

S. Wohlgenuth · B. Ronacher · R. Wehner

Distance estimation in the third dimension in desert ants

Accepted: 22 February 2002 / Published online: 6 April 2002
© Springer-Verlag 2002

Abstract Desert ants of the genus *Cataglyphis* perform large-scale foraging excursions from which they return to their nest by path integration. They do so by integrating courses steered and the distances travelled into a continually updated home vector. While it is known that the angular orientation is based on skylight cues, it still is largely enigmatic how the ants measure distances travelled. We extended the ants' task into the third dimension by training them to walk within an array of uphill and downhill channels, and later testing them on flat terrain, or vice versa. In these tests the ants indicated homing distances that did not correspond to the distances actually travelled, but to the ground distances; that is, to the sum of the horizontal projections of the uphill and downhill segments of the ants' paths. These results suggest a much more sophisticated mechanism of distance estimation than hitherto thought. The ants must be able to measure the slopes of undulating terrain and to integrate this information into their "odometer" for the distance estimation process.

Keywords Path integration · Distance estimation · Odometer · Ants · *Cataglyphis*

Introduction

Desert ants of the genus *Cataglyphis* perform large-scale excursions in rather featureless surroundings from which they return to their nest with astonishing precision by

path integration (dead reckoning: Wehner and Wehner 1990). During their outbound path they continually update a 'home vector', which at any point indicates the homing direction and the distance to the nest. To assess this home vector the ants apply an iterative rule of thumb (Müller and Wehner 1988) by which they integrate the distances they have travelled and the angles of their path segments with respect to an external compass reference (Müller and Wehner 1988, 1994). While the estimation of walking direction is based on skylight cues (both spectral and polarizational: Wehner 1997), the sensory basis of the ants' odometer is still largely enigmatic. Three types of cues have been considered as a possible basis how insects could gauge travelling distances (von Frisch 1965; Seyfarth and Barth 1972; Seyfarth et al. 1982; Mittelstaedt 1983; Esch and Burns 1996; Srinivasan et al. 2000): (1) energy expenditure, (2) self-induced optic-flow, and (3) information derived from the animal's own movements, i.e. *idiothetic cues* (Mittelstaedt and Mittelstaedt 1973). According to earlier experiments (Heran and Wanke 1952; Heran 1956; von Frisch 1965), energy expenditure seemed to be the decisive cue used by foraging bees. However, this hypothesis is no longer tenable because of evidence accumulated during the last decade (Schäfer and Wehner 1993; Esch and Burns 1995, 1996; Srinivasan et al. 2000). Instead, flying bees rely mainly on the integration of optic-flow parameters to gauge distances travelled (Srinivasan et al. 2000; Esch et al. 2001). Interestingly, in desert ants (*Cataglyphis fortis*) optic flow cues play only a minor role for gauging distances. While ventral optic flow had some influence on distance estimation (at least at high contrasts; Ronacher and Wehner 1995), lateral optic flow, which has been invoked as the major cue for bees (Srinivasan et al. 1996, 1997), definitely played no role in the ant's odometer (Ronacher et al. 2000). Even more importantly, the ants arrived at a fairly exact distance estimate if all optic flow cues had been excluded (Fig. 6 in Ronacher and Wehner 1995; cf. also Ronacher et al. 2000). The conclusion from these experiments was that ants mainly rely on idiothetic cues. Probably, for a

S. Wohlgenuth · B. Ronacher (✉)
Department of Biology,
Humboldt University, Invalidenstr. 43,
10099 Berlin, Germany
E-mail: Bernhard.Ronacher@rz.hu-berlin.de
Tel.: +49-30-20938806
Fax: +49-30-20938859

R. Wehner
Department of Zoology,
University of Zürich, Winterthurerstr. 190,
8057 Zürich, Switzerland

walking animal, cues related to its own motor performance constitute a more reliable source of information than optic flow, while the latter is the best choice for flying animals.

In this study we investigated how these ants measure travelling distances in undulating terrain. We extended the ants' task to the third dimension, by training them to walk over a linear series of hills to reach a food source located several meters away from the nest. In our uniformly painted channel system the ants could not rely on optic flow cues, and therefore were likely to use idiothetic cues (cf. also Ronacher and Wehner 1995; Ronacher et al. 2000; Wohlgemuth et al. 2001). The animals could rely on idiothetic cues, for instance use a kind of step counter or monitor the output of a locomotor central pattern generator (CPG) by means of an efference copy. Our present results, however, suggest that the use of idiothetic information cannot be as simple as activating a step counter or monitoring the output of a CPG. Rather information about the slopes of the terrain must also be measured and then integrated into the distance estimation process.

Materials and methods

Experiments were performed on desert ants (*C. fortis*) in a small salt pan near the village of Maharès (Tunisia; 34.58° N, 10.50° E). Additional control tests were performed on a colony of *C. bicolor* reared in our Zurich laboratory.

Experimental set up, training and testing

The basic experimental set up is depicted in Fig. 1. Ants were trained and tested in channel systems, which consisted of aluminium U-profiles (7-cm base, 7-cm walls, see Fig. 1a). The bottom was covered with very fine grey sand glued to the floor in order to facilitate walking behaviour. For two reasons, the inner side walls were sprayed with matte grey paint: to avoid disturbing reflections and to eliminate any contrast cue that could provide optic flow stimuli. The dimensions of the channels were chosen so that ants walking in the middle of the channel – what they usually do ('centering response', Heusser and Wehner 1996) – could still see a substantial part of the spectral and e-vector patterns of the sky (a strip-like window with an angular width of approximately 50°).

The channel system was either flat (horizontal; training B) or consisted of a series of hills (training A, C, D). The hill segments were either symmetric (50 cm ascent, 50 cm descent, slopes 54° from the horizontal) or asymmetric (50 cm and 100 cm, 54° and 24° slopes, Fig. 1). The training distances varied between different experiments and are specified in the figures. At both ends of the training channel (around the nest and the feeder) a circular fence was fixed, so that large numbers of ants were forced to enter the channel. The following test channels were used: (1) horizontal, (2) symmetric hills, and (3) asymmetric hills in both orientations (steep ascent, shallow descent and vice versa). The test channels were aligned in parallel to the respective training channel and were much longer than the training one (Fig. 1b).

Once in the training channel, individually marked ants (marked by a three-digit code) shuttled back and forth between the nest and a food source (pieces of water melon or small biscuit crumbs). An individual ant could be taken from the feeder and transferred to one of the test channels where it performed its homebound run. We then recorded the point at which the ants switched from their steady, straight return path to their typical nest-searching beha-

viour. This transition is marked by a conspicuous 180° (U) turn, followed by a path directed backwards and long lasting oscillatory movements around the turning point (e.g. Wehner and Srinivasan 1981; Ronacher and Wehner 1995). In all figures, the mean distances of these initial U-turns relative to the release point are defined as the ants' distance estimates.

When transferred from the food source to the test channels, some animals refused to commence a normal straight homebound run, but switched to searching behaviour immediately or after a few decimetres. These 'abortive' runs clearly differed from normal ones, as nest-searching behaviour mostly occurred at distances of less than 1 m, only rarely up to 1.8 m. The distribution of abortive runs was clearly separated from the normal runs (Fig. 1c). We decided to set a criterion of 2 m. Tests where the ants exhibited search behaviour at distances less than 2 m were not included in our analysis, while all other runs were included and contributed to the mean distances given in the figures. Note that although abortive runs occurred with a somewhat higher proportion when the animals were tested in a channel that differed from the training situation, they also occurred in about 35% of the tests performed in a test channel that had the same dimension as the training one (Fig. 1c).

Experiments with additional load

Animals were trained in a horizontal channel to a food source 4.2 m away from the nest (ground distance). An ant was taken from the food source, marked and loaded with a piece of tin wire (weight: 10–20 mg) glued to its pronotum with Opalith glue (as used by beekeepers). Most animals were severely disturbed by this procedure and refused to show normal homing behaviour. These ants were taken to the nest, released there, and tested (in the flat and the symmetric hill channel) several hours later, after they had returned (with the artificial load) from the nest to the food source.

Walking speeds

The time spent during walking uphill and downhill was recorded separately for each channel segment (stop watch HANHARD Delta E100). From such individual travelling times we calculated an ant's average travelling speed for ascent and descent walks.

Statistical tests

In most experiments individually marked ants were tested in all (two or three) test conditions. This experimental paradigm allowed us to make pairwise or triple comparisons. We applied Wilcoxon's matched-pairs signed-rank test for paired data (see Figs. 2, 3c, d, 4, 7), and Friedman's test combined with Wilcoxon-Wilcoxon tests for multiple comparisons of data obtained in the repeated measures design (Fig. 3a, b). Correlations between speeds on outward and homebound runs and distances were tested with Spearman's signed rank test (Sachs 1997). Bars in the figures indicate mean values plus standard deviations.

Results

Do ants measure walking distance or ground distance?

The results of two main experiments are described in Fig. 2. In the first experiment the ants were trained along a series of nine hills. They covered an actual walking distance of 8.7 m from the nest to the food source (the ants were captured in the midst of the last descent), which corresponded to a horizontal (ground)

Fig. 1. **a** Dimensions of single channel segments. **b** Schematic side views of the experimental set-up consisting of the channels used for training and testing. **c** Distribution of distances travelled after training A. *Open bars*: distances covered by ants that immediately showed search behaviour instead of normal homebound runs. *Filled bars*: travelling distances of normal homebound runs. *Left diagram*: tests in hill-channel array (control); *right diagram*: tests in horizontal channel

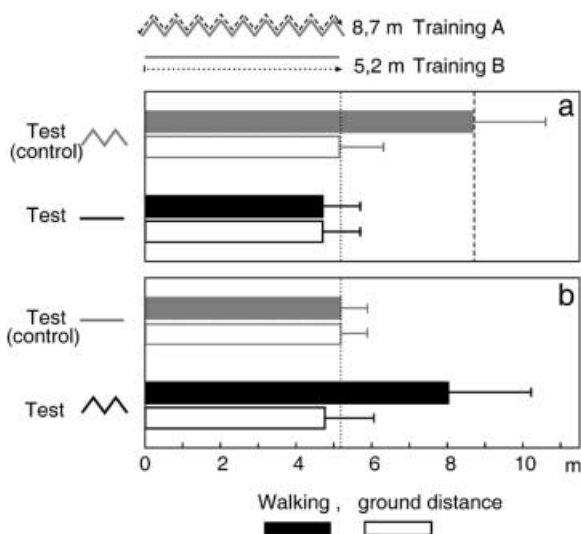
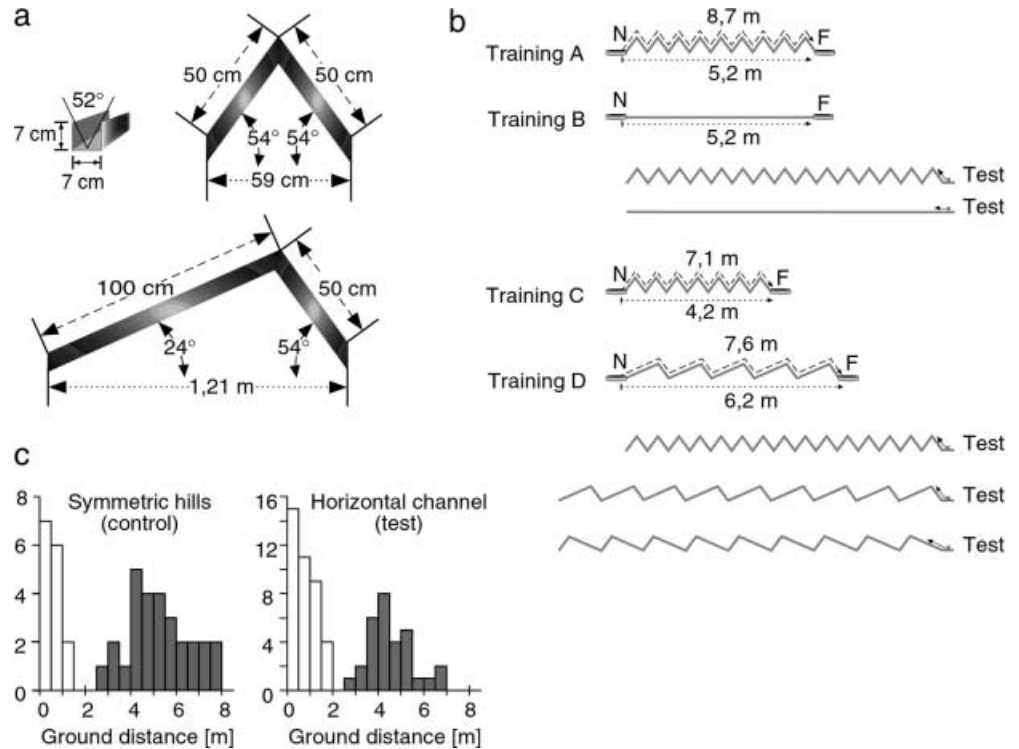


Fig. 2a,b. Homing distances of ants after training A and B. **a** Ants were trained to walk to the food source over nine symmetric hills (training A); walking distance 8.7 m, ground distance 5.2 m (see top). *Filled bars* indicate the actually travelled distance (mean + SD), *open bars* the corresponding ground distances (for tests in the flat channel the two values are the same). *Dotted vertical line*: expected ground distance, *broken vertical line*: expected walking distance. $n = 21$ individuals tested; difference between walking distances in control and test $P < 0.001$ (Wilcoxon matched-pairs signed-rank test); ground distances differed with $P < 0.05$ between control and test. **b** Results of training B, in which the ants were trained to walk to a 5.2-m-distant food source in a flat horizontal channel. $n = 17$, walking distances differed significantly ($P < 0.001$) between control and test, while ground distances did not ($P > 0.05$)

distance of 5.2 m (see Fig. 1b). In the hilly test channel (control as in training) the animals' mean distance estimate corresponded very well with the correct home distance (Fig. 2a; filled bars indicate walking distances, open bars the corresponding horizontal distance). However, when the ants were released in the flat channel, they stopped at a much shorter distance than their outward walking distance (4.7 ± 1.0 m, difference to training control: $P < 0.001$). This distance actually travelled by the ants came close to the ground distance of the training channel (there was, however, a weakly significant undershoot, $P < 0.05$, when compared with the ground distance of the training control).

The reciprocal experiment was performed with a different group of animals. The ants were now trained in the horizontal channel (distance 5.2 m). As in the first experiment, the ants turned at the correct distance in the control tests (upper bars in Fig. 2b). By contrast in the hill-channel device, they covered a much greater distance of 8.1 ± 2.2 m (difference to training control $P < 0.001$). The corresponding ground distance, however, was not significantly different from that travelled in the controls ($P > 0.05$).

Taken together, the results obtained in these two experimental paradigms indicate that, when walking in undulating terrain, the ants' odometer does not refer to the actual walking distance but rather to the ground distance, that is, the sum of the horizontal projections of the uphill and downhill segments of the ants' path. Hence, the ants seem to be able to perceive the inclination of the uphill and downhill slopes and to include this information into their processing of walking distances.

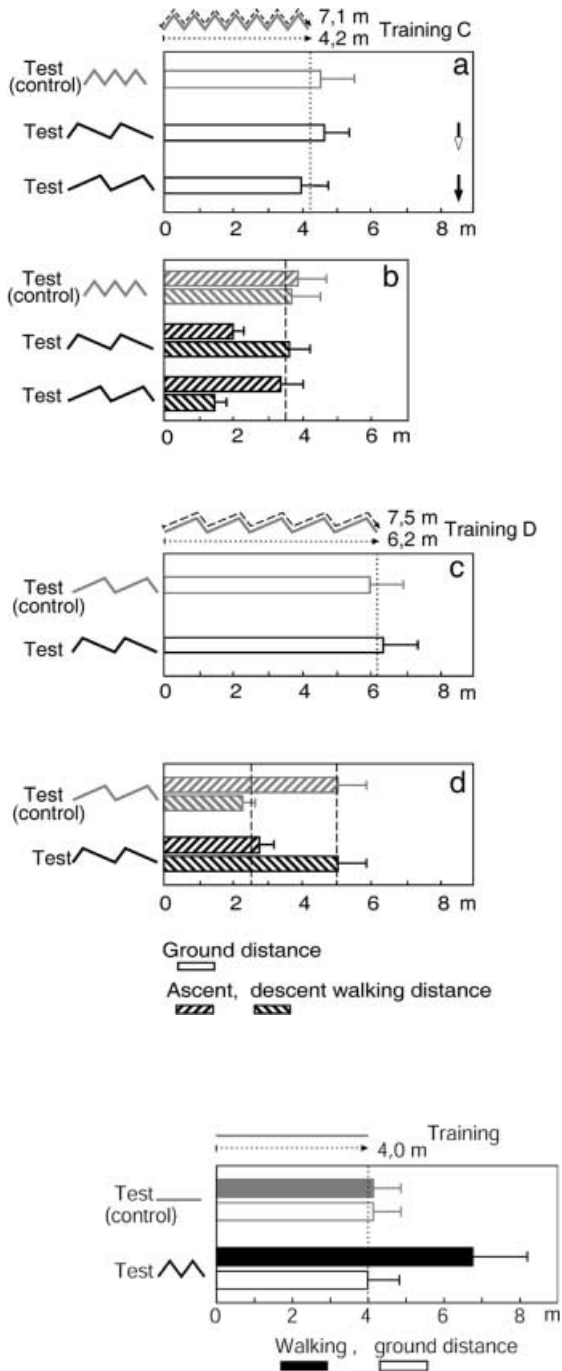


Fig. 4. Results of the laboratory experiment, in which the use of sky light polarization pattern was precluded. Training to a 4-m-distant food source in a flat channel. The homing distance in the control test corresponded to the training distance (4 m, vertical dotted line). In the hill-channel array the ants walked significantly longer than in the control (6.8 m, $P < 0.001$); the corresponding ground distance, however, was not significantly different from control (and expectation); $P > 0.05$. $n = 9$

There are, however, two alternative interpretations by which the results shown in Fig. 2 can be explained without the need to refer to a computation of ground distances. One possibility is that the ants measure walking distances only during the ascent (or descent) parts of

Fig. 3a–d. Results of tests in asymmetric channel arrays: **a, b** after training in a symmetric channel (training C); **c, d** after training in an asymmetric channel (training D). **a** Homing distances of ants after training C. The ground distances covered in the three test arrays did not differ significantly from each other (Friedman test, triple comparison, $P > 0.05$), nor from the training ground distance (dotted vertical line). The arrows indicate the expected ground distances for the asymmetric channels, had the animal's odometer counted ascents only (open arrow) or descents only (filled arrow). $n = 15$. **b** Plot of the cumulative ascent (upper bar of pair) or descent (lower bar of pair) walking distances. Among the ascent distances the middle column differs significantly (Wilcoxon-Wilcox, $P < 0.01$) from the other two (which are not significantly different); for the descent distances the lowest bar differs significantly from the other two ($P < 0.01$). Broken vertical line indicates cumulative ascent or descent distance experienced in the training channel (3.5 m). **c** Corresponding results after training in an asymmetric channel array (training D, see top of **c**). Ground distances covered by the ants did not significantly differ between the two orientations (and from training distance), $P > 0.1$ (Wilcoxon), $n = 18$. **d** Cumulative ascent distance (upper bar of pair) corresponded to the expectation in the upper channel orientation while it was significantly different ($P < 0.01$) in the lower one. For descent distances, the reverse is true. Vertical lines indicate distances experienced during training (left: cumulative descent distances, right: cumulative ascent distances)

the channels, ignoring the descents (or ascents) and not incorporating information about the slopes. Because of the particular dimensions of the symmetric channel segments used in training A and B (see Figs. 1b, 2), the expected home distance for the ascent- (descent-) alone assumption would be 4.5 m. This value is close to the distance actually travelled by the ants (4.7 m; see lower bars in Fig. 2a, b). In order to test this possibility, we trained ants over seven symmetric hill segments (walking distance 7.1 m, ground distance 4.2 m). The ants were then tested in both orientations of an asymmetric channel (Fig. 3a), and, as a control, in the symmetric test channel as well. As shown in Fig. 3a, the ground distances covered by the ants were quite close to the training ground distance (the differences between the three test conditions are not significant, Friedman $P > 0.05$). However, according to the assumption that the ants had taken into account only the ascents they should have stopped at a ground distance of 8.5 m (open arrow in Fig. 3a). Similarly, the results of the lowest column also reject the hypothesis that the ants had counted only the descent walking distances (filled arrow indicates expected ground distance under this assumption). Figure 3b shows the cumulative ascent and descent distances separately, as derived from the data of Fig. 3a. The cumulative ascent distance covered in the test with steep ascents (upper bar, centre pair) differs significantly from that of the control (and the reciprocal test paradigm). The cumulative descents yielded similar results. Here the distances represented by the lower bar of the lower pair differed significantly from the distances in the other two tests. A different group of ants was not only tested but also trained within an asymmetric channel array (Fig. 3c, d). The results of this group completely confirmed the ones shown in Fig. 3a, b; again, the (horizontal) search dis-

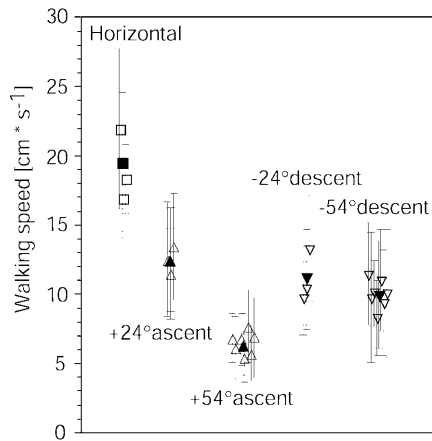


Fig. 5. Walking speeds of ants during homebound runs in different channel arrays. Ascent and descent speeds are shown separately for different slopes. *Open symbols* represents the mean value (\pm SD) of a certain test in the field, *filled symbols* the grand mean for the respective test condition

tances in the two reciprocally oriented channels were not significantly different from the 6.2-m ground distance experienced in the training situation ($P > 0.1$). In summary, the results shown in Fig. 3 do not support the hypothesis that the ants had exclusively relied on the ascents (or descents) to gauge walking distances.

The second objection relates to the ant's use of their polarization compass. Ants derive information about the direction of their paths from the polarization pattern of the sky by means of a specialized dorsal rim region of their compound eyes (Wehner 1982; Fent 1985). Note, however, that during their ascent and descent walks the ants had their head inclined (relative to the skylight pattern) at an angle that differed from the one kept on even ground. This difference could have induced an error in reading polarized-light information from the sky. Thus, it is conceivable that an ant walking in the hill-channel array could have misinterpreted an ascent walk as an angular deviation of its course in the *horizontal* plane. On the other hand, descent walks could have induced an angular deviation pointing in the opposite direction, actually leading to a 'virtual' zig-zag course within the horizontal plane. Such a course would then predict a shorter distance estimate, just as it was observed in the experiments of Fig. 2. According to this hypothesis the ants would not be 'aware' of the slopes, or they would be unable to integrate this information into their odometer reading. It is rather unlikely that this hypothetical misinterpretation yielded distance estimates that fitted the corresponding ground distances so closely. Nevertheless, we performed control experiments using the same channel system as in the field, but set up under laboratory conditions (in Zurich rather than in Maharès). Now the ants could derive information about directions only from artificial illumination that was present on the ceiling of the laboratory.

In these lab experiments training was performed in the flat horizontal channel with the feeder situated at a

distance of 4 m from the entrance of the colony (Fig. 4). In the hill-test channel, the ants turned at a distance of 6.8 ± 1.4 m, corresponding to a ground distance of 4.0 ± 0.8 m; not significantly different from control and expectation. This result obtained in the absence of polarized-light cues confirmed the results shown in Fig. 2, and rejected the hypothesis introduced in the previous paragraph.

Walking speed

In combination with an estimate of walking time, walking velocities could in principle be used to infer travelling distance. To test this, we separately stopped the walking times spent during ascents and descents and used these records to calculate the ants' mean velocities during ascent and descent walking. Velocity data from the homebound runs in all experimental conditions are summarized in Fig. 5. In the horizontal channel the ants' mean speed was around 20 cm s^{-1} (in three experiments between 17 cm s^{-1} and 22 cm s^{-1} , with rather large standard deviations due to variations in animal size and mandibular loads). Compared to this flat-ground speed, velocities were clearly reduced in both the ascent and descent sections of the channels. The strongest reduction in speed occurred during 54° ascents, where the ants were slowed down to about $6\text{--}7 \text{ cm s}^{-1}$, while in the 24° ascents the speed was about twice as high (around 12 cm s^{-1}). Remarkably, on the 24° slopes, ascent and descent walks yielded the same speeds. The ants walked only slightly faster when the descents became less steep.

To test for a possible correlation between outward and inward velocities, individual ants were observed both during their outward run (in an array of symmetric hills) and during their return run in a test channel (same dimensions as in training). There was no correlation between the velocities on the outward and homebound runs (Fig. 6a). During the (unloaded) outbound runs the mean velocities were 10.3 cm s^{-1} and 12 cm s^{-1} for ascents and descents, respectively (Fig. 6b, open triangles). Again, the main reduction in speed during the return run (by ca. 40%) occurred in the ascent sections, while the reduction was only approximately 20% for the descents. This trend was confirmed by tests in asymmetric channels (comparison of outbound and homebound runs for 24° ascents and 54° descents). Again, there was no correlation between an individual's inbound and outward velocities (Spearman rank correlation coefficient: $r = 0.44$, -0.24 ; $P > 0.1$, > 0.2 ; data not shown). The mean in and out velocities for 24° ascents did not significantly differ, nor did they during the 54° descents (Fig. 6c).

Experiments with artificial loading

To derive their ground distances when walking over hilly terrain the ants must measure the inclination of their path and include this information in their odometer

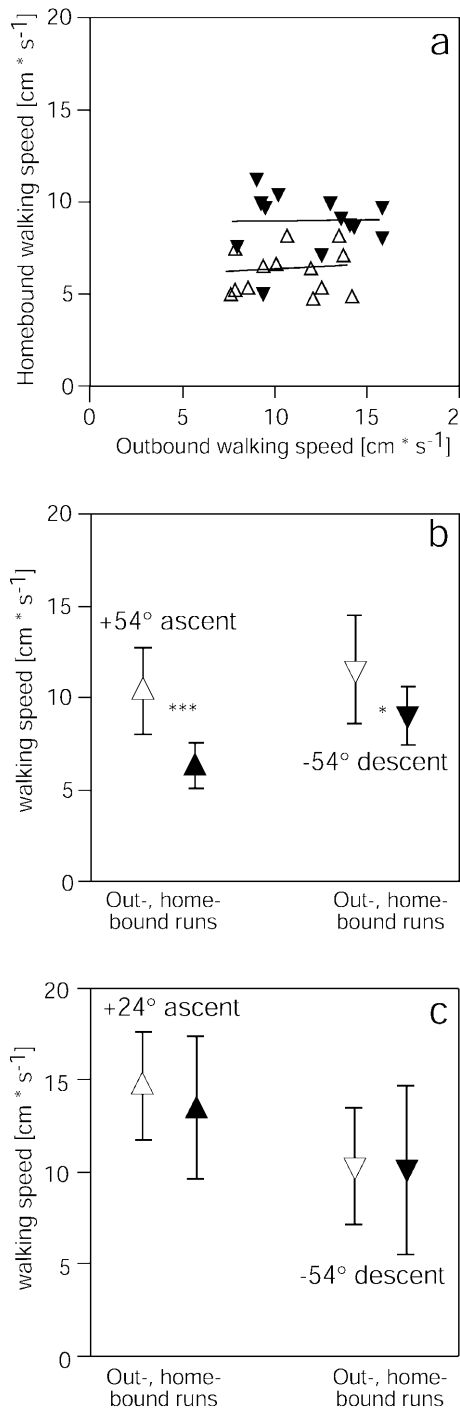


Fig. 6a–c. Comparison of walking speeds during outbound and homebound runs (during which the ants bore a piece of biscuit in their mandibles). **a** Test for a possible correlation of an individual's walking speed during outbound and homebound run (in a symmetric channel array); $n = 13$. Neither for ascent (*open triangles*) nor for descent (*filled triangles*) speeds there was a significant correlation between the inbound and the outbound speeds ($P > 0.2$, Spearman rank correlation). **b** Ascent and descent walking speeds were nearly the same in outbound runs, while during return runs the ants walked much slower on ascents ($n = 13$). Asterisks indicate significant differences between outbound and homebound speeds ($*P < 0.05$, $***P < 0.001$). **c** Speeds in asymmetric channel arrays. Neither in 24° ascents nor in 54° descents did the outbound and the homebound speeds differ significantly ($n = 15$, $P > 0.05$). Note that the ants were faster on a 24° ascent than on a 54° descent

altered and that this alteration would lead to a misjudgement of the slopes of the walking platform. Such an error would reflect itself in a mismatch between the actual ground distance indicated in the hill-channel array and the distance estimated in the flat channel. The loads applied consisted of 1.5- to 2.5-mm-long pieces of tin wire (see Materials and methods). The weight of the tin wires ranged from 10.5 mg to 17.5 mg, which averaged to 1.9 times the body weight of the ants (range 1.1–3.1 times). After the ants had been trained in a flat channel (4.2 m distance), the loads were applied. Since after this procedure almost all ants did not show normal homing behaviour they had to be released into the nest and could be tested only after they reappeared at the food source. Therefore, the animals had borne the additional weight already during their outbound run in the flat channel. The result obtained in the symmetric hill channel did not indicate any influence of the weight on the ants' estimate of the slopes: the ants stopped at the correct ground distance (Fig. 7a). There was no correlation between walking distances and the body weight to load ratio, neither in the flat nor in the hilly channel ($r = 0.02$ and 0.07 ; $P > 0.2$, data not shown). The walking speed was, however, markedly reduced during both the ascents (additional reduction by 35% compared to ants without alitruncal load) and the descents (reduction by around 40%; Fig. 7b). In contrast, in the flat channel the ants were nearly as fast as without loads (speed reduction less than 10%, difference to speed of unmanipulated ants n.s.).

mechanism. According to Markl (1962) ants of the genus *Formica* do measure the inclination of their body against the gravity vector through changes of the relative positions of different body parts (between head and thorax, between thorax and petiole, between petiole and gaster, as well as between thorax and the coxae of the legs). The angular inclinations between these body parts are monitored by several hairplates located at the respective joints. Our working hypothesis for the next experiment was that by applying an additional load on the thorax (alitrunk) the proprioceptive input would be

Discussion

The results presented above suggest that when walking over hilly terrain ants do not gauge the actual walking distance but rather the ground distance, i.e. the sum of the horizontal projections of the uphill and downhill segments of their paths. To do so, they must measure the inclination of the walking plane, or the inclination of the body against gravity. Two alternative explanations were ruled out by the results shown in Figs. 3 and 4: (1) that the ants had measured walking distances only during the

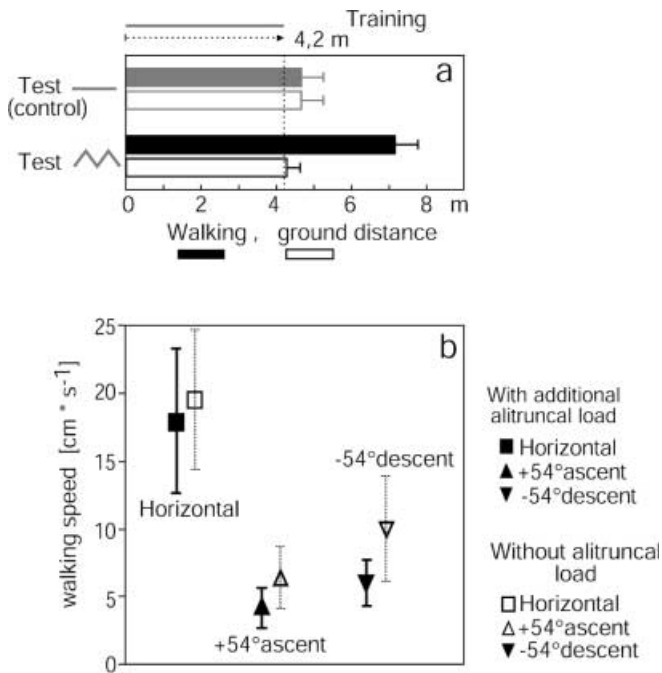


Fig. 7a,b. Experiments with artificial loading. **a** Ants were trained in a horizontal channel to a 4.2-m-distant food source. The loads were applied to the thorax already before the outbound run (see Materials and methods). The average ground distance indicated in the hill-channel array was not significantly different from the control ($P > 0.05$) and corresponded well to the training distance (compare *open bars* in **a**); the actual walking distances, however differed highly significantly ($P < 0.001$); $n = 14$. **b** Speeds of ants with alitruncal load (*filled symbols*), for walking in a horizontal channel, during ascents and during descents. For comparison also the mean (return run) speeds of ants without artificial load are shown (*open symbols*); note that these speeds were not obtained from the same individuals

ascents (or descents) while ignoring slopes and descents (or ascents), and (2) that the different inclination of the ant's head during ascents and descents had induced a misinterpretation of the ants' polarization compass, and thereby of their (horizontal) walking direction (see results of the laboratory experiment shown in Fig. 4).

Rather than projecting their walking trajectories on the horizontal plane, the animals could have computed their 3-D position when walking over undulating terrain. If this were the case, an ant trained to walk on a ramp to a food source located, e.g. at 2 m height, should later try to climb to this height when guided in a flat channel that was provided with opportunities for vertical ascents (cf. Srinivasan 2001). It is also in this case, however, that the ants must be able to measure the slope of the terrain over which they travel (or the inclination of their body against the gravity vector). Our present experimental paradigm does not allow a definite conclusion about this hypothesis, but further experiments are under way to investigate this possibility.

Even though at present we do not know how the ants actually incorporate the information about the inclination of the walking platforms into their estimates of ground distances (or their 3-D vector com-

putations), the results presented in this study allow for some conclusions about the nature of the odometer. We will discuss the three cues invoked earlier (see Introduction), and include combinations of velocity and time cues.

Energy expenditure

Recent experiments have shown that energy expenditure is an unlikely odometric cue in both bees (Esch and Burns 1996; Srinivasan et al. 2000; Esch et al. 2001) and ants (Schäfer and Wehner 1993). Our present results yield additional evidence that the mere energy consumption on the way from the nest to the feeder, without additional information about the slopes of the walking platform, cannot be a useful means of gauging distances travelled. For example, in the hilly test array the ants covered a 1.5-fold distance compared to the flat channel, in which they had been trained (Fig. 2b). Thus, when returning over the hills the ants experienced at least the 1.5-fold energy consumption as on flat terrain. In contrast, when trained over the hills and tested in the flat channel, the ants stopped at about 55% of the walking distance covered in the hilly array (Fig. 2a). If the ants had relied on energy expenditure alone, irrespective of the slopes of the walking platforms, one had to conclude that they had consumed distinctly less energy when walking over the hills than when walking on level ground, or had misjudged their energy expenditure accordingly (cf. Nielsen et al. 1982; Full et al. 1990). Of course, if walking uphill and downhill were more costly for the ants than walking on level ground, this discrepancy would even be larger (cf. Taylor et al. 1972).

Optic flow cues

Of the cues proposed so far as a possible basis for gauging distances travelled (see Introduction), optic flow information was excluded by our present experimental paradigm. The uniformly grey floor and walls of the channels were devoid of any textural cues that could have been exploited by the ants' visual system. However, our earlier experiments had already shown that *Cataglyphis* can measure travelling distances quite well even without any optic-flow information (Ronacher and Wehner 1995; Ronacher et al. 2000).

Walking speed

In gauging distances travelled the ants could rely on some combination of speed and time. By measuring its own speed and the time spent walking, an ant could also arrive at an estimate of travelling distances. In *Cataglyphis* there exists a highly stereotyped relationship between walking speed and stride length as well as stride frequency (Zollikofer 1994a, 1994b). Hence, by moni-

toring, for example, the output of a CPG for leg movements the ants could, in principle, obtain information about their locomotor speed without referring to other sensory cues (e.g. optic flow).

In principle, it would even be sufficient to measure time as the sole parameter, provided that the speed does not vary too much (cf. Wehner and Srinivasan 1981). However, in general this condition is not fulfilled, if one compares walking speeds during outbound and homebound runs. Large differences in speed between outbound and homebound runs necessarily arise when an ant carries a heavy or bulky piece of prey (Zollikofer 1994c; cf. also Fig. 6a, b). Nonetheless, the ants indicated correct distances even when bearing large prey or when their speed was reduced due to eye covers (Ronacher et al. 2000). By the hill experiments presented here an additional variation of walking speeds was introduced (Figs. 5, 6). Thus, the ants could not have relied on measuring walking time alone. In order to derive distances from speed they must have a means to compensate for changes in walking speed. A feasible way to compensate for differences in walking speed would be to monitor the output of the CPG for walking, and to increase or decrease the total time spent walking in proportion to deviations from the basic CPG frequency.

However, a comparison of the results presented in Figs. 2 and 3 and in Figs. 5 and 6 does not support such a mechanism. On the one hand, for example in Fig. 3a, in spite of the different slopes of the channel arrays the ants always indicated the same ground distances (differences between the three test conditions not significant). As a consequence of the different slopes the ants' walking speeds differed substantially (cf. Figs. 5 and 6). In the asymmetric channel with flat ascents (lowest bar in Fig. 3a) the mean return velocity was even larger than during the outbound run (up 13 cm s^{-1} and down 11.5 cm s^{-1} , compared to the mean outbound velocities of up ca. 10 cm s^{-1} , down ca. 12 cm s^{-1} ; Fig. 6b). Hence, one had to assume that the animals precisely compensated for differences in walking speed. This, however, is at odds with the results of Fig. 2. Here, in the hill-channel array the ants walking at low speed stopped at a large walking distance (Fig. 2a). When tested within the flat, horizontal channel, the ants had about twice the speed of the hill-controls. However, the actual walking distance was by 4 m shorter than in the control test (compare filled bars in Fig. 2a). Taken together, it seems rather unlikely that velocity as an isolated cue (irrespective of other odometric cues like slopes) is a useful means of gauging walking distances.

Idiothetic cues

The previous discussion leaves idiothetic cues as the most likely source of information used by the *Cataglyphis* odometer. As mentioned in the Introduction, it is not clear what kind of sensory information and neuronal processing mechanisms can be subsumed under

the term 'idiothetic information'. Our present results clearly demonstrate that in gauging distances travelled the ants must employ more sophisticated means than merely counting numbers of steps or monitoring the output of a central pattern generator. In particular, we must conclude that information about the slopes contributes to the distance estimates. In ants gravity perception, and hence most probably also the measurement of the slopes of the walking platforms, is mediated by proprioceptors located at the joints between the ant's major body parts (Markl 1962). However, it remains an open question how these proprioceptive inputs are integrated into the ant's odometer.

The experiment with artificial loading aimed at introducing an erroneous input into the ant's system of gravity perception whenever the ants were walking over the hills. Even though the ants could not be tested immediately after attaching the loads, and hence were loaded already during their (horizontal) outbound run from the nest to the feeder (see Materials and methods), the artificial loading could have induced a misjudgement of the slopes of the hills. The results shown in Fig. 7a do not indicate that such a misjudgement of distances might have occurred. However, one should take into account that a variety of hairplates contribute to gravity perception, and that the artificial load might not have affected the joints between head and thorax and between petiole and gaster. In *Formica* these joints seem to be of special relevance in gravity perception (Markl 1962). As these various organs may complement each other when one or another is surgically eliminated, it will be nothing but easy to unravel the mechanisms by which the ants gauge walking distances proprioceptively.

Whatever the underlying mechanisms are that *Cataglyphis* uses in navigating over hilly terrain, our experiments clearly show that the ants when walking within an uphill-downhill platform array can compute the ground distance between the points of departure and arrival. Whether this means that they perform true 3-D path integration or merely project all distances travelled in 3-D space onto virtual 2-D dimensions, remains to be elucidated. Experiments aimed at providing answers to this question are under way.

Acknowledgements We thank Heidi Gansner for her help in running the experiments and the members of the Zurich-Maharès crew for their cooperation in the field. We further thank Helmut Heise for the excellent construction of the channel arrays and the Swiss National Science Foundation as well as the Georges and Antoine Claraz Foundation (both grants to R.W.) for financial support.

References

- Esch HE, Burns JE (1995) Honeybees use optic flow to measure the distance of a food source. *Naturwissenschaften* 82:38–40
- Esch HE, Burns JE (1996) Distance estimation by foraging honeybees. *J Exp Biology* 199:155–162
- Esch HE, Zhang S, Srinivasan MV, Tautz J (2001) Honey bee dances communicate distances measured by optic flow. *Nature* 411:581–583

- Fent (1985) Himmelsorientierung bei der Wüstenameise *Cataglyphis bicolor*: Bedeutung von Komplexaugen und Ocellen. Ph.D. Thesis, University of Zürich
- Frisch K von (1965) Tanzsprache und Orientierung der Bienen. Springer, Berlin Heidelberg New York
- Full RJ, Zuccarello DA, Tullis A (1990) Effect of variation in form on the cost of terrestrial locomotion. *J Exp Biol* 150:233–246
- Heran H (1956) Ein Beitrag zur Frage nach der Wahrnehmungsgrundlage der Entfernungsweisung der Bienen (*Apis mellifica* L.). *Z Vergl Physiol* 38:168–218
- Heran H, Wanke L (1952) Beobachtungen über die Entfernungs-meldung der Sammelbienen. *Z Vergl Physiol* 34:383–393
- Heusser D, Wehner R (1996) The centering response of desert ants, *Cataglyphis fortis*: balancing the angular heights of objects in the left and right visual fields. In: Elsner N, Schnitzler H-U (eds) Göttingen Neurobiology Report, vol II. Thieme, Stuttgart, p 330
- Markl H (1962) Borstenfelder an den Gelenken als Schweresinnesorgane bei Ameisen und anderen Hymenopteren. *Z Vergl Physiol* 45:475–569
- Mittelstaedt H (1983) The role of multimodal convergence in homing by path integration. In: Horn E (ed) Multimodal convergences in sensory systems. Fortschritte der Zoologie, vol 28. Fischer, Stuttgart, pp 197–212
- Mittelstaedt H, Mittelstaedt M-L (1973) Mechanismen der Orientierung ohne richtende Außenreize. *Fortschr Zool* 21:46–58
- Müller M, Wehner R (1988) Path integration in desert ants, *Cataglyphis fortis*. *Proc Natl Acad Sci USA* 85:5287–5290
- Müller M, Wehner R (1994) The hidden spiral: systematic search and path integration in desert ants, *Cataglyphis fortis*. *J Comp Physiol A* 175:525–530
- Nielsen MG, Jensen TB, Holm-Jensen I (1982) Effect of load carriage on the respiratory metabolism of running worker ants of *Camponotus herculeanus* (Formicidae). *Oikos* 39:137–142
- Ronacher B, Wehner R (1995) Desert ants *Cataglyphis fortis* use self-induced optic flow to measure distances travelled. *J Comp Physiol A* 177:21–27
- Ronacher B, Gallizzi K, Wohlgemuth S, Wehner R (2000) Lateral optic flow does not influence distance estimation in the desert ant *Cataglyphis fortis*. *J Exp Biol* 203:1113–1121
- Sachs L (1997) Angewandte Statistik. 8. Aufl. Springer, Berlin Heidelberg New York
- Schäfer M, Wehner R (1993) Loading does not affect measurement of walking distance in desert ants *Cataglyphis fortis*. *Verh Dtsch Zool Ges* 86.1:270
- Seyfarth EA, Barth FG (1972) Compound slit sense organs on the spider leg: mechanoreceptors involved in kinesthetic orientation. *J Comp Physiol* 78:176–191
- Seyfarth EA, Hergenröder R, Ebbes H, Barth FG (1982) Idiopathic orientation of a wandering spider: compensation of detours and estimates of goal distance. *Behav Ecol Sociobiol* 11:139–148
- Srinivasan MV (2001) Homing in on ant navigation. *Nature* 411:752–753
- Srinivasan MV, Zhang SW, Lehrer M, Collett TS (1996) Honeybee navigation en route to the goal: visual flight control and odometry. *J Exp Biol* 199:237–244
- Srinivasan MV, Zhang SW, Bidwell NJ (1997) Visually mediated odometry in honeybees. *J Exp Biol* 200:2513–2522
- Srinivasan MV, Zhang S, Altwein M, Tautz J (2000) Honeybee navigation: nature and calibration of the “odometer”. *Science* 287:851–853
- Taylor CR, Caldwell SL, Rowntree VJ (1972) Running up and down hills: some consequences of size. *Science* 178:1096–1097
- Wehner R (1982) Himmelsnavigation bei Insekten: Neurophysiologie und Verhalten. *Neujahrsbl Naturforsch Ges Zürich* 184: 1–132
- Wehner R (1997) The ant’s celestial compass system: spectral and polarization channels. In: Lehrer M (ed) Orientation and communication in arthropods. Birkhäuser, Basel, pp 145–185
- Wehner R, Srinivasan MV (1981) Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J Comp Physiol* 142:315–338
- Wehner R, Wehner S (1990) Insect navigation: use of maps or Ariadne’s thread? *Ethol Ecol Evol* 2:27–48
- Wohlgemuth S, Ronacher B, Wehner R (2001) Ant odometry in the third dimension. *Nature* 411:795–798
- Zollikofer CP (1994a) Stepping patterns in ants. I. Influence of speed and curvature. *J Exp Biol* 192:95–106
- Zollikofer CP (1994b) Stepping patterns in ants. II. Influence of body morphology. *J Exp Biol* 192:107–118
- Zollikofer CP (1994c) Stepping patterns in ants. III. Influence of load. *J Exp Biol* 192:119–127