

Path Integration Provides a Scaffold for Landmark Learning in Desert Ants

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Summary

On leaving the nest [1–9] or a newly discovered food site [10–12] for the first time, bees and wasps perform elaborate flight maneuvers to learn the location of their goal and the lay of the land surrounding it. In all these orientation flights the insects turn back and look [13] at the goal, which they can visually locate by landmark cues directly defining the goal. Here we show that Namibian desert ants, *Ocymyrmex*, when learning new landmarks in the neighborhood of the goal, acquire this landmark information when they cannot see the goal. They do so by performing well-choreographed rotation movements integrated in spiral-like “learning walks.” Within these rotations, short (about 150 ms) stopping phases occur, during which the ants orient themselves in the direction of the nest entrance. On the barren sand surface the nest entrance is invisible, so the ants can aim at it only by reading out the current state of their path integrator [14–17]. Hence, they could associate “snapshot” views [18–20] taken of the nest surroundings during the stopping phases with path integration coordinates. In bees and ants such associations have often been discussed, but evidence has not been obtained yet [15, 20–22].

Results and Discussion

Occurrence and Significance of Learning Walks

Central place foragers such as bees and ants use path integration as their predominant system of navigation [14–16]. However, because this system is inherently prone to cumulative errors [17, 23, 24], visual landmarks are necessary for reliably locating the goal. In desert ants, which have become model systems for the study of animal navigation [25], such visual place recognition is based on view-based image-matching (“snapshot”-matching) routines [18, 20, 26]. Here we investigate how the necessary landmark information is acquired during well-structured learning walks.

The thermophilic ants *Ocymyrmex robustior* inhabit the bare sandflats of the Namib desert, where their path integration system brings them back to the neighborhood of their nest, a tiny hole level with the ground. In the absence of any landmarks, say, a stone here and a pebble there, the ants have to perform lengthy and sinuous search movements to finally pinpoint their goal, but in the presence of even a single landmark they hit the nest entrance rather directly (Supplemental Information available online).

In our experiments, departing ants were confronted with a new landmark within their otherwise featureless visual environment: a black cylinder positioned 0.4 m away from the nest entrance. When leaving the nest under these new

stimulus conditions, the ants slowly circle the nest entrance in a spiral-like way and intermittently stop to rotate about their vertical body axis (Figure 1A). On their first departure, they may perform up to 30 such “pirouettes” within a distance of less than 2 m from the entrance hole. In the subsequent foraging trips, the number of these rotations declines exponentially, and the runs between these rotations straighten out rapidly (Figure 1B). Obviously a quick learning process has occurred, freeing the ants from extensive search movements and enabling them to return to the nest directly. When the landmark is removed while the ants are on their foraging journeys, the search behavior and the subsequent orientation pirouettes immediately recur (Figure 2).

Fine Structure of the Rotatory Orientation Movements

Even with the naked eye, one can observe that a short stopping phase is included into each rotation movement. Video recordings reveal the details. Having stopped their forward runs, the ants rotate either clockwise or counterclockwise about their vertical body axis (“turning-in”: velocity 170°s^{-1} , 95% C.I. $161\text{--}179^{\circ}\text{s}^{-1}$, $n = 101$), stop quickly (“stopping phase” during which the ants stand still: 150 ms, 95% C.I. $130\text{--}170$ ms, $n = 128$), and then rotate back until their longitudinal body axis has roughly reached the orientation in which they had started their rotatory movement (“turning-out”: velocity 423°s^{-1} , 95% C.I. $401\text{--}445^{\circ}\text{s}^{-1}$, $n = 101$; Supplemental Information). Often, the turning-in phase is followed by a much smaller second one in the same direction, as if the ant tried to adjust its longitudinal body axis more precisely in a particular way. This is indeed what happens. During the stopping phase, the ants aim at the location of the invisible nest entrance rather than the landmark (Figures 3 and 4; Supplemental Information). Obviously, whereas the slow turning-in movements lead to adjusting the ant’s longitudinal body axis with the ant nest direction, the fast turning-out movements are just to re-establish the ant’s former angular position.

Frame of Reference

What navigationally relevant visual information does *Ocymyrmex* extract from its environment while it performs its learning walks and rotation movements, and what is the framework within which this information is obtained? In addressing these questions, let us first have a look at the flight maneuvers that bees [1, 5, 6, 9, 11–13] and wasps [2–5, 7, 8, 10] perform when they first leave the nest or a newly discovered food site, i.e., a place to which they intend to return. These orientation flights, which have been recorded and analyzed most extensively and beautifully in *Cerceris* wasps by Jochen Zeil and his coworkers [3–5, 7, 8], consist of a series of arcs roughly centered on the goal and increasing in size as the insect moves away from the goal. In particular, during these pivoting flight maneuvers, the wasps systematically increase their horizontal distance from the nest and their height above the ground. In the learning flights of orchid bees *Euglossa cyanipes*, stationary periods occur, in which the bees hover on the spot and during which they might acquire snapshot views [27]. Wasps might do so at the ends of their flight arcs when the rotational velocities are low [28]. In all these orientation

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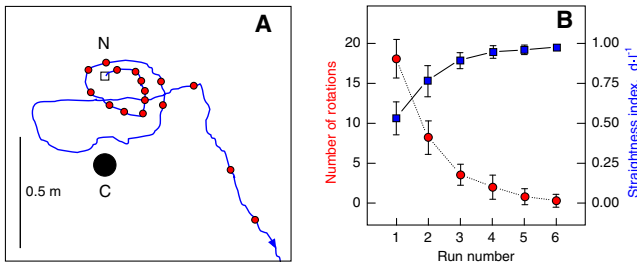


Figure 1. Learning Walks and Pirouettes of *Ocymyrmex* Desert Ants
(A) The first outbound run (learning walk) of an ant after a landmark, a black cylinder, C, had been installed 0.4 m north of the nest, N. The red dots mark the locations where rotatory orientation movements (“pirouettes”) occurred. (B) The number of rotations (red circles) decreased and the straightness of the runs (blue squares) increased, after the ants had first encountered (run no.1) a new landmark in the neighborhood of their nest entrance. Means \pm 95% confidential intervals are given. $n = 63$ runs recorded in 19 ants.

flights, the insects having turned back immediately after take-off [1, 3, 10, 13] can visually locate the goal by landmark cues directly defining the goal.

Walking wood ants, *Formica rufa*, behave differently in so far as they turn back and look at the landmark placed at some distance from the invisible goal—a food site—rather than at the goal itself [29]. The authors of this study assume that by not being able to move sideways and obliquely, as flying bees and wasps can do [12], ants should have a tendency to match landmarks viewed in the frontal visual field. The pirouetting *Ocymyrmex* ants do not exhibit this tendency, but always align their body axis with the direction of the invisible nest. They can do so only by reading out the current state of their path integrator (Supplemental Information). Most probably it is during this alignment phase that a “snapshot” is taken and the view containing the laterally positioned landmark is stored. Of course, behavioral data cannot prove directly that the state of the path integrator—be it the directional component alone or the full vector state—is memorized and associated with the view. Nevertheless, indirect evidence that the ants indeed acquire landmark information while they are stopping and

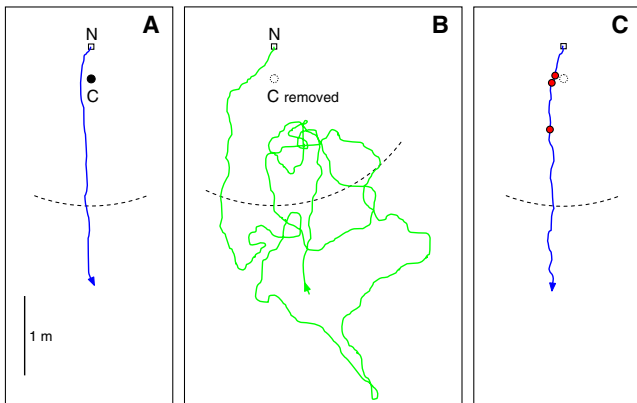


Figure 2. Reappearance of Rotatory Orientation Movements after Removal of Landmark
Rotation movements (red dots) during an ant’s outbound run reappeared (C) after the ant familiar with a landmark (A) had not encountered this landmark on its preceding inbound run (B). Outbound and inbound trajectories are shown in blue and green, respectively. N, nest entrance; C, landmark (cylinder).

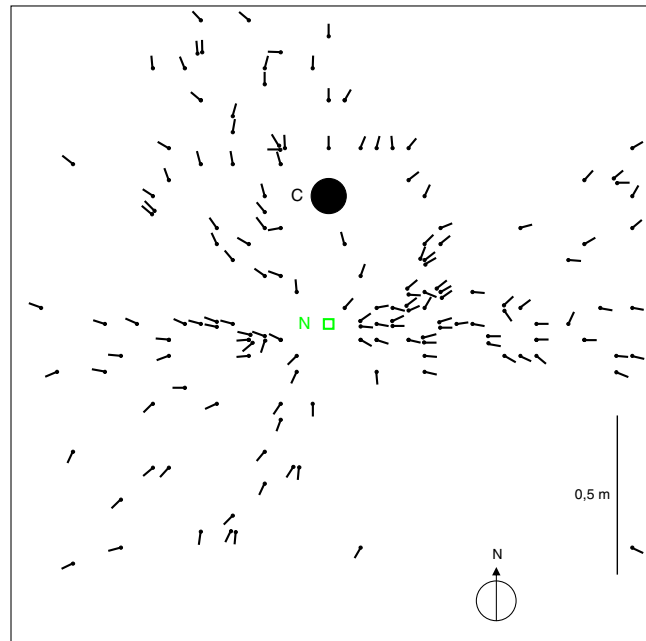


Figure 3. Locations and Viewing Directions of the Ants during the Stopping Phases of the Rotation Movements
The ball-and-stick icons indicate the head positions and the orientation of the longitudinal body axes of the ants during the stopping phases. The uneven distribution of the data points across the 4 m² area centered around the nest entrance, N, is due to recording biases. C, landmark. $n = 154$.

looking toward the nest comes, for example, from the immediate recurrence of circuitous search behavior whenever the familiar landmark is no longer present during the subsequent inbound run (Figure 2).

The overarching question now is what use the ants actually make of these multiple nest-oriented views when later returning to the nest. Do they choose among the various snapshots

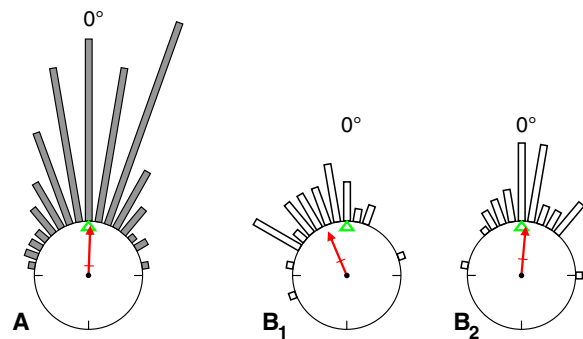


Figure 4. Orientation of the Ants’ Forward Directions during the Stopping Phases
The viewing (forward) directions of the ants are given relative to the direction of the nest (open green arrowhead, 0°).
(A) One-step turning-in movements. $\phi = 1.9 \pm 23.5^\circ$, $r = 0.916$, $n = 163$.
(B) Two-step turning-in movements with B₁ and B₂ referring to the first (large) and the second (small adjustment) turn. Clockwise rotations. The counterclockwise rotations were mirror-imaged on the 0°–180° axis and superimposed. $\phi_1 = -23.3 \pm 28.4^\circ$, $r_1 = 0.877$, $\phi_2 = 5.4 \pm 23.6^\circ$, $r_2 = 0.915$, $n = 51$. The slight overshooting ($\phi_2 = 5.4^\circ$) of the adjustment turn does not significantly differ from the 0° direction. The length r of the mean orientation vector (ϕ, r) is a measure of variance [36]. The radius of the circles corresponds to $r = 1.0$. The small dash indicates $p < 0.01$ (Rayleigh test).

(templates)? Do they store them all or only a few, e.g., the ones that pertain to the direction in which they finally set out for their foraging journey? Or do they rely on the orientation of the closest stored views to recall the nest direction? A first attempt of answering such questions would be to record the ants' return runs in detail, in order to learn what aspects of the learning walks are reflected in the spatial structure of the subsequent return runs. In their return flights, wasps and bees try to mimic certain features of the dynamics of their learning flights [12]. For example they try to match their current views with the views they have obtained during these learning flights [4, 28]. First observations in *Ocymyrmex* show that the returning ants do not consistently view the landmark from all locations at which they have previously acquired their visual templates. The use of arrays of landmarks rather than only a single mark and recording sequences of outbound and inbound walks might help to clarify this point. Another attempt of answering the question posed above could consist in analyzing the ant's orientation walks theoretically, e.g., within a probabilistic Bayesian framework [30], in order to learn whether the walks are structured to optimally extract metric information from the environment. A recent such study of the orientation flights of bumblebees has shown that this is not the case [31].

In the light of our results, we propose the hypothesis that *Ocymyrmex* uses its path integration system as a reference for acquiring landmark information, i.e., labels snapshots with path integration information, and does so for an entire set of places centered about the goal. This hypothesis might lead to rather far-fetched speculations about the potential use of links established between landmark memories and metric path integration coordinates, as surmised for mammals ([32], see also [33, 34]). At the present state, however, the next and more careful step to be taken is to analyze how the landmark information acquired during the learning walks is used in structuring the ants' subsequent return journeys. As the learning walks include clear-cut events—well-localized pirouettes and stopping phases that can easily be recorded under various experimental conditions—*Ocymyrmex* provides a convenient handle for further investigating one of the crucial questions in the study of animal navigation: how landmark information is acquired, processed, stored, and finally retrieved in the animal's overall system of navigation.

Experimental Procedures

Procedures

Observations of the ants' learning walks were made in January 2005 and 2007, and the experiments and recordings were performed in November 2007 on the Kuiseb sandflats next to the Gobabeb Training and Research Centre (23°34' S, 15°03' E) in the Namib Naukluft area, Namibia. The sandflats are inhabited by *Ocymyrmex robustior*, a medium-sized species of the ant genus *Ocymyrmex* (Myrmicinae), which is considered to be the southern African ecological equivalent of the northern African and Asian thermophilic ant genus *Cataglyphis* (Formicinae) [35].

The nests selected for this study were located on bare ground devoid of any nearby visual signpost available to the ants. A black polyvinylchloride cylinder (height 0.30 m, diameter 0.11 m) was used as an artificial landmark placed at a 0.40 m distance from the inconspicuous nest entrance. In order to facilitate the recording of the ants' walking trajectories on graph paper, a 25 m² grid of white threads was mounted on the sand surface. In addition, a video camera (Sony DCR TRV 60E) was used to record the ants' trajectories ("learning walks") as well as their rotatory orientation movements in detail (25 frames s⁻¹). The camera fixed to a horizontally held metal rod was carried along with the moving ant. In this context, the gridwork of threads enabled the experimenter (1) to maintain a constant orientation of the camera while following the ant, and (2) to transfer the video-recorded trajectories positionally correct on to graph paper. For each orientation

walk of an ant, a straightness index d^{-1} was computed. It represents the ratio of the distance d of the ant's position from the nest entrance (in the present case $d = 2$ m) to the path length l actually covered by the ant. Hence, a completely straight run would yield $d^{-1} = 1.0$.

Statistics

Mann-Whitney U and t tests were used to compare the mean values of two sets of linearly distributed data (distributed either nonnormally or normally, respectively). Circularly distributed data were treated by applying the procedures described in [36]. Throughout the present account, mean orientation vectors are given in polar coordinates with the angle ϕ and the length r describing the ants' mean orientation and the amount of scatter about the mean, respectively. In addition the vector length r allows for the computation of a measure of variance that is equivalent to the standard deviation (SD) of linearly distributed data. The Rayleigh test was used to check for uniformity, i.e., to test whether the data were distributed randomly over the entire 360° range. With the Stephens test and the Watson Williams test, we checked whether the mean orientation angle ϕ of a given data set differed significantly ($p < 0.01$) from an expected fixed value and from the mean orientation angle ϕ^* of another data set, respectively.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and two figures and can be found with this article online at [doi:10.1016/j.cub.2010.06.035](https://doi.org/10.1016/j.cub.2010.06.035).

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