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Path integration in a three-dimensional maze: ground distance estimation keeps desert ants *Cataglyphis fortis* on course

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Summary

In this study, we investigate the ability of desert ants to gauge the ground distances of sloped sections in a three-dimensional (3D) outbound path. Ground distance estimation, as opposed to a simple measurement of walking distances, is a necessary prerequisite for precise path integration in undulating terrain. We trained ants to visit a feeder along a path that included an angular turn as well as a ‘hill’, resulting in an outbound path with a distinct 3D structure. We then observed the ants’ return path in a test field on level ground. From the angles of the ants’ return path on the test field one can infer which

property of the hill segment was fed into the ants’ path integration module, the actual walking distance or the ground distance. The results show clearly that it is the ground distance that *Cataglyphis fortis* feeds into its path integrator, and suggest that the ants are able to keep an accurate home vector also in hilly terrain.

Key words: three-dimensional path integration, distance estimation, odometer, ant, *Cataglyphis fortis*.

Introduction

Desert ants of the genus *Cataglyphis* perform large-scale excursions in surroundings devoid of conspicuous landmarks, from which they return to their nest by path integration (dead reckoning), i.e. on a direct, shortcut way (Müller and Wehner, 1988; Wehner and Wehner, 1990; Wehner, 2003). During their outbound path they continually update, with astonishing precision, a ‘home vector’, which at any point indicates the homing direction and the distance to the nest. To assess this home vector, the ants need a source of information about the distances they have travelled, i.e. a kind of odometer, and also about the compass direction of their path segments (Müller and Wehner, 1988, 1994). The polarisation pattern of the sky is the predominant reference system for the estimation of walking directions used by these insects (Wehner, 1997; Labhart and Meyer, 2002). The sensory basis of the ants’ odometer, however, is less well understood. Three types of cues: (i) energy expenditure, (ii) self-induced optic-flow and (iii) idiothetic cues, i.e. information derived from the animal’s own movements, have been proposed as a possible basis for how arthropods could gauge travelling distances (von Frisch, 1965; Mittelstaedt and Mittelstaedt, 1973; Seyfarth et al., 1982; Mittelstaedt, 1983; Esch and Burns, 1996; Srinivasan et al., 1996, 1997, 2000). Desert ants *Cataglyphis fortis* seem to use neither energy expenditure (Schäfer and Wehner, 1993; Wohlge-muth et al., 2002) nor optic flow cues for gauging distances. Heavy loads did not affect the measurements of walking distances (Schäfer and Wehner, 1993), and the ants arrived at a fairly exact distance estimate even if all optic flow

cues had been excluded (Ronacher and Wehner, 1995; Ronacher et al., 2000). The conclusion from these experiments was that ants rely mainly on idiothetic cues, probably on a kind of step counter. Further experiments with ants that were trained to walk over a linear series of hills, however, indicated that the use of idiothetic information cannot be as simple as activating a step counter or monitoring the output of a central pattern generator (Wohlge-muth et al., 2001, 2002). In subsequent tests, the ants indicated homing distances that corresponded to the outbound run’s ground distance, not to the (much longer) distance actually walked over the hills. Ants seem to be able to derive the horizontal projections from the uphill and downhill segments of their path. Hence, the animals must be able to measure the slopes of the terrain and to integrate this information into their process of distance estimation (Wohlge-muth et al., 2002).

In the experiments of Wohlge-muth et al. (2002), the ants were trained and tested in a linear array of hills or in a linear horizontal channel. It was, therefore, not evident whether the animals can integrate this measurement of ground distances into their path integrator module in a more complex, really three-dimensional (3D) task. We set out to investigate if this is, in fact, the case. In order to do so, we employed the following experimental paradigm. If ants are trained to visit a feeder via an L-shaped set of channels, the azimuth steered by the animals on their way back from the feeder to the nest will depend on the lengths of the channel segments. From the angles steered, we can hence infer the relation of the lengths

of both segments, as they were gauged by the ants' odometer. If one section of the L-shaped outbound route is not laid out on level ground but leads up to an apex and back down again (Fig. 1A), and if the other, horizontal, section is of known length, we can determine from the ants' homing direction the length by which the sloped segment added to the state of the path integrator. We assume two possible outcomes. Either, the 'hill' segment is measured by the walking distance, or alternatively, the animals could have integrated this segment only with the (shorter) ground distance. In this paper, we show that sloped parts of an ant's journey are correctly incorporated into the path integrator with their corresponding ground distances. As a consequence, the home vector of desert ants also maintains its accuracy in heavily undulating, 3D terrain.

Materials and methods

Experiments were performed on desert ants of the species *Cataglyphis fortis* Forel 1902 in their natural habitat, a saltpan located at 34.52°N, 10.53°E, near the town of Maharès (Tunisia). Tested animals belonged to four nests, and each animal was tested only once.

Ants were trained from their nest entrance to visit a feeder,

using pieces of watermelon and biscuit crumbs. Training took place in aluminium channels (dimensions: 7 cm wide, height of side walls: 7 cm). A PVC wall surrounded the nest entrance and guided foraging ants into the attached training channel (Fig. 1A). Fine grey sand was glued to the channel's bottom in order to facilitate the animals' walking. The inner side walls were painted grey to prevent possibly irritating reflections from the channel walls' metallic surfaces. The upper end of the walls was evenly covered with khaki-coloured adhesive tape in order to minimise, by its smooth surface, escape attempts. The channels provided no visual contrast cues that could be used to estimate distances.

3D experiment

The first leg of the channel system led away horizontally from the nest entrance for 3 m in a southward direction. The second leg connected at a right angle, leading either towards the east or the west in mirrored test set-ups (in Fig. 1A, the westward orientation is shown). This second leg led upwards at an inclination of 70° for 2 m. It was followed by a short horizontal channel (0.35 m) at a height of 1.9 m above the ground, before a last channel segment led back down to ground level (inclination: -70°, length: 2 m). The end of this downward ramp marked the training location of the feeder, placed in a short channel segment that was closed at its far end (Fig. 1A).

Straight 3D control

In a first control experiment, the path from the nest to the feeder was laid out in a straight line pointing southward, i.e. without leading around a corner. The ascending and descending channel segments of this control followed a level channel segment of 3 m length, and were identical to those of the 3D experiment described above (not shown).

2D controls

In a second set of control experiments, the channels were laid horizontally on the ground (Fig. 1B,C). The first leg was identical with the 3D set-up. The second leg connected at a right angle, but horizontally, pointing either east or west, and led to a feeder at a distance from the bend of 1.4 m or 4.35 m. These distances corresponded to the ground and walking distances, respectively, in the 3D set-up. Thus, the homing azimuths from the critical, 3D test could be compared with results of animals that had walked the corresponding ground distance or walking distance in the horizontal plane.

Animals that had performed several successful foraging trips between the feeder and the nest, as indicated by their unhesitating climb and descent on the sloped parts of the channel, were captured and transferred in a lightproof container to a test

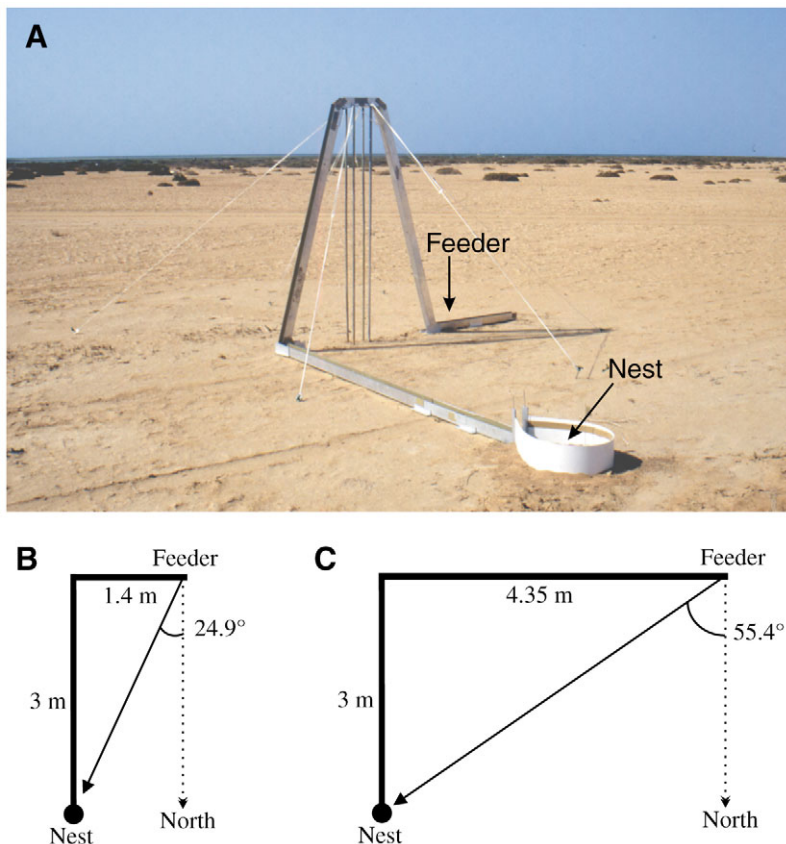


Fig. 1. Training situations. (A) Experimental set-up for 3D outbound runs. (B) Schematic view of 2D ground distance control. (C) Schematic view of 2D walking distance control.

field at some distance to the training site. The test field was a flat area devoid of any vegetation, with a grid (10 m×10 m; grid width: 1 m) consisting of thin white lines painted on the desert floor. An ant was released after ascertaining that it had a food item between its mandibles and was therefore intending to return to the nest. The ant's path across the test field was recorded for 3 min on squared paper.

In order to determine the compass directions of the ants' initial homebound run, we drew a circle corresponding to a test field radius of 1 m and 2 m around the animal's release point and measured the azimuth of the ant path's intersection with both circles (as conventionally done in *Cataglyphis* experiments; see Wehner, 1968). The length of the home vector was measured as the distance between the release point and the position where the ant first made a distinct turn, which usually indicates that the animal has run off its vector and begun making search spirals in order to find the nest entrance (Wehner and Srinivasan, 1981). Furthermore, the complete runs were digitised on a graphic tablet (Digikon 3, Kontron, Eching, Germany) with GEDIT Graphics Editor & Run-Analyser (Antonsen, 1995). The paths of all ants during the first 30 s after release were combined for each treatment, respectively. Also, search densities were determined for each treatment by calculating the animals' walking distance within a particular area (grid width: 0.25 m) in relation to the total walking distance (measured over the 3 min period).

The results gained in our experiments were independent from the overall compass direction of the training. After mirroring data of eastbound trainings on the north–south axis, results did not differ from westbound training (Watson–Williams test, $P>0.05$). Hence, runs from eastward and westward outbounds were pooled for each training situation and are treated in the following as one set of data. The directionality of intersection points of a treatment was examined using the Rayleigh test; differences between mean angles of treatments were checked using the Mardia–Watson–Wheeler (MWW) test with a Bonferroni correction for multiple test comparisons. All statistics were calculated using Oriana circular statistics software (Kovach, 2004).

Results

We trained ants to walk from their nest to a feeder through an L-shaped channel, where the second section led the ant uphill and again downhill to a feeder (Fig. 1A). Their return angles steered were compared with angles of ants in two control experiments, in which the second segment of the outbound channel was laid out horizontally, and had the length of the 3D route's ground and walking distances, respectively (Fig. 1B,C). For all training groups, the combined traces of homebound runs show for the first couple of meters a high number of relatively straight paths in the direction of the expected nest position (Fig. 2). Such straight path segments are followed by a rather sharp turn that indicates the onset of the ants' nest searching behaviour (Wehner and Srinivasan, 1981).

In each training situation, the intersection points of runs at 1 m and 2 m distance from the release point were highly clustered (Rayleigh test, $P<0.001$, Fig. 3), resulting in all cases in high mean vector strengths (for 1 m/2 m radius: 3D: 0.95/0.93; ground distance: 0.96/0.97; walking distance: 0.95/0.98). The mean vectors of the two control groups from L-shaped training (ground distance control and walking distance control) differed strongly from each other (MWW test, $P<0.001$, both at 1 m and 2 m radius). The mean azimuths of these control runs pointed into the expected direction with high accuracy (2 m mean azimuth vs expected azimuth: ground distance control, 25.1° vs 24.9° , Fig. 3B, outer black arrow; walking distance control: 64.7° vs 55.4° , Fig. 3C, outer white arrow).

The mean homebound vector of ants that had performed a 3D outbound run to the feeder (Fig. 3A; azimuth for 2 m radius: 24.3°) did not differ from the angle steered by animals that had been trained to a feeder at the respective ground distance (Fig. 3B; 2 m azimuth: 25.1° ; MWW test, $P>0.10$, both radii), while it differed strongly from controls that had covered the according walking distance (Fig. 3C; 2 m azimuth: 64.7° ; MWW test, $P<<0.001$, both radii). Hence, ants that had been trained in a 3D channel system indicated the same direction to their nest as did ants in a flat training where the second leg equalled the ramp's ground distance (Fig. 3A,B).

Three-dimensional training along a straight path (Fig. 3D, $N=20$, both radii) showed that climbing and descending did not

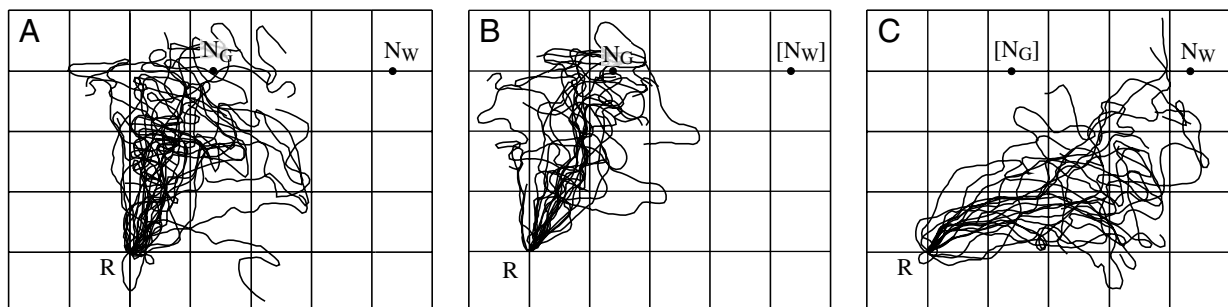


Fig. 2. Homebound paths of individual ants from their point of release, R, plotted for the first 30 s of each search run ($N=27$ in A, $N=22$ in B, $N=21$ in C). N_G depicts the relative nest position according to ground distance in the 3D test (A) and ground distance control (B). N_W is the relative nest position in walking distance controls (C). Square brackets in B and C indicate the predicted nest position of the other control group, respectively, and are shown for comparison.

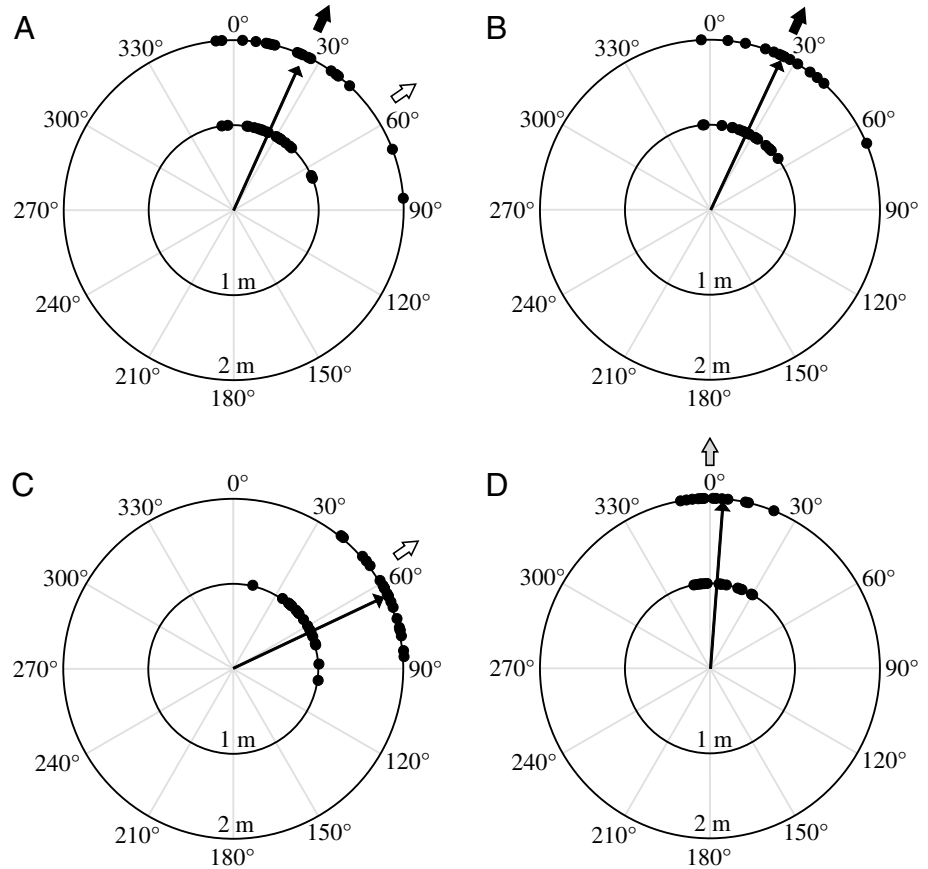


Fig. 3. Intersection points of homeward runs of different individuals of *Cataglyphis fortis*, at 1 m and 2 m radius from the release point. Long arrows depict vector strengths at the 2 m radius, where full radial length equals 1. Short arrows show the true vector to the nest in 3D tests and ground distance controls (black), walking distance controls (white), and straight controls (grey). (A) 3D outbound run ($N=26$ at 1 m, $N=23$ at 2 m radius); (B) ground distance control ($N=22$ at 1 m, $N=20$ at 2 m radius); (C) walking distance control ($N=21$, both radii); (D) straight control ($N=20$, both radii). Note that data points obscure others with identical azimuth.

shift an ant's homing direction: intersection points were highly clustered (Rayleigh test, $P<0.001$) and clearly oriented towards the expected nest position (Fig. 3D, outer grey arrow), located at due north (mean vector strength: $0.97/0.98$; 2 m azimuth: 4.3° ; Fig. 3D).

The outbound path towards the feeder also influenced the length of the ants' home vector, as indicated by the distance between the release point and the onset of search loops. The mean path length was larger in walking distance controls than in ground distance controls or the 3D test (Kruskal–Wallis test, Tukey's test, $P<0.001$; Fig. 4). This is in agreement with the

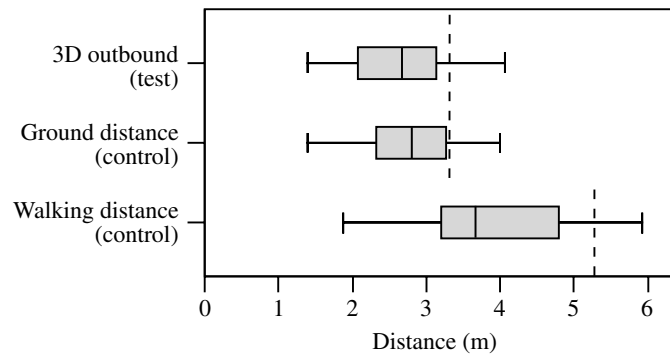


Fig. 4. Average distances covered before the ants start to search for the nest. Shown are the median, quartile range and extremes. Broken lines show the real distance of the nest.

longer overall distance between the nest and the feeder (5.3 m in walking distance controls vs 3.3 m in ground distance controls and the 3D test). The onset of search loops of ants from the 3D test did not differ from ground distance controls (Tukey's test, $P>0.5$). However, a pronounced undershooting of walked distances was common to the mean vectors of all three training groups. The medians were well below the actual distances (Fig. 4, broken lines) between the feeder and the nest.

The search density diagrams of the test and control experiments reveal for all training situations that search densities were highest between the release point and the expected nest position (Fig. 5). In 3D training, ground distance controls, and straight controls, the club-shaped area of high search densities just reaches the expected position of the nest according to its ground distance, with much lower densities in the sector beyond (Fig. 5A,B,D). This distance undershooting is even more pronounced in the case of walking distance controls, where only low search densities were found at the fictive position of the nest (Fig. 5C).

Discussion

The experiments presented here investigated the accuracy of path integration in desert ants that were trained to visit a food source along a complex 3D path. In particular, the question was whether the ants, when walking over slopes, do indeed determine the ground distances, as has been suggested earlier

(Wohlgemuth et al., 2001, 2002). Our experimental design focused on a translation of outbound path lengths, covered in a channel, into an azimuth angle of the home vector shown by ants returning from the feeder (cf. Müller and Wehner, 1988). By this transformation some inaccuracies of measuring homing distances may be avoided, e.g. the frequently observed undershooting of home distances (Müller, 1989; Sommer and Wehner, 2004).

The mean home vectors in the two 2D controls differed distinctly and corresponded closely to the expected directions (compare Figs 3B,C and 1B,C). The mean home vector of ants trained in the 3D setup (Fig. 1A) was indistinguishable from that of the 2D control with the 1.4 m leg (compare Fig. 3A,B), which corresponded to the ground distance of the 3D maze. These results allow two conclusions: first, that *Cataglyphis fortis* is indeed able to derive the ground distance information when walking over hills and, second, that this information is incorporated in a meaningful way into the path integration process. Furthermore, these results provide independent support for and extend the hypotheses developed in Wohlgemuth et al. (2001, 2002): The path integration module is also fully functional in 3D tasks, enabling desert ants to navigate accurately even in landscapes with strong vertical stratification.

The exact mechanism by which the ants determine the slope of a steep ascent or descent remains to be unravelled. In *Formica polyctena*, hair-plates at the joints of the coxae, and on the joints between head and thorax, and between petiolus and gaster, play a role in the perception of relative positions of body parts, which in turn may enable the ant to judge its overall orientation within the gravity field (Markl, 1962). Interestingly, in *Cataglyphis fortis*, the manipulation of hair fields in the neck of the ant, as well as hair fields located between petiolus and gaster, did not yield any change in the distance estimation (Wittlinger et al., 2005).

A second important input source of the ant's path integrator is the pattern of polarised skylight, which is used by *Cataglyphis* (and other insects) as the main allothetic compass cue (Fent, 1986; Wehner, 1997). However, under the present training paradigm two systematic error sources could influence the ant's perception of compass directions. Because of the limited view of the sky within the channel on the way to the feeder, as opposed to a full view on the return trip, a discrepancy exists between the perceived compass directions of the outbound and inbound route (Müller, 1989). The amount and direction of the navigational errors within both channels of the L-shaped 2D control experiments depends on the walking direction (i.e. the channel's compass bearing) and the channel's angle relative to the solar azimuth. At present, a

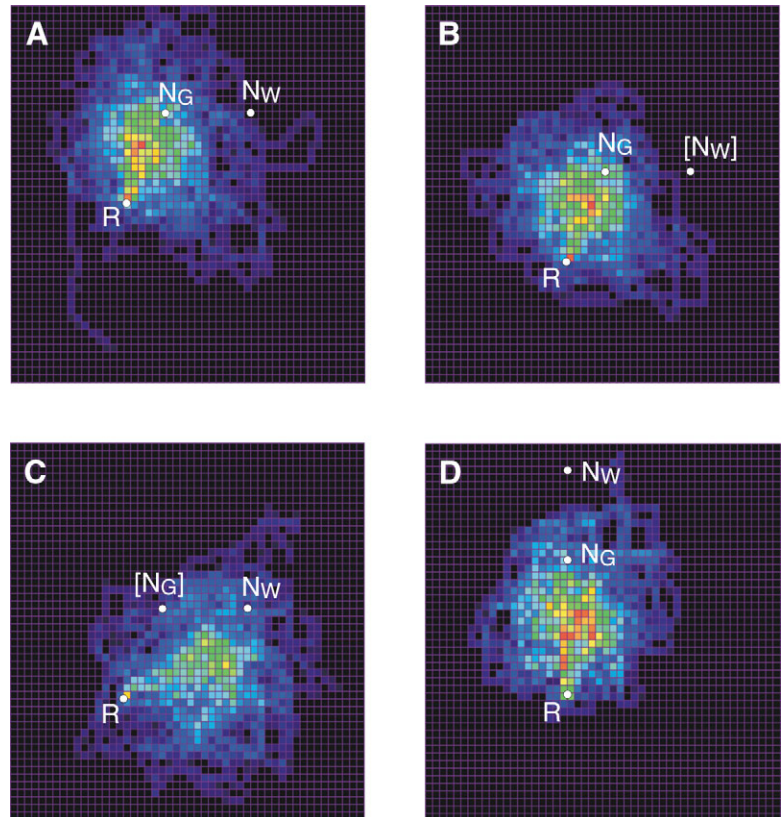


Fig. 5. Search density distributions of ants within the test area after different outbound runs ($N=27$ in A, $N=22$ in B, $N=21$ in C, $N=20$ in D). One pixel represents an area of $0.25\text{ m} \times 0.25\text{ m}$. Densities are defined as the summed path lengths within one pixel, divided by the total path length for all pixels of each test situation. The obtained values for each pixel are colour-coded from black (minimal value; 0) to red (maximal value; 0.845 in A, 0.926 in B and C, 0.773 in D). R, point of release; N_G depicts the relative nest position according to ground distance in the 3D test (A), ground distance control (B), and straight control (D). N_W is the relative nest position in walking distance controls (C). Square brackets in B and C indicate the predicted nest position of the other control group, respectively, and are shown for comparison.

precise estimation of errors that may have been introduced by different view sectors of the sky is not possible.

The straight controls aimed at estimating the extent of this possible error in the ants' determination of the homing direction. The skylight compass can be described as a detector for the orientation of the symmetry plane of the E-vector pattern present in the sky (Rossel and Wehner, 1984, 1986; Wehner, 1998). However, it actually employs an averaging mechanism of polarisation orientations and intensities over a large area of the visible sky (Wehner, 1994). If the sun's azimuth is not aligned with the orientation of the channel in which the ant walks, and if large parts of the sky become invisible for the ant while climbing on a ramp, the axis of symmetry of the polarisation pattern appears under a different azimuth. Hence, the ant may perceive a deviation of her walking course while being on a slope. In the straight control, such an error did not occur (Fig. 3D). We suggest the reason is that the errors of the upward and downward slopes are in

mirrored orientation to each other and therefore cancel out, as long as the orientation of upward and downward slopes is mirrored as well. This symmetry is unaffected by the position of the sun and the resulting orientation of the polarisation pattern.

In addition, we cannot decide to what extent the ants having been trained over extended periods of time have derived the exact compass courses from the sun and the spectral gradients in the sky (for the latter, see Wehner, 1997). Finally, in one-sided detour arrangements systematic errors are to be expected according to what is known about the ant's path integration system (Müller and Wehner, 1988; Müller, 1989; cf. also Hartmann and Wehner, 1995). As all these potential sources of systematic errors are superimposed in ways that vary according to the time of day, it is nearly impossible to predict the total effect these error sources might have on the ants' bearings in the tests. In fact, the ants' bearings in all experiments with L-shaped channel combinations correspond amazingly well with the expected ones (Fig. 3A,B). Only in the walking distance controls (Fig. 3C), ants exhibit a systematic error, turning too far inwards, by 9°, as was described first for *Cataglyphis* (Müller and Wehner, 1988; Müller, 1989), and found in other insects and mammals in L-shaped training situations alike (Etienne et al., 1996; Séguinot et al., 1998). We do not have a convincing explanation why this 'Müller'-error did not occur in the tests of Fig. 3A,B. One possible reason is that the second leg of the L was too short to induce this kind of error. We also checked whether the day-time of testing could have led to a shift that canceled this error (cf. Müller, 1989), but this cause could be ruled out.

The accuracy of the ant's path integrator in a 3D environment can also be estimated by the distance that an ant walks in a straight path before it begins to search for the nest entrance in conspicuous search loops. The results after a 3D outbound run did not differ from the ground distance control, but differed significantly from the walking distance control (Fig. 4, see also Fig. 5). This also suggests that the path integrator treats sloped sections of an itinerary in the same way as their corresponding ground distances. It is worth noticing, however, that the distances covered before the search behaviour started, were in all cases too short. This 'undershooting' is a phenomenon that has been repeatedly observed in experimental set-ups where ants performed an outbound trip within a channel and then were transferred to the open field for their return trip (Burkhalter, 1972; Müller, 1989; Collett et al., 1999, 2003). The most likely explanation for the premature end of the vector run is the discrepancy between the panoramic views that the ants expect in the nest's vicinity and the actual imagery. The memorisation of landmarks in the vicinity of the nest and the ability of actions associated with these 'snapshots' to override the state of the path integrator, could already be demonstrated (Andel and Wehner, 2004). The search density diagrams (Fig. 5) show that the undershooting results in the ants spending most time in an area that lies on the feeder's side of the expected position of the nest. Hence, under natural conditions, the ants would start their search

within an area they are familiar with. They should be able to pick up visual cues that they had passed numerous times just recently while shuttling back and forth between the feeder and the nest, leading them to the nest entrance (cf. Sommer and Wehner, 2004).

One question that this study cannot yet answer is whether the ants possess a 3D representation of their world, or if hills and valleys are only computed with their correct ground distance, with any further information about the position on the vertical dimension being discarded immediately. Recent, preliminary findings suggest, however, that the notion of an elevated food source as being 'above the ground' is present in the ant's representation of space (Grah et al., 2005).

Lastly, there remains the question of ecological relevance for the species examined. *Cataglyphis fortis* lives on salt pans and in the desert, i.e. in only slightly undulating terrain. It does not climb on trees or into bushes, where the third dimension takes on an important role in the definition of a point in space. Most probably, a path integrator that incorporates slopes with their walking distances (instead of their ground distances) would still work reasonably well for this species. But other cataglyphids, like *C. bicolor*, live in more uneven habitats and might very much have to rely on an orientation mechanism that also keeps fully functional in a heavily undulating, 3D environment.

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