Report
Ant Navigation: One-Way Routes Rather Than Maps

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Summary

In recent years, there has been an upsurge of interest and debate about whether social insects—central-place foragers [1] such as bees and ants—acquire and use cognitive maps, which enable the animal to steer novel courses between familiar sites [2–4]. Especially in honey bees, it has been claimed that these insects indeed possess such "general landscape memories" [5] and use them in a "map-like" way [6]. Here, we address this question in Australian desert ants, *Melophorus bagoti*, which forage within cluttered environments full of nearby and more distant landmarks. Within these environments, the ants establish landmark-based idiosyncratic routes from the nest to their feeding sites and select different one-way routes for their outbound and inbound journeys. Various types of displacement experiments show that inbound ants when hitting their inbound routes at any particular place immediately channel in and follow these routes until they reach the nest, but that they behave as though lost when hitting their habitual outbound routes. Hence, familiar landmarks are not decoupled from the context within which they have been acquired and are not knitted together in a more general and potentially map-like way. They instruct the ants when to do what rather than provide them with map-like information about their position in space.

Results and Discussion

In a stimulating and provocative account, Gould [2] has claimed that honey bees acquire and use cognitive maps. Generally, such mental survey maps are geocentric representations, in which the spatial relations between multiple places are defined in cartographic ways. In operational terms, animals are said to use such mental analogs of topographic maps if they are able to compute and steer novel courses between familiar sites within their habitual foraging or home range areas. After quite some conflict of data and ideas about whether honey bees were able to do so [3, 4, 7–10], Menzel and his coworkers have recently tried to answer this question in the affirmative [5, 6]. On the basis of their radar-tracking records of flying honey bees, they argue

that these insects possess "general landscape memories," which enable them to return to their home place from arbitrary locations within their hive environments. Alternative views hold that social insects such as bees, wasps, and ants do indeed make intensive use of landmark information [11–15], but do so by structuring their spatial knowledge in procedural rather than positional ways. Seen in this light, landmarks are used to instruct the animal when to do what, i.e., when to recall particular steering commands, rather than provide it with map-like, topographic information about its position in space [16].

Here, we address this question by taking advantage of the amazing landmark-based navigational performances of visually guided ants. Within the cluttered environment inhabited by *Melophorus* desert ants of central Australia, we record the foraging (outbound) and homing (inbound) journeys of individually marked ants over periods of days, then displace these ants to various points within their foraging area and record their subsequent search and homing paths. We show that within their foraging ranges, which are full of nearby and more distant landmarks, the ants acquire and use rich memories of visual stimuli, but they employ this information in strictly procedural and context-dependent ways. This is the case even though we have deliberately applied an experimental paradigm in which the ants were encouraged to acquire landmark information in rather versatile ways, especially by selecting different routes for their outbound and inbound journeys.

Because of nest-based and feeder-based barriers (height of border = 8 cm), the ants were forced to select different routes for their outbound and inbound journeys (Figure 1A). After the barriers had been established, a sufficiently large number of ants arrived at the feeder without any artificial training procedures involved by the experimenter. Upon their first arrival at the feeder, the ants were marked individually. The feeder-based barrier prevented them from homing along their vector courses directly, but deflected them to the left of these courses. Immediately after their first round trip, they established their own idiosyncratic routes for either way. One out of in total 57 examples recorded in 57 ants is given in Figure 1B.

First, let us mention in passing that there is one feature common to all these paths. After the inbound ants had turned around the free (eastern) edge of the feeder-based barrier, they all did not choose the direct course toward the nest, but deviated from that course to the right. Peculiar as this might appear at first glance, this is exactly what the ants' path-integration algorithm, as derived from the ants' behavior within an array of channels [17], would lead one to predict [18]. If during its outbound journey the ant experiences a bias of turns to, say, the right (as it has been the case in our experimental setup), their inbound trajectories should deviate toward the right as well. The observation that the *Melophorus* ants indeed turned consistently toward the right is
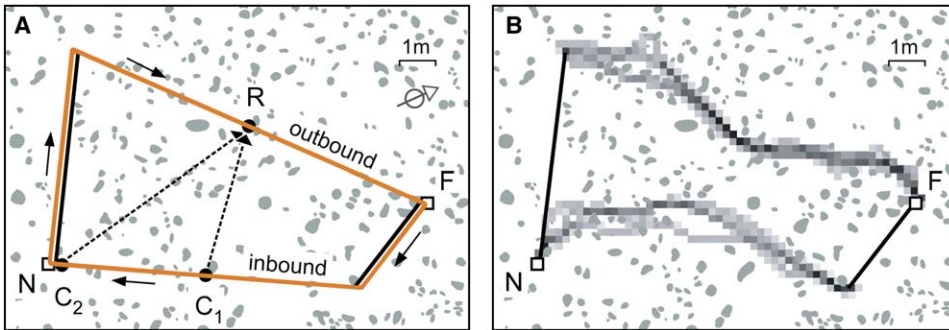
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Figure 1. Experimental Paradigm

(A) Setup. Two barriers (black bars) were used to force the ants to acquire different outbound and inbound paths (orange round-trip lines) from the nest (N) to the feeder (F) and back to the nest. C_1 and C_2 mark points at which inbound ants were captured and displaced to the release point (R). The light-green spots indicate buffle grass tussocks. The open arrow symbol depicts north.

(B) Example of a path-density plot of three round-trip journeys performed by one ant. The plot depicts the frequencies with which the ant has covered 0.2×0.2 m^2 pixels of terrain during its three round trips.

a nice open-field confirmation of the path-integration hypothesis, but it has no implication whatsoever for the questions addressed in the present account.

After the foragers had acquired their specific routes, and after the trajectories of at least three of their specific round trips had been recorded, the experiments started. Inbound ants returning from the feeder were displaced to their outbound routes and released there (at location R in Figure 1). In particular, two types of experiments were performed. After the ants had left the feeder-based barrier, they were captured (1) either half-way along their unconstrained inbound route (at location C_1 in Figure 1A), i.e., when they had not yet run off their global vector ("vector ants"), or (2) after they had fully run off this vector (at location C_2 in Figure 1A) and were just on the point of vanishing into the nest ("zero-vector ants"). Upon release, exactly at a place that the particular ants had passed during their preceding outbound runs (at R in Figure 1A), the vector ants immediately headed off in the direction of their vector courses (Figure 2A, V in Figure 3), as they did when displaced to completely unknown territory (Figure 4). Neither did they follow their outbound route in the opposite

direction (R_{out} in Figure 3), nor did they head directly toward the nest (N in Figure 3). Both R_{out} and N lie well beyond the 95% confidence limits of the directions chosen by the ants.

However, this result in itself does not rule out yet the possibility that the ants were able to retrace their steps by following the sequence of landmarks experienced on their way out in reversed order (i.e., follow R_{out}) or that they were able to compute novel shortcuts (i.e., follow N). It might merely imply that if the ant's path integrator has not yet been reset to zero, vector navigation is still the ant's dominant means of navigation suppressing route following or any kind of map-like behavior.

It is here that the zero-vector ants captured at C_2 directly adjacent to the nest entrance come into play. If these ants, which had already completed their vector courses, were displaced to their outbound routes, they, too, did not retrace their steps along these routes, but engaged in systematic search behavior (Figure 2B). During these systematic searches, they repeatedly crossed their outbound routes, but scarcely showed any sign of recognizing them. In only four out of 41 cases in which they happened to hit these routes, they apparently
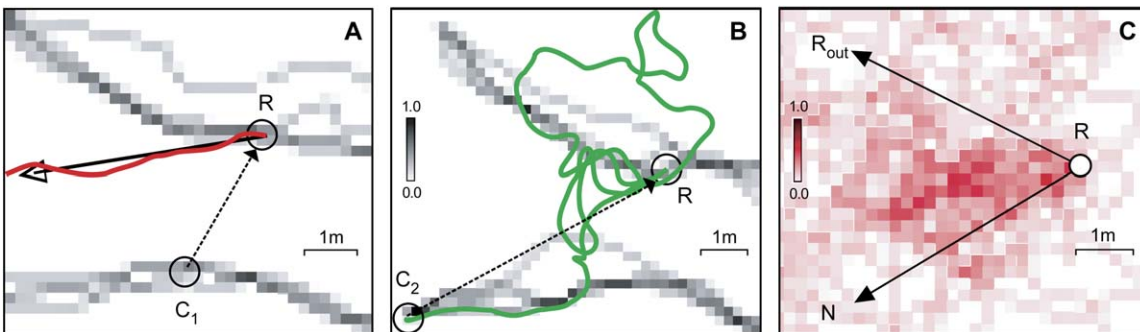

Figure 2. Homing Behavior of Ants Provided with Different States of Their Path Integrator

(A and B) Home runs of "vector ants" ([A], one example: red line) and "zero-vector ants" ([B], one example: green line) displaced from the capture point (C_1 and C_2, respectively) to the release point (R). The habitual outbound and inbound routes (upper and lower trace, respectively) are indicated by gray shading (see Figure 1B). In (A), the open arrow indicates the direction read out from the ant's path integrator.

(C) Search densities of 16 "zero-vector ants." The black arrows mark the directions that the ants should have taken had they reversed their outbound paths (R_{out}) or steered the direct course toward the nest (N). The intensity of the red shading reflects search density.
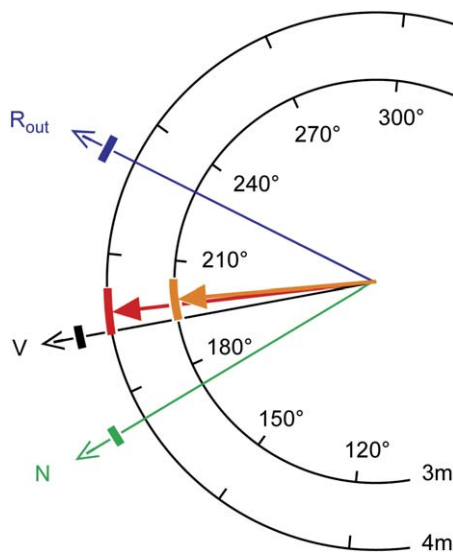
Figure 3. Directional Choices Taken by "Vector Ants"

The ants were displaced from their inbound route, i.e., captured at C_1, to their outbound route, i.e., released at R (see Figures 1A and 2A). The blue, black, and green arrows mark the hypothetical directions that the ants could have taken: the reverse outbound route (R_{out}), the vector course (V) that would lead the ants from C_1 to N, and the novel shortcut course (N) that would enable the ants to reach the nest directly. The ants' actual choices (recorded at distances of 3 m and 4 m from the start at the release point, R) are depicted by the heavy orange arrows. In all cases, the tangential bars mark the 95% confidence limits. n = 20 ants. Because the release points vary among the ants tested in this paradigm, the directions R_{out}, V, and N have to be computed for each ant separately; 0° is north.

following behavior of inbound ants hitting their inbound or outbound paths was highly significant (p < 10^{-4}, χ^2 test, n = 52). Clearly, inbound (homebound) ants do not follow, in reverse order, the sequence of landmarks that they have experienced along their outbound paths. Nor are they able to compute novel shortcuts between two familiar places, in this case between place R, which they have experienced several times during their outbound journeys, and their familiar nest site, N.

Even if the inbound ants did not follow the landmark channel used on their way out and did not steer novel shortcuts toward the nest, their search densities were not radially symmetric, as they would have been if the ants had been transferred to unknown territory [18, 19]. In spite of being rather broad indeed, the search patterns were clearly biased toward the direction in which the nest would have been had the ants not been displaced from C_2 to R (Figure 2C). This directional bias could have only been caused by some larger landmarks, *Acacia* trees, which were present in a loosely scattered, irregular way within the ants' foraging grounds. These larger landmarks presented the animals with an irregularly shaped horizon skyline that could have provided them with information about the general direction toward the nest. As the ants' search behavior (Figure 2C) clearly demonstrates, the ants have exploited the optical information inherent in the array of these landmarks, but they have not used this information and/or the information defining their habitual routes to compute the novel course from R to N. Among 40 ants whose search trajectories had been recorded for 3 min each, there was no single one that during its extensive search behavior had moved toward the actual location of its central place, the nest site. Furthermore, it is very unlikely indeed that the outbound and the inbound information is represented in two separate, noninteracting maps; the ants did not generate novel routes when they were in the outbound (or inbound) mode. Even if close to their habitual routes, the ants continued searching and only followed straight paths when hitting their proper routes.

How do ants store, integrate, and finally retrieve spatial information about the positions of landmarks in their nest environs? A promising way to tackle this question is to study how ants acquire spatial information during the
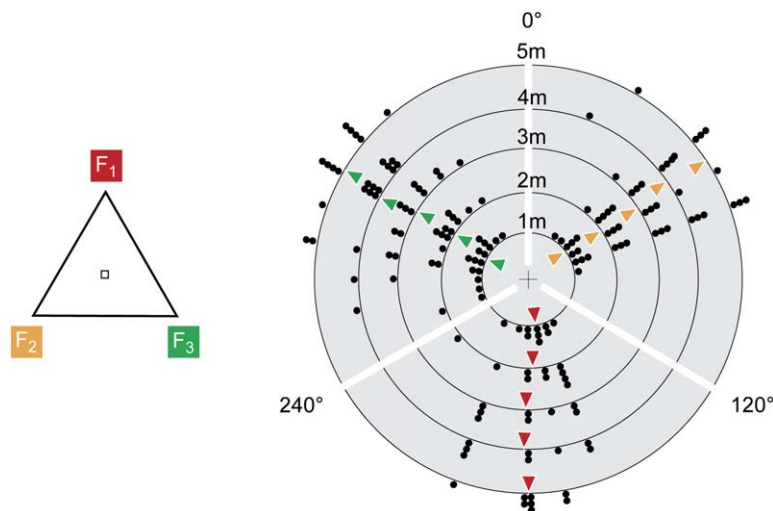
followed them for a very short while, but soon left them again. In the remaining 90.2% of the cases, the ants unhesitatingly crossed these paths and continued their systematic searches. In contrast, when they happened to hit their inbound routes, which were located far more distant from their points of release than their outbound routes had been, in 63.6% of the 11 cases in which this occurred, they immediately channelled in and without breaking out again followed these routes until they reached the nest. The difference in the route-

Figure 4. Vector Navigation within Unfamiliar Arrays of Landmarks

At left is the training paradigm. Three groups of ants belonging to the same colony (white square) are trained to three feeders (F_1, F_2, and F_3), each located at a 10 m distance apart from the colony and separated from each other by an angular distance of 120°. At right is the test result. Shown are the directional choices of ants displaced from the three feeders to an unfamiliar test area in which the distribution of grass tussocks completely differs from that in the training area. The directions taken by the ants (mean angles at circular standard deviation for 5 m circle: 179.96° ± 8.65°, 300.87° ± 11.89°, 56.32° ± 13.19°) do not differ significantly from the hypothetical vector courses 180°, 300°, and 60° for the F_1, F_2, and F_3 ants, respectively.

course of their foraging lives. If an ant starts to venture out into unfamiliar territory, path integration is its only means of acquiring such information. By continually recording the rotational and translational components of its movements, it keeps a record of its net distance and direction from its point of departure, so that at any one time it can make a straight-line return to the nest (during inbound runs) or a frequently visited feeding site (during outbound runs). The ant's path integrator does not require any memory of visual landmarks encountered during previous journeys (for a recent review on path integration in insects, see [20]). It works even if the ants are later tested in terrains that are completely free of landmarks (e.g., in *Cataglyphis* [21]) or covered with arrays of landmarks that are completely different from the ones present in the training area (Figure 4). In the latter case, the *Melophorus* ants have been trained to a feeder within one part of the low-shrub desert and tested after displacement to another part of the desert, in which the array of landmarks differed from that in the training area.

However, in addition to integrating their paths, the ants are able to employ landmarks for guiding their ways along fixed routes to frequently visited feeding sites (*Cataglyphis* [11, 22, 23], *Melophorus* [12]). These landmark-defined routes are acquired while the ant's path integrator is running, but the individual landmark memories can later be retrieved independently of the state of the path integrator with which they have been associated during the acquisition phase of learning [12, 23]. The possibility of uncoupling of landmark-based and vector-based information after the acquisition phase has occurred is considered to be a decisive prerequisite for landmark memories being later used in a map-like way [10, 24, 25].

In the present experimental paradigm, the ants were trained to follow different routes during their outbound and inbound journeys. These routes turned out to be one-way (uni-directional) routes. The information about the landmarks defining these routes could be used by the ants only in the sequence in which the ants had acquired this information during their outbound and inbound journeys. This is in accord with the observation that local vectors or trajectories can be linked to particular landmark views [26, 27]. The area in which these adjacent routes were acquired was rich in nearby (local) and more distant (global) landmarks, tussocks and trees, respectively. As our results show, the ants make use of both types of visual information, but do so in strictly route-bound and context-specific ways. If inbound ants are displaced to their outbound routes, they either follow their path-integration course (if the path integrator has not been reset to zero) or exhibit systematic search behavior (if the path integrator has been reset to zero), but they do not retrace their steps along their outbound routes. In contrast, regardless of the state of their path integrator, if they hit their inbound routes, they immediately recognize them, channel in, and follow them until they reach the nest ([12] and this study). Hence, *Melophorus* ants do not only form chain-like memories of landmark sequences, but prime these memories to particular (inbound and outbound) states of their foraging round trips. Of course, our findings do not imply that ants during their outbound trips were

not able to acquire information later used in homing. In fact, the rotational turn-back movements observed in foraging wood ants (*Formica rufa* [28, 29]) and the frequent 360° full rotations performed by outbound desert ants (*Cataglyphis bombycina* [30]) are likely candidates for types of behavior by which the animal could acquire exactly this kind of information (maybe alongside skylight information picked up by the dorsal rim area of the eye [20]). Our findings, however, do imply that the long-term visual memories of narrowly defined paths through cluttered environments are not decoupled from the context within which they have been acquired and are not knitted together in a more general, context-independent, and potentially map-like way. Of course, because we have not been able to record the exact number of (at least three) round trips that the ants had performed prior to the experiments, we cannot decide whether a shorter or longer training period would have influenced the ants' behavior in any predictable way (see, e.g., the effect of cumulative experience in visual discrimination tasks in honey bees [31]). However, given that the behavior of all 57 ants tested was very uniform indeed, we do not think that varying numbers of round trips preceding the experiment would have led to different results (see also [12]).

In their influential account "The Hippocampus as a Cognitive Map," O'Keefe and Nadel [24] distinguish a "locale system," which is based on a geocentred mental representation of the spatial relationships among arrays of landmarks, from a "taxon system," in which the animal maintains specific egocentric relationships with sequences of landmarks. If we stick to this dichotomy, *Melophorus* ants certainly employ the latter system.

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