

Hair plate mechanoreceptors associated with body segments are not necessary for three-dimensional path integration in desert ants, *Cataglyphis fortis*

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Accepted 28 November 2006

Summary

In formicine ants, the hair fields associated with the neck and the petiole (alitrunk–petiole and petiole–gaster joints) have long been established to function in graviception. Here, we examine a possible role of these hair receptors in three-dimensional (3-D) path integration of the (formicine) desert ant, *Cataglyphis fortis*. *Cataglyphis* judge the ground distance when travelling over hills, allowing correct homing even in (unpredictably) uneven terrain. We eliminated the function of these hair sensors in graviception either by shaving the hairs or by immobilising the joints monitored by the hair plates. With that major component of their sense of graviception eliminated, one would expect the ants to disregard, or at least misgauge, the ascents and descents performed across hills during outbound journey. The ants should thus

consider the (much longer) actual walking trajectory, instead of the base distance, when calculating their homing distance. Surprisingly, neither shaving nor immobilisation of the hair sensillae affected correct path integration, across both uneven terrain (3-D) and level surface. If anything, the ants underestimated homing distance, which may reflect a general, safety-oriented navigation strategy. Animals that had performed the outbound journey with their gaster fixed in a horizontal position underestimated their homing so dramatically that this latter explanation cannot hold.

Key words: desert ant, *Cataglyphis*, navigation, 3-D path integrator, graviception.

Introduction

Desert ants, *Cataglyphis fortis*, perform dead reckoning, or path integration (Mittelstaedt, 1983; Müller and Wehner, 1988), as a major means of orientation when foraging in their typically flat and featureless desert habitat. Path integration relies on two input components. The first is the direction of travel, measured by a celestial compass. This compass is sensitive to the polarisation pattern of sky light, to the sun's azimuth and to spectral gradients of sky light (Wehner, 1992). The second component for path integration is distance measurement, provided by an odometer module. The ant odometer is basically a stride integrator that also considers stride length or stride frequency (Wittlinger et al., 2006; Wittlinger et al., 2007).

Path integration in desert ants is surprisingly accurate and successful, due to a number of compensatory and backup mechanisms that deal with the inevitable navigation errors inherent in all integration mechanisms (Müller and Wehner, 1988). This accuracy is not too surprising for the compass module, which relies on exact external directional cues, namely sun azimuth and sky light pattern. The odometer module, by contrast, has to rely primarily on idiothetic cues, namely

proprioceptive signals that measure leg movement or monitor the output of a locomotor central pattern generator (Wehner, 1992; Wittlinger et al., 2007). It might thus be expected to be more error-prone than the directional component of the path integrator. All the more surprising are unexpected features of the odometer module that have been reported in recent years. Most notably, the odometer is able to determine travel distance not just in the typical flat desert pans but also in hilly terrain with slope inclinations of up to 60° (Wohlgemuth et al., 2001; Wohlgemuth et al., 2002; Grah et al., 2005). Ants walking over such hilly terrain determine the ground, or base line, distance irrespective of the actual shape of the surmounted hills. This allows accurate return to the nest on a different route from that taken during outbound travel, independent of the substrate structure on these routes. Not only is this feature of the ant odometer surprising but also its accuracy is comparable to that achieved on level ground.

It is as yet completely unclear how base line distance is determined by the ants when walking on hilly terrain. It is clear, however, that the ants must be able to measure the slope of their walking substrate quite exactly to achieve this feat. In the present study, we examine one particular hypothesis of how

desert ants might be able to determine the inclination of the ground they travel on. According to the detailed analyses of Markl, ants determine the relative positions of their body parts, such as head, thorax (or in ants, alitrunk) and abdomen (or in ants, gaster), by means of hair fields associated with the joints between these body segments (Markl, 1962). And since the pull of gravity on these segments is dependent on body position and inclination, these hair fields might indeed serve as graviceptors involved in adjusting the odometer module to substrate inclination.

Materials and methods

Animals and experimental site

The field site for our experiments was located near Maharès, Tunisia (34°30'N, 19°29'E). Large and viable nests of *Cataglyphis fortis* Forel 1902 (Wehner, 1983) were selected. The experimental seasons lasted from the middle of June to the start of September in the years 2004 and 2005.

Preparation

To manipulate graviception, in a first set of experiments (exp. data I) the hair sensillae in the neck region and/or those associated with the petiole were eliminated by shaving with a razor splinter. There are two groups of hair plates associated with the petiole, one between alitrunk and petiole and a second between petiole and gaster (Fig. 1). In a second set of experiments (exp. data II), the joints between head and alitrunk and those between alitrunk and gaster were immobilised with a beeswax–resin mixture (1:2 v/v). In detail, the head was fixed to the alitrunk in a normal attitude, while the gaster was fixed to the alitrunk either in an extended position (i.e. gaster, petiole and alitrunk forming a roughly straight line, 180°) or in an erect position (the angle between alitrunk and gaster was <90°) (Fig. 2).

Experimental set-up

The basic experimental set-up was adapted after Wohlge-muth and co-workers (Wohlge-muth et al., 2001; Wohlge-muth et al., 2002). Ants were trained to forage at a feeder they could reach only *via* a series of artificial hills (hill training) (Fig. 3), affording a walking distance of 10 m. That walking distance corresponded to a distance on ground level between nest entrance and feeder of 6 m. As a control, a group of ants was trained to walk a 10 m distance in a flat channel (flat training) (Fig. 3). For testing, the experimental ants were put into a horizontal channel, 21 m long and oriented in parallel to the outbound (hill or flat training) channel (Fig. 3) (test). Both the artificial hill channel set-up for training (10 symmetrical triangular ‘hills’, consisting of 50 cm ascent and 50 cm descent, each with slopes of 54°) and the flat channel set-up for control training and testing consisted of alloy U-profiles. Width and height of the channels were 7 cm (see Fig. 3, top left), such that the ants experienced a strip-like view of the sky of approximately 54° when walking in the centre of the channel profile (centring response) (Heusser and Wehner,

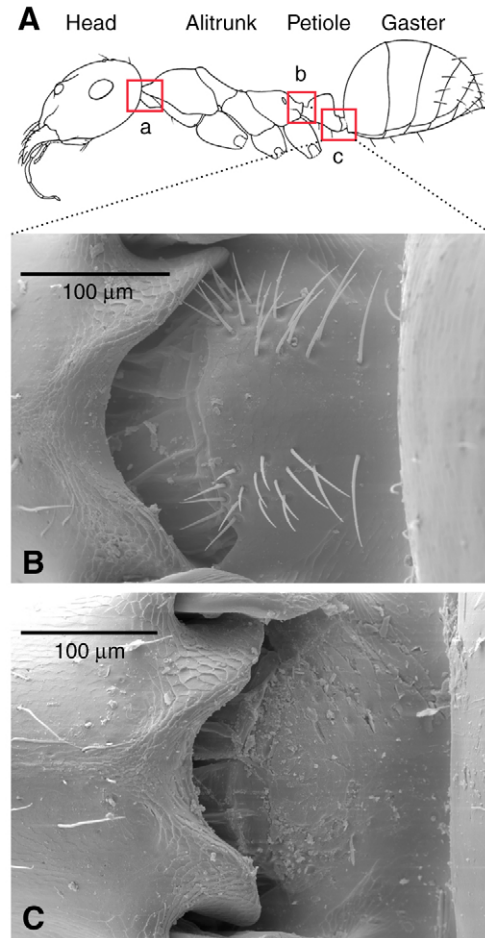


Fig. 1. Manipulated hair plates. (A) Schematic drawing of a *Cataglyphis* worker ant, lateral view. The positions of the manipulated hair plates are indicated (red rectangles); (a) neck joint, (b) alitrunk–petiole joint, (c) petiole–gaster joint. Drawing adapted from (Wehner, 1983). (B) Scanning electron micrograph (SEM) of the petiole–gaster joint; ventral view. Hair plates are in the centre of the image, not manipulated. (C) SEM of the petiole–gaster joint, ventral view; the hair plates had been shaved with a razor splinter (one of the experimental animals that contributed to the data in Fig. 4B).

2002) to read the skylight pattern. To provide traction for walking, the channel floor was coated with grey quartz sand, and to reduce optic movement cues and avoid distracting reflections the walls were painted with matt grey varnish.

In all experiments, each ant was marked by an individual three- or four-digit colour code, so that each animal of an experimental group could be run individually through the particular series of treatments and tests. The animals were caught and operated under a dissection microscope (Wild M8; magnification 50×; Heerbrugg, Switzerland) at the feeding site and then placed into a small container with an assortment of food. As soon as a given ant had picked up a food item it was placed into the test channel to perform its homebound run. With a food item in their mandibles, the animals were highly motivated to return to their nest (Wehner, 1982) and performed

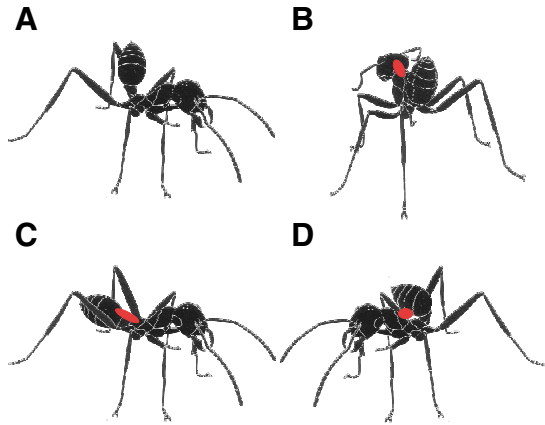


Fig. 2. Immobilisation of body parts. (A) Body posture in walking ants, *Cataglyphis fortis*. (B) Animal with its head fixed to the alitrunk. (C) Gaster (metasoma) fixed to the alitrunk in a prolate position of approximately 180°. (D) Gaster fixed onto the alitrunk in an erect (<90°) position. Drawing adapted from (Wehner, 1983). Beeswax–resin glue indicated in red.

determined homebound runs. This experimental group performed the outbound travel in a normal condition ('0'), and the homebound travel in a manipulated condition ('1'), and is thus termed '0–1' throughout the text. After this first test, the ants were released into their nest. A further (control) test was performed in these manipulated ants after they had re-emerged from the nest and performed another journey to the feeder (outbound manipulated – homebound manipulated; '1–1' ants). In animals with immobilised body segments (head–alitrunk or alitrunk–petiole–gaster joints incapacitated), additional tests were carried out. Namely, one test was made after removal of the beeswax–resin glue at the feeding site, thus making the previously immobilised body parts again free to move (outbound manipulated – homebound normal; '1–0'), and one final control test was made after these 1–0 animals had re-emerged from the nest, being in a normal condition again (outbound normal – homebound normal; 0–0a; as opposed to 0–0, as the group of ants tested prior to any manipulation, except colour marking). Of course, the shaving of hair plates could not be reverted in this way, the final test for these animals being 1–1.

Once transferred into the (flat) test channel, the ants performed their homebound runs. We recorded the point at which the ants switched from their steady, straight return path to their typical nest-searching behaviour. This point is marked by a conspicuous U-turn, followed by a run pacing back and forth around the initial turning point. The median distances of the six initial U-turns, relative to the release point, and the search densities were evaluated (see Figs 4–6). The test channel was divided into 10 cm bins for distance recording. Search density distributions (Figs 4–6, upper panels) were evaluated for each experimental situation. The bins of the test channel covered by an ant during its search were noted and cumulated, i.e. the more often a channel segment (bin) was visited during

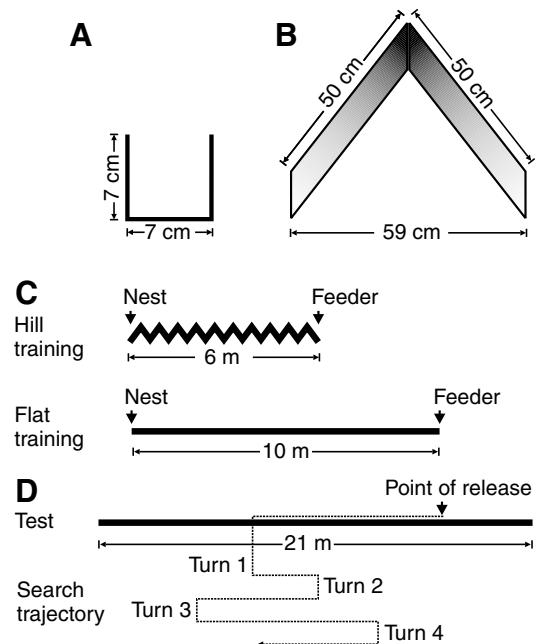


Fig. 3. Experimental situation and channel layout. (A) Channel cross section; (B) single channel segment for hill training; (C) hill training and flat training channels; (D) test channel. The search behaviour exhibited by *Cataglyphis fortis* foragers after having run off their home vector is illustrated schematically below the test channel (search trajectory). Not drawn to scale.

the search, the higher its value in the density distribution. Search density distributions were normalised to their peak values.

Statistical tests

For descriptive statistics, box and whisker plots (box plots) are shown (see Figs 4–6, lower panels). They display median values (bar in the box) and interquartile ranges (IQR) as measures of statistical dispersion, with first and third quartiles (the box margins) and the 5th and 95th percentiles (whisker margins). For all tests, we performed non-parametric statistics. Friedman Repeated-Measures ANOVA on Ranks compared effects of a series of different experimental test situations on a single group. If a difference was found, Tukey's test was performed as *post hoc*-test for multiple comparisons between test situations (Sachs, 1992). All statistical analyses were made with SigmaStat Version 2.03 (SPSS Inc., Chicago, IL, USA).

Results

Shaving of hair fields

We trained ants to walk from the nest entrance to a feeder over an array of artificial hills (Fig. 3) (hill training). The actual walking distance for the animals was 10 m, corresponding to a distance of 6 m on ground level. Ants that had reached the feeder in this artificial hill set-up were caught and subjected to experimental manipulation, and their homing distances were

subsequently measured in a flat channel (see Materials and methods). In accordance with previous studies (Wohlgemuth et al., 2002), control animals without any manipulation exhibited homing distances close to the actual ground distance of the training set-up (0–0 in Fig. 3A–C). In experimental animals, the hair plates between head, alitrunk and gaster were manipulated by shaving the hair sensillae in a first set of experiments. Unexpectedly, none of the shaving operations changed the animals' homing distances and, in particular, they did not extend them towards the 10 m actual walking distance experienced during the outbound journeys (Fig. 4). If anything, the ants slightly underestimated, rather than overestimated, the distance to the nest. This held true for all combinations of hair plate manipulation, shaving of the hair sensillae in the neck region, of the hair plates associated with petiole and gaster, and shaving of all these sets of hair plates (summary in Table 1). The slight underestimation of homing distance just noted was statistically significant only for the animals that had all these hair sensillae incapacitated and were tested after they had accomplished their first manipulated homing run (1–1 animals, $P < 0.05$, Tukey test) (Fig. 4C).

Shaving of hair fields – flat channel training controls

In these control experiments, the ants were trained from the nest entrance to the feeder over a 10 m distance in a flat, linear

channel, instead of the artificial hill array used otherwise. The ants were tested in the usual 21 m long flat channel. Interestingly, the slight underestimation of homing distance after the shaving operations also occurred with the flat channel training array (Fig. 5A,B). Actually, animals that re-emerged from the nest after having previously been shaved in the neck region (1–1) significantly ($P < 0.5$, Tukey test) undershot in their homebound runs, compared with the control recordings in these same animals (0–0). Animals with their hair sensillae shaved in the petiole–gaster region showed a significant underestimation of their homing distance, compared with the control situation (0–0), in both tests that followed the manipulation (0–1 and 1–1, both $P < 0.5$, Tukey test). These slight underestimations of travel distance correspond to those observed with training in the artificial hill array.

Immobilising body parts

There are two major differences between the shaving of hair plates and the immobilisation of body segments. First, the hair plates associated with immobilised body parts will constantly signal the particular fixed body posture, while signalling is absent or corresponds to a 'null' position after shaving. Second, the immobilisation of body parts – here, head–alitrunk and alitrunk–petiole–gaster joints – is reversible. This expanded the test runs to be performed for any given ant by another two runs:

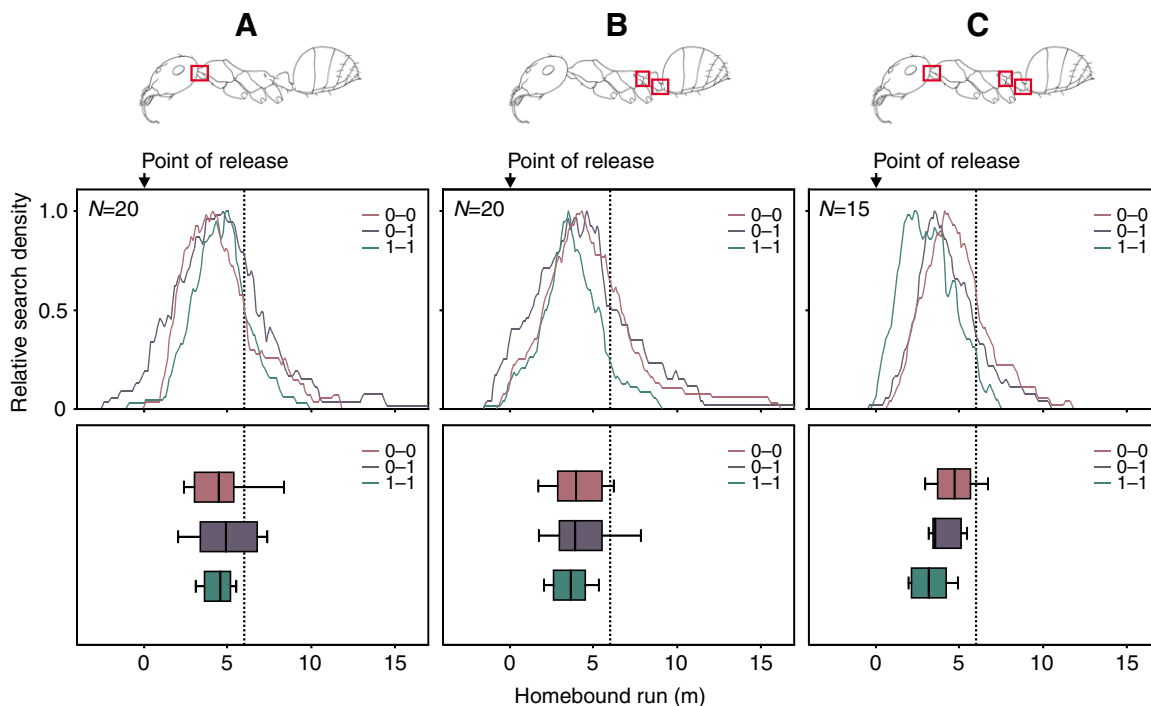


Fig. 4. Training across the artificial hill set-up (compare Fig. 3C), experimental data I (shaving). The top panels show search density plots (abscissae, homing distances; ordinates, cumulated relative search densities between the first and sixth turning points; see Materials and methods). The bottom diagrams display box-and-whisker plots (medians of the initial six turning points), derived from the same data sets ($N=15$ – 20 ants for each experimental situation). 0–0, 0–1 and 1–1 are double-digit codes for the particular test situation, the first digit represents the outbound run and the second digit represents the homebound run; 0 denotes the normal situation, 1 denotes the manipulated condition. (A) Animals with the hair plates in their neck region shaved. (B) Animals with the hair plates in the petiole–gaster region shaved. (C) Animals with both neck and petiole–gaster regions shaved.

Table 1. Statistical data of all experimental groups including all test situations

Experiment	N	Test situation	Median (m)	IQR (m)	P (Friedman test)	Tukey test (P<0.05)
Neck shaved Hills	20	0-0	4.45	2.35	0.311	-
		0-1	4.875	2.40		-
		1-1	4.55	1.55		-
Petiole-gaster shaved Hills	20	0-0	4.2	2.60	0.607	-
		0-1	3.975	2.35		-
		1-1	3.55	1.70		-
Neck-petiole-gaster shaved Hills	15	0-0	4.7	1.96	0.038*	1-1
		0-1	3.55	1.66		-
		1-1	3.15	2.08		0-0
Neck shaved Flat	18	0-0	8.95	2.55	0.029*	1-1
		0-1	8.55	4.20		-
		1-1	8.1	3.05		0-0
Petiole-gaster shaved Flat	20	0-0	9.6	2.30	0.007*	1-1, 0-1
		0-1	8.55	1.55		0-0
		1-1	8.5	1.45		0-0
Gaster fixed 180° Hills	15	0-1	4.75	1.54	0.012*	1-0, 0-0a
		1-1	3.45	0.92		-
		1-0	2.65	1.50		-
		0-0a	3.30	1.46		-
Gaster fixed <90° Hills	18	0-1	5.10	1.65	≤0.001*	1-1, 1-0
		1-1	1.525	2.45		0-1, 0-0a
		1-0	3.0	1.90		0-1
		0-0a	4.9	1.20		1-1
Head fixed Hills	15	1-1	3.7	1.51	0.725	-
		1-0	3.7	2.30		-
		0-0a	3.55	1.86		-
Gaster fixed <90° Flat	20	0-1	10.25	1.33	0.005*	1-1
		1-1	6.35	1.0		-
		1-0	9.275	3.4		-
		0-0a	9.175	1.95		-

Asterisk indicates significance.

outbound journey, manipulated – homebound journey, normal (1-0), and outbound journey, normal – homebound journey, normal (0-0a) (in addition to the usual 0-1 and 1-1 tests). That is, the animals were tested right after removal of the beeswax-resin glue at the feeding site (1-0) and later, after they had once again re-emerged from the nest and travelled to the feeder (0-0a).

Unfortunately, ants with their head fixed to the alitrunk could not be tested right after this manipulation, even when care was taken to adjust the head in a fairly normal posture. They were confused, had problems cleaning their antennae with the comb on their front legs and thus refused to accept a food crumb. Carrying food in their mandibles, however, is evidence of the ants' normal motivation to carry their booty home (Wehner, 1982) and was thus a prerequisite for recording homing distances (see Materials and methods). Nevertheless, the operated animals appeared one day later from the nest with

their heads still immobilised, now apparently without problems, and travelled to the feeder. The 1-1 test series could thus be performed, although without the normal preceding 0-1 test run. No differences were observed in the homing distances between these tests and the subsequent 1-0 and 0-0a tests (Fig. 6B). In all these tests, the ants appeared to slightly underestimate ground distance, instead of overestimating it due to the much longer outbound walking distance of 10 m across the artificial hills array (see above).

Animals that had their gaster fixed in an extended position (180°) were tested immediately after the gaster had been glued to the alitrunk at the feeder. These ants, too, slightly underestimated their homeward travel distance on level ground. In the subsequent tests (1-1, 1-0, 0-0a), they searched even closer to the release point than right after the manipulation (0-1) (differences significant in 1-0 and 0-0a, compared with 0-1, $P < 0.05$, Tukey test). The search density distributions in

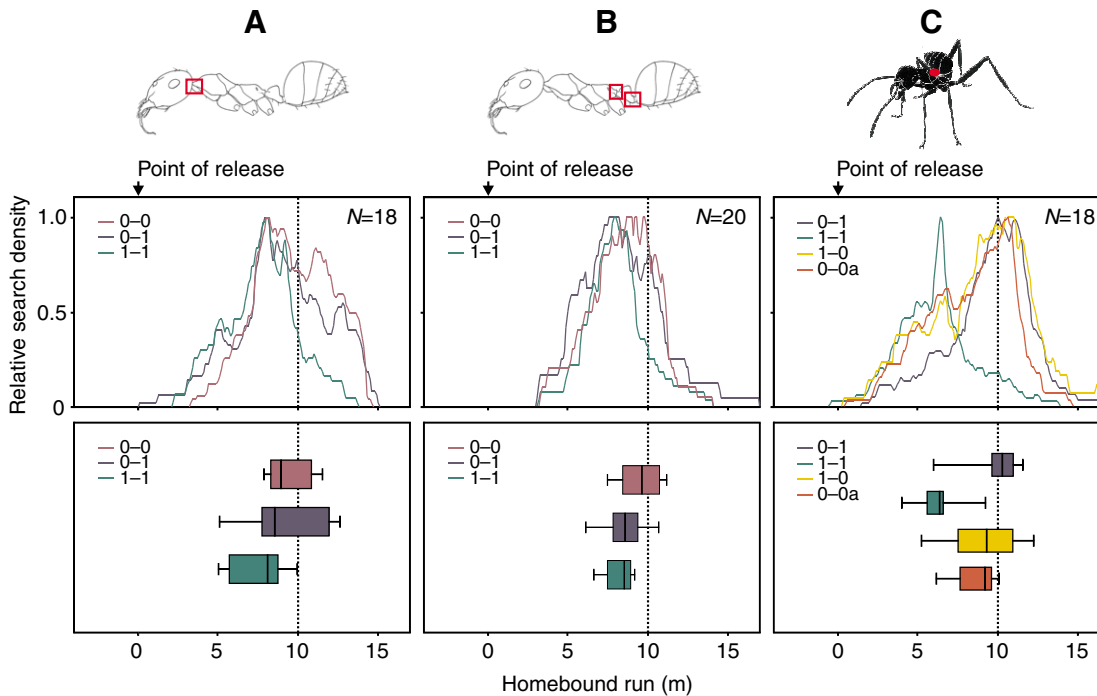


Fig. 5. Training across the flat channel set-up, experimental data I (A,B) and II (C). Diagrams and details of presentation are the same as described in Fig. 4. (A) Animals with the hair plates in their neck region shaved. (B) Animals with the hair plates in their petiole–gaster region shaved. (C) Animals with their gaster fixed in an erect ($<90^\circ$) position.

Fig. 6A (upper panel) demonstrate that this undershoot was quite distinct, the distribution of test 0–1, by comparison, showing a consistent shift towards larger distances.

The most striking results were observed in ants that had their gaster fixed in an erect position ($<90^\circ$). Ants that had their gaster immobilised during outbound as well as homebound runs (1–1) significantly underestimated homing distances, both after training in the horizontal channel and in the artificial hill array ($P < 0.05$, Tukey test) (see Fig. 6C, Fig. 5C). Very distinct displacements of the search density distributions towards the shorter homing distances were observed in these experiments (Fig. 6C, Fig. 5C, upper panels). This held true to some extent even after removal of the immobilising glue before the animals started their homebound journey (1–0) (see Fig. 6C). This pronounced underestimation in the 1–1 and 1–0 tests of the artificial hill training and in the 1–1 tests of the flat channel training were conspicuous indeed, particularly when considering the rather consistent results of all the other experiments.

The above results are summarised in Table 1.

Discussion

Path integration on slopes, and graviception

One might expect that, after elimination of the hair plates between adjacent body segments that were previously established to function as their major sensory system for graviception (Markl, 1962), ants foraging in the artificial hill

channel array would have no perception of the surmounted up- and downward slopes. They should thus perform homebound journeys in the flat test channel that correspond to the actual walking distance of 10 m of their outbound journey in the artificial hill array (in the critical 1–1 tests). At the very least, one would expect the animals to extend their search for the nest entrance well beyond the base line distance of 6 m. In contrast to this expectation, the experimental animals consistently performed homebound journeys that corresponded to the ground level distance of their outbound journeys. In several instances, the ants actually searched for the nest entrance at even shorter distances from the release point. This was true for both experimental interferences, i.e. shaving of the hair fields and immobilisation of the body parts monitored by these position sensors (summarised in Table 1). These results demonstrate that manipulated animals were still able to perform (almost) correct path integration during their up- and downhill outbound journeys.

This result is surprising when considering, first, that *Cataglyphis* ants usually keep their gaster in an upward (erect) position (see Fig. 2A) and, second, that, due to their long legs and elevated centre of mass, the gaster would lend itself as a major means of detecting terrain slope. More significantly, in his careful behavioural study of graviception in formicine ants, Markl identified the hair sensillae in the neck and petiole regions as important sensors for graviception (Markl, 1962).

In the above experiments, the hair plates associated with the legs and antennae still remain as possible sensors of the

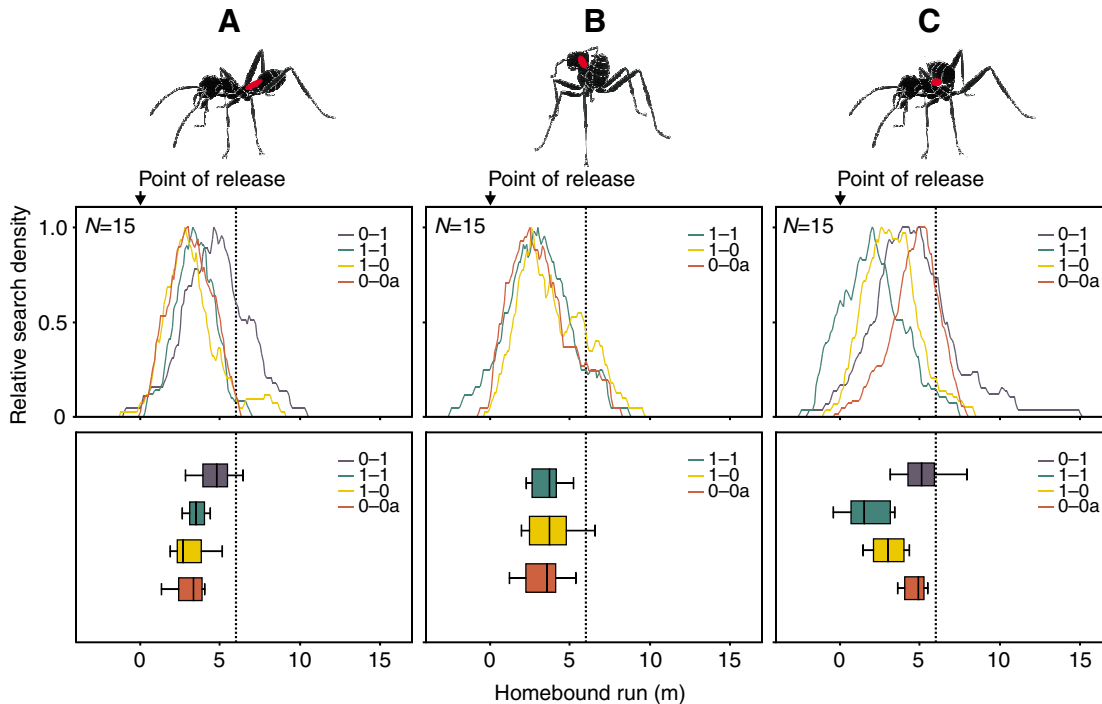


Fig. 6. Training across the artificial hill set-up, experimental data II (immobilisation). Diagrams and details of presentation are the same as described in the legend of Fig. 4. (A) Animals with their gaster fixed in a prolate ($\sim 180^\circ$) position. (B) Animals with their head fixed in a normal position. (C) Animals with their gaster fixed in an erect ($< 90^\circ$) position.

slopes of ascent and descent during outbound travel. Unfortunately, the hair fields of coxa and trochanter are not accessible for operation or immobilisation, at least not without incapacitating the animals and thus preventing further homing experiments. Operating the antennae has similarly severe effects. However, Markl suggests that the neck joint and the alitrunk–petiole–gaster joints are of particular importance for graviception and slope detection (Markl, 1962). At the very least, the relative contributions to graviception of these hair plates and those associated with the legs are in the same order of magnitude and cannot completely replace each other. Thus, the hair plates remaining on the legs would not appear to be responsible for the largely unaffected path integration in uneven terrain. Wohlgemuth and co-workers demonstrated, in an experimental set-up similar to the one used here, that additional loads applied on the alitrunk did not induce misjudgement of base line distance (Wohlgemuth et al., 2002). Presumably, thus, hill slopes were also judged correctly. The authors conclude that the artificial load could only have affected the legs, and thus the hair sensillae associated with the joints between leg segments, but could not have impaired other body parts such as head, petiole and gaster. Hence, the detection of slopes must have remained unaffected with altered leg load and slightly changed leg coordination.

In summary, it appears that desert ants do not measure terrain slope by means of sensory systems employed in graviception,

namely neither by hair fields associated with neck and petiole nor by those associated with the legs. At least, these organs are dispensable for 3-D path integration and their loss can be compensated. It remains to be examined whether the ants use different sensory modalities altogether, such as vision and the detection of sky light polarisation, to assess the slope of their walking substrate.

Possible reasons for underestimation of homing distance

Apparent underestimation of homing distance was observed in several of our experiments (see e.g. Figs 4, 6; summarised in Table 1). Modest undershoot may in fact represent an element of homing strategy, rather than a genuine mistake in distance estimation. Starting to search for the nest after a homing distance that is shorter than the actual estimate by the average margin of error will lead the animal to the familiar side of the nest surrounds, rather than to unfamiliar terrain beyond the nest (see also Sommer and Wehner, 2004; Wolf and Wehner, 2005). Such undershoot in the range of about 5–10% of homing distance is thus frequently observed in homing experiments, not only in desert ants (see Sommer and Wehner, 2004). This effect may become more pronounced in cases where the animals experience disturbances or are even disabled. In such cases, it may be advantageous to opt for more safety at the expense of homing speed. According to this line of argument, a more severely impaired ant should exhibit shorter homing distances, at least within the short-distance

ranges examined here (6–10 m, compared with more than 100 m in some recorded foraging runs; for these distances this argument may not be valid any more).

Gluing the gaster to the alitrunk in an (extremely) erect position ($<90^\circ$) had the most noticeable effects on homing distance, both in the up- and downhill channel training and in the flat channel training (Fig. 5C, Fig. 6C). In these experiments, the undershoot was pronounced to an extent that makes the above general explanation for shortened homing distances very unlikely. At the same time, this manipulation had the largest impact on body posture, since the position of an ant's centre of mass is noticeably influenced by fixing the heavy gaster onto the alitrunk (see Fig. 2D) (Zollikofer, 1988). In the artificial hill training, these animals considerably underestimated their travel distance, by an average 75.6%, when tested after they had emerged with their fixed gaster at the feeding site (1–1). This held true when the manipulation was reversed at the feeder and the animals were tested again, although the undershoot was somewhat smaller (50%) (1–0) (Fig. 6C). Intriguingly, the ants also misgauged their travel distance in the flat channel (control) experiment, though only when the gaster was fixed during both outbound and homebound runs (1–1). They did not undershoot when the manipulation was reversed before the homebound run was performed (1–0) (Fig. 5C).

Outbound journey with the gaster fixed in an extreme erect position thus seems to be the major determinant in misgauging homing distance in these experiments. At present, one can only speculate about the possible reasons for these observations.

We thank Stefan Sommer, Tobias Seidl and Markus Knaden for a lot of support during the field work and many stimulating discussions. This study was funded by the

Volkswagen Stiftung (I/78 580 to R.W. and H.W.), by the Swiss National Science Foundation (3100-61844 to R.W.), and by the University of Ulm and Zurich.

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