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Integrating two-dimensional paths: do desert ants process distance information in the absence of celestial compass cues?

B. Ronacher^{1,*}, E. Westwig^{1,†} and R. Wehner²

¹Department of Biology, Humboldt University, Invalidenstr. 43, D 10099 Berlin, Germany and ²Department of Zoology, University of Zürich, Winterthurerstrasse 190, CH 8057 Zürich, Switzerland

*Author for correspondence (e-mail: Bernhard.Ronacher@rz.hu-berlin.de)

†Present address: American Museum of Natural History, Department of Mammalogy, Central Park West at 79th Street, New York, NY 10024, USA

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Summary

When performing foraging trips desert ants of the genus *Cataglyphis* continuously process and update a ‘home vector’ that enables them to return to their nest on the shortest route. This capacity of path integration requires two types of information: (i) information about the travelling directions, and (ii) odometric information about the distances travelled in a particular direction. We have investigated how these two necessary pieces of information interact within the path integration processor. The specific question is: how do the ants process distance information if there is no simultaneous input from the sky compass available. Ants were trained to forage in a ‘Z’-shaped channel system, the three segments of which joined at right angles. Individual animals were transferred from the feeder to a test field where their homing paths could be observed. In the crucial tests the middle segment of the

maze was covered by orange Perspex that did not transmit the UV part of the spectrum, and thus precluded the perception of polarization patterns. Changes of the ant’s processing of odometric information within this channel segment directly translate into a change in homing direction on the test field. The results indicate that the odometric information about travelling distance is largely ignored for path integration if there is no simultaneous input from the sky-view-based compass. They further show that idiothetic information cannot adequately substitute for the polarization compass to infer travelling directions.

Key words: path integration, odometer, polarization compass, desert ant, *Cataglyphis*.

Introduction

Desert ants of the genus *Cataglyphis* are renowned for their path integration capacities (Wehner and Wehner, 1990; Wehner, 2003). Individual foragers perform large scale excursions from which they return to their nest on the shortest route. This navigational feat is accomplished with remarkable precision by a path integrator, which allows for an approximate form of dead reckoning (Wehner and Wehner, 1986; Wehner and Wehner, 1990; Müller and Wehner, 1988; Wehner and Labhart, 2006). To perform path integration the animals need two types of essential information, that is, directional information (with reference to an external compass cue), and information about the distances travelled in a particular direction [(Müller and Wehner, 1988; Wehner, 1994); for a discussion of the necessity of distance information, however (see Biegler, 2000)]. It is well established that ants as well as other insects rely on polarizational (and, to a lesser degree, on intensity and spectral) sky-light cues, for determining their travelling direction (e.g. Wehner, 1982; Wehner, 1997; Dacke

et al., 2003). Concerning the measurement of travelling distances, evidence is accumulating that *Cataglyphis* uses idiothetic cues, their odometer seems to be based on a kind of step counter or an efference copy of a locomotor central pattern generator (Wohlgemuth et al., 2001; Wohlgemuth et al., 2002; Thiélin-Bescond and Beugnon, 2005; Wittlinger et al., 2006). Idiothetic information can be used also by some arthropods to identify changes in walking directions (Seyfarth et al., 1982; Mittelstaedt, 1985; Moller and Görner, 1994) (cf. Chittka et al., 1999).

However, these two pieces of information, about distance and direction, must be processed in a meaningful way, in order to yield a correct home vector. On the basis of a detailed analysis of directional errors produced by *Cataglyphis*, when trained in a channel with sharp bends, Müller and Wehner proposed that the ants use an approximate iterative algorithm to continuously update their home vector on the basis of compass and odometric information (Müller and Wehner, 1988). The aim of the present study was to further investigate the interplay of these two

essential inputs to the path integrator. In particular, we asked how travelling distance is processed in a two-dimensional path if the ants are deprived of any sky-light-based compass information during parts of their path. Ants were trained in a Z-shaped channel system, the middle part of which was covered with orange Perspex that excluded any short-wavelength light, and therefore prevented the perception of polarization patterns, as these are received by UV receptors in the dorsal rim region (Wehner, 1994; Labhart, 2000; Labhart and Meyer, 2002). The parcours in the channel maze was designed in a way that any change in the ant's processing of walking distances while travelling in the Perspex covered part of the maze should translate into a change of homing direction when the animals returned to the estimated (fictive) nest position on a test field. The main message from our data is that the odometric information about travelling distance is largely ignored for path integration, if there is no simultaneous input from the sky-view-based compass. This paper extends and confirms a recent study (Sommer and Wehner, 2005), which explored the influence of celestial cues on the processing of distance information in a linear channel array.

Materials and methods

Experiments were performed in 2002 and 2005 on desert ants of the species *Cataglyphis fortis* Forel 1902 in a salt pan located at 34.52°N, 10.53°E, near the town of Maharrès (Tunisia). Tested animals belonged to two nests; except for the data shown in Fig. 5 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 laid out on the desert floor. The dimensions of the channels (width, 7 cm; height of side walls, 7 cm) allowed a view of the sky in a streak of 55° to 60°, depending on the ant's size and position. 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 travelling distances (see also Ronacher et al., 2000). A PVC wall surrounded the nest entrance and guided foraging ants into the attached training channel.

Straight control

In a control experiment, a 4-m channel leading from the nest to the feeder was laid out in a straight line, pointing southward (see inset in Fig. 1C).

First 'Z' experiment

The first leg of the channel system led away from the nest entrance for 2 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 (see Fig. 1). This second leg

was 4 m long and connected, again at a right angle, to another 2 m segment pointing to the South. The two 90° turns were arranged in opposite directions in order to minimize the possible errors that are induced by one-sided turns [cf. fig. 2 in Müller and Wehner (Müller and Wehner, 1988)]. The dimensions were chosen to yield the same total lengths in the N–S segments and the E–W segment. Hence, the expected homing directions in the 'open' controls were 315° and 45°, respectively. In the crucial experiments, the compass information based on sky-light cues was completely withheld for the middle segment (see Fig. 2). This was achieved by covering the channel with orange Perspex that was completely non-transparent to UV radiation, and thereby precluded the perception of polarization patterns which depends on UV receptors [(Duelli and Wehner, 1973; Labhart, 2000); the Perspex, no. 478, Röhm and Haas, Darmstadt, excluded all wavelengths below 540 nm – see curve e in fig. 43 in Wehner (Wehner, 1982)]. In addition, wooden plates of 60 cm width were arranged above the channels at a height of approximately 80 cm above ground. These screens prevented the direct view of the sky and in particular of the sun's position. In the experiment shown in Fig. 2, the Perspex cover extended by 15 cm into the N–S segments, so that an ant entering the middle segment had to perform its 90° turn without sky view. However, in a modification of this experiment the bends were left open (open section extending 15 cm into the middle segment of the 'Z'; see Fig. 3). Hence, in this set-up the ants could perform their 90° turns while still relying on sky compass information.

Directional errors induced by a partial versus complete view of the sky

The approximate path integration algorithm proposed for the ants (Müller and Wehner, 1988; Wehner, 1994) works well under natural conditions but induces systematic navigational errors if an ant is trained in a straight channel, which restricts its view of the sky, and is later released on a test field (Müller, 1989). Such errors may have been relevant also in our experimental set-up, although the design of the Z-shaped maze with its perpendicularly oriented segments should minimize this influence, as the opposite deviations caused by the N–S segments and those caused in the E–W segment should largely cancel out (see Fig. 1A,B). However, if the sky view in the middle segment was occluded, then the errors induced by the remaining open segments should be unveiled. The sign and size of this type of directional errors depend on the orientation of the channel and the time of day. For a N–S direction of the channel, Müller found that the deviations were maximal, up to 20°, between 10:00 and 11:30 h, and, in the opposite direction, between 13:00 and 14:30 h [(Müller, 1989), fig. 10 therein]. Provided that the tests are evenly distributed over the whole day, positive and negative deviations, although increasing the standard deviations, should roughly cancel out. This held true for the straight control (Fig. 1C), but in the experiments shown in Fig. 2B and Fig. 3B, the sampling times were biased towards the afternoon (see Results).

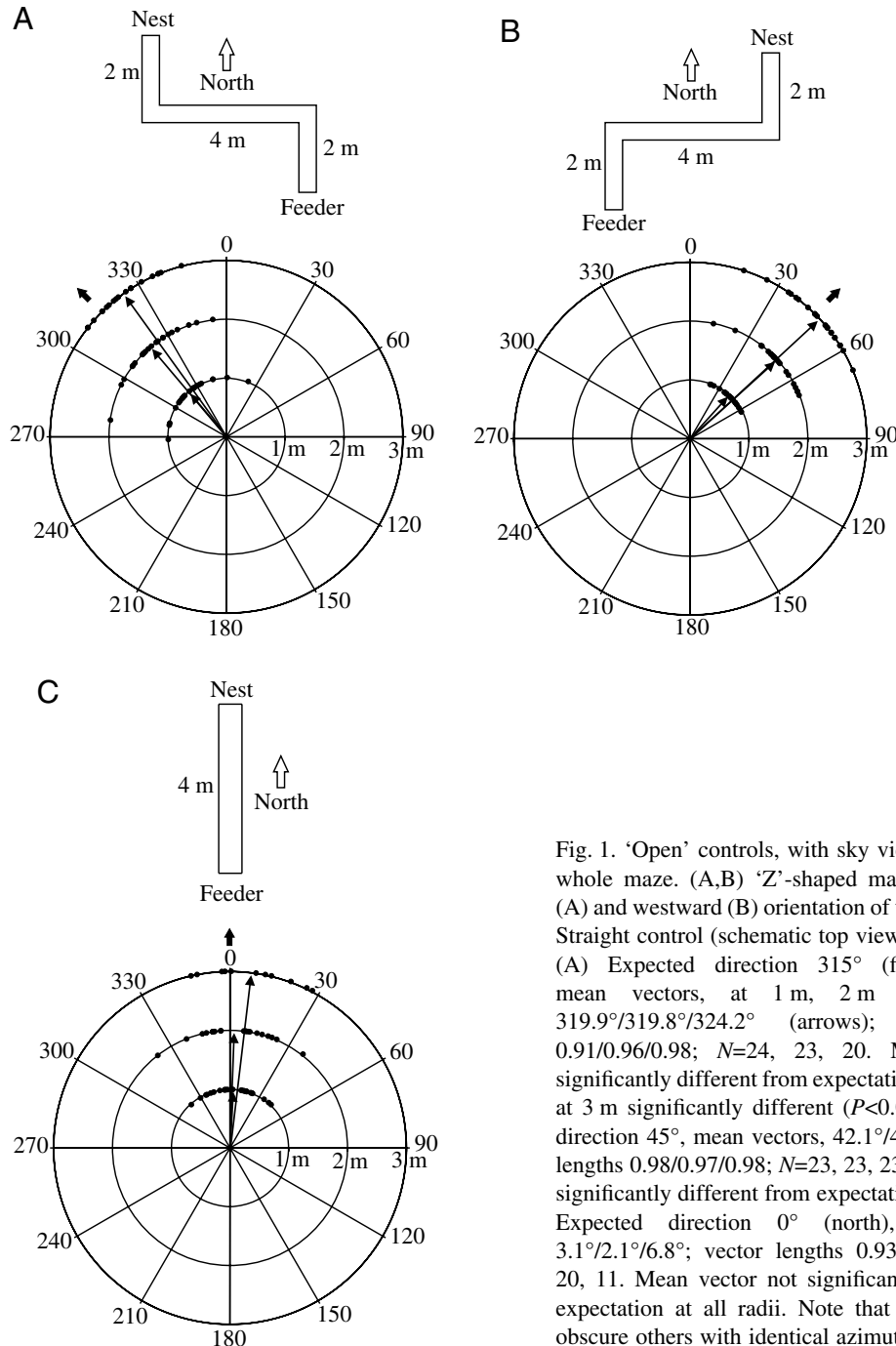


Fig. 1. 'Open' controls, with sky view throughout the whole maze. (A,B) 'Z'-shaped maze, with eastward (A) and westward (B) orientation of the middle leg. (C) Straight control (schematic top views of all channels). (A) Expected direction 315° (filled arrowhead), mean vectors, at 1 m, 2 m and 3 m radii: $319.9^\circ/319.8^\circ/324.2^\circ$ (arrows); vector lengths 0.91/0.96/0.98; $N=24, 23, 20$. Mean vector not significantly different from expectation at 1 m and 2 m; at 3 m significantly different ($P<0.01$). (B) Expected direction 45° , mean vectors, $42.1^\circ/47.9^\circ/47.2^\circ$; vector lengths 0.98/0.97/0.98; $N=23, 23, 23$. Mean vector not significantly different from expectation at all radii. (C) Expected direction 0° (north), mean vectors, $3.1^\circ/2.1^\circ/6.8^\circ$; vector lengths 0.93/0.96/0.97; $N=25, 20, 11$. Mean vector not significantly different from expectation at all radii. Note that some data points obscure others with identical azimuth.

Second 'Z' experiment

We therefore decided to repeat the experiment of Fig. 2 by choosing those times of day (14:30 to 17:30 h) and an orientation of the uncovered channels (E–W) that should result in only small errors [of less than 5° , see fig. 10 in Müller (Müller, 1989)]. In this second experiment the channel segments were chosen somewhat longer (2.65 m, 4.85 m and 2.20 m), and only the N–S direction of the middle segment was used (see inset in Fig. 4), since the results of the first experiment [and those of others (see Grah et al., 2005)], revealed no influence of the compass direction in the mirror

symmetric arrangements. For the crucial experiment, the middle leg of the Z was covered with orange Perspex, including the bends, and as before the direct view of the sky and the sun was prevented (in this experiment 20 cm wide wooden plates were arranged above the channels at a height of 15–20 cm above the ground).

Animals that had performed at least three successful foraging trips between the feeder and the nest, as indicated by their unhesitating passage of the covered segment of the channel, were captured and transferred in a lightproof container to a test field at some distance to the training site. The test field was a

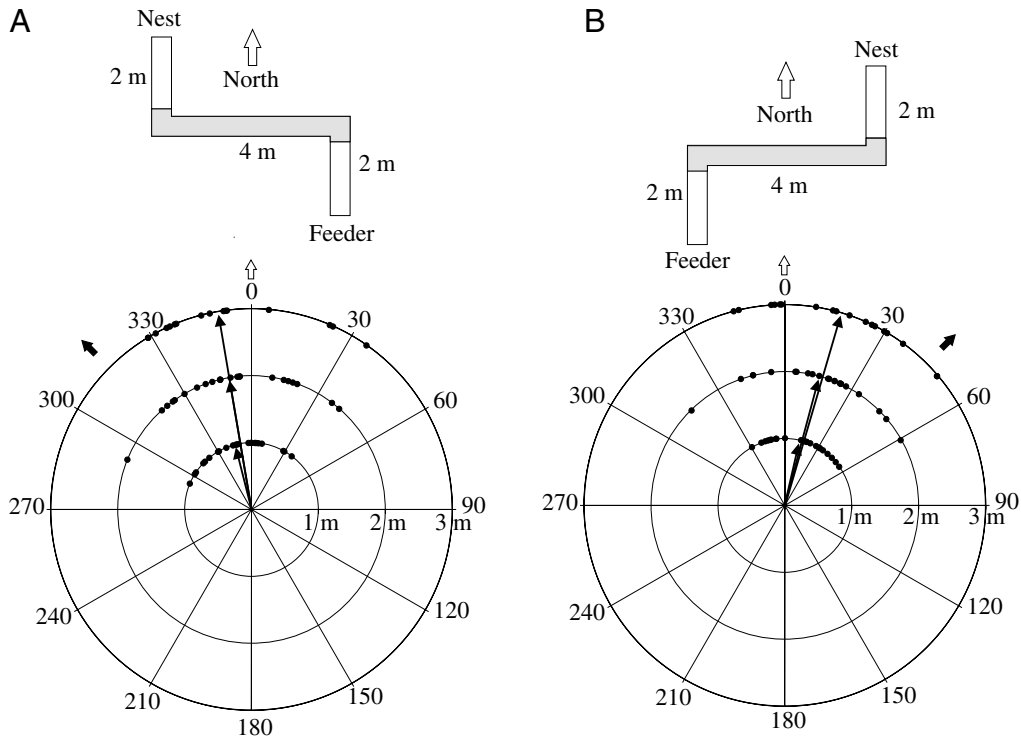


Fig. 2. Maze with covered middle segment, same orientations and dimensions as in Fig. 1A,B. The Perspex cover excluding UV radiation extended by 15 cm into the N–S-channel segments on both sides. (A) Eastward orientation. Mean vectors, at 1 m, 2 m and 3 m radii: $345.8^\circ/350.3^\circ/350.4^\circ$; vector lengths 0.89/0.90/0.94; $N=23, 23, 16$. Mean vector not significantly different from 0° (open arrowhead) at all radii, but highly significantly different from 315° (filled arrowhead). (B) Westward orientation. Mean vectors $12.9^\circ/15.0^\circ/16.3^\circ$; vector length 0.91/0.92/0.95; $N=22, 22, 18$. Mean vector not significantly different from 0° at 1 m, but significantly different from 0° at 2 m and 3 m. $P<0.05$. At all radii highly significantly different from 45° . Mean vectors of A and B significantly different (Watson–Williams test with Bonferroni correction, $P<0.01$).

flat area devoid of any vegetation, with a grid (10 m \times 10 m; grid width, 1 m) consisting of thin white lines painted on the desert floor. An ant was released after it was ascertained that it had a food item between its mandibles and therefore intending to return to the nest. The ant's path across the test field was recorded on squared paper until it switched to search spirals (cf. Wehner and Srinivasan, 1981).

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, 2 m, 3 m, and, if possible, 4 m around the animal's release point and measured the azimuth of the ant path's intersection with these 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 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).

The directionality of intersection points of a treatment was examined using the Rayleigh test, and the agreement with a theoretical value was checked by calculating the 99% confidence intervals [chapter 5 in Batschelet (Batschelet, 1981)]. Differences between mean angles obtained in different treatments were checked using the Watson–Williams test,

with a Bonferroni correction for multiple comparisons if appropriate. All statistical parameters were calculated using Oriana circular statistics software (Kovach, 2004).

Results

The compass directions of the ants' homing paths in the control conditions are summarized in Fig. 1. Each point gives the intersection of the ant's path with a 1-m, 2-m, or 3-m circle (see Materials and methods). Controls were performed in the Z-shaped channel system without a Perspex cover, and in addition in a straight channel (pointing to the South; see insets in Fig. 1). In these control conditions the ants' mean homing directions were close to the expected values of 315° , 45° and 0° [at 2 m, $319.8^\circ\pm 21.2^\circ$, $47.9^\circ\pm 12.9^\circ$ and $2.1^\circ\pm 16.9^\circ$, respectively; $N=23, 23, 20$, Fig. 1A–C; vector lengths >0.95 , means at all distances (except for the 3-m circle in Fig. 1A)] not significantly different from the three theoretical values.

This picture changed drastically when the compass information was withheld in the middle segment of the Z (Fig. 2). Now the mean homing directions at 2 m were $350.3^\circ\pm 26.0^\circ$ and $15.0^\circ\pm 23.7^\circ$, respectively ($N=23, 20$). In Fig. 2A the mean homing directions were not significantly different from the zero direction (i.e. north) at all distances, nor

from the straight control ($P>0.05$, Watson–Williams test), but significantly different from the respective Z controls with an open sky view (compare Fig. 1A, $P<0.01$, after Bonferroni correction). In Fig. 2B the mean at 1 m was not significantly different from 0° , whereas those at 2 m and 3 m were significantly different from the theoretical value of 0° , according to the 99% confidence intervals (see Materials and methods). However, at all distances the mean homing directions shown in Fig. 2B were not significantly different from the straight control (Fig. 1C; Watson–Williams test $P>0.10$), but significantly different from the open controls at all distances (compare Fig. 1B; all $P<0.001$).

There are several possible reasons for this result. For the moment let us focus on only one of them, i.e. that the ants were unable to perceive, or simply ignored, the 90° turns when entering the occluded channel segment (the channel was covered for up to 15 cm from the bends; see Materials and methods). If the ants did not take into account these 90° turns, they should have ‘added’ the 4 m of the mid-segment to their north-bound home vector at a rather small angle. (In the last leg the ants had an open sky view again, so that this travelling distance must also have been assigned to the north-bound vector.) Hence, under this assumption, the path lengths should

have been much larger than in the straight and open controls – which was not observed. The lengths of the straight homing path segments, before the ant switched to its typical search loops, were 3.43 ± 1.11 m and 3.36 ± 1.08 m for the data in Fig. 2A,B [difference to the open controls: not significant (n.s.) and $P<0.01$, for a, b, respectively]. Although this was 27% and 24% larger than the mean path length in the straight control (2.70 ± 0.77 m, Fig. 1C; differences n.s.; t -test with Bonferroni correction), these homing distances were much smaller than the 8-m prediction from the above hypothesis, but, most importantly, still smaller than the distances observed in the open controls (4.04 ± 1.32 m and 4.46 ± 1.11 m for Fig. 1A,B). The path lengths observed in the experiment shown in Fig. 3 were 3.9 ± 1.97 m and 3.18 ± 1.03 m (both n.s. different from those of Fig. 2). Hence, the estimated nest distances are by no means compatible with the assumption mentioned above. Note that the path lengths observed in the controls were also distinctly smaller than the expected values of 4 m and 5.66 m ($P<0.001$). A similar undershooting of walking distances, however, has been frequently found if training and testing conditions were rather different, as in the present experiments (e.g. Grah et al., 2005).

There is an additional result which makes the above

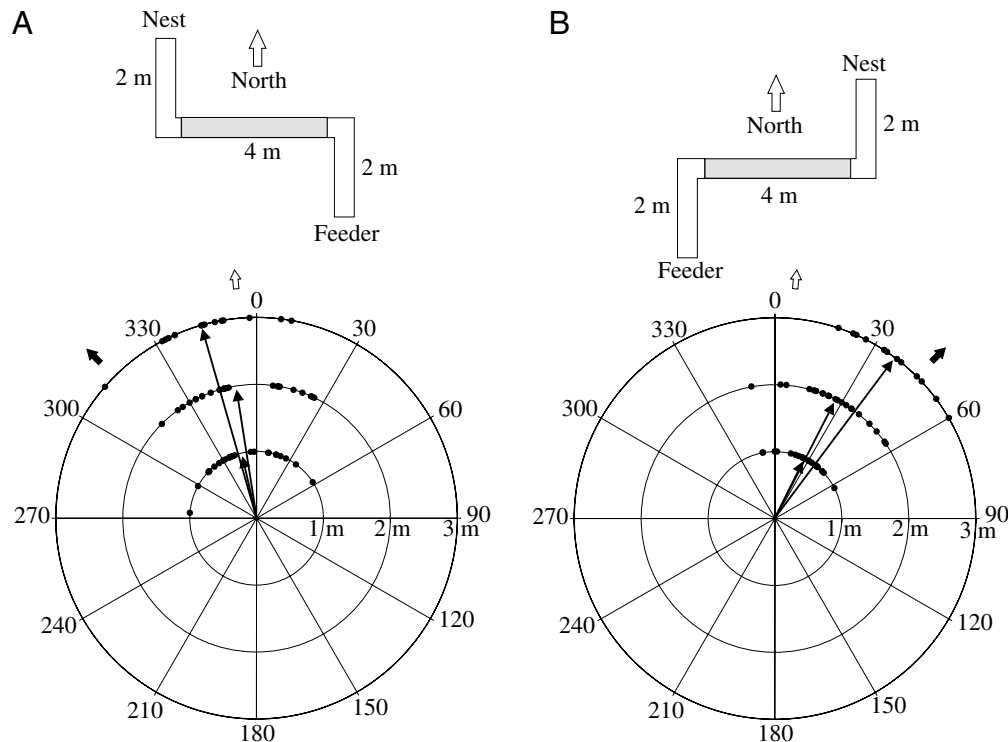


Fig. 3. Maze with covered middle segment and open bends. The Perspex did not cover the bends, allowing a view of the sky up to 15 cm into the middle segment on both sides. (A) Eastward orientation. Conventions as in Fig. 2: mean vectors $347.2^\circ/351.1^\circ/344.0^\circ$; at all radii not significantly different from 355° (open arrowhead), but highly significantly different from 315° ($P<0.01$); vector lengths 0.86/0.94/0.97; $N=25, 25, 15$. Note that in this maze a -5° or $+5^\circ$ deviation from a purely northern course is now expected, even if the ants had ignored the covered middle segment, since an uncovered middle segment of 30 cm has to be taken into account for the calculation of the expected home vector. (B) $26.4^\circ/27.1^\circ/36.8^\circ$; 0.95/0.96/0.98; $N=21, 21, 12$. At all radii mean vectors significantly different both from 5° (open arrowhead) and from 45° ($P<0.01$), except at 3 m radius (not significantly different from 45°). Mean vectors of A and B significantly different (Watson–Williams test with Bonferroni correction, $P<0.01$ to 0.001).

interpretation of a misperception of the 90° turns very unlikely. We ran a control experiment in which the bends were left uncovered so that the ants could perform their 90° turn still with an open view of the sky (Fig. 3). If, in the situation with covered 90° bends (Fig. 2), the ants had wrongly perceived only the turning angle, while the distance estimate was unaffected, the experiment shown in Fig. 3 should yield a clearly different picture, as the ants now performed their 90° turn under open sky. But the path directions shown in Fig. 3 closely resemble those of Fig. 2 (data of Fig. 3A and Fig. 2A not significantly different at all radii, $P>0.3$; data of Fig. 3B and Fig. 2B not significantly different at 1 m and 2 m radii, only at 3 m: $P<0.02$; Watson–Williams test with Bonferroni correction).

Hence, the shift of homing path directions seen in Fig. 2 (compared with Fig. 1) cannot be solely explained by an incorrect perception of the 90° turns. Rather, it must be the processing of distance information within the path integration module that has been affected by the exclusion of compass information. A puzzling result, however, is the remaining angular deviation from a purely northern direction, of 10° and 15° (Fig. 2A,B). In this context the directional errors induced by a partial *versus* complete view of the sky must be considered [(Müller, 1989); see also Materials and methods]. Indeed, the 10–15° deviations found in Fig. 2 are in the range of the sizes of errors observed by Müller (Müller, 1989). As in the

experiments shown in Fig. 2B and Fig. 3B the sampling times were biased towards the afternoon, this bias could have contributed to the observed ‘deviation’ from a pure northern direction. For the ‘left’ condition (E–W orientation of the mid-segment; Fig. 2A, Fig. 3A), there was a smaller bias towards testing in the morning. We tentatively corrected for these effects by subtracting the values reported in fig. 10 of Müller (Müller, 1989) from individual data points, according to the time of day of testing. Although this procedure did shift the mean angles towards the expected 0° value (in Fig. 2A from 350.3° to 352.5°, and in Fig. 2B from 15° to 11.5°), it could not completely account for the deviations from 0° seen in Fig. 2 (for Fig. 3B this correction shifted the mean angle from 27.1° to 23.1°, at 2-m distance, whereas that of Fig. 3A was unaffected).

In order to reduce the possible confounding influence of angular errors caused by the different sky views when ants walked within the channel and on the test field, we repeated the experiment of Fig. 2 at times of day that minimized potential systematic errors to less than 5° (see Materials and methods). The paths of the ants in the control situation (middle leg open) and in the crucial test (middle leg covered) were in the mean directed towards NW and to W (not significantly different from the expectations of 315° and 270° in Fig. 4A,B at all distances). These results confirm those of Fig. 2. Although for the crucial experiment (Fig. 4B), the deviations from the expected point in

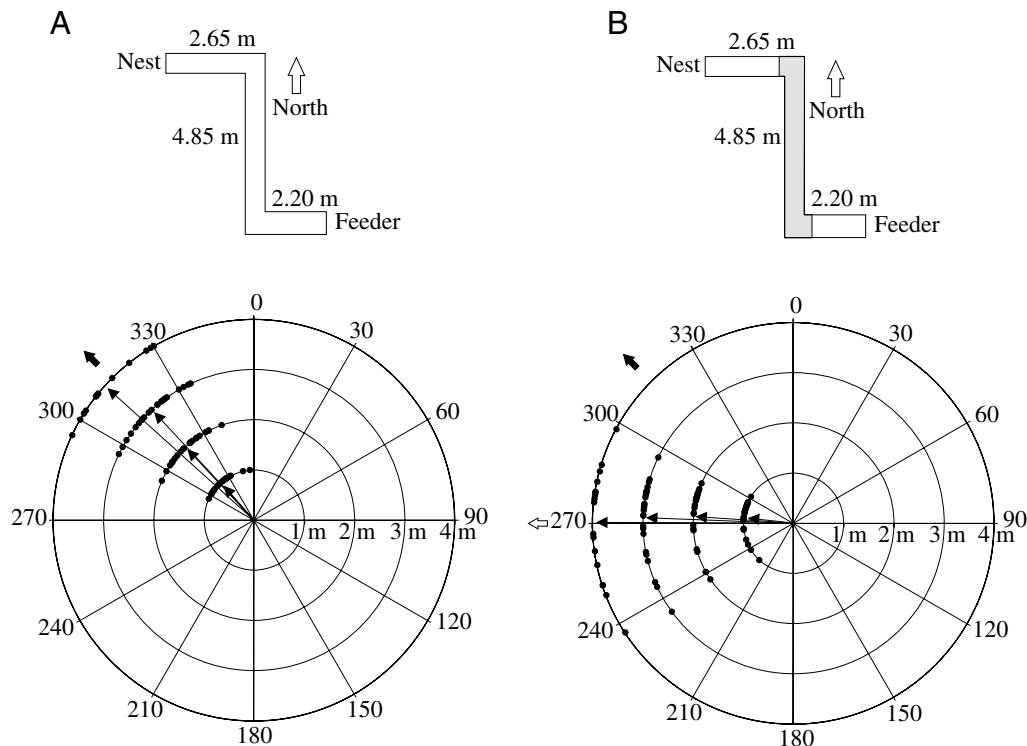


Fig. 4. Z-shaped maze in a different orientation (in 2005, first and third leg pointing to the east, middle to the south) (see Materials and methods). (A) Open control. Expected orientation 315° (filled arrowhead), mean vectors: 319.1°/316.8°/317.1°/312.0° (at 1 to 4 m radii); not significantly different from expected 315° at all radii; v.l. 0.97/0.98/0.98/0.98; $N=22, 22, 22, 13$. (B) Maze with covered middle segment. Mean vectors: 276.1°/273.8°/272.2°/270.2°; v.l. 0.95/0.96/0.97/0.97; $N=25, 25, 25, 18$. Mean vectors not significantly different from expected 270° (open arrowhead) at all radii.

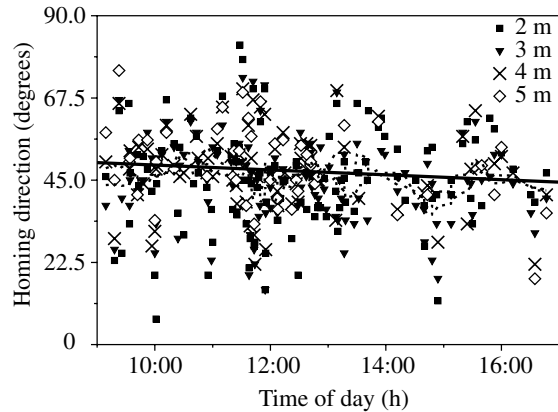


Fig. 5. Homing directions after training in open control maze, in relation to time of day. Expected values 45° and 315° . After mirroring the data of eastbound training they were not significantly different from those after westbound training (see Fig. 1A,B), and therefore the former data were mirrored for this plot. No larger deviations from 45° at some times of the day, nor a significant overall trend was visible, indicating that directional errors induced by the restricted sky view within the channels had been cancelled out due to the perpendicular orientation of segments in the 'open' controls.

the same direction as those of Fig. 2 (i.e. towards the direction of the first turn in the channel), these deviations were now only 6.1° , 3.8° , 2.2° and 0.2° for the 1-m, 2-m, 3-m and 4-m distance (mean values not significantly different from the expectation of 270°). Deviations of a similar size also occurred in the control situation (4.1° , 1.9° , 2.1° and -3.0° ; Fig. 4A).

In Fig. 5 the data of all individual runs obtained in the control situations, with an open view of the sky, are plotted against the time of day (data of 2002 and 2005 combined). As predicted, the systematic errors induced by the two rectangularly oriented channel segments seem to largely cancel out. There is no systematic trend visible as a gliding average yielded only small deviations from the expected 45° value, and also a linear regression yielded no significant trend ($r^2=0.0144$ and 0.0139 , $P=0.18$ and $P=0.29$, for the 3 m and 4 m data, respectively). The mean angles correspond well to the expectation of 45° (the data of Fig. 1A and Fig. 4A were mirrored): $44.8^\circ \pm 13.3^\circ$ ($N=125$), $44.3^\circ \pm 11.4^\circ$ ($N=122$), and $47.7^\circ \pm 10.8^\circ$ ($N=81$) for the 2-m, 3-m and 4-m circles, respectively.

Discussion

Our experiments were aimed at elucidating the interplay between the two essential inputs to the path integration module, odometric information and information from the celestial compass. A follow up question was, to what degree ants can fall back upon idiothetic information to measure changes in walking direction if deprived from celestial compass cues. Such idiothetic cues have been invoked to guide orientation in spiders (e.g. Seyfarth et al., 1982; Mittelstaedt, 1985; Moller and Görner, 1994) and *Cataglyphis cursor* (Thiélin-Bescond and Beugnon, 2005). It seemed quite conceivable that the large

turns involved in our experiments could also be measured by proprioceptors, e.g. by means of hair plates located on the leg joints. Hence, idiothetic information by itself could still provide sufficient directional information for path integration – at least with the comparatively small distances involved in the present experiments.

The main result was a dramatic change in homing directions induced by covering the middle segment of the Z-shaped maze to exclude UV radiation (Fig. 2, Fig. 4B). There are several conceivable explanations of this result: (1) An incorrect interpretation of only the turning angle when entering and leaving the covered channel segment – whereas the distance was measured and processed correctly. (2) A malfunction of the odometer within the covered channel. (3) A combination of 1 and 2. (4) A different weighting of odometric information if the path integrator is deprived of compass information.

(1) One possible explanation of the results with the covered middle segments (Figs 2–4) is that the ants did not perceive the 90° turns correctly, when entering the occluded channel segment (the bends were covered up to a 15 cm distance), and therefore simply 'added' to their north-bound vector the 4 m distance travelled within the middle segment. This interpretation is ruled out by the results of the control experiment (Fig. 3), which yielded very similar homing directions as the critical experiment (Fig. 2). Furthermore, the lengths of the respective return path segments were only larger than in the straight control by 24% and 27%, contrary to an expected factor of 2 under this hypothesis (see Results).

(2) A faulty perception of walking distance by the odometer is not likely either, since, first, in the uncovered part the channel floor and walls offered no contrasting structures that could have contributed to a visually driven odometer. Second, earlier experiments have demonstrated that the ants arrive at a reasonable distance estimate even if all optic flow cues were eliminated by partial ventral eye covers (Ronacher and Wehner, 1995; Ronacher et al., 2000). Walking bumble bees can measure distances in total darkness (Chittka et al., 1999), and recently *Cataglyphis cursor* has been reported to measure small distances correctly when walking in darkness, though only after intensive training (Thiélin-Bescond and Beugnon, 2005). Hence, a malfunction of the odometer seems unlikely, and also a combination of 1 and 2 (explanation 3) seems to be an unrealistic assumption.

We therefore favour explanation 4: that it is not the (peripheral) measurement of walking distance *per se* that has been affected by the exclusion of sky compass cues but rather the *processing* of this input within the path integration module. A still open question is whether the ants completely omitted the distance information obtained within the occluded channel segment, or whether it has been fed into the path integration module with a reduced weight. A small weighting factor, e.g. of about 0.1, could result from the sky compass input persisting with a certain decay time. Such an after effect would have led to a noticeable, though reduced, input into the path integrator of the distance travelled in the covered maze segment. Note

that by this assumption it is still necessary that the 90° turns have been perceived idiothetically in the experiment shown in Fig. 2. In the experiment in Fig. 3, the somewhat larger deviations from 0° could also have been caused by such a lagging decay function. However, the rather close agreement between mean vector and expected direction (270° in Fig. 4B), as well as the data of Sommer and Wehner (Sommer and Wehner, 2005), do not favour of this assumption of persisting sky compass information. As the direct view of the sky and the sun was prevented by additional screens (see Materials and methods), it is highly unlikely that the ants could have relied on intensity or spectral gradients as compass information (see also Wehner, 1982). Further experiments will be necessary to explore whether there is a decay function of the compass input that has led to the deviations from a purely northern course in Fig. 2, and if so, what its time course may be.

However, irrespective of this possibility of a very small weighting factor the clear message from our data is that the odometric information about travelling distance is nearly completely ignored for two-dimensional path integration, if there is no simultaneous input from the celestial compass. This conclusion is in accord with the one drawn from experiments with *Cataglyphis* trained in linear channels (Sommer and Wehner, 2005). Most importantly, the data presented here for the two-dimensional paradigm rule out that *Cataglyphis* can maintain the path integration process solely on the basis of idiothetic information. The latter possibility would have been a rather likely hypothesis, since earlier as well as recent experiments strongly suggest that (i) the ant's odometer operates on the basis of a step counter (Ronacher et al., 2000; Wohlgehmuth et al., 2001; Wohlgehmuth et al., 2002; Wittlinger et al., 2006), and (ii) idiothetic information can be used by other arthropods to infer changes in walking directions (see Introduction). Remarkably, while using different aspects of visual information [polarization, intensity and spectral cues (Wehner, 1982; Wehner, 1997)], the compass module of *Cataglyphis* apparently is not able to substitute visual cues by idiothetic information.

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