Uncertainty about nest position influences systematic search strategies in desert ants

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Summary

Foraging desert ants return to their starting point, the nest, by means of path integration. If the path-integration vector has been run off but the nest has not yet been reached, the ants engage in systematic search behavior. This behavior results in a system of search loops of ever increasing size and finally leads to a search density profile peaking at the location where the path integration system has been reset to zero. In this study we investigate whether this systematic search behavior is adapted to the uncertainty resulting from the preceding foraging run. We show first that the longer the distances of the foraging excursions, the larger the errors occurring during path integration, and second that the ants adapt their systematic search strategy to their increasing uncertainty by extending their search pattern. Hence, the density of the systematic search pattern is correlated with the ants' confidence in their path integrator. This confidence decreases with increasing foraging distances.

Key words: desert ants, path integration, systematic search behavior, distance, uncertainty, nest position.

Introduction

Foraging desert ants, *Cataglyphis fortis*, return to their nest by keeping a running total of their distance and direction from the nest. This mode of navigation was called path integration by Mittelstaedt and Mittelstaedt (Mittelstaedt and Mittelstaedt, 1982), who provided the first systematic studies of this phenomenon, and vector navigation by Wehner (Wehner, 1982; Wehner, 1983). More recent reviews and considerations on path integration are given elsewhere (Wehner and Srinivasan, 2003; Merkle et al., 2006). By path integration the ants acquire a home vector that enables them to return at any time along the beeline, so to speak, to the nest. However, after having played out their home vector, they do not always arrive exactly at the entrance of their nest, a tiny hole in the desert floor. Even small deviations or inaccuracies within the compass, the odometer or the integration system lead to overall errors that might result in remarkable discrepancies between the tip of the home vector, i.e. the nest position as computed by the ant's path integrator, and the actual position of the nest. This should lead to an increasing uncertainty about the goal with increasing foraging distances. That such an uncertainty can cause a change in behavior has already been shown (Wolf and Wehner, 2005). Wolf and Wehner demonstrated that desert ants when leaving the nest deviate from the direct global vector course with the direction of the blowing wind, and then head towards a food source against the direction of the wind, i.e. they

approach the feeder in a way that enables them to head straight upwind towards the feeder by following the odor plume emanating from it. The upwind approach distance depends on the length of the foraging trip. The authors interpret this behavior as being an error compensation strategy due to navigation uncertainty, and regard it as one tool that outbound ants apply to deal with the errors they perform during path integration. Here we aimed to test ants on their way back from the feeder to the nest, i.e. inbound ants, and tried to quantify the correlation between uncertainty about the path integrator and the length of the foraging runs.

If an ant fails to find the nest after having 'run off' its home vector, it terminates its almost straight inbound run and starts a systematic search for the nest (Wehner and Srinivasan, 1981). During this search *C. fortis* performs loops of increasing radius around the supposed nest position (Wehner and Wehner, 1986). At regular intervals, it reverts to the starting point of the systematic search, i.e. the nest position as calculated by the path integrator, and then changes the direction in which it heads off next. Desert ants as well as desert isopods (*Hemilepistus reaumuri*) spatially broaden their search the farther they have ventured out during their foraging trips (Hoffmann, 1983a) [fig. 3.35 in (Wehner, 1992)].

The ultimate reason for this change of the search pattern with increasing distance of their foraging journeys could be an ongoing accumulation of errors during the egocentric path

integration process. We designed and applied an experimental paradigm, which allowed us to compare the orientation errors resulting from different homing distances with the spatial layout of the subsequent search. By this we investigated whether the search density profile is adapted to the degree of uncertainty inherent in the path integration process. In particular, our experiment was intended to reveal (i) whether different lengths of the foraging paths account for differences in the errors produced by the path integrator, and, if this were the case, (ii) whether *Cataglyphis* ants adjust their systematic search behavior accordingly.

If this again were the case, the search pattern would reflect the ant's degree of confidence in the output of its path integrator.

Materials and methods

The experiments were performed within a salt-pan near Maharès, southern Tunisia (34.58°N, 10.50°E) from June to September 2004. All ants belonged to the same colony, which had not changed its nest location over at least 5 years (Dillier and Wehner, 2004).

Training procedure

Desert ants *Cataglyphis fortis* (Forel 1902, Wehner 1983) were trained to feeders south of their nest (Fig. 1A). The distances between nest and feeder were varied systematically (5 m, 10 m, 20 m, Fig. 1A). All ants were marked at the feeder at least 1 day prior to the tests in order to ensure that the ants used in the experiments had performed a sufficient number of foraging trips before they were tested (Åkesson and Wehner, 2002). There were no obvious landmarks within the range of vision of the foraging ants on their outbound and inbound runs as well as around the nest and the feeder. Thus, the ants had to

rely upon their celestial compass information exclusively, i.e. they had no landmarks to reduce possible errors that had accumulated during path integration.

Test procedure

Our experiment aimed at testing whether the foraging distance affects the errors accumulating during foraging as well as the range of the subsequent search pattern. Ants that were trained to a feeder 5 m (in the following called 5-m ants, *N*=51), 10 m (10-m ants, *N*=53), or 20 m (20-m ants, *N*=50) south of the nest were captured at the feeder, transferred in small black plastic flasks to the test area, and released there with a piece of biscuit or a dead fly in their mandibles. The test area was about 100 m apart from the training area. A sandy bank separated the nest and the test area. Thus, it was very unlikely that the ants had ever been in the test area before. Like the training area the test area did not contain any obvious landmarks. The paths of the ants were recorded by means of a white grid (20×30 m) that had been painted on the flat ground [for recording paradigms, see (Wehner, 1982)].

The ants ran off their home vectors, and then switched on their systematic search program. The trajectories of all ants were recorded for 5 min on graph paper. Only for the 20-m ants, were the trajectories recorded for 10 min each, because of the larger loops and the longer home runs of these ants.

Data analysis

The recorded trajectories were digitized using a graphics tablet and GEDIT Graphics Editor and Run Analyser (Antonsen, 1995). For all animals that still had to run off the home vector, home vectors and systematic searches were digitized separately. The switch from playing out the home vector to systematic search behavior was defined as the point at which the overall direction of the path changed by at least 30°. An additional condition was that the animal did not revert to the former general direction for the next 3 m. In most cases, one could discover this point easily as a sharp turn performed by the animal (Fig. 1B).

To test whether the three different groups of ants captured at the nest (5-m ants, 10-m ants, 20-m ants) varied with regard to the accuracy of their home vectors, we determined for each ant the

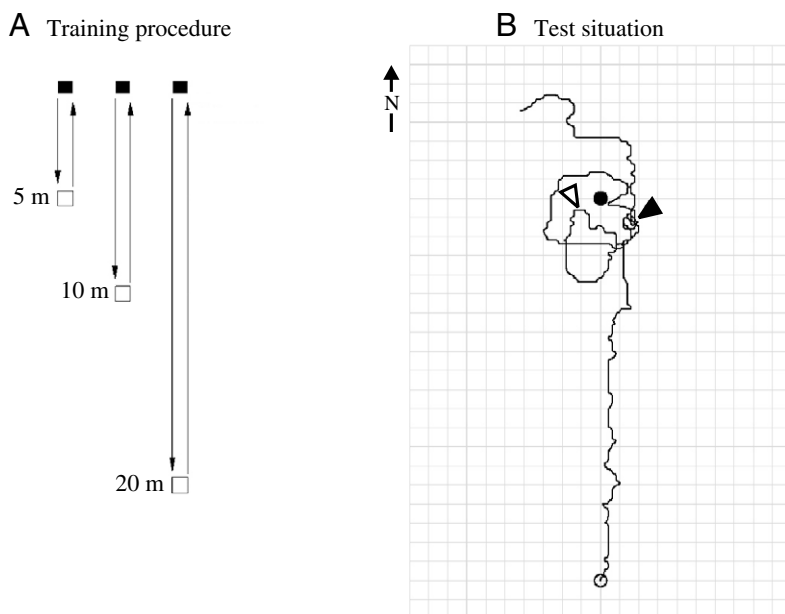**A** Training procedure

5 m

10 m

20 m

B Test situation

N

Fig. 1. Experimental paradigm. (A) Training situation. Ants trained to a feeder located either 5 m, 10 m or 20 m south of the nest entrance were captured at the feeder and transferred to the test field. Filled square, nest; open square, feeder where the ants later were captured and transferred to the test field. (B) Example of a trajectory of an ant transferred from the feeder to the test field. Open circle: point of release; filled circle: correct position of the (fictive) nest; open triangle: end of home vector; filled triangle: center of systematic search (for definition of end of home vector and center of systematic search see data analysis); mesh width of grid was 1 m.

distance between the end of each home vector and the fictive position of the nest (Fig. 1B). In addition, we calculated the distance between the center of the systematic search and the correct position of the nest. The center of the systematic search was defined as the square (0.5 m×0.5 m) that contained the highest path density, i.e. in which the ant's path length divided by the total path length of the systematic search of this particular ant reached its maximum (Fig. 1B). If the density in two squares was the same, the respective ant was excluded from the systematic search analysis. This was the case in only about 10% of all cases (N=154). Thus, the error performed during path integration was measured for both the home run (distance between end of straight home run and correct position of nest) and the subsequent systematic search (distance between center of search and correct position of nest).

In order to compare the systematic search patterns among all ants, we have cut the systematic search runs at a path length of 40 m, i.e. each ant had completed at least two search loops. Animals with systematic search runs shorter than this criterion were excluded from this analysis (16% of all runs, N=154). The distances between the most extreme values along both the x and the y axes were than multiplied by each other. This resulted in an area characterizing the spatial extension of the systematic search.

Statistics

Multiple comparisons between the groups were done using the Kruskal–Wallis one-way analysis of variance (ANOVA). Tests between single groups were performed using Dunn's *post-hoc* test.

Results

Since we do not know the exact position at which an ant suspects its nest to be, we used two different parameters to measure the accuracy of the ant's path integration system. Various procedures have been applied to determine the 'end point' of an ant's home run, i.e. the point at which the ant assumes its nest to be (e.g. Wehner and Srinivasan, 1981; Collett et al., 1998; Bisch-Knaden and Wehner, 2003). However, one cannot be sure whether this point really reflects the ant's guess of its nest position, or whether at this point the ant has already started its first search loop. As an ant should focus its search at that position, at which it assumes its nest to be, the position of the ant's search density peak might yield clearer results about the ant's perspective of the position of the nest. Fig. 2 correlates the ends of the home runs determined as described in the Materials and methods section, and the centers of the systematic search with the correct position of the nest for all three groups. By using these data sets we compared the distance between the end of each home run and its corresponding center of search with the average distance to the centers of search by all ants. As a result, the end of the home run of a particular ant is closer to the center of systematic search of this particular ant (5-m ants: median=2.08 m, N=49; 10-m ants: median=3.12 m, N=41; 20-m ants: median=3.78 m,
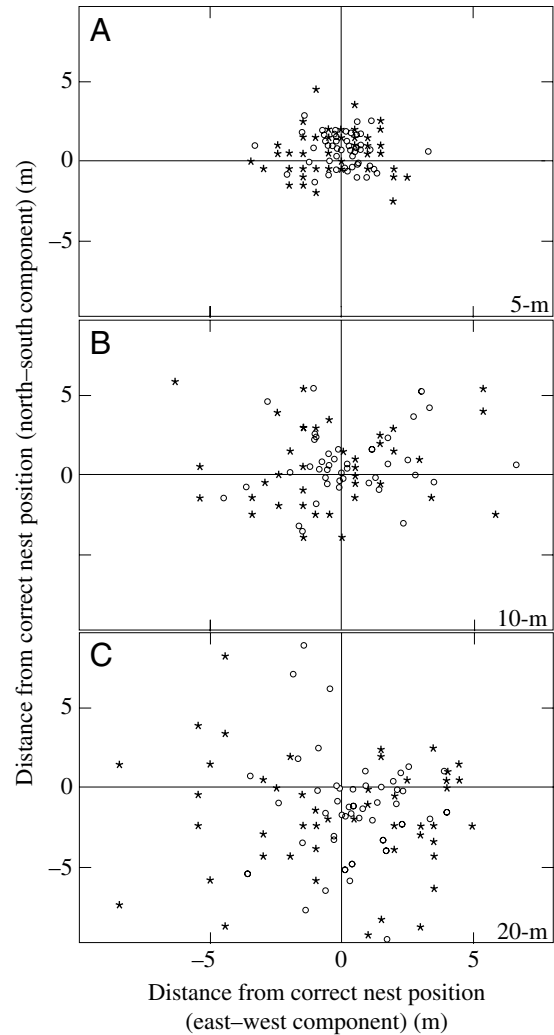

Fig. 2. End points of home runs (circles) and systematic search centers (stars) of (A) 5-m, (B) 10-m, and (C) 20-m ants. The trajectories were recorded for five respective 10 min searches (see Materials and methods). The correct position of the nest was at the intersection of 0/0.

N=49) than to the centers of systematic search of all other ants (5-m ants: median=2.24 m, N=49, Wilcoxon matched-pairs signed-ranks test: P=0.395; 10-m ants: median=3.76, N=41, P<0.05; 20-m ants: median=5.05 m, N=49, P<0.01). Therefore, we can conclude that for each individual ant there is indeed a correlation between the end of the home run and the center of systematic search. Nevertheless, since the median distance between the end of the home run as determined by the experimenter and the center of the ant's search is rather large, for further analyses we decided to take both parameters into account (Fig. 3).

The main focus of the present account was to test whether the ant's accuracy in pointing at the nest position is affected by the length of the preceding foraging trip. The accuracy was reduced after longer foraging trips. Ants that returned from a feeder 10 m and 20 m away from the nest started their
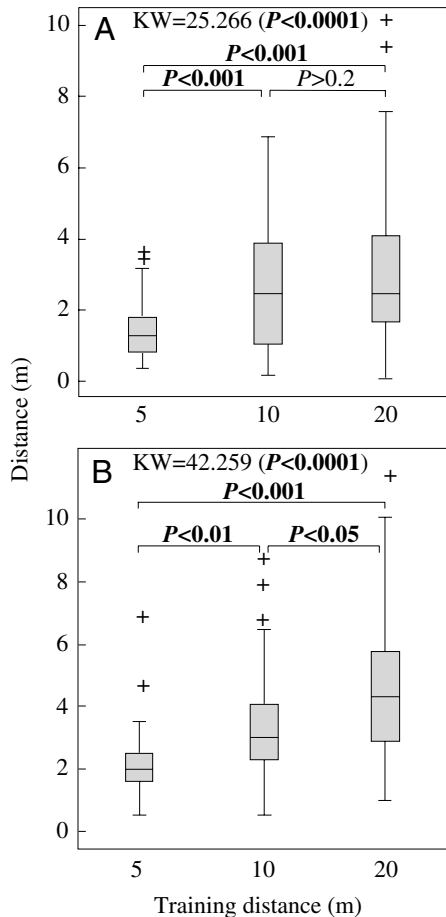
Fig. 3. Accuracy of the path integrator. (A) Distances between the end of the home run and the correct position of the nest for ants captured at the feeder (5-m ants: median=1.27 m, N=51; 10-m ants: median=2.45 m, N=53; 20-m ants: median=2.47 m, N=50). Boxplots give the median, 25% and 75% quartiles, whiskers and outliers (+). (B) Distances between the center of the systematic search and the correct position of the nest for ants captured at the feeder (5-m ants: median=2.00 m, N=49, 10-m ants: median=3.04 m, N=41, 20-m ants: median=4.30 m, N=49). The values for the Kruskal–Wallis (KW) one-way ANOVA are given at the top, the P values of pairwise comparison are given underneath. P values that show significant differences at a level of at least 5% are printed in bold types.

systematic search behavior farther away from the fictive nest position than ants that returned from a distance of only 5 m (Fig. 3A). Furthermore, the distance between the center of the systematic search and the correct position of the nest increased with increasing foraging distance (Fig. 3B).

Is this increasing error also reflected in the ants' confidence in their path integrator? In trying to answer this question, we compared the range of the systematic search patterns of the three different groups. Again, the ants that had returned from a distance of only 5 m differed dramatically from those that had foraged over longer distances (Fig. 4). Hence, the ants seem to be aware of the correlation that obviously exists between the errors accumulated during path integration and the foraging distance (Fig. 3), and respond accordingly by broadening their search pattern with increasing foraging distance (Fig. 4).

Discussion

Do different lengths of foraging runs cause larger errors of the path integrator?

Animals perform path integration by summing up all angles and distances (Mittelstaedt and Mittelstaedt, 1980). Errors concerning the determination of the correct homing direction (Wehner and Wehner, 1986; Müller and Wehner, 1988) as well as errors due to misestimation of distances (Sommer and Wehner, 2004) have been shown to exist for desert ants and also for other invertebrates such as honey bees (Srinivasan et al., 1997; Cheng et al., 1999). Inaccuracy results from the measurements of rotations performed and distances covered, and rotations and distances integrated, and should lead to a route-dependent overall error, and this error should be correlated with the length of the foraging excursion.

We tested whether longer distances of foraging trips account for larger errors in the path integrator. Both the accuracy of the home vector and the systematic search behavior were more accurate for ants heading back after shorter foraging excursions (Fig. 3). Therefore, longer distances do lead to a decreasing accuracy of the path integrator. This increase of the path integration error with the covered distance leads us to the next question: Is this
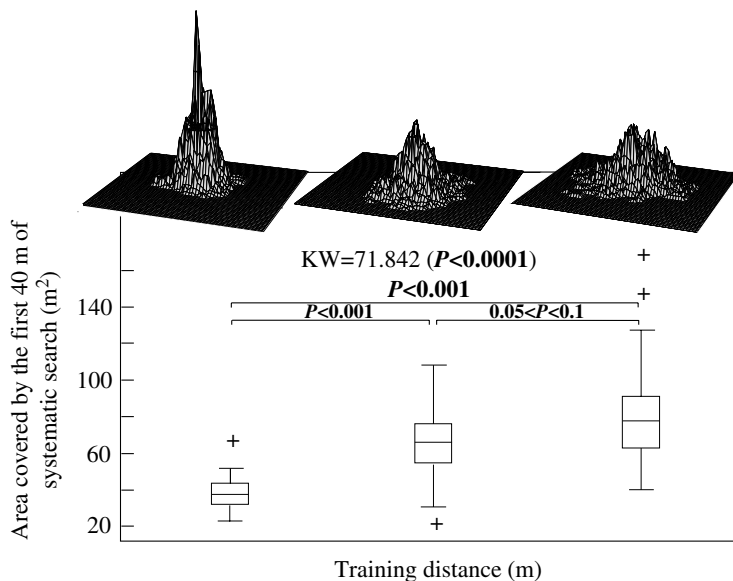

Fig. 4. Areas covered by the first 40 m of systematic search (5-m ants: median=37.77 m², N=45; 10-m ants: median=66.28 m², N=35; 20-m ants: median=77.81 m², N=50). Conventions as in Fig. 3. Corresponding search-density profiles are shown above. For conventions, see Fig. 3.

increasing error also reflected in the ants' confidence in their path integrator?

Several models describe the search behavior of desert arthropods as mathematical functions (Wehner and Srinivasan, 1981; Hoffmann, 1983a; Hoffmann, 1983b; Alt, 1995). The systematic search program of desert ants is not an equidistant spiral, but rather concentrated around the area in which the nest is most likely to be found (Müller and Wehner, 1994). Hence, the search density profile gets adapted to the probability density function of the target. Now, does the search pattern also get adapted to path integration errors, which, as shown above, increase with larger foraging distances? *Cataglyphis* indeed adapts its search behavior to the larger errors by widening its search loops (Fig. 4). Obviously, its confidence in its path integrator seems to be lower, the larger the foraging distance it has covered before finding a food item. Ecologically speaking, it is essential for the ants to reach the nest in the shortest possible time. If the errors to be expected are small, the ants should concentrate their searches around the end of the home vector, and this is exactly what they do. On the other hand, the bigger the uncertainty of the ants gets, the wider the spread of the loops, and again this is what we observed.

Uncertainty is an inherent property of the odometer, the compass and the path integrator and, therefore, surely cannot be measured by the ants. Thus, it seems to be a successful strategy to take the uncertainty into account by widening the systematic search after longer foraging excursions as shown in our experiment. However, it might well be that in the very same training situation an ant behaves as if it decreased the size of its uncertainty range [e.g. during an upwind approach to the feeder (see Wolf and Wehner, 2000)]. Other experiments, in contrast, have shown that during continuous training the ants are not able to increase the accuracy of their outbound or inbound runs (T.M. and R.W., unpublished).

To sum up, our results provide clear evidence that the ant's systematic search behavior is not a fixed program that is just reeled off after the animal has completed its home vector. Rather, the search program is highly adaptive and enables the ants to take errors into account that necessarily accumulated during path integration.

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