

## LATERAL OPTIC FLOW DOES NOT INFLUENCE DISTANCE ESTIMATION IN THE DESERT ANT *CATAGLYPHIS FORTIS*

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Accepted 27 January; published on WWW 9 March 2000

### Summary

The present account answers the question of whether desert ants (*Cataglyphis fortis*) gauge the distance they have travelled by using self-induced lateral optic-flow parameters, as has been described for bees. The ants were trained to run to a distant food source within a channel whose walls were covered with black-and-white gratings. From the food source, they were transferred to test channels of double or half the training width, and the distance they travelled before searching for home and their walking speeds were recorded. Since the animals experience different motion parallax cues when walking in the broader or narrower channels, the optic-flow hypothesis predicted that the ants would walk faster and further in the broader channels, but more slowly and less

far in the narrower channels. In contrast to this expectation, neither the walking speeds nor the searching distances depended on the width or height of the channels or on the pattern wavelengths. Even when ventral-field visual cues were excluded by covering the eyes with light-tight paint, the ants were not influenced by lateral optic flow-field cues. Hence, walking desert ants do not depend on self-induced visual flow-field cues in gauging the distance they have travelled, as do flying honeybees, but can measure locomotor distance exclusively by idiothetic means.

Key words: odometry, optic flow, distance estimation, insect, vision, ant, *Cataglyphis fortis*.

### Introduction

To perform their remarkable feats of path integration, desert ants must continuously determine the course they have steered and the distance they have travelled (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 odometer of the ants is still enigmatic. From experiments performed using mainly honeybees and ants, four types of cue have been considered: (i) time spent while travelling in a particular direction, (ii) energy expenditure, (iii) idiothetic cues (some kind of step or wingbeat counter), and (iv) self-induced optic flow (see von Frisch, 1965; Esch and Burns, 1996; Mittelstaedt, 1983; Seyfarth and Barth, 1972; Seyfarth et al., 1982; see also Etienne et al., 1996).

For many years, the second hypothesis was the one favoured by most authors. According to experiments carried out in the 1950s and 1960s (Heran and Wanke, 1952; Heran, 1956; von Frisch, 1965), energy expenditure seemed to be the decisive cue used by foraging bees. Neese (1988) suggested that, instead of directly monitoring their energy consumption during flight, bees might measure the decrease in the amount of nectar in their crop by means of stretch receptors. In recent years, however, the use of energy expenditure as a cue was rendered unlikely for several reasons. In the field, bees were trained to

collect nectar on the roof of a high building or at an elevated source attached to a balloon (Goller and Esch, 1990; Esch and Burns, 1995, 1996; see also Esch et al., 1994). In spite of the higher energy demands associated with the 'up-hill' flight, these bees did not indicate larger distances travelled when performing their recruitment dances. Similarly, results obtained in ants carrying heavy loads (Schäfer and Wehner, 1993; see also Nielsen et al., 1982) contradict the predictions of the energy hypothesis. Instead, several pieces of evidence have now accumulated to suggest that bees use self-induced optic-flow parameters to gauge the distance they have travelled. For example, in the experiments mentioned above in which bees were trained to feed from an elevated nectar source, their subsequent dances indicated a shorter rather than a longer distance (compared with the ground-level distance), as would have been expected according to the energy hypothesis (Esch and Burns, 1995, 1996). This underestimation of distance flown is compatible with the assumption that distance estimation is based on the rate of self-induced optic flow (which decreases with increasing distance from the ground). Orientation to optic cues had already been suggested by von Frisch and Lindauer (1955), Heran (1956), Heran and Lindauer (1963) to explain the observations that bees flying under head-

or tail-wind conditions partly compensate their flight speed for the influence of the wind and that the less visual structure they experience from the ground, the closer they fly to it.

In the laboratory, Srinivasan et al. (1996, 1997) trained bees to collect nectar in channels that had their lateral walls covered with gratings. When the widths of the channels were changed, the bees adjusted their flight speed to the changing apparent angular speed of movement of the pattern (Fig. 2 in Srinivasan et al., 1996; see also Heran and Lindauer, 1963; David, 1982; Srinivasan et al., 1991, 1993). Probably also as a consequence of this optically induced flight velocity control, the estimation of distance was influenced by the width of the channel (Srinivasan et al., 1996, 1997). Somewhat surprisingly, in these experiments, the optic flow from the ventral visual field had only negligible effects. According to Srinivasan and coworkers, distance estimation in bees is based on the visual flow-field experienced in the lateral visual field. This conclusion is at odds with the results of the long-distance experiments performed by Esch and coworkers (for a summary, see Esch and Burns, 1996).

In the present account, we investigate whether walking ants, like flying bees, exploit optic-flow cues within their lateral visual fields of view to gauge the distance they have travelled. Are walking speed and searching distance influenced by changes in the flow-field patterns and speeds? We trained ants to visit a food source placed several metres from the nest. The ants were guided to the food source by walking through a channel of a certain width. The inner walls of the channel were covered with high-contrast black-and-white gratings. For their subsequent homebound runs, they were transferred to a channel aligned parallel to the training channel but with a different width, and the homing ants therefore experienced different motion-parallax cues. Under these experimental conditions, the homing distance as gauged by a trained animal (searching distance) can be easily recorded by a sharp 180° turn performed by the homing ant (Wehner and Srinivasan, 1981; Ronacher and Wehner, 1995).

### Materials and methods

Experiments were performed on desert ants (*Cataglyphis fortis*) in a salt pan near the village of Maharès, Tunisia (34.58° N, 10.50° E).

#### Experimental arrangement, training and testing

The basic experimental arrangement is depicted in Fig. 1A. Ants were trained to walk through a channel to a food source (pieces of water melon or small biscuit crumbs) placed 11 m from the nest. A circular fence (devoid of optical gratings) was fixed at both ends of the training channel (around the nest and the feeder) so that large numbers of ants were forced to enter the channel. The training channel had a width of either 20 cm or of 10 cm, while the widths of the test channels in most experiments were 20, 10 or 5 cm (see Fig. 1A). Unless mentioned otherwise (e.g. in Fig. 4), the heights of the walls were the same as the widths of the channels (see insets at the

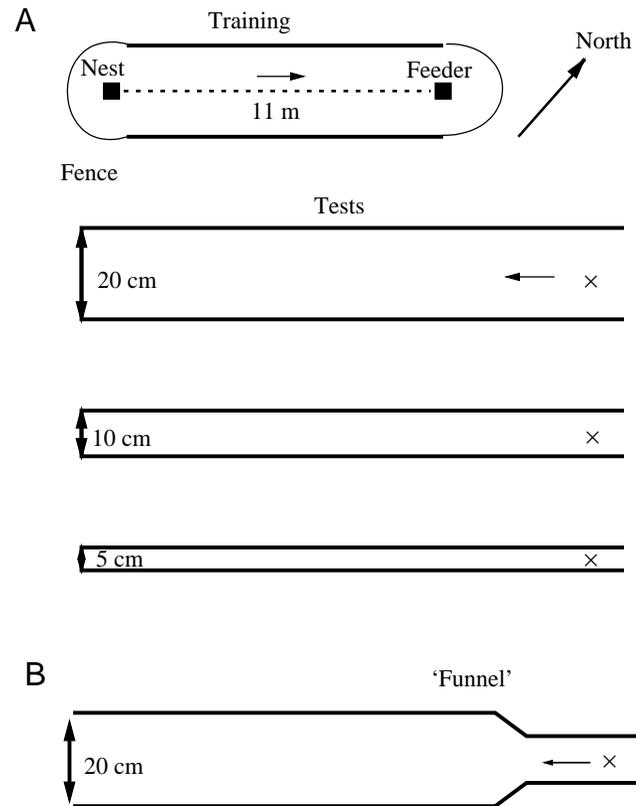


Fig. 1. (A) Schematic top view of the experimental arrangement consisting of the training channel and the three test channels. Note that the widths and lengths of the channels are not drawn to scale. The width of the training channel was usually 20 cm, but occasionally 10 cm. The distance between the nest entrance and the feeder was 11 m; the test channels were 16.5 or 18 m long. × in the test channels denotes the points at which the individuals were released for their homebound runs. (B) 'Funnel' experiment (see text for explanation).

top of Fig. 2). Thus, for ants walking in the middle of the channel, which is what they usually do ('centering response'; Heusser and Wehner, 1996), the walls covered approximately 70° of their lateral visual fields. However, they could still see a substantial part of the e-vector pattern of the skylight (compass) patterns (a strip-like window of angular width of more than 50°). In the training channel, the individually marked ants (marked by a three-digit code) shuttled back and forth between the nest and the feeder. From the feeder, an individual ant could be taken and transferred to one of the test channels (aligned parallel to the training channel). There, it performed its homebound run. We recorded the point at which the ants switched from their steady straight path to their typical nest-searching behaviour. This transition is marked by a very conspicuous 180° (U)-turn followed by a path directed backwards (see Wehner and Srinivasan, 1981; Ronacher and Wehner, 1995). In all figures, the mean distances (plus standard deviations) of these first U-turns are defined as the ants' searching distance. From the individual travelling times and searching distances, we calculated the ant's average

travelling speed. Runs during which an ant was slowed down to less than  $20 \text{ cm s}^{-1}$  by an especially bulky piece of food were generally excluded from the calculation of the mean speeds shown in the figures. This limit of  $20 \text{ cm s}^{-1}$  seems justified because speeds as low as this were observed in only 0.8% of runs with normal loads.

We tested how the width (experiments 1 and 2) and the height (experiment 4) of the channels and the spatial period of the patterns (experiment 3) influenced walking speed and searching distance. We further examined whether a sudden change of pattern would induce a reset (experiment 5) and, as a control, whether optical information from the ventral visual field had a stabilizing influence (experiment 6).

In most training and test protocols, the walls were covered with black-and-white gratings (stripes perpendicular to the long axis of the channel). The black stripes were photocopied onto very light grey paper and glued to the channel walls, which were constructed from light plywood. We chose a light-grey paper to avoid bright reflections, which seemed to disturb the animals. Nevertheless, the contrast of the pattern was still very high ( $>0.8$ ). We used gratings of different spatial periods (as specified in the figure captions). In most experiments, the pattern wavelengths ( $\lambda$ ) were adjusted to the widths of the channels to minimize the difference between the test and training situations (e.g.  $\lambda=8 \text{ cm}$  in the 20 cm channel,  $\lambda=4 \text{ cm}$  in the 10 cm channel and  $\lambda=2 \text{ cm}$  in the 5 cm channel; the visual angle of the patterns seen from the middle of the respective channels was approximately  $44^\circ$ ). Thus, the main difference between the three test channels, as experienced by the ants, was the apparent angular speed of self-induced pattern movement.

The floor of the channels consisted of the hard desert salt-pan surface. We were careful to choose a nest opening surrounded by a very uniform sand desert floor to provide the animals with identical conditions in both the training and test channels.

In most experiments (nos. 1 and 3–6), the test channels had a uniform width along their entire (16.5 m or 18 m) length. However, we performed a control experiment (experiment 2) in which the test channel began with the training width of 10 cm and widened to double this width after 3 m (the intermediate funnel-shaped part of the channel had a length of 1 m; see Fig. 1B). The pattern period was  $\lambda=4 \text{ cm}$  in the 10 cm and funnel part and  $\lambda=8 \text{ cm}$  in the 20 cm wide part of the channel.

In experiment 6, individually marked ants had the ventral parts of their eyes covered by black light-tight enamel paint (see Wehner and Müller, 1985; Ronacher and Wehner, 1995). Painting of the eyes and checking the paint after the completion of the test runs were performed under a stereo microscope (Wild M3).

#### *Statistical analyses*

In most tests, individually marked ants were tested in all (two or three) the different conditions. This experimental paradigm allowed us to make pairwise or triple comparisons.

We used the *t*-test or Wilcoxon matched-pairs signed-rank test for paired data and Friedmans's test combined with Wilcoxon–Wilcox tests for multiple comparisons of data obtained in the repeated-measures design.

## **Results**

Our first series of experiments examined whether ants would behave in a manner similar to bees and adjust their locomotor speed to the apparent angular velocities experienced in their lateral visual fields. Furthermore, we investigated whether the ants' method of estimating distances (their 'odometer') would also be influenced by this kind of optic-flow information.

### *Experiment 1: variation of channel width*

In the main experiment, the ants were trained in a channel 20 cm wide ( $\lambda=8 \text{ cm}$ ), and then tested on their way home in channels of different widths: 20 cm (control), 10 cm and 5 cm (see Fig. 1A). The heights ( $h$ ) and wavelengths ( $\lambda$ ) of the patterns in the narrower channels were adjusted to keep the angular values of  $\lambda$  and  $h$  identical under all test conditions. Thus, the main difference between the three test situations depicted in Fig. 2A was the apparent angular velocity of the lateral patterns, which was determined by the distance between the ant and the walls.

If ants were to behave like bees (Fig. 2 in Srinivasan et al., 1996), they should decrease their walking speeds in the two narrower channels by factors of 0.5 and 0.25 (see arrows in Fig. 2A) compared with the controls (training width). The ants did not follow this expectation. Their mean walking speeds were virtually identical for all three conditions (Fig. 2A, filled columns). The searching distances (the locations of the first U-turns) did not differ significantly between the three test channels (Fig. 2A, open columns, Friedmans test,  $P>0.10$ ) and were not significantly different from the training distance (11 m). The mean walking speeds and searching distances in the 5 cm and 10 cm channels, however, were completely different from those predicted by the optic-flow hypothesis (see arrows in Fig. 2A,  $P\leq 0.001$ ). This result is corroborated by a second series of tests in which the training width was 10 cm, and in which the ants were tested in the 20 cm, 10 cm or 5 cm channels (Fig. 2B). Again, neither the mean speeds nor the mean walking distances of the ants differed significantly between the three test conditions ( $P>0.20$  in both cases). Taken together, these results clearly show that neither a reduction of the channel width by a factor of up to 4 nor a widening by a factor of up to 2 affected the walking speeds of the ants or their searching distances.

### *Experiment 2: 'funnel'*

It seemed conceivable (although not very likely) that the ants adjusted their walking speed to the optic-flow cues present at the start of their homebound run. We therefore performed a control experiment by using a test channel that had the training width (10 cm) at its beginning and then widened to 20 cm (cf. Fig. 1B, 'funnel'). Neither the speed ( $P>0.1$ ) nor the searching

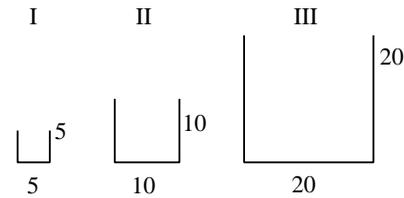
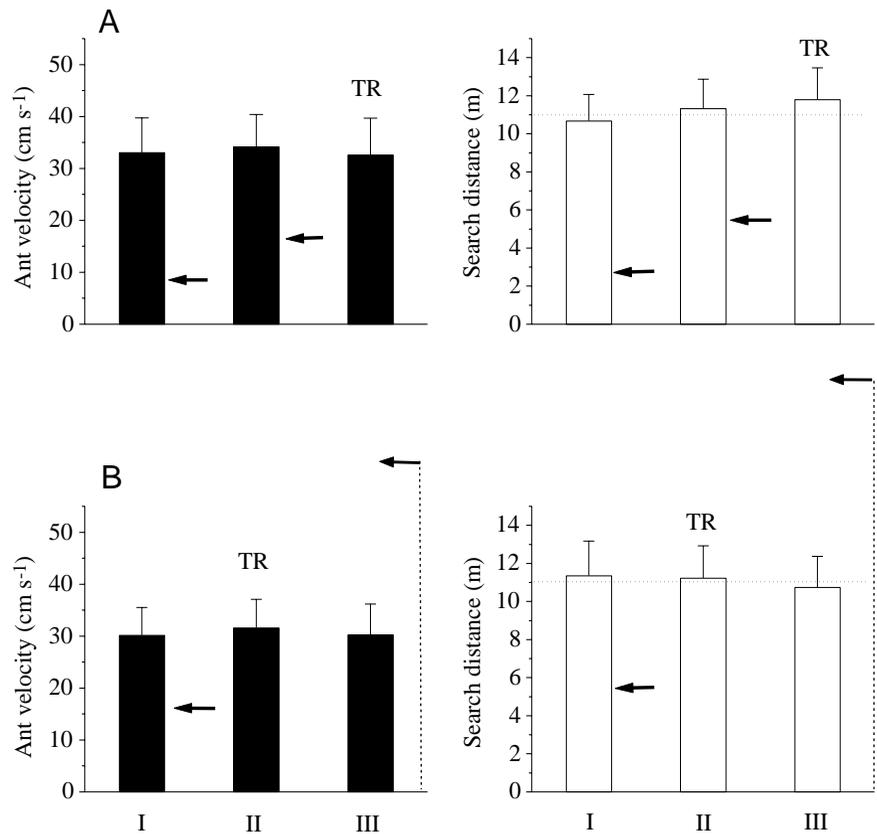


Fig. 2. The effects of variation in channel width. (A) Training in the 20 cm channel (period of stripe pattern  $\lambda=8$  cm), tests in the 5 cm, 10 cm or 20 cm channels. The heights of the channel walls were the same as the respective widths of the channels. Pattern wavelength  $\lambda=2, 4$  and 8 cm, respectively, corresponding to an angle subtended at the ant's eye of approximately  $44^\circ$  as seen from the midline of the channel. Training width is indicated by 'TR' above the columns. Left-hand diagram (filled columns): ant velocities ( $\text{cm s}^{-1}$ ). Values are means and standard deviations of 24–28 runs by 18 individuals. Right-hand diagram (open columns): searching distances (m). Values are means and standard deviations for the same runs; the dotted line indicates the training distance (11 m). Differences in mean velocities and mean distances are not significant according to Friedman's test. (B) Training in the 10 cm channel ( $\lambda=4$  cm), tests as in A. The 16–23 runs by more than 10 individuals yield no significant differences between the tests and the control (middle columns). The arrows in A and B indicate expectations according to the optic-flow hypothesis. The inset at the top of this and the following figures shows cross sections of the channels with dimensions in centimetres.



distance ( $P=0.5$ ) differed significantly from those obtained in the channel with the (constant) training width (Fig. 3, compare middle and right-hand columns).

#### Experiment 3: variation of pattern wavelength

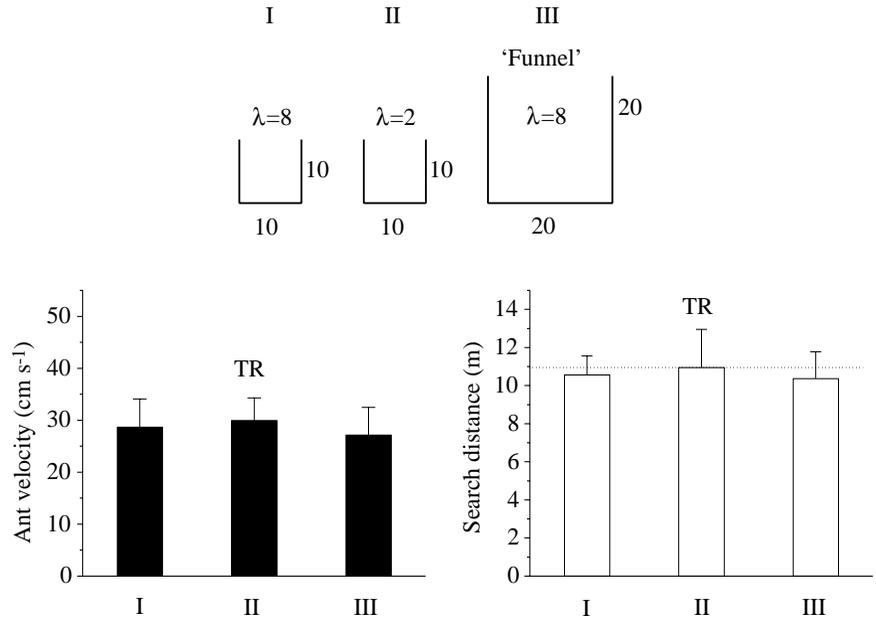
We investigated the possible influence of the pattern wavelength by training ants in a 10 cm channel whose walls were provided with a stripe pattern of  $\lambda=2$  cm. In the tests, the pattern wavelength was either 2 cm (as in the training situation) or 8 cm (channel width was 10 cm in both cases; see inset at the top of Fig. 3). Increasing the pattern period by a factor 4 had no influence on speed or searching distance (compare the left-hand and middle columns in Fig. 3).

#### Experiment 4: variation of channel height

In the previous experiments, the heights of the walls of the test channels were adjusted to the widths of the channels, so that the patterned walls appeared at the same visual angle for ants running in the middle of the channel (as they usually do; see centering response; Heusser and Wehner, 1996). In this respect, the channels used for the tests shown in Fig. 2 differed from the experimental situation in the bee experiments of

Srinivasan et al. (1997) (see their Fig. 3). To determine whether this difference in the experimental arrangement had substantially influenced the results, we trained ants in a channel 20 cm wide and 10 cm high (pattern wavelength  $\lambda=4$  cm). The test channels were all the same height (10 cm), but were 10 cm (apparent wall height seen from the centre approximately  $70^\circ$ ), 20 cm (apparent height as in training approximately  $47^\circ$ ) or 40 cm wide (apparent height approximately  $27^\circ$ ; pattern wavelengths were constant at  $23^\circ$ , i.e.  $\lambda=2$  cm,  $\lambda=4$  cm and  $\lambda=8$  cm respectively). The results of these tests are shown in Fig. 4A. Whereas the walking speeds were virtually identical in all three conditions, the searching distances were reduced in both the narrower and the wider channel by 1.9 and 1.2 m, respectively (compared with the control). According to the Friedman and the Wilcoxon–Wilcoxon tests, only the mean searching distances between the 10 cm and the 20 cm channels differed significantly ( $P<0.01$ ). However, it must be emphasized that the mean searching distance observed in the 10 cm channel was still much larger than that expected according to the optic-flow hypothesis (see arrows in Fig. 4A), while it was much smaller than that expected in the 40 cm channel. We repeated this experiment with the same channel

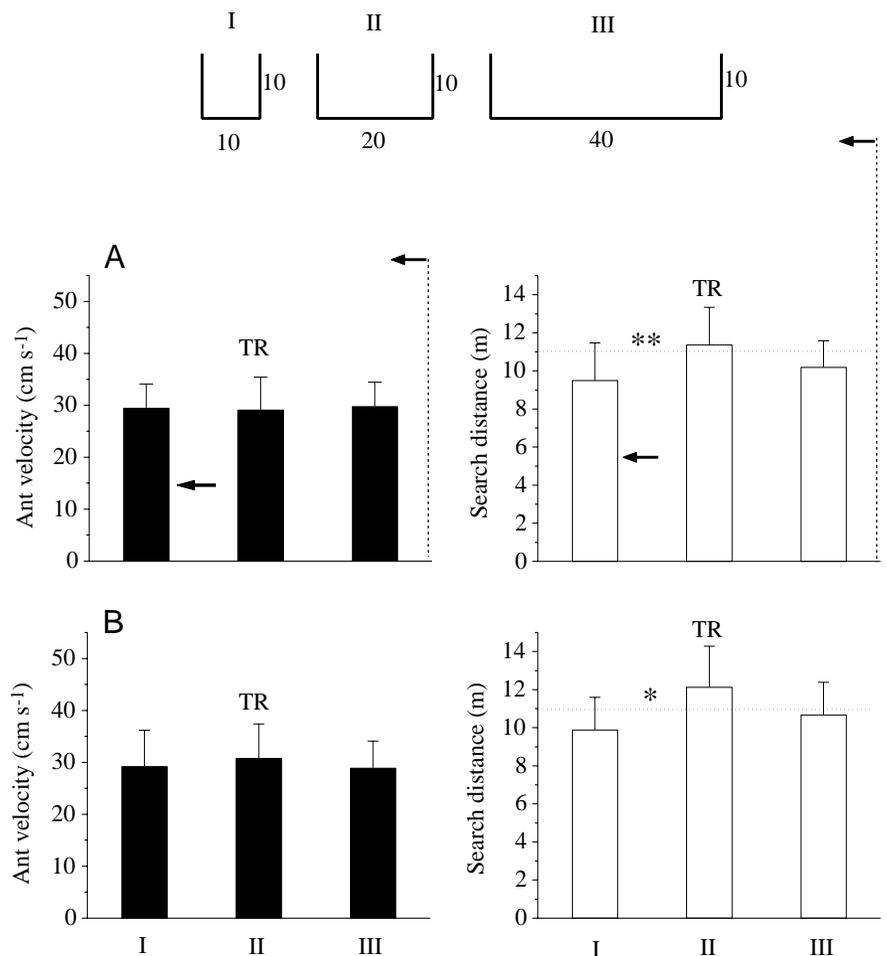
Fig. 3. Influence of pattern wavelength and the 'funnel'. Left-hand and middle columns: training in the 10cm channel (period of stripe pattern  $\lambda=2$ cm), tests in the 10cm channel with  $\lambda=8$ cm (angle subtended at the ant's eye  $77^\circ$ ) or (as control)  $\lambda=2$ cm ( $23^\circ$ ); see inset at top, I and II. Data are from 15–18 runs by nine (left-hand column) and 12 (right-hand column) individuals. There were no significant differences between the test and the control condition (middle column, denoted by TR). Right-hand columns (III): results of the 'funnel' experiment (see Fig. 1B and Materials and methods). The pattern wavelength of the 20cm channel section was increased by a factor of 2 with respect to the 10cm section so that the angle of the pattern period subtended at the ant's eye ( $\lambda=44^\circ$ ) remained constant (and Materials and methods); 15 runs by nine individuals. There were no significant differences between the test (III) and the control (II) condition. Values are means  $\pm$  S.D.



dimensions, but now using walls without any pattern (plain plywood that exhibited few if any structures of very low contrast). The results (Fig. 4B) were very similar to those of Fig. 4A, suggesting that the observed reduction of the

searching distance of the ants in the 10cm channel cannot be attributed to lateral optic flow, but rather seems to be a nonspecific effect pertinent to this experimental paradigm (see Discussion).

Fig. 4. Effects of variation in the angle subtended at the ant's eye of the walls of the channel. Training was in a channel 20cm wide and 10cm high. Tests were performed in channels of various widths (10cm, 20cm or 40cm) and apparent heights (angle subtended  $70^\circ$ ,  $47^\circ$  or  $27^\circ$ ). (A) Training and tests in channels with patterned walls (period of stripe pattern  $\lambda=2, 4$  and  $8$ cm). Data are from 21–28 runs by 26 individuals, 16 of which were tested in all three conditions. A Friedman test combined with the Wilcoxon–Wilcox test revealed a significant reduction of search distance in the 10cm channel ( $\chi^2=13.87$ , difference between summed ranks for the 10cm and 20cm channels 21,  $**P<0.01$ ). Ant velocities did not differ significantly between the three test paradigms. The arrows indicate the expectations according to the optic-flow hypothesis. (B) Training and tests in channels with unpatterned walls of plain wood. Channel dimensions as in A. Data are for 21–25 runs by 23 individuals, 17 of which were tested in all three conditions. There were no significant differences in velocities, but there was a significant difference in searching distances between the tests in the 10cm (I) and 20cm (II) channels (difference between summed ranks 16,  $*P<0.05$ ). Values are means  $\pm$  S.D. TR, training condition.



*Experiment 5: 'reset' experiment*

In the next test, we examined whether the lateral channel walls had any effects on the behaviour of the ants or whether lateral optic cues were totally ignored. We trained ants in a channel (width and height 10 cm) in which the walls exhibited a pattern ( $\lambda=4$  cm) during the first 6 m (starting from the nest) and then changed to a 4.5 m section without any pattern. In the test channels, the pattern-free section (from which the animals started their homebound run) was either extended to 7.5 m or shortened to 2 m. However, the 'landmark' induced by the change from the pattern-free to the patterned section (see Srinivasan et al., 1997) did not induce any obvious reset (compare the actual searching distances with the expectations indicated by the arrows in Fig. 5).

Nonetheless, this test situation led to several additional observations, which clearly demonstrate that the patterns on the lateral walls indeed influenced the behaviour of the ants. (i) Several individuals exhibited some kind of 'hesitant' walking pattern within the pattern-free section of the channel. At the contrast border, this movement pattern changed immediately to a more 'fluent' one. This behaviour most certainly accounts for the small (although not significant) increase in mean walking speed within the channel in which

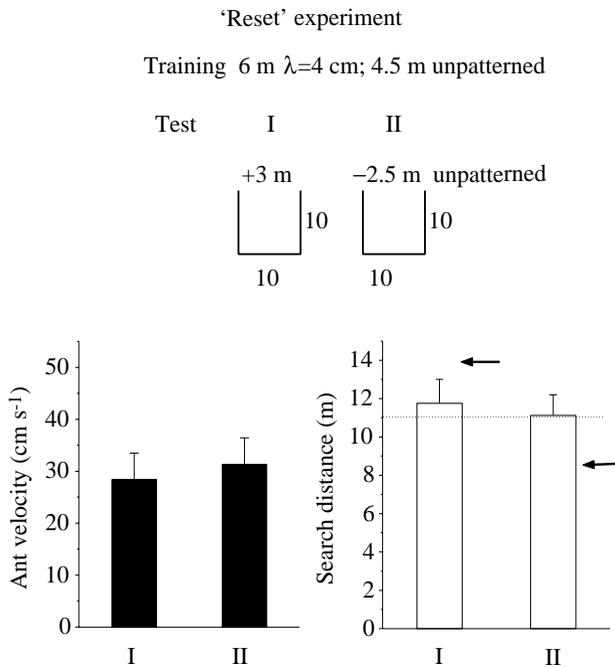


Fig. 5. The 'reset test'. Training was performed in a channel whose walls exhibited a pattern (period of stripe pattern  $\lambda=4$  cm) during the first 6 m from the nest, followed by 4.5 m of unpatterned walls (channel width 10 cm). Test channels: prolongation of the unpatterned section by 3 m (7.5 m unpatterned, followed by 10.5 m with  $\lambda=4$  cm) or shortening of the unpatterned section by 2.5 m (2 m unpatterned, followed by 15 m with  $\lambda=4$  cm); channel width 10 cm as in training. Results are for 33 runs by 16 individuals. There are no significant differences between the two conditions ( $P>0.05$ ); right-hand diagram: mean search distances differ significantly ( $P<0.001$ ) from the expectations, see arrows. Values are means  $\pm$  S.D.

the pattern-less section had been shortened (Fig. 5, left). (ii) Some individuals preferred to run near or even along one of the walls after they had entered the unpatterned section. Once they returned to the patterned section, they immediately switched to a centered running position within the channel. (iii) During training, many ants tried to escape from the channel in the unpatterned section, but they very rarely did so in the patterned section. Both these latter two effects, the frequent attempts to escape from the training channel and the tendency to walk near one of the walls, might have been due partly to the previous training experience of the ants within a continuously patterned channel.

*Experiment 6: excluding ventral-field visual cues*

In previous experiments, we have shown that the searching distance of *Cataglyphis fortis* is influenced, to some degree, by optic-flow components within the ventral parts of its visual field (Ronacher and Wehner, 1995). Hence, it is conceivable that the possible influence of ventral-field cues had suppressed any influence on distance estimation of lateral-field cues. To test for this possibility, we tested ants that had the ventral parts of their compound eyes covered by light-tight black enamel paint. In this way, any possible effect of ventral optic-flow components on course stabilization could be excluded. The ants were obviously hampered by the eye covers, and some individuals

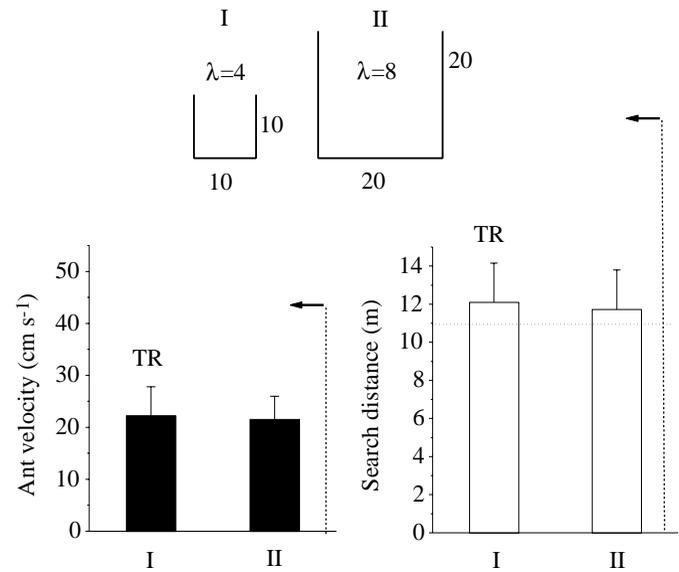


Fig. 6. Effects of occlusion of the ventral visual fields of the ants with paint. Training was performed in a 10 cm channel (period of stripe pattern  $\lambda=4$  cm), and tests were performed in the 10 cm channel (control,  $\lambda=4$  cm) and the 20 cm channel ( $\lambda=8$  cm). Eye occlusion was checked in each case after completion of runs using a stereo microscope. The expectation was that there should be an increase in mean velocity and searching distance (see arrows). Results are for 24 and 22 runs by 10 individuals. The differences in velocities and searching distances between the two conditions are not significant (paired comparisons  $t=0.67$  and  $t=0.44$ ,  $P>0.5$ ). Values are means  $\pm$  S.D. TR, training condition.

made frequent attempts to escape from the test channels. Nonetheless, those that performed uninterrupted runs showed mean searching distances that were fairly accurate (Fig. 6).

We followed several individuals that escaped early from the test channels on their path outside the channels. These animals often maintained a rather straight course, more or less parallel to the channel from which they had escaped, up to a total distance of between 10 and 13 m, and they then began their search for the nest even outside the channels. These observations again indicate that the lateral optic cues provided by the channels were not necessary for distance estimation by the ants.

### Discussion

#### *Cataglyphis fortis* does not use self-induced visual-flow parameters experienced within its lateral fields of view

In contrast to our expectation (based on the experiments on bees of Srinivasan et al., 1996, 1997), the present account clearly demonstrates that neither the walking speed nor the searching distance of ants is influenced by self-induced optic flow in the animal's lateral visual fields (Figs 2–4). In the experiments in which ventral optic cues were excluded, the ants still ignored lateral-field optic-flow cues (Fig. 6). This latter result indicates that a possible influence of lateral optic flow has not been compensated for by stronger ventral flow components in ants with unobstructed ventral vision. In most cases, and under all experimental conditions, a wider or narrower channel had no effect on the ants' estimation of distances that were compatible with the flow-field hypothesis. There was only one case in which the distance estimates of the ants differed when channels of different widths were used (Fig. 4A, left-hand column of right-hand panel). For several reasons, however, even in this case the difference in searching distance cannot depend on the apparent speed of pattern movement. (i) With an optic-flow-based odometer at work, a considerably greater searching distance (compared with the controls) would have been expected within the 40 cm channel. In contrast, the ants tended to stop even sooner than they did in the controls (compare the middle and right-hand open columns in Fig. 4A). (ii) The mean walking velocities are virtually identical in all three test situations (Fig. 4A, filled columns). (iii) Very similar results were obtained in channels without a pattern (Fig. 4B).

Thus, optic flow within the lateral visual field is neither sufficient (e.g. Figs 2, 6) nor necessary for correct distance estimation (cf. tests in a Perspex channel with uniformly painted walls and a patternless floor; Fig. 6 in Ronacher and Wehner, 1995). In this respect, the results obtained in ants differ substantially from those in bees (Srinivasan et al., 1996, 1997).

Could this difference have been caused by the use of another range of pattern wavelengths? This possibility can be ruled out because Srinivasan et al. (1996, 1997) used mainly stripe periods of 21°, and in some experiments also 26°, 52° and 78°; this range was also covered in our experiments. (In the lateral field of view, the sampling intervals, i.e. the interommatidial

angles, of bees *Apis mellifera* and ants *Cataglyphis* spp. vary at maximum by a factor of 2; Baumgärtner, 1928; Hecht and Wald, 1929; Kunze, 1961; Wehner and Srinivasan, 1984; Zollikofer et al., 1995.) Furthermore, in the experiments of Srinivasan et al. (1991, 1993, 1996, 1997) and as in earlier experiments with ants (Ronacher and Wehner, 1995) and fruit flies (*Drosophila hydei*) (David, 1982), pattern wavelength did not influence the results decisively. This was true even for a fourfold difference in pattern wavelength (Fig. 3). Furthermore, if the ants had somehow counted contrast changes, a searching distance of 44 m would have been expected in the experiment described in Fig. 3 (left-hand open column). In the bee experiments, a distinct change in the side-wall pattern induced a reset of the odometer (Srinivasan et al., 1997, their Fig. 7). In a similarly designed experiment, the ants showed no indication of any such reset induced by a distinct change in their visual surround (Fig. 5).

#### *Influence of ventral optic-flow cues on walking speed and distance estimation*

In contrast to foraging bees, foraging ants are walking animals and, hence, are more likely to use optic-flow components in their ventral rather than their lateral field of view. Because their eyes are held at a more-or-less constant distance from the ground, ventral optic-flow parameters are more reliable cues than lateral ones. In fact, as Ronacher and Wehner (1995) have shown, self-induced ventral flow-field parameters can contribute to gauging the distance travelled. However, as described in the present study, individuals wearing ventral eye covers move more slowly than untreated animals, but their distance estimation is still fairly accurate. Most importantly in the present context, however, distance estimation was not influenced by the distance of the only visual cues available (i.e. in the lateral visual field; Fig. 6, open columns) even in animals with their ventral visual fields occluded.

From the data presented here, we must conclude that neither the speedometer nor the odometer of *Cataglyphis fortis* is coupled to optic-flow cues experienced within the lateral visual field. As shown in our previous experiments on this topic (Ronacher and Wehner, 1995), self-induced visual flow perceived in the ventral visual fields can be used, at least to some extent, by *Cataglyphis fortis* to obtain information about distances travelled. This would make sense for a walking animal, because the distance between any gravel-floor pattern and its detector (the animal's eyes) is constant for any particular individual. In contrast, this distance varies in largely unpredictable ways for objects perceived within the lateral visual field. Furthermore, taken together with the earlier study mentioned above, the present study clearly shows that *Cataglyphis fortis* can gauge distances without referring to any visual cue: the ant's odometer seems to be based mainly on idiothetic information.

#### *How do bees compare with ants?*

Because *Cataglyphis fortis* often take quite different paths

on their way home from those on their way out (e.g. Wehner and Wehner, 1990), any reliance on lateral optic-flow cues would be prone to substantial errors. Similar arguments also apply to bees. To make the lateral optic-flow measurements reliable, a bee should return home the same way that it flew out to the feeding site. This might be true for an experienced forager bee visiting the same food source for several days. But relying predominantly on lateral visual cues will be as dangerous for bees performing exploration flights as it is for foraging desert ants.

Because foraging bees and ants employ different locomotor strategies – flying and walking, respectively – their locomotor behaviour may impose different constraints on the sensory basis of their odometer devices (see Zanker and Collett, 1985). Nevertheless, the question remains of whether lateral or ventral cues would be the more reliable ones in a flying animal. Little is known about how constant is the height above ground maintained by a foraging bee. There are only a few comments in earlier papers concerning the effects of flight height on flight speed: bees experiencing a head wind on their outward flight increase their flight velocity, and thereby try to keep their ground speed constant; in addition, in their dances, they signal a greater distance to the food source (and a shorter distance in a tail wind). But it is only in a strong head wind that they fly lower than in a wind-free situation (von Frisch and Lindauer, 1955; Heran and Lindauer, 1963; Bräuninger, 1964). However, it is not clear whether they try to adjust the speed of their optic flow to their lower ground velocity or whether they simply choose a lower height to fly in a zone with lower wind speed (Bräuninger, 1964, p. 93; see also von Frisch and Lindauer, 1955, p. 378). Heran and Lindauer (1963, pp. 47, 50) mention that bees tend to fly more slowly when they fly lower, but without providing precise data (see also Steiner, 1953). At least we know that the lower the contrast provided by the structure of the landscape, the lower the bee flies (lake experiments of Heran and Lindauer, 1963).

In the experimental results on the use of ventral and lateral flow-field information, there is an obvious discrepancy between the outdoor experiments of Esch and coworkers and the laboratory-based experiments of Srinivasan and coworkers. The former authors report a strong influence of ventral flow-field information, while the latter authors find that this information has little influence and that bees rely predominantly on lateral-field cues. Perhaps part of this discrepancy is due to the rather different scales of training distances investigated by the two groups of authors. In the indoor experiments of Srinivasan et al. (1996, 1997), the training distance was usually 1.8 m (in one case up to 5.6 m), but in the outdoor experiments of Esch and Burns (1996) it was up to 650 m. Furthermore, the bees studied by Srinivasan et al. (1997, p. 2515) flew at extremely low speeds of approximately  $0.25 \text{ m s}^{-1}$  (indeed at lower speeds than those achieved by our walking *Cataglyphis fortis*), while bees normally attain speeds of  $8 \text{ m s}^{-1}$  or more (e.g. von Frisch and Lindauer, 1955; Heran and Lindauer, 1963). It is not clear what had caused the bees to fly so slowly (possibly the low illumination level; see Heran,

1959, p. 156) nor how this might have affected their speedometer and odometer. In any case, the small distances investigated and the extremely low locomotor speeds used by the bees flying within the channels make it somewhat doubtful how the mechanism deduced by the elegant experiments of Srinivasan et al. (1996, 1997) applies to the situations normally encountered by bees on their foraging flights.

We are very grateful to the inhabitants of Maharrès (Tunisia) for their kind hospitality. We further thank H. Heise for his excellent technical assistance and all members of the Zurich–Cataglyphis research crew for their help in providing us with the appropriate working and living conditions at our field station in Maharrès.

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