

RESEARCH ARTICLE

Establishing food site vectors in desert ants

Siegfried Bolek, Matthias Wittlinger and Harald Wolf*

Institute of Neurobiology, University of Ulm, D-89069 Ulm, Germany

*Author for correspondence (harald.wolf@uni-ulm.de)

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SUMMARY

When returning to the site of a successful previous forage, where does one search for the goodies? Should one rely on experience from the previous homebound journey, or should one consider the outbound journey as well, or even exclusively? Desert ants are particularly well suited for pursuing this question because of their primary reliance on path integration in open and featureless desert habitats. Path integration has been studied particularly with regard to homing after lengthy foraging trips. The ants also use path integration to return to plentiful feeding sites, but what is memorised for revisiting the feeder remains controversial. Here, we demonstrate that desert ants consider, and indeed linearly average, both outbound and inbound travel for their return to a familiar feeder. This may be interpreted as a strategy to reduce navigation errors.

Key words: desert ant, navigation, food site vector, distance estimation, *Cataglyphis*.

INTRODUCTION

Desert ants *Cataglyphis fortis* live in North African salt pans typically devoid of landmarks, making path integration their primary means of navigation. This allows the ants to return to their nest after foraging runs that may cover a few hundred metres in distance and last for more than an hour. The ants also use this system to return to previously visited food sites if these are plentiful. The portion of an ant's visit to a feeder that is used to establish distance and direction to the food source for a future approach – here termed 'food site vector' – has not been well studied, however (Cheng and Wehner, 2002), although this question is relevant for all central place foragers, from ants and honeybees to hoarding rodents and wolves.

Nonetheless, previous studies in desert ants suggest that the directional component of food site vectors is dominated by the outbound journey (Collett et al., 1999; Wehner et al., 2002). This is indicated by experiments where ants were trained to visit a feeder in one direction from the nest, but were transported to a different location with their food morsel and released to return to the nest. After this translocation, the animals headed off in the familiar homing direction and thus found the nest only after searching. In subsequent foraging trips, the outbound trajectories were dominated by the previous outbound trip, although minor directional recalibration with regard to the previous return trajectory occurred. For the distance component, by contrast, inbound travel appeared to be decisive (Cheng and Wehner, 2002). As in the experiments investigating homing direction, the animals' homebound trip was manipulated, although by increasing homing distance, rather than by changing homing direction. On their next outbound trip the ants nonetheless searched for the feeder at about the distance familiar from the previous outbound journey, apparently ignoring the manipulation of the preceding homebound travel. In honeybees, similarly ambiguous results exist, with some studies reporting outbound travel as decisive in distance estimation (Srinivasan et al., 1997), and others reporting averaging of outbound and inbound journeys (Otto, 1959). The experimental procedures of Otto (Otto,

1959) were similar to those described above for desert ants. The animals' homebound journeys were manipulated by transporting the feeding station with the alighted bees closer to or further away from the hive. Perceived distances were determined through analysing the dances performed by the bees after homing.

Generally, it appears essential for desert ants to use the vector produced by path integration during the present foraging trip in homebound travel. Different foraging trips of an individual ant usually differ considerably in their meandering food search paths, making any consideration of previous trips useless [except with regard to the learning of landmarks for piloting and related strategies; see Cheng et al. (Cheng et al., 2006) and Narendra et al. (Narendra et al., 2007) for a comparison of African and Australian desert ant species]. The situation is different for re-visiting familiar feeding sites, as indicated above. Here, it is necessary to consider the experience from the previous foraging trip to that site. The most conservative strategy would be inversion of the preceding homebound path. The averaging of the previous outbound and inbound vectors, by contrast, should not just lead the animal back to the feeder but should also increase navigation accuracy. Linear averaging appears most straightforward, but different forms of averaging might adapt navigation performance to different situations (Cheng et al., 2007).

Here, we addressed some of the controversial findings noted above by studying in detail how the distance component of food site vectors is established in *Cataglyphis* desert ants. We placed particular emphasis on controls to decide between alternative interpretations.

MATERIALS AND METHODS

Animals and location

Cataglyphis fortis ants (Forel 1902) (Wehner, 1983) were studied near the Tunisian village of Maharès in July and August 2010. Ants were marked individually with a colour code, using car paint.

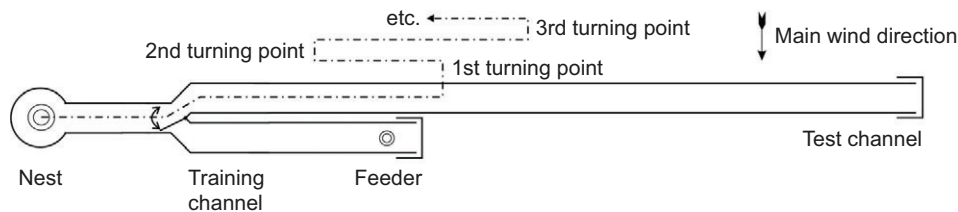


Fig. 1. Experimental arrangement. Nest and feeder were connected by a training channel; a test channel was arranged in parallel close to the training channel on the upwind side. This avoided food odours being blown into the test channel and distracting the ants. Experimental animals were guided into either the test or training channel by a swing door. Above the test channel, desert ants' search behaviour around the assumed feeder position is illustrated schematically. The initial three turning points are indicated; the initial six turning points were evaluated.

Experimental procedure

To examine how the distance component of food site vectors is established in desert ants, we manipulated the animals' homebound journey. Individually marked *C. fortis* ants were trained to visit a feeder (3.2 cm Petri dish filled with cookie crumbs about 1.5 × 1.5 mm in size) 20 m from the nest through a straight channel (aluminium channel, U-shaped in cross-section, floor width and wall height 7 cm, floor coated with sand) (Fig. 1). The channel arrangement not only excluded visual landmarks in the surroundings but also ensured straight travel and selective assessment of the distance component, or odometer, in the ants' navigation. Once an ant had reached the feeder and taken up a food item, it was captured and released closer to home, just 10 m from the nest, thus halving the distance of the return journey. On its next foraging trip, the ant was guided into a test channel running in parallel close to the training channel. The animal's search for food was recorded until completion of the initial six U-turns (Sommer and Wehner, 2004; Wittlinger et al., 2007) (Fig. 1), and search density distributions were constructed from these data (Fig. 2A). Ants were guided into training or test channels through a Y-shaped channel segment with a switch door (Fig. 1). The switch door allowed selection of the appropriate channel without disturbing the ants. Test and training channels were immediately adjacent to each other, with the test channel always on the upwind side (Fig. 1). This arrangement prevented any food or ant odours from being blown from the training channel into the test channel. Food odour would otherwise have distracted the ants being tested. The length of the training channel was 21.5 m for the 20 m training condition and 11.5 m for the 10 m training condition (see below). The length of the test channel was chosen to avoid the tested ants ever reaching the end of the channel during their search. For the 20 m and the 10 m training experiments, the ants were tested in channels of 41.5 and 35.5 m length, respectively. Only naïve ants that had never foraged in the channels before took part in the experimental groups. Each animal performed at least one training run before being tested and was trained and tested in only one test condition.

Test group

Ants from the test group were trained to walk to a feeder 20 m from the nest. Once they had taken up a food item, they were captured at the feeding site and released for homing at half the distance (10 m). Thus, the ants' outbound distance was 20 m, whereas the homebound distance was 10 m.

Controls

Three control groups of ants were tested. A first control group was trained to forage at a feeder 10 m from the nest, and a second control group was trained to forage at a feeder 20 m from the nest, each without interference during the homebound run; that is, without changing homing distance. A third handling control group was also trained to a feeder 20 m from the nest. These animals were captured and carried like the experimental ants, but released back into the channel at a distance of 20 m from the nest.

Data analysis

The number of visits made to 10 cm bins of the test channel was calculated from the above recordings. Search density distributions were constructed by summing the visits to each channel segment (Fig. 2A). Box-and-whisker plots were calculated from the recorded turning points using Sigma Plot 9.01. Specifically, the medians of the turning points of each individual ant were taken to calculate search medians and percentiles (Fig. 2B). The means of first turn distances with corresponding standard deviations were also calculated and are shown in Fig. 2B. Statistical analyses were carried out with the program Sigma Stat 3.11, using ANOVA and Holm–Sidak *post hoc* tests.

RESULTS

Animals from the 10 m and the 20 m control groups reliably searched for food at 10.6 and 22.2 m distance (medians) from the nest, respectively, during their subsequent foraging trips (Fig. 2B, Table 1). The first turn distances for these groups had mean values of 11.1 and 23.8 m, respectively. The handling control animals, which were captured and released back at a distance of 20 m,

Table 1. Food search distances

	10 m control	20 m/10 m test group	20 m control	20 m handling control
Median search distance (m)	10.6	17.0	22.2	21.8
Normalized s.d.	0.26	0.19	0.21	0.08
Mean search distance (m)	11.2	17.3	23.5	22.0
First turn distance (m)	11.1 (2.9)	16.9 (3.8)	23.8 (5.2)	22.6 (4.1)

Median values, mean values (arithmetic averages) and mean first turn distances are shown for all groups. Standard deviations (s.d.) of the first turn distances are in parentheses; standard deviations for the search distance medians (second row) are normalised to the median search distances (see Discussion).

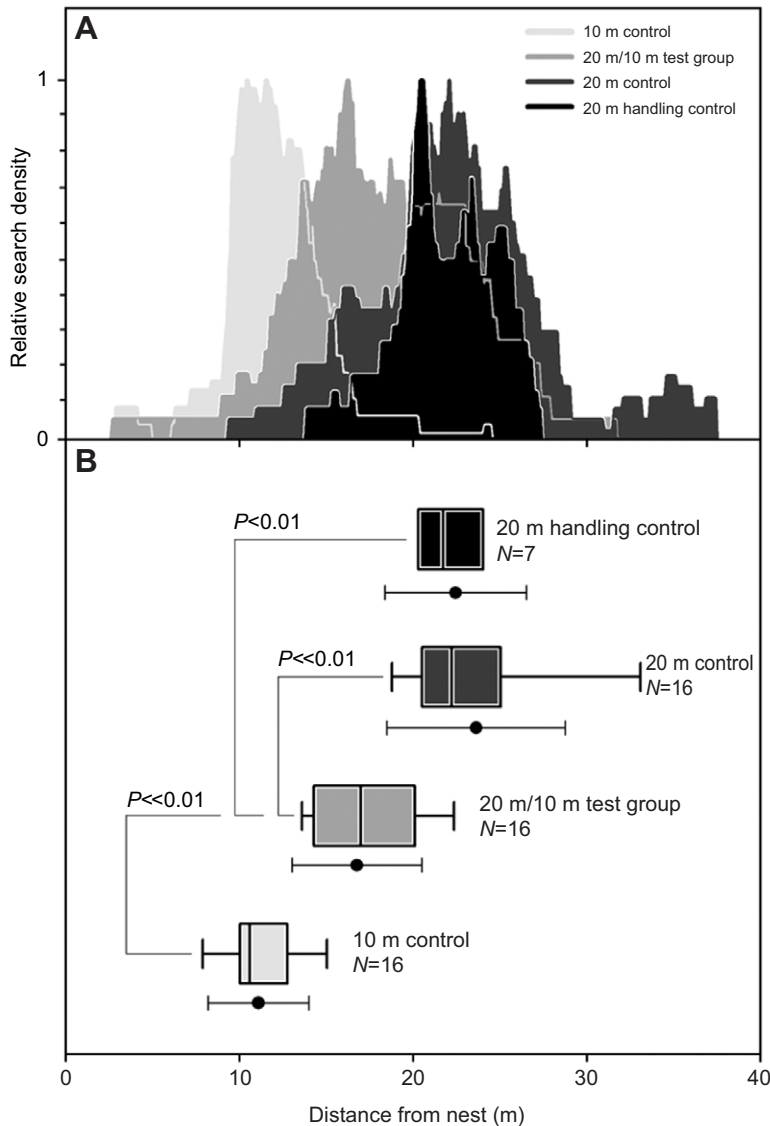


Fig. 2. Search behaviour of desert ants on their outbound journey, from the nest to the site of a previously present feeder. (A) Normalised search densities (no. of visits per 10 cm bin of test channel). (B) Corresponding box-and-whisker plots (boxes, medians and 25th and 75th percentiles; whiskers, 10th and 90th percentiles); abscissae, distance from the nest. Corresponding grey shading is used in A and B. Data in B represent, from top to bottom, 20 m handling control group (black), 20 m control group (dark grey), 20 m outbound/10 m inbound test group (grey), and 10 m control group (light grey). Numbers of animals are indicated, as are significant differences, including significance levels. Medians of the turning points of the food searches of the ant individuals were used to calculate ANOVAs, with pair-wise comparisons according to Holm–Sidak *post hoc* test. The corresponding means of first turn distances and their standard deviations are shown below the box-and-whisker plots in B.

searched for food at 21.80 m from the nest (22.6 m for the first turns); that is, at a distance statistically indistinguishable from the 20 m control group (see also Table 1).

Compared with these control groups, the experimental (test) ants searched for the food at an intermediate position; namely, 17.0 m (median) from the nests (mean and first turn distance are given in Table 1). This distance is significantly different from the search distances of all control groups (values of statistical comparisons in Fig. 2B). Averaging their outbound and inbound journeys, and adding the average overshoot observed in the control groups (8.5%), yields an expected search distance of 16.3 m (see Introduction). A similar estimate is obtained when averaging the search distances of the 10 m and the 20 m control groups above; namely, 17.3 m. Together, these data indicate that the desert ants indeed average outbound and inbound journeys from their last foraging trip to estimate the distance to the feeder on their subsequent foraging trip.

DISCUSSION

The above results clearly indicate that the length of food site vectors is computed by averaging the distances covered during the outbound and inbound segments of a foraging trip. In particular,

the search distance of the experimental animals – who covered just half the distance on their homebound journey compared with that on their outbound trip – is significantly different from that of all control groups (Fig. 2B). The controls reliably searched a small distance (an average 8.5%) past the position of the feeder during their last foraging trip. And averaging the actual search distances of the 10 m and the 20 m control groups yields an almost exact fit with the search distance of the experimental group (as does averaging the inbound and outbound walking distances of the experimental animals with an added average overshoot; see Results). This further indicates that the averaging process is linear, an observation made previously in honeybees (Srinivasan et al., 1999). It has to be considered, however, that for the measurement of short distances, linear and geometric averages are usually indistinguishable (for desert ants, ‘short’ in this context is below ~30 m) [see e.g. Sommer and Wehner (Sommer and Wehner, 2004), particularly their fig. 2].

It is further notable that the variance of the searches is similar between the experimental ants and the control groups, when normalised to the median search distances (Table 1). Normalisation is necessary as many parameters, and notably search variance, scale with navigation distance (e.g. Cheng et al., 2006). There were

actually no significant differences between the 10 and 20 m controls and the experimental group with regard to variance. This indicates that no further variance is introduced by the averaging process, for instance by variance associated with (variable) weights assigned to the outbound and inbound distances.

Our result of – perhaps linear – averaging is in good agreement with previous findings in the honeybee (Otto, 1959) (see Introduction). It is, however, still open to discussion how food site vectors are established in honeybees (Srinivasan et al., 1997). By contrast, previous reports on desert ant odometry (Cheng and Wehner, 2002) appear to be at variance with our present finding. Closer scrutiny of these data unexpectedly reveals almost exact agreement, however, thus actually supporting our conclusions. Desert ants that had travelled 6 m to the feeder and 12 m back on their last foraging trip, for instance, searched for food close to 9.50 m from the nest [see fig. 5 in Cheng and Wehner (Cheng and Wehner, 2002)]. The expected search distance according to our present data would have been 9.77 m – if one assumes averaging of inbound and outbound distances, and adds a further 8.5% (calculated from the weighted average overshoot of the three different control groups; see above). Extension of search distances in this range is often observed in ants that travel across familiar terrain during homing (e.g. Cheng and Wehner, 2002; Wittlinger et al., 2007) (but see Sommer and Wehner, 2004). And when outbound and homebound distances were 6 and 9 m, respectively [see fig. 5 in Cheng and Wehner (Cheng and Wehner, 2002)], the ants searched around 7.52 m, with our expectation at 8.14 m.

This line of argument holds for the distance of the first turns in the ants' homing runs, another measure of homing distance (Cheng and Wehner, 2002) in addition to search medians. As shown in Table 1, first turns of experimental animals were at 16.9 m, with expectations at 17.2 m derived from linear averaging of the outbound and inbound distances, and adding 14.6% overshoot derived from our controls. Corresponding numbers from Cheng and Wehner (Cheng and Wehner, 2002) are 9.5 *versus* 10.3 m (first turns *versus* expectation) for the 12 m homebound experiment and 7.5 *versus* 8.6 m for the 9 m homebound experiment. Again, the overshoot was assumed to be 14.6% as there are no 9 or 12 m controls in Cheng and Wehner's study (Cheng and Wehner, 2002).

Despite the unexpected agreement with the data from Cheng and Wehner (Cheng and Wehner, 2002), it has to be noted that their study is focused on homing distance rather than outbound travel. Consequently, the data set on outbound searches is not ideal for the present comparison. Notably, there were no significant differences between the food searches of control ants and those that had experienced an experimentally extended return travel previously [pooling the different experimental conditions, however, yielded a

significant difference to the control situation (Cheng and Wehner, 2002)].

In the present situation, with almost straight journeys to and from a familiar feeding site, the strategy of averaging the two parts of travel is likely to reduce navigation errors. It will be interesting to scrutinise whether or not the weighting of outbound and inbound travel changes during typical food searches that exhibit a different layout. Outbound search trajectories are usually tortuous and long, while the homebound paths are straight and short (Wehner and Wehner, 1990). Here, increased weight on the homebound journey may appear advantageous with regard to minimising navigation errors.

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