstacle. We again forced the ants to deviate from their straight homebound paths around an extended barrier, but this time the obstacle was rather inconspicuous and vanished completely from the field of view of the ant as soon as it had reached the edge of the barrier and started to turn around it. This experimental design allowed us to distinguish between hypotheses 2 and 3. What happens when this obstacle is rotated relative to the training situation? Do the ants follow an allocentric course (the habitual compass direction) or does their course alter to match the rotation of the barrier? If the latter were the case, the ants would have defined their courses with respect to the locomotor course taken before reaching the edge of the obstacle and must, therefore, have relied on egocentric (idiothetic) information. In the present study, we show that this is, in fact, the case.

Materials and methods

Animals and location of experimental site

The experiments were performed during July and August 1999 at our *Cataglyphis* Field Station near Maharès, Tunisia, within the area of salt-pans between Maharès and Chaffar inhabited by *Cataglyphis fortis*. Each monodomous *C. fortis* colony contained approximately 50 individually searching foragers. These ants travel away from the nest for mean distances of 90.6±31.9 m (mean ± S.D., N=15) (Wehner, 1987).

Training

The nest selected for the experiments was located within a flat open area, with the nearest natural landmarks (some shrubs, <0.5 m high) at least 40 m away. A feeding site F was established 13 m to the south of the nest entrance N. Between the nest and the feeder, a V-shaped barrier was placed with its tip pointing towards the feeder (Fig. 1A). The barrier consisted of two wooden shelves, each 6 m long and 5 cm high, enclosing an angle of 120 °. Ants heading for the feeder could easily climb over the obstacle because a flat ramp of sand had been constructed on the inner side of the V-shaped array (Fig. 1B). The ants then had to jump down from the top of the barrier to run straight to the feeder, and did so unhesitatingly. Ants returning from the feeder, however, were not able to cross the barrier because some smooth tape had been glued to it on the feeder-facing side. On their first homebound path, the ants tried repeatedly to cross the barrier and ran back and forth along the obstacle until they finally managed to turn around its end and head for the nest. Approximately half the ants chose the left detour around the barrier, and the other half chose the right detour. Subsequent home runs were observed until the ants detoured around the barrier without any hesitation. The ants were then marked with a coloured dot depending on whether they had chosen the left (red) or right (green) detour direction.

Testing

To exclude unwanted visual or olfactory cues such as the presence of nest mates, distant landmarks or nest odours, all tests were performed in an area unfamiliar to the ants located approximately 250 m from the nesting site.

Ants were tested in two different states of homing behaviour. They were captured either at the nest entrance after they had returned from the feeder and completed their homebound run (so-called zero-vector ants) or at the feeder before they had started their homebound run (vector ants). The term ‘zero-vector ants’ refers to the fact that, upon arrival at the nest entrance, the ants have ‘paid out’ their home vector. If these ants were displaced to unfamiliar terrain, they would switch on a systematic search program (Wehner and Srinivasan, 1981). Accordingly, the term ‘vector ants’ means that the ants taken from the feeder have their full home vector ($F \rightarrow N$) still to be paid out.

Well-trained ants, detectable by their red or green colour mark, were transferred individually to the test area, provided with a biscuit crumb, and released. Zero-vector ants were released at the tip of a barrier identical to the one used for training. The barrier was presented either in the same orientation as during training (N=36) or rotated through 45 ° to either the west (N=22) or the east (N=27). In addition, ants were released on the bare test area without any barrier (N=22). Vector ants (N=22) were released at the geographical position of the feeder relative to the barrier, which was oriented as during training.

A grid of white lines (mesh width 1 m, square dimension 25 m×25 m) was painted on the desert floor so that the trajectory of the ant could be recorded on graph paper (square dimension 1 cm). After 5–10 min of recording, the ant was captured again, marked with a blue dot, and released into the entrance of its nest. Each ant was tested only once.

Data analysis

The first path segment after the ant, approaching the barrier from the insurmountable (feeder-based) side, had turned round one end of the barrier was analysed. This path segment expresses the directional information the ants had associated with the barrier. In the following, it is called the ‘detour vector’ in order to use a neutral term that could be applied irrespective of whether the ants behaved according to hypothesis 1, 2 or 3. Some zero-vector ants (14 out of 85 ants) did not manage to

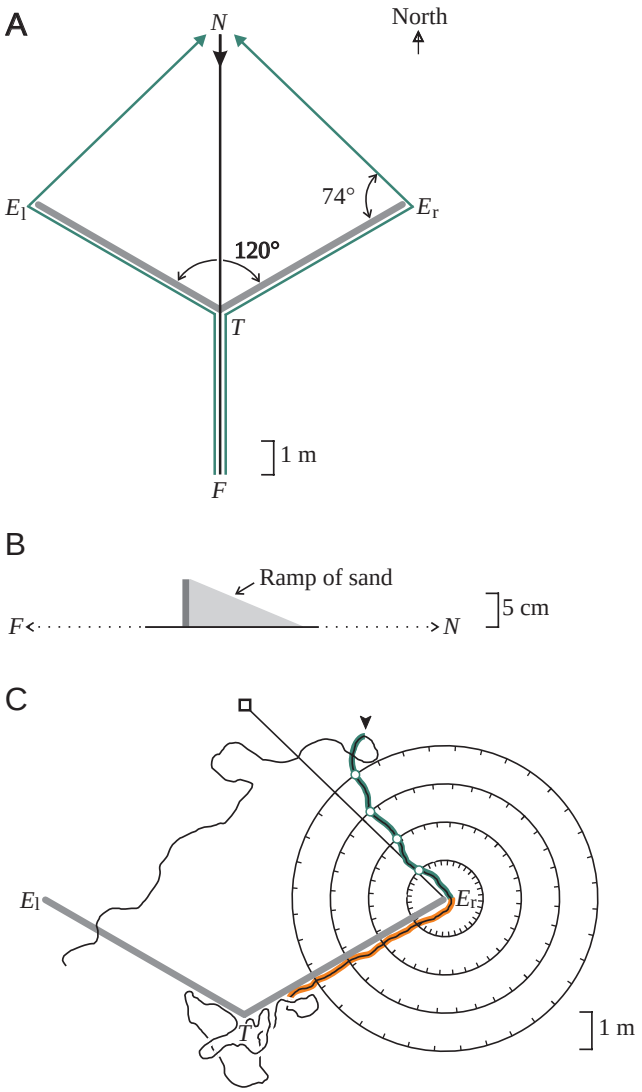

Fig. 1. (A) Training arrangement. The outbound and inbound paths of ants are indicated by black and green arrows, respectively. The heavy grey line marks a V-shaped barrier, each arm of which is 6 m long and 5 cm high, enclosing an angle of 120 °. A sandy ramp (see B) attached to the inside of the V-shaped array enabled the ants to pass the barrier on their way from the nest *N* to the feeder *F*. In the opposite direction, *F* to *N*, smooth, light-brown tape glued to the feeder-facing side of the barrier forced the ants to detour around the left (E_l) or right (E_r) end of the barrier. *T*, central tip of the V-shaped barrier. Lengths of path elements: $N \rightarrow F$, 13 m; $F \rightarrow T$, 5 m; $T \rightarrow E_l$ and $T \rightarrow E_r$, 6 m; $E_l \rightarrow N$ and $E_r \rightarrow N$, 7.2 m. (B) Transverse section of the barrier. (C) Data analysis. Example trajectory of a zero-vector ant tested with the barrier in the training orientation. The ant was released at *T* and its path was recorded for 5 min. The following variables were analysed: (i) the walking distance along the barrier immediately before the ant turned around E_r (orange); (ii) the length of the subsequent path segment (green, 'detour vector') measured from the intersection of the trajectory with the imagined extension of the barrier until the ant made a sharp turn of more than 90 ° compared with its preceding running direction (arrowhead); (iii) the angular deviation of the detour vector from a line connecting E_r and the fictive position of the nest relative to the barrier (□). For this purpose, the intersections (small circles) of the trajectory of the ant with concentric circles (radii 1, 2, 3 and 4 m) centred on E_r were determined.

get round the barrier during 10 min of recording time. These runs were omitted from the evaluation. Furthermore, analyses were restricted to those ants that detoured around the same end of the barrier that they had used during training (for numbers of ants, see Results).

To determine the directions of the detour vectors, four concentric circles (radii 1, 2, 3 and 4 m) were drawn around the ends of the barrier (Fig. 1C). The first intersections of the path of the ant with each of these four circles were recorded. The lengths of the detour vectors were defined as the distance from the intersection of the trajectory with the imagined extension of the barrier to the endpoint of the trajectory. This point was judged by eye; it is characterised by a deviation of at least 90 ° from the previous mean running direction of the ant. In addition, the walking distance along the barrier immediately before the ant turned round it was recorded. Results are presented as means ± S.D.

In experiments without a barrier, the direction of the first points of intersection of the trajectories of the ants with concentric circles (radii 1, 2, 3 and 4 m) centred on the point of release was determined.

Statistical treatment of circularly distributed data

The Rayleigh test was used to test whether sample points were distributed non-randomly. To test whether mean angles differed from expected directions, 95 % confidence limits were used. The Mardia–Watson–Wheeler test was applied to detect differences between the mean angle and/or angular variance of two samples (Batschelet, 1981).

Results

Tests with a barrier: walking distances along the barrier and lengths of detour vectors

Ants caught close to the nest entrance and transferred to a distant test area perform a systematic search pattern that is symmetrically centred on the point of release (Wehner and Srinivasan, 1981). In the present experiments, these so-called zero-vector ants encountered a familiar obstacle, the barrier, which markedly influenced their behaviour. After initially searching in small loops, the ants ran alongside the barrier to the left or right before they finally turned round one of its ends. Most of them (96 %, N=71) chose the side that they had chosen during training.

Ants caught at the feeder ('vector ants') and released at the geographical position of the feeder relative to the test barrier (the fictive feeding site) chose their preferred detour around the barrier in 86 % of cases (N=22). Although the ants had performed several foraging trips in the training area before they were tested, none of them took the short cut from the release point to the end of the barrier. Instead, all the ants headed towards a point close to the tip of the V-shaped barrier and then ran alongside the barrier for a distance of 5.7±1.3 m (N=19).

This value did not differ significantly from the mean distance that the zero-vector ants had walked along the barrier immediately before turning around it (5.0±2.6 m, N=68; P=0.8, z=–0.206, Mann–Whitney test).

In zero-vector ants, the mean lengths of the detour vectors were the same irrespective of the test situation (barrier in training orientation, 5.1±2.0 m, N=25; barrier rotated through 45 °, 5.3±1.7 m, N=43; P=0.8, z=–0.318, Mann–Whitney test). However, the mean lengths of the detour vectors differed between zero-vector ants and vector ants (P=0.02, Kruskal–Wallis test). In addition, the mean lengths of the detour vectors for vector ants (6.7±2.0 m, N=19) closely corresponded with the distance from the end of the barrier to the fictive location of the nest (7.2 m, P>0.2, t-test), while the corresponding path lengths in zero-vector ants were significantly shorter (5.1±2.0 m, N=25, P<0.001, t-test).

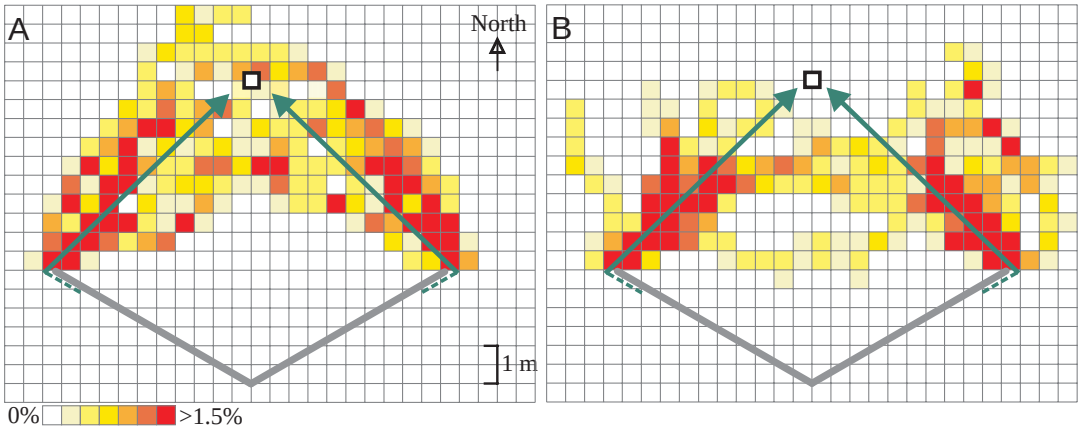

Fig. 2. Detour vectors associated with the barrier in the training orientation. (A) Vector ants (left side N=9, right side N=10) were released at the fictive position of the feeder relative to the barrier (5 m south of the tip of the barrier). (B) Zero-vector ants (left side N=13, right side N=12) were released at the tip of the V-shaped barrier. The green arrows point towards the fictive position of the nest relative to the barrier (□). The fictive position of the nest relative to the home vector of the ant coincides with □ in A and is located at the tip of the V-shaped barrier (the release point) in B. The normalised path density histograms were obtained by determining the path lengths of the detour vectors in squares of 0.5 m×0.5 m. These values were then assigned to seven classes ranging from 0 % (white) to more than 1.5 % (red) of the total path length of the detour vectors at each of the ends of the barrier.

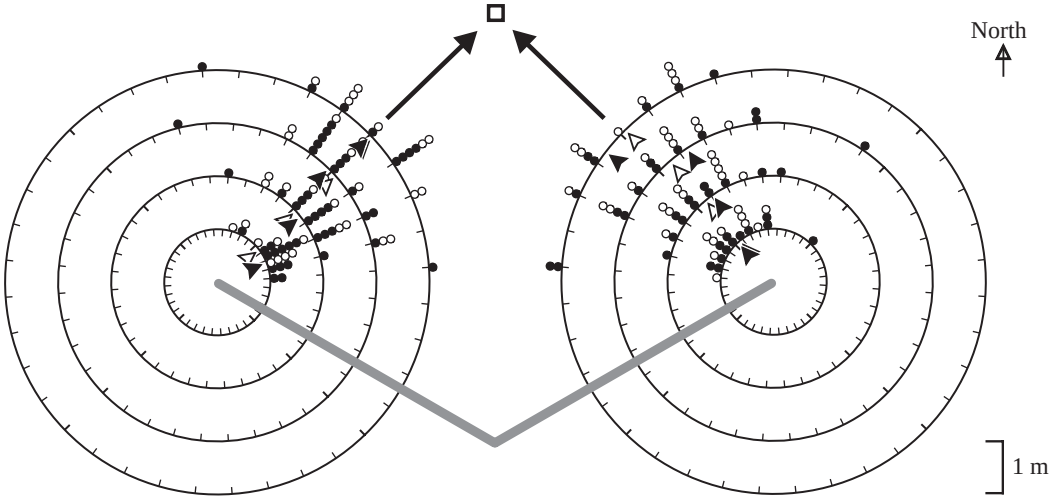

Fig. 3. Angular distribution of detour vectors in vector ants compared with that of zero-vector ants. Circles represent the first intersections (open circles, vector ants; filled symbols, zero-vector ants) between the trajectories of the ants and concentric circles (radii 1, 2, 3 and 4 m) centred on the ends of the barrier. Vector ants (open arrowheads) and zero-vector ants (filled arrowheads) do not differ in their mean angles and angular variations (P>0.05, Mardia–Watson–Wheeler test) at each of the circles. In both groups of ants, the mean angles do not deviate from the line (0 °, arrow) connecting the end of the barrier with the fictive position of the nest relative to the barrier (□); angles are given clockwise from this direction. A comparison of the statistical details for vector ants and for zero-vector ants (values given in parentheses) at the 3 m circle for the left side of the barrier shows: mean angles 1.7 ° (359 °); r-values 0.952 (0.941); number of ants 9 (13); 95 % confidence intervals 347.9–15.5 ° (348.9–13.1 °); for the right side of the barrier, mean angles 5.4 ° (13.2 °); r-values 0.969 (0.880); number of ants 10 (10); 95 % confidence intervals 355.1–15.7 ° (352.5–33.9 °).

To justify the use of the term ‘detour vector’, we compared the mean lengths of detour vectors of vector ants, which are assumed to have their home vector (nest-to-feeder) still to be paid out, with those of zero-vector ants with the barrier in the training and in the rotated positions. The distributions of detour vector lengths pertaining to these three experimental situations could not be distinguished statistically (P=0.6, Kruskal–Wallis test). Detour vectors in zero-vector ants therefore seem to have a defined length, although this length was too short to cover the distance between the edge of the barrier and the fictive position of the nest relative to the barrier.

Direction of the detour vector with the barrier in the training orientation

After passing the barrier, both vector ants (Fig. 2A) and zero-vector ants (Fig. 2B) continued in a direction that led towards the fictive position of the nest relative to the barrier. There was no difference between the mean directions and angular variances of the detour vectors exhibited by vector ants and zero-vector ants (Fig. 3).

Direction of the detour vector with the barrier rotated through 45°

In this crucial test, zero-vector ants encountered the familiar barrier rotated through 45° compared with its orientation during training (Fig. 4). This experimental design enabled us to distinguish between two alternative ways in which local directional information associated with the barrier could be stored in the brain of the ant. The first possibility is that the direction of the detour vector is defined egocentrically with respect to the previous walking direction of the ant along the barrier (74° to the left or right of the barrier). The second is that it might be encoded allocentrically in geographical terms (46° west or east of north) and, hence, be independent of the orientation of the barrier. The ants clearly behaved according to the former hypothesis. As shown in Fig. 5, their detour vector was rotated by almost the same angular amount as was the barrier.

Tests without a barrier

If zero-vector ants were released within the test area without a barrier, their search patterns were symmetrically arranged around the point of release (Wehner and Srinivasan, 1981). Hence, the ants did not move in any preferred direction while they were searching (Fig. 6).

Discussion

This study attempted to determine whether directional information associated with landmark obstacles (in the following termed the ‘detour vector’) is stored allocentrically (as a specific compass direction) or egocentrically (as a direction relative to the locomotor course taken by the ant around the obstacle). Ants were trained to detour around a barrier that obstructed the route between an artificial feeder and the nest. By confronting zero-vector ants with the barrier at a remote test area, we were able to show that the ants associated local directional information with this obstacle. The barrier-bound detour vector pointed towards the position of the nest relative to the barrier (Figs 2, 3). If the ants encountered the familiar barrier rotated through 45° at the test area, they exhibited a detour vector with its direction rotated through the same amount as the rotated barrier (Figs 4, 5). Tests with ants released at the test area without any barrier showed that the ants were not influenced by possible orientation cues such as distant landmarks, wind direction or the presence of the experimenter (Fig. 6).

According to the hypothesis that detour vectors are stored as a constant bearing as ‘local vectors’ *sensu* Collett et al. (1998), the direction of the detour vector should have been the same irrespective of whether the barrier had been rotated (see Introduction, hypothesis 1). This was not the case. There are two possible explanations to account for this result. First, the ants might have remembered a constant direction relative to their previous walking direction along the barrier and thus might have defined the direction of the local vector within an

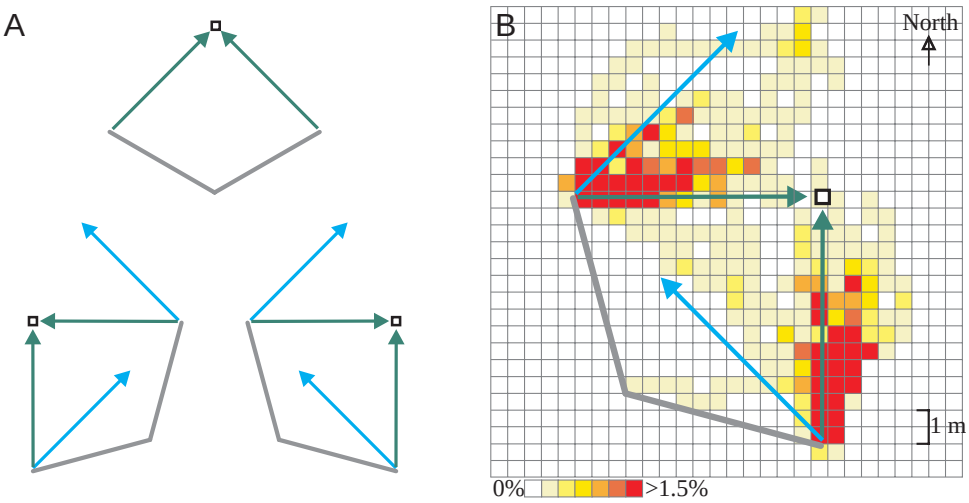

Fig. 4. Detour vectors associated with rotation of the barrier through 45°. (A) Top: barrier oriented as during training; the green arrows point to the position of the nest relative to the barrier (□). Bottom: barrier rotated through 45° to the west (left) and east (right); the arrows indicate the hypothetical directions of detour vectors according to hypothesis 1 (allocentric system of reference, blue) and hypothesis 3 (egocentric system of reference, green). (B) Zero-vector ants were released at the tip of a barrier rotated either to the west (left side N=9, right side N=9) or to the east (left side N=13, right side N=12). The path density histogram shows the trajectories from the east-rotated barrier together with the mirror-reversed trajectories from the west-rotated barrier. For further explanation, see Fig. 2.

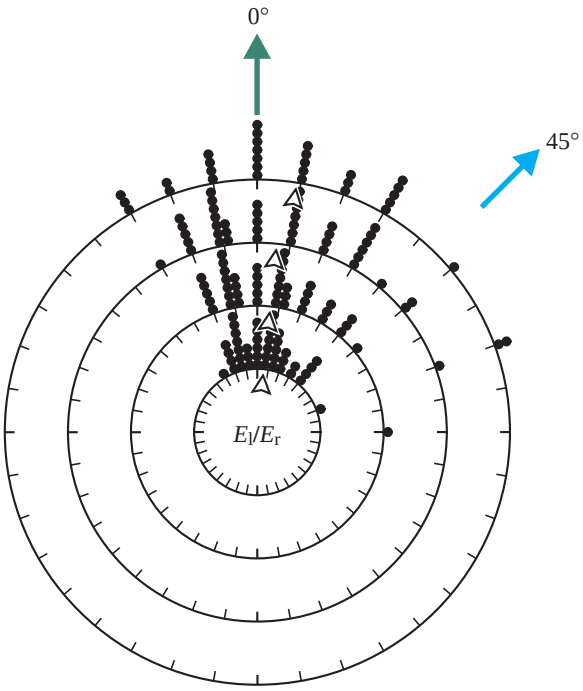

Fig. 5. Angular distribution of detour vectors associated with the rotated barrier. Detour vectors of zero-vector ants are superimposed and rotated in such a way that 0° marks the direction of the detour vector defined within an egocentric system of reference (hypothesis 3, green arrow). The arrow at 45° indicates the direction of the detour vector defined within an allocentric system of reference (hypothesis 1, blue arrow). The filled circles represent the first intersections of the trajectories of the ants with concentric circles (radii 1, 2, 3 and 4 m) centred on the end of the barrier (E_l/E_r). The mean directions (arrowheads) do not deviate from 0°, but they are significantly different from 45°. Statistical details for the 3 m circle: mean angle 7.0°; *r*-value 0.926; number of ants 42; 95 % confidence limits 359.9–14.1°.

egocentric system of reference (see Introduction, hypothesis 3). Alternatively, the sight of the landmark might have guided the ants (see Introduction, hypothesis 2). An example of the latter hypothesis was recently reported using a somewhat similar experimental paradigm. In this case, the obstacle consisted of a large black wall placed at right angles to the home vector of the ant (Collett et al., 2001).

Compared with the obstacle used in the present study (sand-coloured, height 5 cm, visual angle seen from the feeder 0.4°), the obstacle in the wall experiment was very conspicuous (black, height 50 cm, visual angle seen from the feeder 5°). This difference affected the behaviour of the ants when they approached it during training. In the experiment using a black wall, most of the ants returning from the feeder (eight out of 11 recorded training trajectories) headed directly towards the end of the wall, indicating that the sight of the black wall guided the trajectories of the ants on their entire homing trip. In contrast, ants trained with an inconspicuous barrier, as in the present experiments, never took a shortcut to the end of the barrier. Even after lengthy training, they always ran first to a point close to the tip of the V-shaped barrier and then walked along the obstacle before they finally turned round the end. The barrier seemed to be noticed only after the ants had approached it closely. After the ants had turned round the edge of the barrier, it became inconspicuous because of the ramp of sand attached to the nest-side of the obstacle. Hence, we can exclude hypothesis 2 and conclude that the directional choices of the ants seem to be defined within an egocentric system of reference (hypothesis 3).

The existence of hypothesis 3 detour vectors associated with a running direction along an almost invisible obstacle can also be inferred from other recently published data (Collett et al., 1998). In these experiments, desert ants were trained to run the first part of their homeward journey from a feeder to the nest inside a narrow east-pointing channel that forced them to deviate from their straight homebound path. Having left the channel, the ants had to make a 90° turn to the right and run further in this southward direction to reach their nest (Fig. 7A). Since the channel was hidden in a trench, visual stimuli were absent after the ants had left the channel. Zero-vector ants were tested in channels of different lengths rotated through 45°. If the test channel had the same length as during training, the ants behaved according to either hypothesis 1 or hypothesis 3: half walked southwards, while the others made a 90° turn to the right at the end of the channel (Fig. 7B). Ants released in a test channel half the length of the training channel, however, seem to follow a compromise course (Fig. 7C). Only if the rotated test channel was reduced to a quarter of the training length did the ants display allocentric local vectors (hypothesis 1, Fig. 7D).

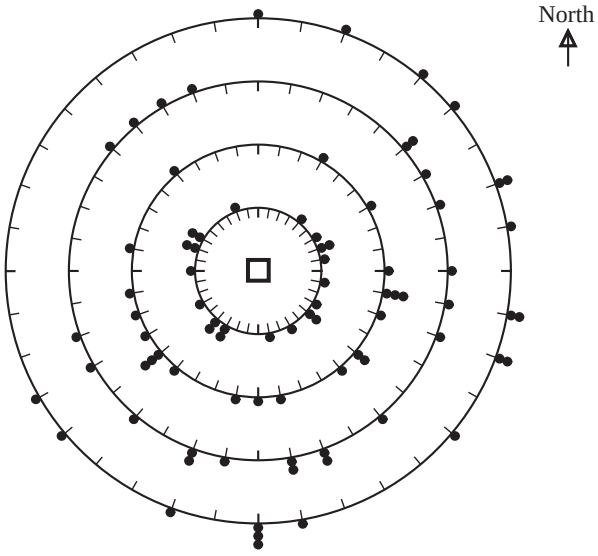

Fig. 6. Angular distribution of zero-vector ants released within the test area without barrier. The ants (N=22) were released within a test area devoid of landmarks, and their trajectories were recorded for 5 min each. The first intersections (filled circles) of their trajectories with concentric circles (radii 1, 2, 3 and 4 m) centred on the point of release (□) do not show any directional preference (P>0.2 for all circles, Rayleigh test).

In addition, clear allocentrically defined local vectors were found in training situations in which distinct landmarks (small black cylinders with a diameter of 20 cm and varying heights between 20 and 53 cm) were used. The cylinders flanked the first part of the route between the feeder and the nest during training and did not force the ants to deviate from their home vector course. The local directional information associated with the landmark panorama thus coincided with the direction of the home vector. If the whole array was rotated compared with the training orientation, the ants exhibited allocentric local vectors (see fig. 4 in Collett et al., 1998). In the present study, however, the compass direction of the detour vector associated with the barrier differed considerably from the direction of the global home vector computed at the feeder (which was still stored in the memory of the ant) (see Fig. 8). Hence, it is possible that the ants rely more heavily on egocentric information (hypothesis 3), the more local and global vectors deviate from each other.

One might regard the behaviour of the ants as they detour around a familiar obstacle as a kind of motor learning. The motor learning hypothesis (Stamps, 1995) states that animals may learn serial motor programmes and thus increase their ability to move rapidly in a home range containing obstacles or barriers to locomotion. Seen in this light, the consistency shown by the ants in choosing a particular detour side round the barrier and their constant walking distance along this obstacle before passing it are prerequisites for exhibiting a motor programme. The motor programme in the present training situation might consist of the following rules once the ant encounters the barrier: turn to the left (or right) and run along the barrier for approximately 5 m; then, if the end of the barrier is reached, turn through 74 ° to the right (or left) and run further in this direction.

The ants in our experiments might even have relied on a fixed motor sequence on their entire return trip to the nest because, during training, they were constantly kept from following their home vector by the presence of the barrier. Some vertebrates are able to learn fixed pathways in a cluttered, familiar environment without reverting to external signals; for example, shrews (Grünwald, 1969), rats (Gallistel, 1990) and hamsters (Georgakopoulos and Etienne, 1994). A similar behaviour was reported for honeybees trained to follow a complex route through a series of obstacles to reach a feeder. After the obstacles had been removed in a test, the bees continued to fly the same detour trajectory that they had followed during training when the obstacles were present (Collett et al., 1993).

The desert ants behaved differently in a corresponding test situation: if the ants that had been trained with the barrier were released at the test area without any barrier, they followed their global home vector (feeder→nest) although they had never been able to do so during training (Fig. 8). The mean length of their homebound runs within the test area (13.1±2.7 m, N=18) was not significantly different from the net foraging distance (13 m, P=0.9, t-test). The detoured homebound path was not, therefore, governed solely by a stereotyped sequence of motor instructions but was initially

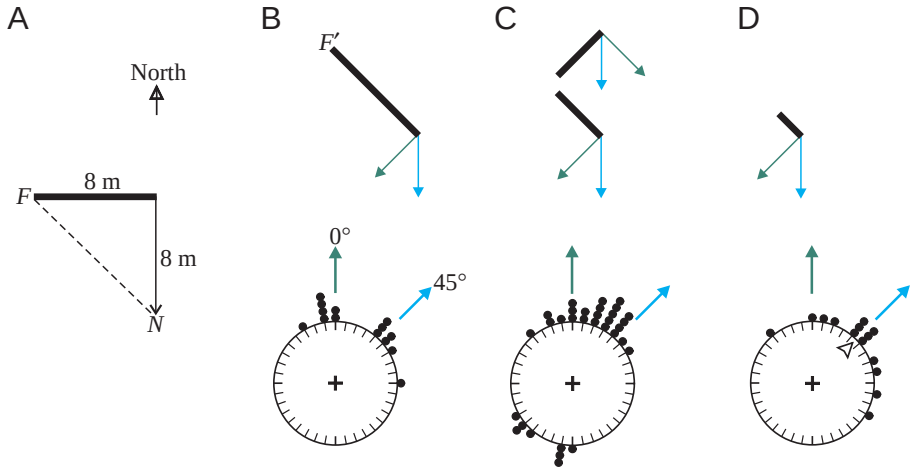

Fig. 7. Detour experiments with a channel. Recently published data (see fig. 3d–g in Collett et al., 1998) were re-evaluated according to the method used in the present study. (A) Training array. Desert ants were trained to travel the first half of their homeward journey from a feeder F to the nest N inside an east-pointing channel (marked by the heavy black line) hidden in a trench. The ants were therefore forced to deviate from their straight homebound path (indicated by the dashed line). The thin arrow marks the paths taken by ants when travelling from the exit of the channel southwards to N over open ground. (B–D) Test situations (top) and results (bottom). Ants were captured close to the nest entrance and released at a feeder F' inside test channels of different lengths (B, 8 m; C, 4 m; D, 2 m). The channels were rotated through 45 ° to the south (B, C and D) or north (C). The arrows indicate the hypothetical directions of detour vectors defined in egocentric (90 ° relative to the channel, green) and allocentric (south, blue) systems of reference. Circular diagrams show the angular distributions of the trajectories of the ants after they had left the rotated channels. Dots represent the first intersections of these trajectories with a circle (radius 1 m) centred on the exit of the channel (cross). Runs that did not reach this 1-m circle were excluded from the evaluation (B, 3 runs out of 17; C, 11 runs out of 43; D, 11 runs out of 25). The remaining trajectories are superimposed in such a way that 0 ° marks the direction of detour vectors defined in egocentric systems of reference and 45 ° marks detour vector direction using allocentric systems of reference. In B and C, the angular distributions seem to be bimodal, so mean directions could not be calculated. In D, the mean direction (arrowhead) coincides with the allocentrically defined direction of the detour vector (hypothesis 1) but deviates significantly from the egocentrically defined one (hypothesis 3; mean angle 45 °; r-value 0.970; number of ants 14; 95 % confidence limits 23–67 °).

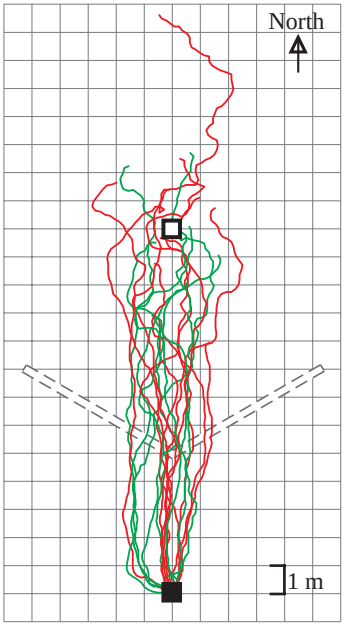

Fig. 8. Trajectories of vector ants released within the test area without a barrier. The ants (N=18) were captured at the feeder and released within a test area devoid of landmarks. During training (see Fig. 1), the ants chose to detour around the left (N=10, red) or the right (N=8, green) end of the barrier. The dashed lines mark the fictive position of the barrier relative to the point of release (■). The trajectories are shown until the ants started to search. □, fictive position of the nest relative to the point of release.

guided by the home vector, which is thought to be defined within an allocentric system of reference, the skylight compass (Wehner, 1982). Hence, desert ants seem to be able to use both allocentric and egocentric systems of reference during a single foraging excursion if they encounter obstacles that force them to deviate from their straight homing course.

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