

The visual centring response in desert ants, *Cataglyphis fortis*

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Summary

When negotiating their way through cluttered environments, desert ants, *Cataglyphis fortis*, tend to run along the midlines of the alleys formed by adjacent low shrubs. This ‘centring response’ was investigated by inducing foraging ants to walk through artificial channels. The sidewalls of the channel were either homogeneously black or provided with stationary or moving black-and-white gratings. The speed of motion and the spatial period of the gratings and the height of the walls could be varied independently on the left-hand and right-hand sides of the channel. The results clearly show that the ants, while

exhibiting their centring responses, try to balance neither the self-induced image speeds nor the contrast frequencies seen in their left and right visual fields, but the vertical angle subtended by the landmarks on either side. When manoeuvring through the channel, the ants always adjust the lateral positions of their walking trajectories in such a way that the vertical angles subtended by the walls are identical for both eyes.

Key words: centring response, optic flow, landmark vision, navigation, ant, *Cataglyphis fortis*.

Introduction

Saharan desert ants of the genus *Cataglyphis* are remarkable long-distance navigators. Some species (e.g. *C. bombycinus*) travel along straight trajectories over bare sand-dune surfaces and finally approach and enter one of the widely scattered shrubs, in which they search for food (Wehner and Wehner, 1990). Other species (e.g. *C. bicolor*, *C. savigny* and *C. mauritanicus*) negotiate their way through cluttered environments, low-bush steppes or gravel plains, while searching for arthropod carcasses lying on the desert floor (Wehner et al., 1983, 1996). These latter species ‘mind the gap’ between adjacent bushes. They run along the middle of the passageway formed by the natural landmarks to the right and to the left of their outbound and inbound courses. This behaviour is also observed in *Cataglyphis fortis*, which forages over large distances on the featureless surfaces of wide salt-pan areas, but also moves about areas covered with salt-bush vegetation. The functional significance of this ‘centring response’ (see fig. 7 in Santschi, 1913, p. 411) might be to keep the ants at maximal distances from rocks and shrubs, which are convenient hiding places for lurking predators such as spiders, robber flies and lizards.

In a series of elegant experiments, Srinivasan et al. (1991) have shown that honeybees fly through the middle of a tunnel, i.e. along its longitudinal axis, by balancing the apparent motions of the images of the walls on the two sides. Flying insects also exploit self-induced optic-flow information in many other contexts of visually guided behaviour; for example, in distinguishing between objects at different distances (Srinivasan et al., 1989) or in gauging distances travelled

(Srinivasan et al., 1997; Esch et al., 2001). In the latter case, bees derive odometric information from flow-field cues presented in their lateral visual fields. In this respect, walking ants differ from flying bees. In monitoring distances travelled, *Cataglyphis* ants rely much more extensively on proprioceptive cues than on the optic flow induced by visual patterns presented within their left and right fields of view (Ronacher and Wehner, 1995; Ronacher et al., 2000). This difference between flying bees and walking ants in their reliance on self-induced optic flow makes one wonder whether, in desert ants, the centring response is mediated by optic flow-field information in the same way as it is in honeybees.

Materials and methods

The experiments were performed at our *Cataglyphis* Field Station near Maharès, Tunisia (34.58°N, 10.50°E). Within this area, *Cataglyphis fortis* inhabits the coastal salt pans extending between Maharès and Chaffar. These areas are occupied either by low-shrub halophilic vegetation or by bare desert ground devoid of any vegetation. *C. fortis* may forage in both types of habitat.

Experimental design, training and testing procedures

Ants were trained to walk from the nest to a feeder positioned 20 m to the south of the nest entrance. While they were shuttling back and forth between the nest and the feeder, using path integration as their main navigational aid, individual ants were captured at the feeder, marked with two dots of paint

(one on the alitrunk and one on the gaster) and transferred to the test area. The colour marking of the animals ensured that each ant was tested only once. Within the test area, the ants performed their homeward runs by traversing a 4 m long channel consisting of walls 20–40 cm high positioned 1.5 m apart and oriented in the north–south direction, i.e. parallel and symmetrical to the ants' homebound paths. Hence, as seen from the centre of the channel, the upper rims of the walls appeared to subtend visual angles of 15–28°. At the entrance to the channel, two small plates (1.5 m long and 0.05 m high) formed a funnel that guided those ants that upon release deviated by more than 25° from their homeward courses into the channel. The dimensions of the channel, i.e. the distance apart and height of the walls, were taken from the average spatial dimensions of the landmarks present in the animals' natural habitat.

During the tests, the ants experienced the walls for the first time in their foraging lives. They had been captured at the feeder and displaced (in the dark) to a point 1.5 m south of the 4 m channel. There they started their homebound runs. After they had been released, they sometimes walked around the channel rather than entering it. Therefore, a funnel array consisting of two low walls (1 m long and 5 cm high) was attached to the entrance of the channel (Fig. 1). Within the channel, the inner sides of the walls were either painted uniformly black or covered with vertical black-and-white gratings (square-wave intensity profiles with periods of 29.5 or 59.0 cm, i.e. subtending 22.3 and 42.9°, respectively, as seen from the centre of the channel). The gratings were fixed on sheets of cloth stretched around a pair of drums. By coupling a direct-current motor (ESCOP 28LT, 12 V) to one of the drums, the pattern on one of the walls could be moved with variable speed with or against the ant's direction of motion.

A gridwork of white lines was painted on the desert floor to facilitate the recording of the ants' trajectories (Fig. 1) (for methods, see Wehner and Srinivasan, 1981). This gridwork was not displayed within the channel, i.e. within the area between the two walls. There, tiny dots forming a square lattice (mesh width 0.15 m) were used as recording aids.

Analysis of walking paths

The walking paths of individual ants were monitored by using the recording grids on both the test floor and the recording tablet (recording scale 1:50). The ants loaded with food (biscuit crumbs, which they had picked up at the feeder) passed through the channel steadily and in a straight line. In total, the homeward trajectories of 463 ants were recorded, digitized and analysed statistically (see Wehner and Srinivasan, 1981).

We determined the lateral positions of the ants within the channel at fictive cross sections through the channel and the running speeds while the ants were traversing the channel. In the following, we refer mainly to the positions recorded when the ants had run half-way through the channel, i.e. when they were 2 m away from both the point at which they had entered the channel and that at which they would leave it. The data are

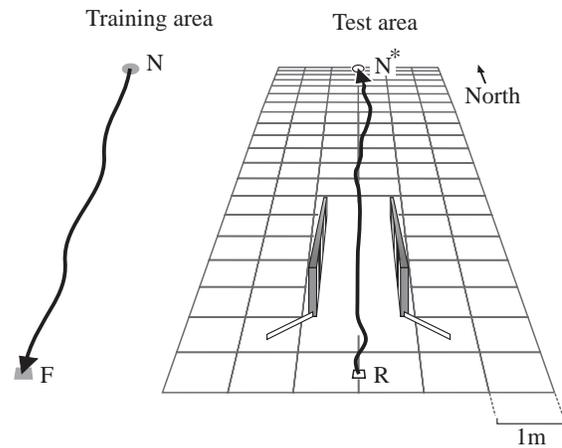


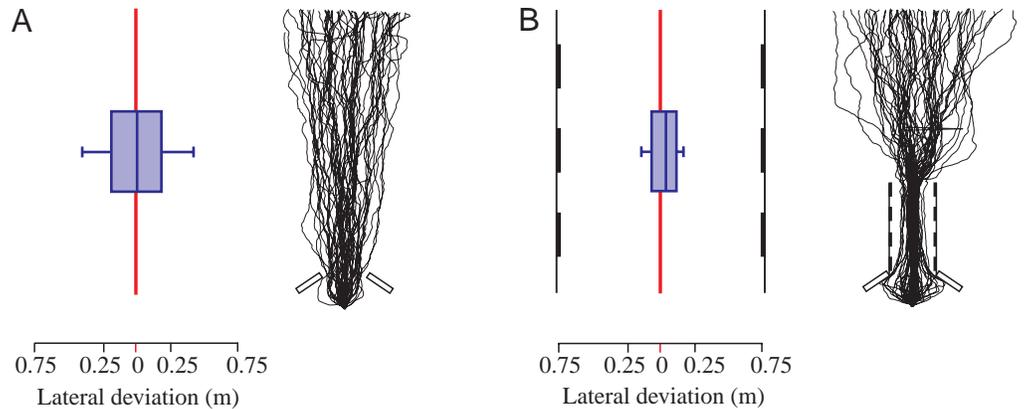
Fig. 1. Experimental arrangement: the training (left) and test (right) situations. Ant foragers that have left the nest (N) and have walked straight to an artificial feeder (F) are captured at F and displaced to the test area. Upon release at R, they immediately head off in their homebound runs, they have to pass through a 4 m long and 1.5 m wide experimental channel. Having arrived at the fictive position of the nest (N*), they are returned to N. The visual patterns on the inner sides of the walls forming the channel and/or the heights of the walls can be varied independently on the left and right sides of the channel. At the entrance to the channel, a funnel formed by two narrow plates serves to guide the ants into the channel.

presented in box-plot form (medians and quartiles). We used Mann-Whitney *U*-tests for pairwise comparisons of data sets obtained under different test conditions and binomial tests to check data obtained experimentally against values expected theoretically (Siegel, 1956).

Results

We first tested how widely the ants' homeward trajectories were scattered when the animals were allowed to perform their homeward journeys in open territory, as they did in the training area. Immediately upon release, the ants headed for home (Fig. 2A). Their trajectories were well centred about the vector course leading from the feeder to the nest (binomial test, $P > 0.99$). The scatter in the data, however, was considerable. The amount of scatter immediately decreased when the homebound ants were presented with the walls of the artificial channel aligned parallel to the animals' home vector. As soon as the ants entered the channel, the distribution of their homeward trajectories became markedly compressed, but it widened again, and did so substantially, after the ants had left the channel (Fig. 2B). The scatter within the distribution of the ants' courses was significantly smaller than in the distribution of trajectories shown in Fig. 2A (Mann-Whitney *U*-test, analysis of variance; $P < 0.001$). In the experiment described in Fig. 2B, the left and right walls of the channel carried the same black-and-white square-wave grating (period $\lambda = 29.5$ cm, i.e. 22.3° as seen from the centre of the channel) and were of equal height (height $h = 20$ cm, i.e. 14.9° as seen from the centre of

Fig. 2. (A) Results from a control experiment with the channel removed. Walking trajectories of 49 ants (one run per ant). Left: box-plot representation of the lateral positions of the ants' trajectories at a distance of 3.5 m north of the point of release, i.e. when the ants are half-way through the channel (compare with Fig. 1). The vertical blue line inside the box depicts the median of the ants' positions. The left and right boundaries of the box indicate the quartiles, which demarcate the range including 25% of the data to the left and right of the median; the horizontal bars indicate the 75% range of the data. Red line, direct homeward course (R-N* in Fig. 1). Abscissa, lateral deviation from direct homeward course (in m). (B) Both sides of the channel are provided with vertically oriented black-and-white square-wave gratings (period $\lambda=22.3^\circ$ and height $h=14.9^\circ$ as seen from the centre of the channel). $N=59$. For conventions, see A.



the channel). When these conditions were met, the ants' trajectories clustered tightly about the midline of the channel (binomial tests; $P>0.25$). The same held true if the period of the grating on one side of the channel was doubled ($\lambda=59.0$ cm; Fig. 3A; binomial test, $P>0.70$). This means that increasing the temporal frequency of the intensity fluctuations (the so-called 'contrast frequency') by a factor of two had no effect on the ants' homeward courses.

Quite surprisingly, however, the ants again passed through the middle of the channel when one of the gratings was moved either in the ants' direction of motion (Fig. 3B, left) or in the opposite direction (Fig. 3B, right). Had the animals tried to balance the apparent angular speeds of the gratings as seen by the left and right eyes, they should have walked closer to the moving grating in the first case and closer to the stationary grating in the second case (Fig. 3B left and right, respectively). They did not do this (binomial test, $P>0.44$, Fig. 3B, left; $P>0.72$, Fig. 3B, right).

The amount by which the ants should have deviated from the centre of the channel if they had tried to balance the image speeds experienced by the left and right eyes can be calculated

as follows (see also Srinivasan et al., 1991). Let d_m and d_s be the theoretically expected distances from the moving and stationary grating, respectively, and let v_a and v_p be the ant's walking speed and the (linear) speed of the pattern, respectively. Then:

$$d_m/(d_s + d_m) = (v_a - v_p)/(2v_a - v_p).$$

Note that v_p is positive for patterns moving in the same direction as the walking ant and negative for patterns moving in the opposite direction. In Fig. 3B, the expected distances computed in this way are indicated by the green lines. In both cases, the distributions obtained experimentally deviated significantly from the expected values (binomial tests; $P<0.001$). Hence, in the experiments described in Fig. 3A,B, neither contrast frequency nor image speed accounts for the ant's centring response.

Next, we removed the patterns from the walls and presented the ants with homogeneously black surfaces. In spite of this quite substantial change in the stimulus situation, the ants moved through the middle of the channel as precisely as they had done with the patterned walls (Fig. 4A; binomial test, $P>0.88$).

Fig. 3. (A) Results from experiments in which the gratings presented on the left and the right walls are stationary, but the spatial period of the right-hand grating ($\lambda=42.9^\circ$) is twice that of the left-hand grating. $N=26$. (B) The left-hand grating is moved at a speed of 0.1 m s^{-1} in the same direction as the ant's direction of motion (left) or at a speed of 0.2 m s^{-1} in the direction opposite to the ant's direction of motion (right). The right-hand grating has the same spatial period ($\lambda=22.3^\circ$) but is stationary. Open arrow, direction of pattern motion. Red line, midline of channel. Green line, position at which the speeds of image motion experienced by the ant's two eyes are balanced. $N=30$. For further conventions, see Fig. 2A.

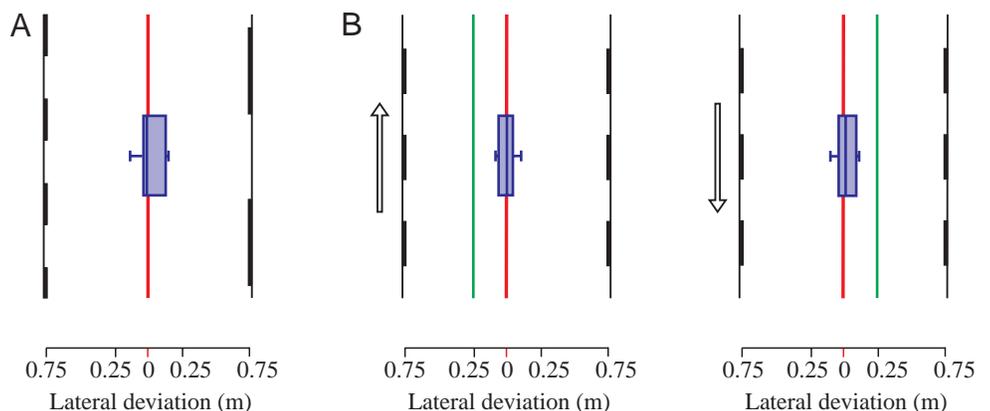
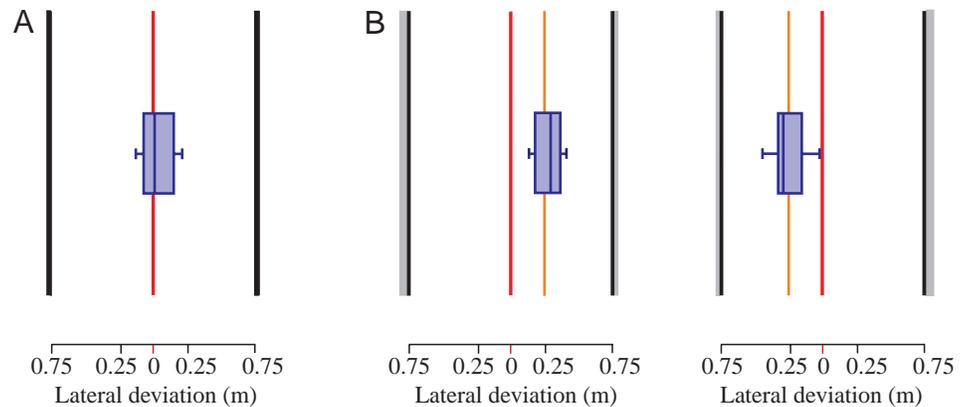


Fig. 4. (A) Results from experiments in which both walls are uniformly black and of equal height ($h=0.2$ m corresponding to 14.9° as seen from the midline of the channel). $N=48$. (B) Either the left-hand or the right-hand wall (left or right figure, respectively) is increased to double the linear height ($h=0.4$ m corresponding to 28.1° as seen from the midline of the channel). Orange line, position at which the heights of the left and the right walls appeared to subtend equal visual angles. $N=22$ (left figure) and $N=21$ (right figure). For further conventions, see Fig. 2A.



However, when one wall was increased to double the linear height ($h=40$ cm, i.e. 28.1° as seen from the midline of the channel), the ants shifted their trajectories away from that wall towards the lower one by exactly the amount necessary to balance the angular heights of the two walls (Fig. 4B). The ants' lateral positions within the channel coincided with the positions computed for equal angular height (see orange lines in Fig. 4B; binomial tests, $P>0.52$, Fig. 4B, left; $P>0.88$, Fig. 4B, right), but differed significantly from the midline of the channel (red line; binomial test, $P<0.001$ in both cases). Exactly the same results were obtained when the two unequally sized walls carried the linear gratings used in the earlier experiments (Fig. 5B). In conclusion, the apparent (angular) height of the walls of the channel was the only parameter that affected the ants' centring response.

Of course, the plates forming the black and patterned sidewalls of the channel could have provided the ants with a rather artificial environment with little bearing on what the animals would usually experience within their natural habitat. However, fortuitously, we were able to weaken this argument. One year after the experiments described above had been performed, two rows of chenopodiacean plants common in the surrounding salt-pan areas had grown in the furrows within which the walls of the channel had previously been mounted on the ground (Fig. 6A). Although the plants neither formed continuous walls nor were of equal height (mean angular

heights of the left-hand row and right-hand row were $9.8\pm 4.6^\circ$ and $13.5\pm 5.3^\circ$; means \pm s.d.), respectively, as seen from the centre of the naturally formed alley), they nevertheless induced the ants to perform remarkable centring responses, with their walking trajectories running closer to the lower (left-hand) side of the alley (Fig. 6B). The variance in the animals' lateral walking positions was significantly smaller than that of the controls shown in Fig. 2A (Mann-Whitney U -test, analysis of variance, $P<0.001$), and the median of the data was shifted towards the position at which the plants in the left-hand and right-hand rows appeared, on average, to subtend equal visual angles. However, even though the lateral positions of the ants' trajectories did not deviate significantly from this equal-angular-height position (binomial test, $P>0.99$), neither did they deviate significantly from the midline position of the alley (binomial test, $P>0.16$).

Discussion

The most striking conclusion that can be drawn from the present account is the difference existing between a flying (honeybee) and a walking (desert ant) insect species in visually manoeuvring through gaps flanked by landmarks. While exhibiting their 'centring response', desert ants, unlike honeybees (Srinivasan et al., 1991), estimate the distances of landmarks occurring on either side of their locomotor trajectories not in

Fig. 5. (A) Same as Fig. 2B (shown for comparison with B). (B) Results from experiments in which the left-hand and the right-hand walls carry stationary black-and-white square-wave gratings of equal spatial period ($\lambda=14.9^\circ$), but one of the walls (the left-hand wall in the left figure and the right-hand wall in the right figure) is higher ($h=0.19$ m) than the other ($h=0.11$ m). Red line, midline of channel; orange line, position at which the heights of the left and the right walls appear to subtend equal visual angles (compare Fig. 4B). $N=23$ (left figure) and $N=34$ (right figure). For further conventions, see Fig. 2A.

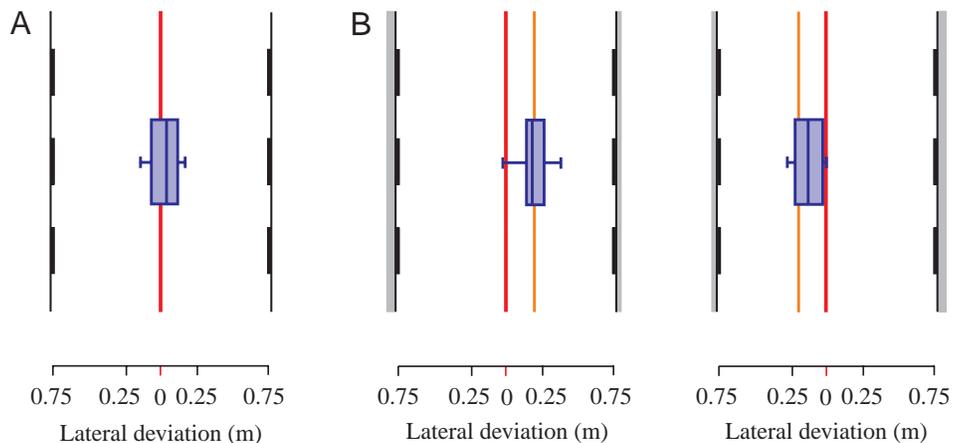
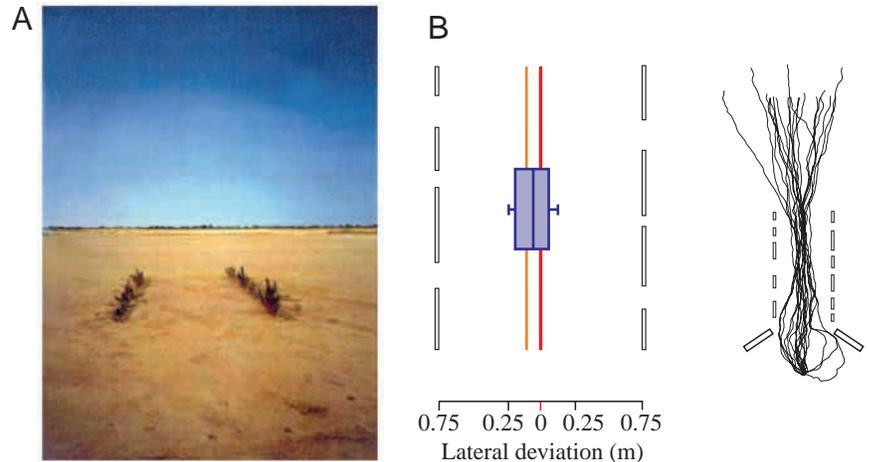


Fig. 6. (A) The natural alley formed by plants that had grown in the furrows used in the previous year to mount the walls of the channel. (B) The trajectories of ants passing through the natural alley. In the box-plot representation, the orange line marks the position at which the left and the right rows of plants appeared to subtend equal visual angles. Since the number (29 in the left row and 23 in the right row) and the linear heights (0.13 ± 0.06 m in the left row and 0.18 ± 0.07 m in the right row; means \pm s.d.) of the plants varied between the left and the right sides of the alley, the orange line represents only an approximate mean value. Nevertheless, the ants' trajectories are shifted towards it (see text). Red line, midline of alley. $N=19$.



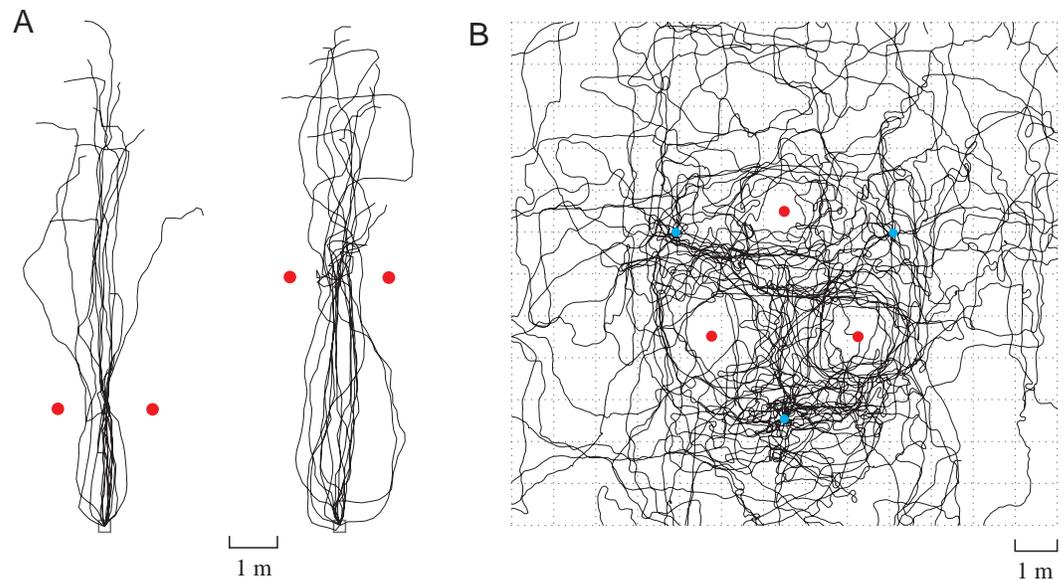
terms of the apparent motion of the images of the landmarks, but in terms of the angular heights of the landmarks. In particular, when they accomplish the centring task, they tend to balance neither the apparent image speeds nor the contrast frequencies of the images of the landmarks, but the vertical angles subtended by the landmarks on either side of the animal's left and right visual field. In our experiments, *Cataglyphis fortis* had to run through a channel in which the left and right walls differed in height. Under these conditions, the ants always adjusted the lateral positions of their trajectories in such a way that the two walls appeared to be of equal angular height.

The marked difference that obviously exists between bees and ants in steering centred courses is related to the different stimulus conditions encountered by flying and walking animals. While flying, an animal can assess its speed of locomotion (its track speed) only by monitoring the speed of the optic image flow

induced by the combined effects of the animal's speed relative to the air (flight speed) and the air speed relative to the ground. This agrees well with the recent discovery that honeybees gauge distance travelled by exploiting self-induced optic flow (Srinivasan et al., 1996, 2000) and that the message conveyed by successful foragers to their hive mates is based on optic-flow parameters rather than on absolute distances (Esch et al., 2001).

In contrast, walking desert ants do not depend on self-induced visual flow-field cues when gauging the distance travelled, but are able to measure locomotor distance exclusively by idiothetic means (Ronacher and Wehner, 1995; Ronacher et al., 2000). For a walking animal, this is a sensible strategy, because during walking the speed of locomotion is due predominantly to the animal's own motor activity and is not influenced passively by the movement of the medium within which the animal proceeds. Furthermore, as a walking

Fig. 7. (A) Walking paths of ants trained to walk from an artificial feeder to the nest, then captured at the feeder and displaced to the position marked by the open square. On their homeward runs towards the fictive position of the nest, they were presented with two black cylinders (0.40 m high, 0.25 m wide and 2.0 m apart from each other; see filled red circles). $N=15$ (left figure) and 16 (right figure). Recordings taken by B. Michel. (B) Walking paths of ants trained to return to a place (their nesting site) surrounded by three black cylinders (0.40 m high and 0.25 m wide, see filled red circles) positioned at the corners of an equilateral triangle and 2.0 m apart from the entrance of the nest. After training, the three-cylinder landmark array was established within a distant test area where 45 trajectories of 3 min search paths of 17 ants were recorded. While concentrating their search about the fictive position of the nest (the centre of the landmark array), the ants avoided the immediate neighbourhood of the landmarks. The three blue dots mark the positions at which the ants were released. Recordings taken by P. Antonsen.



animal, unlike a flying one, maintains a constant distance above the ground, the apparent (angular) heights of landmarks located to the left and right of frequently travelled paths (Wehner et al., 1996) provide the animal with reliable visual cues. *Cataglyphis* ants use these skyline cues irrespective of whether the walls of an artificial alley are visually homogeneous, e.g. uniformly black, or whether they carry contrast-rich visual patterns and irrespective of whether, in the latter case, the patterns on the walls provide them with equal or different apparent image speeds and contrast frequencies.

In the present study, the visual stimulus parameters used in the experiments were adapted as closely as possible to the stimulus conditions encountered by the animals in their natural environment. When *Cataglyphis fortis* forages in the cluttered environment of its salt-bush habitat, it has been observed to run through the middle of gaps 1.68 ± 0.74 m ($N=31$) wide. The mean angular height of the local skyline as experienced from the midlines of these natural alleys is $20.2 \pm 8.9^\circ$ ($N=62$) (means \pm s.d.). Both values correspond well with those used in the present experiments (1.5 m and 14.9 – 28.1° , respectively).

The centring response can be observed in a variety of natural as well as experimental conditions (see e.g. Fig. 7A). It is related to the ant's tendency to stay away from the immediate vicinity of large objects. For example, when *Cataglyphis fortis* is trained to locate a particular place within an array of black cylinders, its search density distributions contain 'haloes' of 'no-ants-land' around the cylinders (Fig. 7B). These haloes increase in diameter as the cylinders increase in height. It remains to be determined whether the ants are able to learn to view particular landmarks subtending particular angles when steering their idiosyncratic routes around bushes and other obstacles (Wehner et al., 1996). Whatever the answer turns out to be, the sensory mechanisms involved in the centring response will undoubtedly be related to the mechanisms mediating more elaborate landmark-based navigational performances, e.g. linking particular landmarks to particular places (Wehner and R ber, 1979; Nicholson et al., 1999), routes (Wehner et al., 1983, 1996) and vectors (Collett et al., 1998; Bisch-Knaden and Wehner, 2001).

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