The Journal of Experimental Biology 209, 3336-3344
Published by The Company of Biologists 2006
doi:10.1242/jeb.02364

Visual and tactile learning of ground structures in desert ants

Tobias Seidl and Rüdiger Wehner*
University of Zurich, Institute of Zoology/Neurobiology, Winterthurerstrasse 190, 8057 Zurich, Switzerland
*Author for correspondence (e-mail: rwehner@zool.unizh.ch)

Accepted 5 June 2006

Summary

Place defining landmarks that have been studied intensively in insect navigation are large, voluminous objects visible to the insect from quite some distance. Here, we show that in desert ants, *Cataglyphis fortis*, local variations in ground properties can also serve as landmarks. The ants were trained to forage within a linear channel, in which the floor adjacent to the nest entrance was altered in optical and tactile properties. When ants were later tested within a test channel that ran parallel to the training channel, they recognized this landmark and centred their search on the part of the ground structure during training that was closest to the nest entrance. Hence, physical properties of the ground can be learnt and used as cues defining, for example, the position of the nest. In a second series of experiments the ants were presented with ground structures that differed in their visual and tactile properties from the training structure. We show that the absence of either the correct tactile properties or the correct optical properties of the ground structure make the ants reject the previously accepted structure. Hence small ground structures are recognized by the ants as familiar landmarks only if both visual and tactile information coincides with what the ants have experienced during training.

Key words: *Cataglyphis fortis*, orientation, ground landmark, tactile learning.

Introduction

Desert ants of the genus *Cataglyphis* live in wide, featureless salt-pan areas that provide almost no terrestrial orientation cues. Owing to the sparsely distributed food sources (i.e. dead insects that have succumbed to the environmental stress conditions) and the high temperatures the ants have to perform wide ranging individual foraging journeys and do not recruit by, for instance, laying odour trails. Path integration serves as their main means of navigation (e.g. Wehner, 1992; Collett and Collett, 2000; Wehner and Srinivasan, 2003; Wehner et al., 2002). This mode of navigation relies on acquiring egocentric information on the nest position by continuously integrating the path run by the animal, and doing so by integrating directional information provided by celestial cues and distance information provided, for example, by proprioceptive cues. The outcome of this computational process enables the ant to return to the nest without detour once an appropriate food item has been found. However, due to the egocentric nature of the path integration process the position of the nest entrance as defined by the path integrator (in the following referred to as the PI-position) is subject to a continuous accumulation of errors. In trying to eliminate this navigational uncertainty, desert ants will, whenever possible, take advantage of landmark information, in order to finally pinpoint the goal, the nest entrance, by recalling a previously learnt panoramic image of the goal and comparing this reference image with the current retinal image (Wehner and Räber, 1979; Cartwright and Collett, 1983; Wehner et al., 1996; Wehner, 2003). A basic setup for testing the significance of landmark navigation with respect to path integration consists in presenting the nest-defining landmarks in a position (in the following referred to as the LM-position) that does not coincide with the PI-position (e.g. Wehner et al., 1996; Knaden and Wehner, 2005).

The landmarks used so far in this kind of cue competition experiment have mostly been black cylindrical objects up to 50 cm high and 50 cm wide, i.e. landmarks that have been several orders of magnitude larger than the animal itself, but have mimicked the salt-bush vegetation at the borders of, and sometimes within, the salt pans inhabited by *Cataglyphis fortis* (Heusser and Wehner, 2001). Owing to their sheer size, these landmarks could be recognized by the ants from quite some distance. The area within which an animal can identify such landmarks and use them for orientation is called the catchment area of the landmark(s) in question (Cartwright and Collett, 1983); hence, the larger the object, the wider its catchment area.

In addition, there are already a few hints that ants can recognize minor ground variations and use them during nest finding behaviour [Santschi, fig. 4 (Santschi, 1913); Wehner (Wehner, 1968), and R.W., unpublished observations]. Inspired by these episodic remarks we designed an experimental setup that enabled us to test whether local variations in the ground properties perceived by the ant's ventral retina can be learnt,

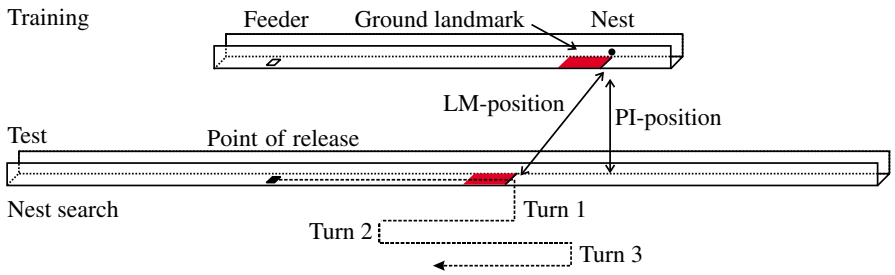

Fig. 1. Schematic view of the experimental setup. Training took place in a 10 m channel with an exit hole on the side, where ants were able to enter and leave the setup and forage to a feeder 9 m down the channel. The coloured rectangular area denotes the position of the ground landmark during training (PI-position). For tests, the ants were transferred into another channel 18 m long and aligned parallel to the training channel. Within this test channel ants were presented with a ground landmark at varying positions (LM-position) relative to the position indicated by their path integrator (PI-position, experiment 1), or with ground landmarks differing from the training landmark in visual or tactile properties (experiment 2). The first six U-turns of the ant's search behaviour were recorded. Drawings are not to scale.

recognized and used as landmarks in a potentially similar way as *Cataglyphis fortis* has been shown to use large, panoramic landmarks that extend upwards from the ant's visual horizon. We further tested whether ground structures can also be perceived by tactile rather than only by visual means.

In a first set of experiments we trained ants to a specific ground structure close to the location of the nest, and later presented this structure in a test situation, in which the LM-position differed from the PI-position. Because of the flat geometry of such ground landmarks ants will cross them quite easily. Therefore the ants might be able to use sensory cues other than visual ones, e.g. tactile ones, for recognizing these ground landmarks. It is well known that in the tarsi of arthropods cuticular mechanoreceptors reach a high level of sensitivity and perceptual sophistication: crickets (Gnatzy and Hustert, 1989); flies (Seifert and Heinzeller, 1989); spiders (Albert et al., 2001). However, apart from the moth, *Manduca sexta*, which uses mechanoreceptors on its proboscis to locate nectar sources by exploiting tactile properties of flower petals (Goyret and Raguso, 2006), there have been no studies published yet that demonstrate the use of tactile cues in any navigational tasks. Hence in a second set of experiments we focussed on the type of stimuli used by the ants in recognizing the ground landmark. Again, the experiments were designed in such a way that the LM-position and the PI-position were set into competition, but now the test landmarks differed from the training landmarks either in their visual or tactile properties.

Experiment 1

In the first set of experiments we tested whether ground landmarks can be used by ants at all and, if they can, how they compete with the ant's path-integration system. Answering the latter question enables us to place the importance of ground structures into the broader context of the ant's navigational toolkit. For example, it enables us to compare the significance of these ground structures with the one of large, panoramic landmarks i.e. landmarks extending above the ant's visual horizon. Until now it has been only the latter type of landmark that has been studied in *Cataglyphis* navigation (e.g. Wehner and Räber, 1979; Wehner et al., 1996; Åkesson and Wehner, 2002; Bisch-Knaden and Wehner, 2003), and that has been set into competition with the ant's path-integration system (Bregy and Wehner, 2003; Knaden and Wehner, 2005).

Materials and methods 1

All experiments (i.e. experiments 1 and 2) were performed with wild, free-ranging salt-pan ants, *Cataglyphis fortis* Forel 1902 (Wehner, 1983), at our Maharès study site (southern Tunisia) during the months July to September of the years 2004 and 2005.

Ants (nest coordinates: N43° 31.720′, E010° 32.278′) were trained to forage to a biscuit-crumb feeder located 9 m north of their nest. While foraging, the ants had to run back and forth between nest and feeder within a linear channel (height: 9 cm, width: 7 cm), with walls made of plywood boards and the base was natural salt-pan (Fig. 1), which they were not able to leave by themselves. During landmark training a piece of dark and very rough abrasive paper (1 m long, 7 cm wide) was placed on the ground of the channel as close to the nest entrance as possible (for detailed training situations see Table 1, column 3; Fig. 2). The foraging ants were forced to cross this piece of abrasive paper, and by this to experience optical and tactile cues that differed from the ones in the remainder of the channel. Furthermore the channel walls inhibited the ants from having a lateral view of the surroundings and thus prevented them from seeing additional natural landmarks potentially occurring in the vicinity of the experimental device.

Ants arriving at the feeder were marked with a day-specific colour code and tested 1 or 2 days later. This training-and-test schedule ensured that the ants had completed about 30 foraging round trips, before they were tested (Åkesson and Wehner, 2002). In the critical tests the ants were captured at the feeder and, while still carrying their food item, transferred to a separate test channel (length: 18 m) running parallel to the training channel. The test channel was free of foraging nest mates and food items. This procedure assured that homebound ants searching for their nest could only rely on within-channel landmarks or on their egocentric vector information.

Table 1. *Overview of experimental subsets of setup 1*

Experiment	Rear boarder of landmark (m)			Test area (m)	Search densities[1] (%) in test area			*P* value (*U*-test)
	N	Training	Test		Experimental group		Control group	
Control 1	20	–	–	8.5-9	1.31±1.03	*vs*	1.20±0.95[2]	0.66
Control 2	20	9	–	8.5-9	1.20±0.95	–	–	–
1A	15	9	9	8.5-9	2.96±2.33	*vs*	1.20±0.95[2]	<0.01
1B	20	9	7.5	7-7.5	2.70±1.59	*vs*	1.32±1.09[2]	<0.01
1C	20	9	6	5.5-6	2.58±1.70	*vs*	1.10±1.10[2]	<0.01
1D	20	9	2	1.5-2	0.61±1.10	*vs*	0.29±0.82[2]	0.13
1E	20	–	7.5	8.5-9	0.71±1.35	*vs*	1.31±1.033[3]	<0.03

All landmarks used were of dark colour with a rough surface. The rear boarder of the 1-m landmark defines the LM-position. For each experiment a certain area of interest was determined and compared statistically to the data of the same area from a control group using the *U*-test.

[1]All values given are mean ± s.d.

[2,3]The search densities at the test area specified in column 5 were tested against the analogue data section from: [2]control 2, [3]control 1.

Depending on the experimental paradigm the tested ants were confronted with an identical reproduction of the ground landmark used during training, but presented at varying positions relative to their point of release (tests 1A–E, Table 1). Once the ants had run off their home vector, they would start their systematic searches centred on the point where they expected the nest to be (Wehner and Srinivasan, 1981). Within the linear test channel this kind of behaviour usually performed in two-dimensional space is restricted to one dimension. Constrained by the channel walls the back-and-forth running ants have to execute sharp turns of direction (Sommer and Wehner, 2004). During this 'linear search' six turning points were recorded with a precision of 0.1 m. A turn was considered complete if the ant continued to run in the new direction for at least 0.2 m. Each ant was tested only once throughout the whole experiment. Tests in which the ants lost their food item or left the test channel before completing the required number of six turns or did not approach the landmark for 0.5 m were considered unsuccessful and therefore excluded from the analysis.

Data analysis

As already mentioned an ant will change its behaviour after it has run off its home vector in a straight path, and will search for the nest by systematic back-and-forth movements centred on the fictive position of the nest entrance. This behaviour allows us to calculate search density distributions. In order to determine the search density distribution in each individual ant, we divided the channel into virtual 0.1-m bins and calculated how often each bin was visited by the ant. For normalization we then divided the number of visits within each bin by the total number of visits within all bins.

Search densities of different test paradigms were compared to those of control groups ('control 1' or 'control 2'; for details, see Table 1, column 7) by Mann–Whitney *U*-tests (Mann and Whitney, 1947). The analysis focussed on those sectors of the compared data sets that included relevant points ('test area', see column 5 in Table 1), e.g. the nest position as defined by the landmark (LM-position) or the nest position as defined by the ant's path integrator (PI-position).

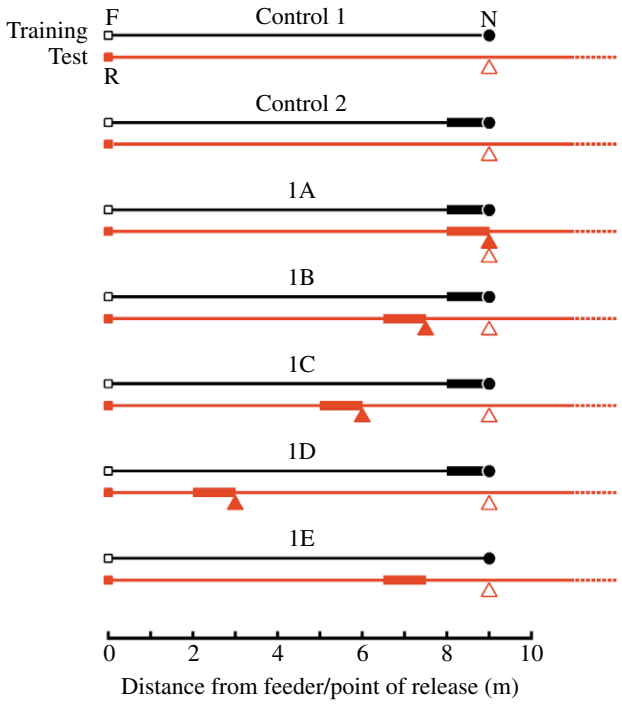

Fig. 2. Schematic representation of the position of the nest (N) as defined by the path integrator (PI-position, open arrowhead) and as defined by the ground landmark (LM-position, filled arrow) in the different sub-sets of experiment 1. During training both positions coincided, but in the test situations the LM-position was usually shifted away from the PI-position towards the point of release (R). This decoupling of PI-position and LM-position ensured that within the test channel the ants encounter the landmark before they have run off their home vector, i.e. before they have reached the PI-position. F and open square, feeder in the training channel; filled square, point of release in the test channel; N and filled circle, nest in the training channel; heavy bar, ground landmark.

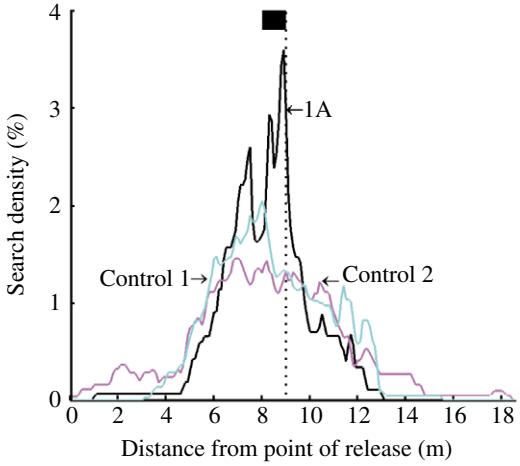

Fig. 3. Search density distribution of the ants' nest search behaviour exhibited under different training and test conditions. Control 1: ants were trained and tested without any landmark. Control 2: ants were trained with a landmark located at the nest entrance but tested without one. Test 1A: ants were trained and tested with a landmark at the nest entrance. Black square, position of landmark; dotted line, position of path-integrator-defined nest.

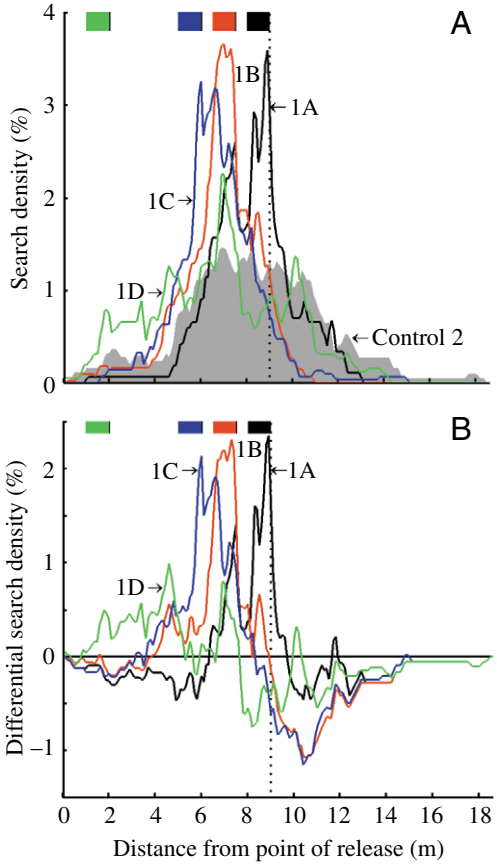

Fig. 4. (A) Search density distribution and (B) differential search density distribution of the ants' nest search behaviour exhibited under different test conditions. All ants were trained with a landmark (black square) directly by the nest and tested with a displaced landmark (coloured square). Test 1A: LM-position was identical to the one in the training situation: 9 m (black line and square). Test 1B: LM-position, 7.5 m (red line and square). Test 1C: LM-position, 6 m (blue line and square). Test 1D: LM-position, 2 m (green line and square). Control 2: no landmark present during test. Note: in B the data of control 2 (in A) were subtracted from each of the other data sets for display reasons.

Results 1

Do ants use ground landmarks?

The first set of experiments was aimed at determining whether *Cataglyphis* ants, once transferred to the test channel, focussed their nest search behaviour more sharply on the fictive position of the nest if the ground landmark were present than if it were not. This was indeed the case (Fig. 3). When ants were trained with a landmark at the nest and confronted with the identical setup in the test channel, i.e. with the LM-position coinciding with the PI-position (Fig. 3: test 1A), the ants searched mainly and consistently at the fictive position of the nest as defined by both the landmark and the state of the path integrator. The height and sharpness of the search peak significantly differed from that of ants that had been trained and tested without any landmark (Fig. 3: control 1) or that had been trained with the landmark at the nest position, but had later been tested without it (Fig. 3: control 2). In fact, the ants' search behaviour did not significantly differ between both types of control (Table 1, last column, first row), but did so highly significantly between control 2 and test 1A (Table 1, last column, third row). Hence, ground structures such as the ones used in the current set of experiments are effectively used by the ants as signposts marking the nest entrance.

Displaced ground landmarks and nest search

In the next set of experiments the ground landmark was set in competition with the ant's path integrator. In technical terms, the LM-position and the PI-position did not coincide. This was achieved by presenting the ants with the landmark at a location at which they had not yet run off their home vector, so that they had to decide between the PI-position and the LM-position of their goal (Fig. 4). As a control we used ants for which the landmarks present during training had been removed in the test situation, so that they had to rely exclusively on their path integrator (Fig. 4A, control 2).

If the LM-position differed from the PI-position by 1.5 m (Fig. 4A: test 1B) the search density at the LM-position (7.5 m) was significantly higher than that at the corresponding position of the control animals. Actually, it was as high as the one obtained when the LM-position coincided with the PI-position (Fig. 4A: test 1A). If the LM-position was moved even closer to the ants' point of release, i.e. even further away from the PI-position (3 m; Fig. 4A: test 1C), the ants still focussed their search at the LM-position (6 m) more strongly than the control animals did (highly significant statistically). However, if the ants encountered their nest landmark very close to the point of their release, i.e. if the LM-position differed from the PI-position by 7 m (Fig. 4A: test 1D), the ants no longer used the

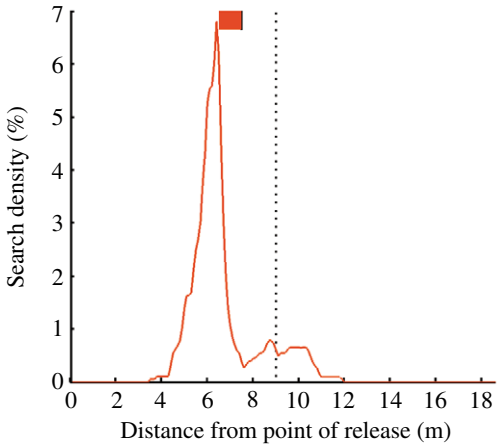

Fig. 5. Search density distribution of ants that faced a landmark for the first time (test 1E). Ants were trained without a landmark, but were presented with a landmark (LM-position: 7.5 m) in the test situation.

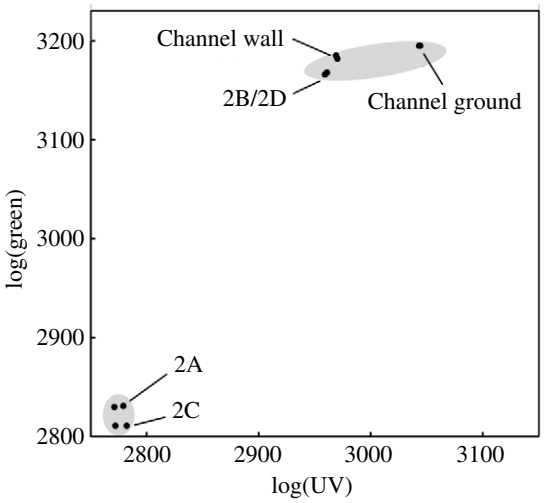

Fig. 6. Visual properties of the landmarks used during experiment 2. The optical properties have been determined following Kollmeier (Kollmeier, 2005) by measuring the remission properties under natural (sunlight) conditions at the specific wavelengths of the ant's light receptors (absorption maxima: green 500 nm, bandwidth 90 nm; UV 350 nm, bandwidth, 60 nm). The optical properties of the landmarks are predominantly defined by the paint used and not by the surface roughness.

landmark as an orientation cue. Their search density at the LM-position (3 m) did not differ from the corresponding one in the control 2. Mean values, standard deviations, and *P* values of all statistical tests mentioned in the paragraph above are given in the last three columns of Table 1.

Effect of unknown ground structures

As shown above, ants do use ground landmarks for orientation. But how do they deal with a structure on the ground that they have never encountered before? If ants were trained without a landmark but were presented with one during the test (Fig. 2: test 1E), their searches exhibited a prominent peak in front of the landmark and far away from both the LM-position and the PI-position (Fig. 5). Their behaviour was significantly different from that of naïve ants that did not encounter a landmark during both training and testing (Fig. 3: control 1; Table 1, last column, last line). In contrast to the latter control situation, the ants rigorously tried to avoid the landmark, and as they could not leave the channel, they ran back and forth without crossing the landmark and hence never got close to the PI-position.

Experiment 2

In contrast to panoramic visual landmarks, which can be perceived from a distance, ground landmarks can be detected only when the ant walks over them. In doing so, the ants come into direct contact with the ground structure not only visually, but also mechanoreceptively. Therefore, we examined whether the ants were able to exploit this tactile input as well. In particular, we investigated whether the ants can detect mechanical properties of the ground structure, such as the roughness of the surface, and use them for orientation.

Materials and methods 2

In the second set of experiments the ground landmark was altered stepwise in both its optical and its tactile properties. All ants were trained with a landmark that was black and rough, delivering high visual and tactile contrast to the channel surroundings. Later, they were tested with landmarks differing in their optical and tactile properties and having been displaced from the PI-position towards the point of release of the ants, by 1.5 m (LM-position: 7.5 m; Fig. 7).

The ants (nest coordinates: N34° 31.745′, E010° 32.333′) again had to forage for 9 m to a feeder, in a north–south oriented channel (height 7 cm and width 7 cm) with walls and the base made of aluminium. The original nest entrance was connected to the channel by a thin tube. The interior of the channel was spray-painted grey (for optical properties see Fig. 6) with the ground additionally being covered with light brown sand. The training landmark consisted of the abrasive paper mentioned above, but it was now spray-painted black in order to increase the visual contrast between structure and ground. The use of the identical paint on the different landmark materials (abrasive paper, cardboard) also eliminated possible different olfactory cues from the different structures. During training the landmark was again placed at the nest entrance (Fig. 7, LM-position and PI-position: 9 m), whereas in the tests its position was moved slightly towards the point of release (LM-position: 7.5 m; compare Fig. 2: test 1B).

In analyzing the type of stimuli being used by the ants, in the test situation different types of landmarks were applied (see Table 2, columns 3 and 4 for landmark description and Fig. 6 for their optical properties): a black and rough landmark identical to the training landmark (test 2A); a landmark painted

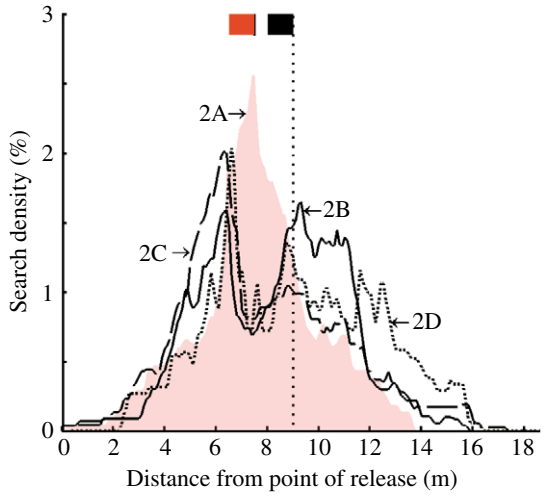

Fig. 7. Search density distribution of ants that faced different types of landmark stimuli. Ants were trained with a black and rough landmark at the nest entrance (black square) and later tested with a landmark of different properties defining the nest entrance at 7.5 m (red square, LM-position). Test 2A (shaded area): Control experiment with a black and rough landmark (same experimental situation as test 1B, but new data set). Test 2B (thin solid line): a grey and rough landmark deprived the ant of the visual contrast. Test 2C (broken line): a black and smooth landmark changed the surface roughness, but left the visual contrast intact (as compared to the training situation). Test 2D (dotted line): the lower hemispheres of the ants' eyes were covered with light-tight paint depriving the ant from any visual cues from below.

in the background colour of the channel but identical in tactile cues with the training landmark (test 2B); and finally a black-sprayed piece of cardboard providing the same optic but different tactile cues as the training landmark (test 2C). In a further experiment we covered the lower hemispheres of the ants' eyes by applying light-tight acrylic paint (after the ants had been trained) and put the ants back into the nest (test 2D). Once the treated ants had reappeared at the feeder, we provided them in the test situation with a grey and rough landmark. Now the ants did not experience any visual cues – not even diffuse ones – that could indicate the position of the ground structure (Antonsen and Wehner, 1995). After a successful test (see above) each ant was examined under a binocular microscope to confirm that the coverage was still intact. As a result of this post experimental test five of the 17 treated ants had to be excluded. In each ant the search behaviour was recorded and the search density was computed by following the same protocol as in experiment 1. The search density profiles of the four experimental subgroups mentioned above were compared by applying the Kruskal–Wallis test (Kruskal and Wallis, 1952) accompanied by the Dunn–Sidak Multiple Comparisons post test (Hochberg and Tamhane, 1987).

Results 2

Relevant stimuli for ground landmark recognition

In the control experiment (test 2A), in which the optical and tactile properties of the landmark coincided with the ones during training, the ants searched consistently at the LM-position. However if either parameter of the landmark was changed (optical properties: test 2B; tactile properties: test 2C), the ants behaved similarly to the ones in experiment 1 in which the ants had never seen a landmark during training but were presented with one in the test (Fig. 5: test 1E): they avoided trespassing the altered landmark. This behaviour resulted in a clear peak positioned directly in front of the landmark, far away from both the LM-position and the PI-position (Fig. 7: tests 2B and 2C).

However, the search density distribution of the ants confronted with the invisible landmark (test 2B) was bimodal, exhibiting a second peak at the PI-position. If the ants had once happened to cross the landmark, they avoided the LM-position and searched at the PI-position. This bimodal distribution with maxima in front of the landmark and at the PI-position could also be observed if, prior to testing, the ants had been deprived of vision in their ventral field of view by covering the lower hemispheres of their eyes with light-tight paint (Fig. 7: test 2D). Even though the half-blind animals subsequently encountered a familiar tactile landmark, they nonetheless avoided trespassing it. The results of statistical tests are given in Table 2.

Table 2. *Overview of experimental subsets of setup 2*

Experiment 2	*N*	Landmark properties		Search densities at rear end of landmark[1] (%)	*P* value[2]	Group
		Visual	Tactile			
2A	24	Black	Rough	2.38±1.47	–	a
2B	25	Grey	Rough	0.74±0.61	<0.001	b
2C	19	Black	Smooth	0.83±0.68	<0.01	b
2D	12	Invisible	Rough	0.89±0.99	<0.05	b

Throughout the whole experiment the ants faced a black and rough landmark in position 9 during training. For tests, landmark properties were altered but all landmarks were presented in the LM-position=7.5 m, i.e. with the rear end of the landmark at 7.5 m. Mean search densities of all experiments at the rear end of the test landmark (test section: 7–7.5 m) were compared statistically. Different letters (last column) indicate significant difference at α=5%.

[1]All values given are mean ± s.d.

[2]*P* values for pair-wise comparison against test 2A (Kruskall–Wallis test with Dunn post test).

General discussion

Ants perceive and use ground landmarks

Our experiments show that marginal variations in ground properties do play a role during an ant's search for the nest. In their natural environment ants can use such local structures to memorize and later recall minute characteristics of the ground surface in the immediate vicinity of the nest entrance. Similarly to what happens in the presence of large panoramic visual landmarks defining the position of the nest (Wehner et al., 1996; Bregy and Wehner, 2003), small ground structures are used as nest-defining landmarks only within certain states of the ant's path-integration vector: if an ant has learnt a nest landmark, later, during homing it expects this landmark to occur after it has fully run off its home vector. But as all vector navigation is error prone, landmarks of any kind will help in finally pinpointing the goal. Particularly, ants might accept a landmark at different states of their home vector, i.e. even though they have not yet completed their vector-based home run. In the present study, the ground landmark was accepted by the ant as a nest-defining orientation cue at vector states of 100%, 83% and 66% (Table 1: tests 1A–1C), but it was ignored at the 22% state (Table 1: test 1D). This result is very similar indeed, even in quantitative terms, with the results obtained by using large panoramic landmarks as nest defining cues (Bregy and Wehner, 2003).

However, the influence a familiar ground landmark has on the ant's search pattern is limited: the centre of search cannot be shifted by the ground landmark as drastically away from a position defined by the ant's path integrator as is the case with panoramic landmarks (e.g. Knaden and Wehner, 2005). This can easily be explained by the reduced catchment area of ground marks. Whereas large panoramic landmarks can be seen from far away, a ground landmark can be recognized by the ant's ventral field of view and by the mechanoreceptors of the ant's tarsi only if the ant is directly above it. If the ant leaves the structure and loses it not only tactilely, but also visually, it instead continues to rely on its path-integration vector. Knaden and Wehner (Knaden and Wehner, 2005) have shown a similar effect with panoramic visual landmarks. If in the test field a set of nest-defining cylindrical landmarks was placed at a position that differed from the position defined by the ant's path integrator, i.e. if the LM-position and PI-position did not coincide, the ants first searched, unsuccessfully of course, at the PI-position and – after the landmarks had been installed – switched to the LM-position, but after removal of the landmarks by the experimenter, returned immediately to the PI-position. This shows that the path integrator keeps running all the time, even if the ants happen to rely, at a particular instance, on landmark information.

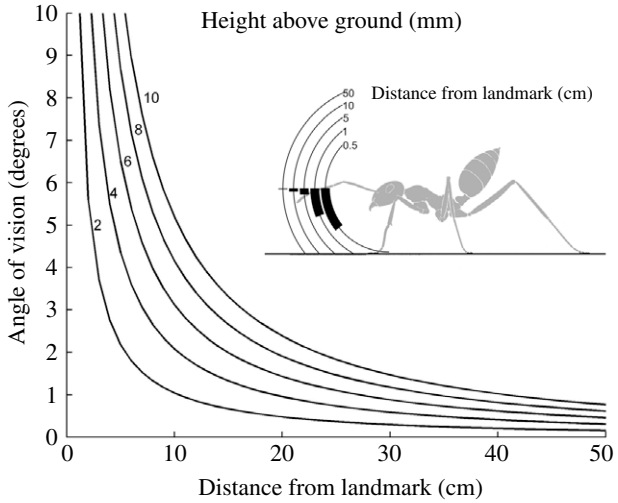

Fig. 8. Ants perceive a ground landmark only from a short distance. The angle of vision under which the ground landmark (length, 1 m; width, 0.07 m) appears in the ant's visual field depends strongly on the distance of the ant from the landmark (shown here for distances <0.5 m). The height of the eye above ground (2–10 mm) has a minor effect. (Inset) Vertical expansion of the ground landmark used in the current experiments within the ant's visual field at different distances of the ant from the landmark (eye 4 mm above ground). The landmark remains extremely small (<1°) up to an approach of about 20 cm. Then it rapidly expands covering a large part of the ant's ventral visual field.

Visual and tactile properties play a role

As to the visual perception of the ground structures we can deduce from our field observations, i.e. from short stops or unrecorded turns performed by the ants close to the landmark border, that within the test channels the ants can most certainly recognize the landmarks visually from a distance of about 10–15 cm. We calculated the angular subtense of the landmark within the ant's visual field of view for various distances between ant and landmark, and for various heights of the ant's eyes above ground (Fig. 8). The calculations show that the landmark remains small within the ant's field of view until the ant has approached it for a distance of about 0.2 m. From that distance onwards the retinal image of the landmark increases dramatically in size until it covers almost the entire ventral visual field (e.g. lateral expansion: 166°, ventral expansion: 188° if the ant's eye is located 4 mm above ground).

The importance of the tactile properties of a ground landmark could be shown most directly in the experiments in which the ventral halves of the ant's eyes were covered with light-tight paint, so that any visual input from the ground structure was abolished. Yet the ants, if forced to perform their home run in the test channel, avoided a novel ground mark. Hence mechanosensory information alone suffices in detecting ground structures. But visual information alone does so as well. In fact, whenever in the test situation the ground landmarks were changed relative to the training situation in either their optical or their tactile properties, the ants exhibited an avoidance response (Fig. 7: tests 2B and 2C). Obviously, in either case the landmarks were no longer recognized as the ones with which the ants had been familiar in the training situation.

But how exactly did the animals perceive the tactile information provided by the ground structures offered in the

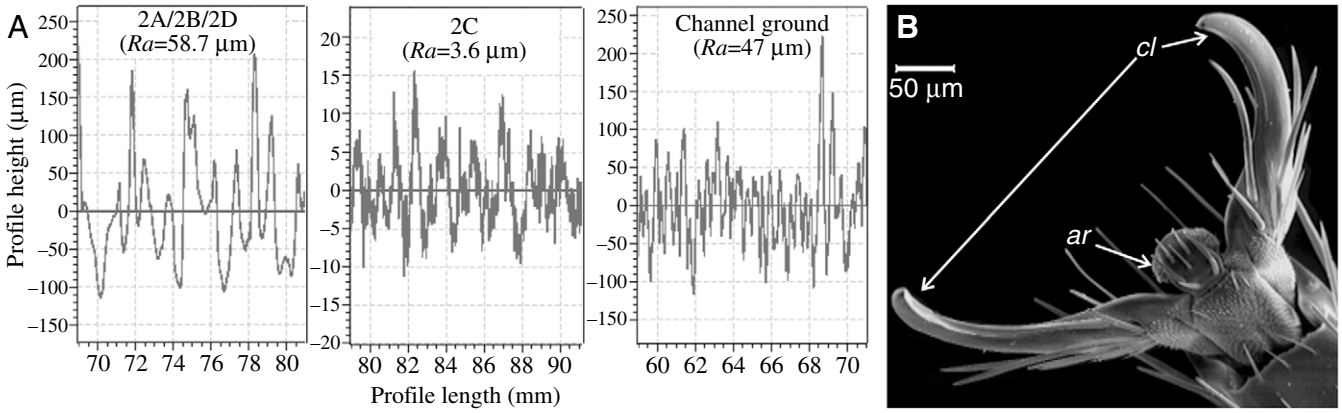

Fig. 9. (A) Typical surface profiles of the structures used in experiment 2, determined using a contact-profilometer. The roughness is characterized by *Ra*, defined as the arithmetic mean of the deviations from the base line measured over an evaluation length (DIN EN ISO 4287). The mean diameter of the grains deposited on the abrasive paper used for experiments 2A, 2B and 2D (compare Table 1) is 270 μm, the sand glued to the channel ground had a mean diameter of 200 μm. In contrast to the abrasive paper the sand grains are deposited next to each other without gaps. (B) Dorsal view of a tarsus of *Cataglyphis fortis* (ar, arolium; cl, tarsal claws). Tarsal claws are separated from each other by approximately 320 μm. (SEM micrograph courtesy of Andrew Martin.)

present case? The structures used in this study most obviously differed in surface roughness, i.e. in the height and the frequency of the deposited grains. As a qualitative analysis of numerous high-speed video recordings (e.g. Seidl et al., 2004) did not provide any hint that the ants used their antennae for evaluating surface structures during locomotion, the tarsi are the most probable appendages for analysing the geometric surface properties. If we compare the geometry of an ant's tarsi with the surface profiles of the ground structures used in this study (Fig. 9), we find that on the sanded channel ground the ant's tarsi would come to lie on top of a layer of densely deposited grains, whereas in the case of the abrasive paper they would fit in between the gaps of the loosely spread substructures of the paper. Tactile hairs on the tarsi could determine the geometry of the surface structure by monitoring both grain height and deposition frequency. Another possible way for the ants to monitor surface structures would be to exploit surface elasticity by, e.g. campaniform sensilla within the cuticle or muscular strain sensors during touch down or lift off of the tarsi. Even though mechanoreception is a well known sensory capacity in insects (e.g. Römer, 2003), most studies deal with mechanoreceptors located at the antennae (e.g. Martin and Lindauer, 1966). Tarsal mechanoreceptors have so far been studied in spiders (e.g. Foelix, 1970), but not yet in insects.

We thank Markus Knaden in our laboratory for helpful comments and Matthias Wittlinger (University of Ulm) for technical support in the field. Ralf Möller and Frank Röben (University of Bielefeld) kindly determined the optical properties of the landmarks used in setup 2. Bernhard Bringmann (ETH, Zurich) measured the roughness properties of the landmarks. We thank one anonymous referee for detailed comments on the manuscript. The research was financed by the Swiss National Science Foundation (3100-61844) and the Volkswagen Foundation (1/78 580) (both to R.W.).

References

Åkesson, S. and Wehner, R. (2002). Visual navigation in desert ants *Cataglyphis fortis*: are snapshots coupled to a celestial system of reference? *J. Exp. Biol.* **205**, 1971-1978.

Albert, J. T., Friedrich, O. C., Dechant, H.-E. and Barth, F. G. (2001). Arthropod touch reception: spider hair sensilla as rapid touch detectors. *J. Comp. Physiol. A* **187**, 303-312.

Antonsen, P. and Wehner, R. (1995). Visual field topology of the desert ant's snapshot. *Proc. Neurobiol. Conf. Göttingen* **23**, 42.

Bisch-Knaden, S. and Wehner, R. (2003). Landmark memories are more robust when acquired at the nest site than en route: experiments in desert ants. *Naturwissenschaften* **90**, 127-130.

Bregy, P. and Wehner, R. (2003). Beacon versus vector navigation in homing ants, *Cataglyphis fortis*. *Neurobiol. Conf.* **29**, 574.

Cartwright, B. A. and Collett, T. S. (1983). Landmark learning in bees: experiments and models. *J. Comp. Physiol. A* **151**, 521-543.

Collett, M. and Collett, T. S. (2000). How do insects use path integration for their navigation? *Biol. Cybern.* **83**, 245-259.

Foelix, R. (1970). Structure and function of tarsal sensilla in the spider *Araneus diadematus*. *J. Exp. Zool.* **175**, 99-124.

Forel, A. (1902). Les fourmis du Sahara algérien. *Ann. Soc. Entomol. Belgique* **46**, 147-158.

Gnatzy, W. and Hustert, R. (1989). Mechanoreceptors in behaviour. In *Cricket Behaviour and Neurobiology* (ed. F. Huber, T. E. Moore and W. Loher), pp. 198-226. Ithaca, London: Cornell University Press.

Goyret, J. and Raguso, R. A. (2006). The role of mechanosensory input in flower handling efficiency and learning by *Manduca sexta*. *J. Exp. Biol.* **209**, 1585-1593.

Heusser, D. and Wehner, R. (2001). The visual centring response in desert ants, *Cataglyphis fortis*. *J. Exp. Biol.* **205**, 585-590.

Hochberg, Y. and Tamhane, A. C. (1987). *Multiple Comparison Procedures.* New York: Wiley.

Knaden, M. and Wehner, R. (2005). Nest mark orientation in desert ants *Cataglyphis*: what does it do to the path integrator? *Anim. Behav.* **70**, 1349-1354.

Kollmeier, T. (2005). Spektrale Kontrastanalyse zur beleuchtungsinvarianten Detektion von Landmarken. Diploma thesis, University of Bielefeld, Germany.

Kruskal, W. H. and Wallis, W. A. (1952). Use of ranks in one-criterion variance analysis. *J. Am. Stat. Assoc.* **47**, 583-621.

Mann, H. B. and Whitney, D. R. (1947). On a test whether one of two

random variables is stochastically larger than the other. *Ann. Math. Stat.* **18**, 50-60.

Martin, H. and Lindauer, M. (1966). Sinnesphysiologische Leistungen beim Wabenbau der Honigbiene. *Z. Vergl. Physiol.* **53**, 372-404.

Römer, H. (2003). Mechanorezeption. In *Lehrbuch der Entomologie* (ed. K. Dettner and W. Peters), pp. 281-298. Heidelberg, Berlin: Spektrum.

Santschi, F. (1913). Comment s'orientent les fourmis. *Rev. Suisse Zool.* **21**, 347-425.

Seidl, T., Weihmann, T., Blickhan, R. and Wehner, R. (2004). Kinematic analysis of ants running at different inclinations. *Comp. Biochem. Physiol.* **137A**, S102-S103.

Seifert, P. and Heinzeller, T. (1989). Mechanical, sensory and glandular structures in the tarsal unguitractor apparatus of *Chironomus riparius* (Diptera, Chironomidae). *Zoomorphology* **109**, 71-78.

Sommer, S. and Wehner, R. (2004). The ant's estimation of distance travelled: experiments with desert ants, *Cataglyphis fortis*. *J. Comp. Physiol. A* **190**, 1-6.

Wehner, R. (1968). Optische Orientierungsmechanismen im Heimkehrverhalten von *Cataglyphis bicolor* (Formicidae, Hymenoptera). *Rev. Suisse Zool.* **75**, 1076-1085.

Wehner, R. (1983). Taxonomie, Funktionsmorphologie und Zoogeographie der saharischen Wüstenameise *Cataglyphis fortis* (Forel 1902) stat. nov. (Insecta: Hymenoptera: Formicidae). *Senckenb. Biol.* **64**, 89-132.

Wehner, R. (1992). Arthropods. In *Animal Homing* (ed. F. Papi), pp. 45-144. London: Chapman & Hall.

Wehner, R. (2003). Desert ant navigation: how miniature brains solve complex tasks. *J. Comp. Physiol. A* **189**, 579-588.

Wehner, R. and Räber, F. (1979). Visual spatial memory in desert ants, *Cataglyphis bicolor* (Hymenoptera: Formicidae). *Experientia* **35**, 1569-1571.

Wehner, R. and Srinivasan, M. V. (1981), Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J. Comp. Physiol. A* **142**, 315-338.

Wehner, R. and Srinivasan, M. V. (2003). Path integration in insects. In *The Neurobiology of Spatial Behaviour* (ed. K. J. Jeffery), pp. 9-30. Oxford: Oxford University Press.

Wehner, R., Michel, B. and Antonsen, P. (1996). Visual navigation in insects: coupling of egocentric and geocentric information. *J. Exp. Biol.* **199**, 129-140.

Wehner, R., Gallizzi, K., Frei, C. and Vesely, M. (2002). Calibration processes in desert ant navigation: vector courses and systematic search. *J. Comp. Physiol. A* **188**, 683-693.