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Desert ants *Cataglyphis fortis* use self-induced optic flow to measure distances travelled

Abstract While foraging, desert ants of the genus *Cataglyphis* use a vector navigation (route integration) system for homing. Any vector navigation system requires that the animal is able to evaluate the angles steered and the distances travelled. Here we investigate whether the ants acquire the latter information by monitoring self-induced optic flow. To answer this question, the animals were trained and tested within perspex channels in which patterns were presented underneath a transparent walking platform. The patterns could be moved at different velocities (up to > 0.5 the ant's walking speed) in the same or in the opposite direction relative to the direction in which the animal walked. Experimental manipulations of the optic flow influenced the ant's homing distances (Figs. 2 and 4). Distance estimation depends on the *speed* of self-induced image motion rather than on the *contrast frequency*, indicating that the motion sensitive mechanism involved is different from mechanisms mediating the optomotor response. Experiments in which the ants walked on a featureless floor, or in which they wore eye covers (Fig. 6), show that they are able also to use additional (probably kinesthetic) cues for assessing their travel distance. Hence, even though optic flow cues are not the only ones used by the ants, the experiments show that ants are obviously able to exploit such cues for estimation of travel distance.

Key words Orientation · Vector navigation · Optic flow · Distance estimation · Ants · *Cataglyphis*

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Introduction

Desert ants of the genus *Cataglyphis* use a vector navigation system for homing. This system enables an animal to return to its starting point on the direct route rather than by retracing its outbound path. Obviously, at each stage of a foraging trip the ant is aware of its position relative to home, that is it must continously compute the vector pointing towards its nest. To accomplish this "dead reckoning" (route integration) task, the animal must evaluate the angles steered as well as the distances travelled (Müller and Wehner 1988; Wehner 1992).

In order to determine the directions of their paths ants (as well as other arthropods) use a celestial compass based on the pattern of polarized light and/or the direct light of the sun (see Wehner 1992, 1994 for reviews). However, as regards the second necessary information needed for route integration, there exist at least three hypotheses how arthropods could estimate the distances travelled in a given direction: (i) by measuring their energy expenditure (e.g. Heran and Wanke 1952), (ii) by monitoring their locomotor activity (idiothetic orientation, Mittelstaedt and Mittelstaedt 1973), or by (iii) utilizing self-induced optic flow parameters (Wehner 1982, 1992).

Energy expenditure as a cue for distance estimation was proposed by Heran and Wanke (1952) and Heran (1956) on the basis of experiments with honeybees that were trained to forage on steep slopes (see also Neese 1988). This hypothesis has been revisited recently for bees (Goller and Esch 1990; Esch and Burns 1995) as well as for ants. An additional load up to four times the body weight did not affect the measurement of walking distance in *Cataglyphis fortis* (Schäfer and Wehner 1993). Evidence for an idiothetic orientation stems mainly from experiments with spiders (Görner 1958, 1966; Seyfarth and Barth 1972; Mittelstaedt and Mittelstaedt 1973; Seyfarth et al. 1982; for review see

Wehner 1992). Indeed the spider *Cupiennius salei* is able to evaluate travel distance on the basis of idiothetic cues (Seyfarth et al. 1982).

Here we present, for the first time, a direct test of the third hypothesis, i.e. a direct answer to the question whether ants are able to use self-induced optic flow components to estimate travel distances. Based on indirect evidence, this was recently reported to be the case in bees (Esch and Burns 1995). As in the natural habitat of *C. fortis* landmarks are scarce, small, and often inconspicuous, and as the angular velocity of optic flow components in the lateral visual field depends strongly on the distance between animal and landmark surroundings, we focus on the *ventral* flow components deriving from patterns on the floor over which the ant moves. While walking it keeps its head in a rather constant position and at a constant height above ground (Wehner 1982). Furthermore, it maintains a rather constant speed of movement (Wehner and Srinivasan 1981). Hence, the ventral components of optic flow could provide the animal with reliable information about travel distances.

The animals were trained and tested in transparent perspex channels with stationary or moving black-and-white gratings or random dot patterns presented underneath. Different pattern wavelengths were used in order to decide whether image speed (as in the centering response of honey bees, Srinivasan et al. 1991) or contrast frequency (as in the optomotor response of bees and flies, Kunze 1961; Götz 1964, respectively; rev. Reichardt 1969; Wehner 1981), is the decisive parameter.

Methods

Apparatus

A 10-m channel and a 20-m channel aligned in parallel (in the north-south direction) were used for training and testing, respectively. The frame of the channels consisted of 2-m pieces of aluminium profiles that could be firmly connected by clamps. Inside these channels a wooden support (pieces of 1-m lengths) could be inserted at an appropriate height (see cross section in Fig. 1A). An endless band provided with black and white gratings or dot patterns was put on the support. Finally, a perspex channel (pieces of 1-m length) was firmly inserted into the aluminium profile (Fig. 1A). The ants walked inside the perspex channel. The distance between the pattern and the running ant's head was ≤ 10 mm. The floor of the perspex channel was slightly roughened. This ensured that, on the one hand, the animal's gait was not disturbed by the smoothness of the walking platform, and, on the other, that the black-and-white pattern was still clearly visible. In order to prevent ants from leaving the channel, the upper rims were bent downward (see Fig. 1). This left a slitlike aerial window, so that the ant could see a substantial part (angular width ca 75°) of the e-vector pattern in the sky. The walls of the perspex channel were painted with a mat brown paint as to minimize lateral reflections of polarized light. Ants walking in the experimental channel were unable to see any natural landmarks.

The endless band could be moved at different velocities (up to 15.5 cm·s^{-1}) by a battery driven motor (Escap- 12V, 5200 rot/min, Portescap, La-Chaux-de-Fonds, Switzerland) positioned at one end
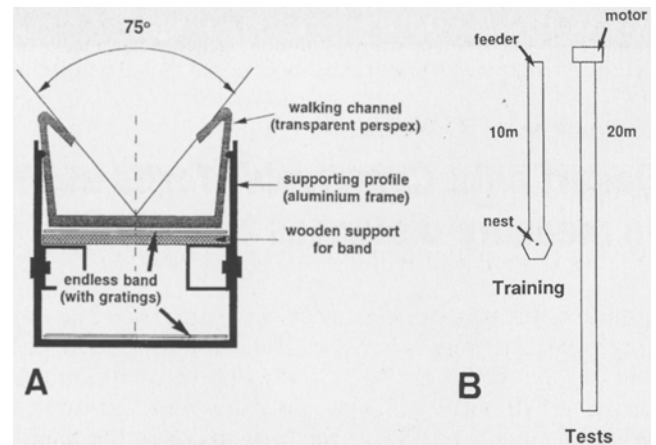

Fig. 1 Experimental set up; cross section (**A**), and arrangement (**B**) of training and test channel (sizes of channels not drawn to scale)

of the channel. At the other end the band passed over a roll and turned back beneath the wooden support at the bottom of the aluminium frame.

Training and testing

The north end of the training channel was situated near a nest of *Cataglyphis fortis*. Ants were induced to enter the training channel by a fence around the nest that had an opening towards a ramp leading into the channel (Fig. 1B). Ants were trained to forage in the shorter perspex channel at a food source (small biscuit morsels) located at a distance of 10 m from the nest. A stationary rectangular black-and-white grating or a stationary random dot pattern was presented underneath the transparent walking platform (Fig. 1A). After successful training the animals were transferred directly from the food source to a 20-m channel aligned in parallel with the training channel (Fig. 1B). In this test channel, the homing distances were recorded, i.e. the points at which the ants terminated their straight homebound runs and turned around by 180° (start of search pattern, see Wehner and Srinivasan 1981; Wehner and Wehner 1990). During the tests patterns were either kept stationary or moved (at 5.5–15.5 cm·s^{-1}) in or opposite to the direction in which the ants walked.

Patterns

Three different gratings and three random dot patterns were used. S5: stripe width 5 mm (spatial wavelength $\lambda = 10$ mm) S10: 10 mm stripes ($\lambda = 20$ mm); S20: 20 mm stripes ($\lambda = 40$ mm); P5: random dot pattern consisting of square-shaped dots with edges 5 mm long; P10: square dots with 10 mm edges; P20: rectangular dots (20 mm long, 10 mm wide, the longer side was aligned parallel to the axis of the channel). In one training condition and in some tests a uniformly white band was used in order to eliminate any optic flow cues.

Patterns were constructed on a personal computer and printed by silk-screen processing equipment onto white, 5 cm wide nylon-bands (No. 841, Fa Ott Fuchs AG, CH 5401 Baden, Switzerland).

Statistical tests

Normality was tested with Lilliefor's modification of the Kolmogorov Smirnov test (Sachs 1984). Homogeneity of variances was tested according to Bartlett (Sokal and Rohlf 1981). Mean values

were compared by using ANOVA (in some cases after log-transformation in order to correct for non-homogeneous variances), or according to Snedecors test of equality of means (Sokal and Rohlf 1981).

Results

Moving floor patterns influence travel distances

Ants were trained to forage at 10-m distances, while the stationary pattern S10 was presented underneath the walking platform. In the following tests the same pattern S10 was moved at different velocities ($5.5-15.5$ cm$\cdot$s^{-1}) either in the forward or in the backward direction (as compared with the animal's walking direction; this convention is used throughout this paper). Tests with a stationary S10 pattern served as a control. In these controls the ants slightly underestimated the homing distance (mean travel distance 9.5 ± 2.2 m, Fig. 2). A pattern moving at a velocity of $v > 9$ cm$\cdot$s^{-1} in the forward direction led to prolonged travel distances, while backward movement decreased the path lengths. A linear regression analysis resulted in a positive slope for the pattern moving in the forward direction (regression coefficient $r = 0.247$, r different from zero at $P < 0.001$), and a smaller negative slope for the backward movement ($r = -0.134$, $P < 0.05$). The two slopes are also highly significantly different from each other, $P < 0.0001$. In conclusion, the movement of the floor patterns indeed influenced the ant's
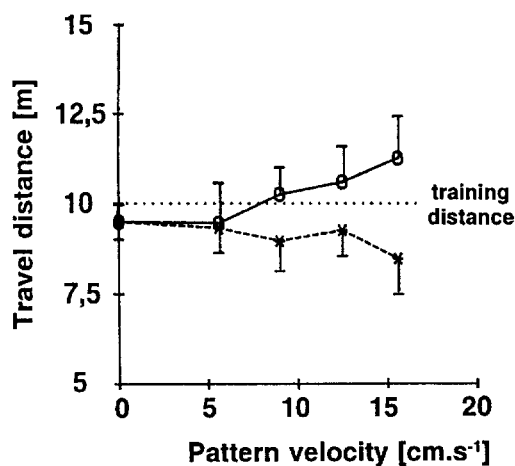

Fig. 2 Pattern movement in the forward direction ($\circ$) leads to increased travel distances, while movement in the opposite direction ($*$) decreases the lengths of the ant's paths. Training pattern: S10, stationary; test pattern: S10, moving. *Abscissa*: pattern velocity; *ordinate*: distance travelled by the ants during their return (homing) runs. *Bars* indicate 99% confidence intervals. Linear regression for both (forward and backward) conditions: $r_1 = 0.247$ ($n = 327$), $r_2 = -0.134$ ($n = 317$); comparison of r_1 and r_2: $z = 4.27$, $P < 0.0001$, Sachs (1984, p. 333). A point to point comparison yields signification differences between the two conditions for pattern speeds > 9 cm$\cdot$s^{-1} ($P < 0.01$; $P < 0.001$ at 15.5 cm$\cdot$s^{-1})

travel distance. However, the effect of pattern movement on the travel distance was smaller than expected if the ants had relied exclusively on the experimentally manipulated optic flow cue. This is especially obvious for pattern movements in the forward direction. In this case the expected travel distance at maximum pattern velocity is 26 m (according to formula (1); mean ant speed 25 cm$\cdot$s^{-1}). In the case of pattern motion in the backward direction the expected value of distance travelled depends on the sum of v_{ant} and $v_{pattern}$. Here, the differences between expected and measured distances are smaller.

$$\text{Distance} = 10 \cdot v_{ant}/(v_{ant} - v_{pattern}) \qquad (1)$$

Since in our experiments the optic flow did not only depend on the velocity (and the direction of movement) of the pattern but also on the walking speed of the ant we checked for a correlation between travel distances and walking speeds of individual ants in individual runs. In the range of $16-40$ cm$\cdot$s^{-1} of the ant's walking speeds there was no significant correlation between the animal's speed of movement and their homing distances (regression coefficients ranging between -0.08 and -0.0153 for different patterns and different movement conditions; all values are not significantly different from zero). Only for runs with very low speed ($v_{ant} < 15$ cm$\cdot$s^{-1}) there was a (weak) trend towards increased travel distances. Such increases were also observed in the stationary (control) condition, and less often with backward movements. Most probably, then, they were not caused by the optic flow component. They could have been caused by an especially bulky load (an unhandy piece of biscuit) which the animals were carrying home in the test channel. Finally, it should be emphasized that in the forward condition ant speeds < 15 cm$\cdot$s^{-1} (with a pattern speed of 15.5 cm$\cdot$s^{-1}) result in directionally inverted optic flow patterns. If the ants relied exclusively on optic flow cues, they should then have turned around and run in the opposite direction. Then, however, the compass direction would have been inverted, and, in fact, the ants never showed this behaviour.

Furthermore, there was no indication of "movement trapping". Such movement trapping should lead to higher or lower walking speeds depending on whether the pattern moved in the forward or backward direction, respectively. If there was any such effect at all, it was neither significant nor in the predicted (but rather in the opposite) direction. Ant walking speeds with pattern S10 (for the stationary, forward and backward condition, pattern velocities 15.5 cm$\cdot$s^{-1}) were 25.2 ± 6.4, 25.4 ± 6.8 and 28.1 ± 6.5 cm$\cdot$s^{-1}, respectively. With pattern P10 the corresponding values were 24.9 ± 7.1, 23.9 ± 8.8 and 23.8 ± 8.1 cm$\cdot$s^{-1}. Results obtained with other patterns (S5, S20, P5, P20) were similar. The ants' mean walking speed was virtually identical for the stationary and forward condition, while in the backward condition there was a tendency

to slightly higher mean walking speeds – which is contrary to the expectation of a movement trapping. In all, however, the ants' mean speed did not differ significantly between tests with stationary patterns and tests with patterns moving in the forward or backward direction (ANOVA, $P > 0.4$).

Pattern wavelength does not influence travel distances

In the intensively studied optomotor responses of flying and walking animals belonging to quite a variety of taxa, *contrast frequency* turned out to be of crucial importance. However, if the animal measured travel distance by self-induced optic flow, reliance on contrast frequency would lead to navigational errors, because contrast frequency (but not image speed) depends on the (generally unknown) spatial structure, or frequency content, of the pattern over which the animal moves. Hence, *image speed* is the parameter to be used (Wehner 1981, 1992; cf. Srinivasan 1992; Srinivasan et al. 1991, 1993). The following experiments are to investigate whether in the mode of behavior considered here, the ant's visual system relies on image speed or on contrast frequency.

Figure 3A shows results of tests with stationary patterns of different spatial wavelengths (training pattern: S10, stationary; test patterns: S5, S10, P10, S20, stationary); Figure 3B shows corresponding data after training on a stationary P10 pattern (test patterns: P5, P10, S10, P20, stationary). Neither the type of pattern nor the spatial wavelength (grain) of the pattern had any significant influence on the ant's travel distances (ANOVA, $P = 0.28$ in Fig. 3A and $P = 0.53$ in Fig. 3B). With the highest pattern velocity available we tested also for effects of pattern wavelength (Fig. 4). Again, travel distance did not depend on pattern wavelength. An ANOVA test reveals a highly significant influence of the direction and velocity of movement

Training pattern: S10, stationary

Test situations:

forward movement   backward movement   stationary

Fig. 4 Tests with moving patterns of different spatial wavelengths (S5, S10, S20, at $v = 15.5$ cm·s^{-1}, forward and backward direction; stationary patterns as control). Analysis of variances reveals a highly significant influence of the direction of movement ($P < 0.0001$), but no significant influence of the type of pattern ($P = 0.12$). The same result was found in tests with random dot patterns (movement: $P < 0.0001$, pattern: $P = 0.54$, data not shown). *Small horizontal bars* indicate standard deviations

($P < 0.0001$), but there was no significant effect of the type of pattern ($P = 0.12$; $P = 0.54$ for the random dot patterns; no significant two-factor interactions).

In Fig. 5 the total number of contrast changes that the ants had experienced during a homebound run, is plotted as a function of the type of the test pattern (S5, S10, S20) and the conditions of movement (stationary, forward, and backward, $v_{pattern} = 15.5$ cm·s^{-1}). The total number of contrast changes was calculated

Fig. 3A, B Results of tests with stationary (grating or random-dot) patterns of different spatial wavelengths. A Training pattern S10, stationary; test patterns S5, S10, P10, and S20, all stationary. B Training pattern P10, stationary; test patterns: P5, P10, S10, and P20, all stationary. All travel distances did not significantly differ from each other (ANOVA $P = 0.28$ in A; $P = 0.53$ in B; number of runs: $n = 28 - 147$ per column). *Small horizontal bars* indicate standard deviations
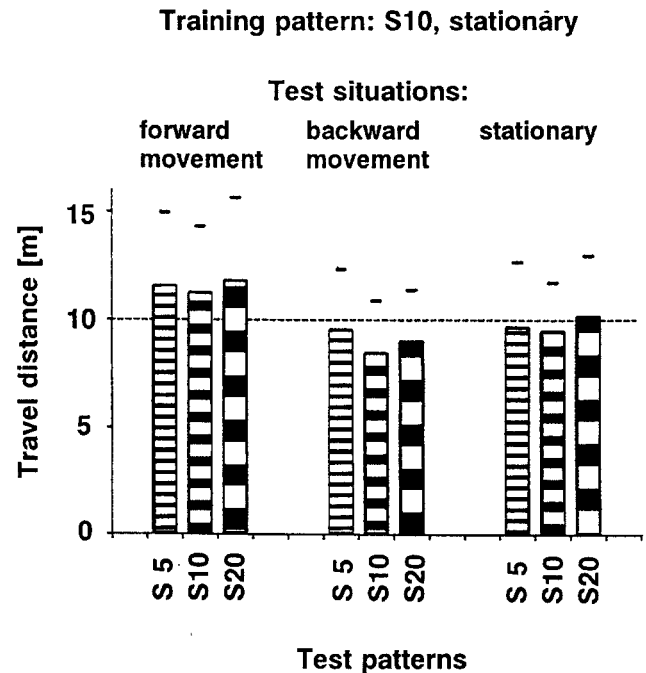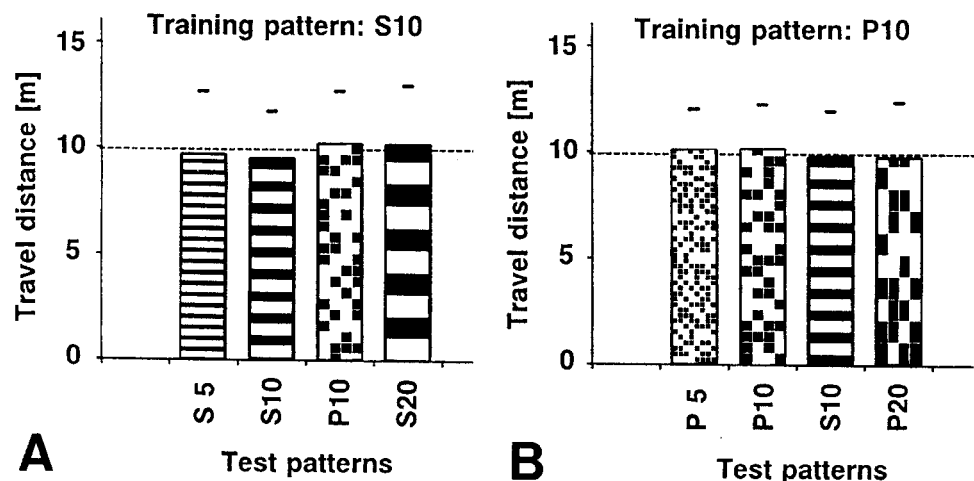

Training pattern: S10

Test patterns

A

Training pattern: P10

Test patterns
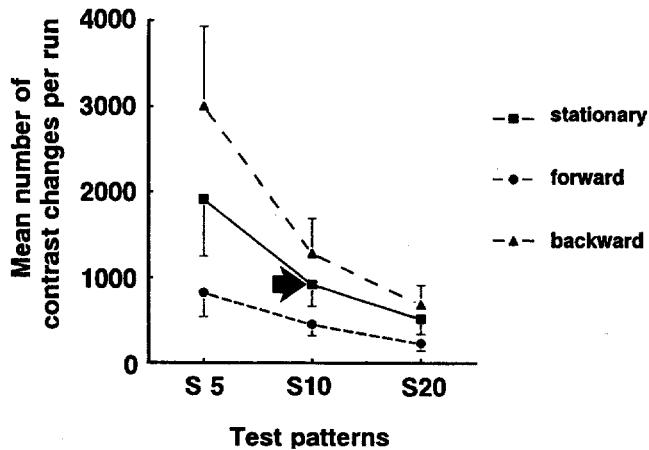
B

Stationary patterns

Fig. 5 Mean number of contrast changes per return run (*ordinate*) for different patterns (*abscissa*) and different movement conditions (*upper curve*: pattern movement ($v = 15.5$ cm·s^{-1}) opposite to the ant's walking direction; *middle curve*: stationary pattern; *lower curve*: pattern movement ($v = 15.5$ cm·s^{-1}) in the ant's walking direction. In all three curves runs with $v_{ant} < 16$ cm·s^{-1} were not included in order to exclude data with a sign reversal of optic flow in case of patterns moving in forward direction. The *arrow* marks the number of contrast changes obtained under control conditions. *Bars* indicate standard deviations that were calculated according to the rules of error propagation from the respective standard deviations of mean distance and mean walking speeds

Fig. 6 Results of tests with stationary (grating or random-dot) patterns, structureless floors, and ants that had the ventral halves of their eyes covered with light-tight paint. The training pattern was always S10. *White column*: 114 runs of more than 10 individuals tested with a white featureless floor. *Black column*: 53 runs of 10 individuals with the ventral halves of their eyes covered. In each individual, eye covers were checked after the tests by microscopic control, in addition, eye covers of five individuals were checked by scanning electron microscopy. The mean return run distances in this experiment were not significantly different (ANOVA, $P > 0.05$) from those observed in ants (without eye covers) that walked over patterned floors (see *left part of histogram*)

from the mean distances travelled and the mean walking speeds of the ants. If the ants, for example, had determined their travel distances by loading a 'counter' for contrast changes during outbound runs, and emptying that counter during homebound runs, in Fig. 5 all points should lie close to the value of the control (S10, stationary, see arrow). In contrast to this expectation, all values (with the exception of one, S5, forward moving pattern) are highly significantly different from the control ($P < 0.001$). There is still another observation supporting the view that image speed rather than contrast frequency is evaluated by the ants. The mean walking speeds in the experiment S5 at $v_{pattern} = 15.5$ cm·s^{-1} and S10, $v_{pattern} = 9$ cm·s^{-1} (both in forward direction) differed slightly and in such a way that the ants experienced exactly the same mean contrast frequencies (18 and 18.2 s^{-1}, respectively). If the ants were guided by the contrast frequencies, the respective homing distances are expected to be equal. The mean travel distances, however, differed significantly (9.87 ± 1.96 and 11.24 ± 3.23, $P < 0.05$).

All these results suggest that it is not the contrast frequency but the speed of the self-induced image motion that influences the homing distance travelled by *C. fortis*.

Are optic flow cues necessary for distance evaluation?

The question phrased above can be answered most straightforwardly by training ants on structured
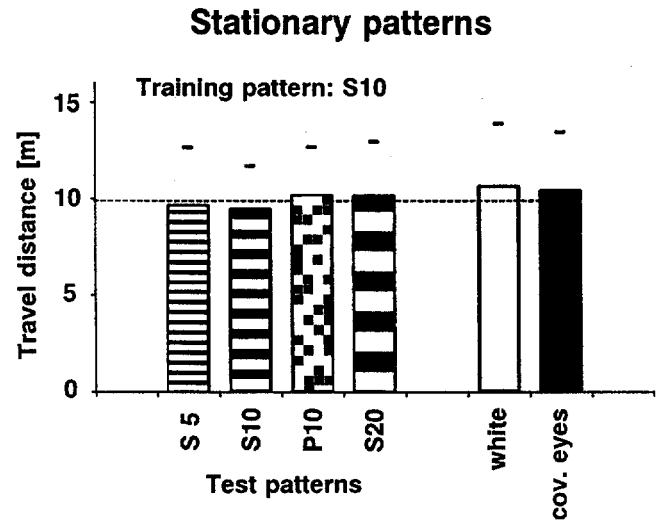
ground (e.g. on S10 or P10), and testing them in a channel that contains a structureless floor (a uniformly white band). As indicated by the white column in Fig. 6, there is a small increase in the distance travelled, as compared with the travel distances obtained above structured ground. But this difference was significant ($P < 0.01$) only after training on S10, not after training on P10 ($P > 0.05$, data not shown in Fig. 6). In an additional experiment ants were trained on a featureless floor and tested on different patterns. Again, there were no significant differences in homing distance between ants walking on structureless or patterned floors. The standard deviations, however, increased significantly in the white band test after training had occurred on pattern S10 or on the white band itself (Bartlett's test for homogeneity of variances $P < 0.001$; $P < 0.01$), but this was not the case after training on P10 ($P > 0.05$). These results show that in spite of a moderate increase in mean travel distance (Fig.6) and an increase in variance, the ants performed rather well in this low contrast condition, and still were able to obtain a reasonable estimate of distance travelled.

In a final experiment, individually marked ants had the ventral half of their eyes covered with light-tight black paint (Wehner and Müller 1985). This treatment prevented the animals from experiencing any ventral flow fields at all. One to two days after the eye covers had been applied, treated ants were found to forage in

the training channel. (A "training pattern" S10 was present but, of course, could not be seen by the experimental animals). After two or three foraging trips the ants were transferred to the test channel as described before. The animals ($N = 10$) which could not see the patterns over which they moved, were still able to assess the appropriate homing distance (black bar in Fig. 6). The mean travel distances did not differ significantly from the controls (ANOVA, $P > 0.05$).

Discussion

The main results presented in this account (Fig. 2 and 4) clearly demonstrate that optic flow parameters influence the ant's estimate of homing distances, and thus can be used by the animals to infer distances travelled. One might feel inclined to conclude from Fig. 2 that estimating distance from measuring self-induced image flow is not fully reliable, because the observed overshoot and undershoot in distances travelled is always smaller than expected. However, due to the artificial test situation this smaller effect should not be too surprising. The pattern that is moved underneath the walking platform covers not the entire ventral visual world of the walking ant. If the animal walks along the midline of the channel (what it usually does), the pattern covers an angular width of ca 135°. It is only within this strip-like region of the ant's ventral hemisphere that the visual flow field of the walking animal was manipulated experimentally. Outside this strip the animal experienced its "uncontaminated", exclusively self-induced image motion (even though we had taken special care that on the walls of the channel there were as few cues available as possible). In addition, the test procedure created yet another situation anomalous to the animal. When the ant while running home inside the channel stopped for a short while, it still experienced the (not self-induced) image motion of the moving belt. Hence, in our experiments the ants were necessarily exposed to somewhat anomalous flow field conditions, both spatially and temporally, and so it is not to be expected from the outset that the distances travelled by the ants fully agree with the ones one would compute from the artificial (external) pattern velocities.

An important result is that distance estimation by flow-field evaluation depends on image speed rather than on temporal contrast frequency (Figs. 3–5). The motion-sensitive mechanism mediating the assessment of distances travelled thus seems to be different from the mechanism involved in the optomotor response. Srinivasan et al. (1991, 1993, see also David 1982) have arrived at the same conclusion for the centering response of flying honeybees.

Of the three hypotheses how animals could measure distances travelled (see Introduction) the energy hypothesis was favoured for a long time, but recently conflicting evidence has accumulated for bees (Goller

and Esch 1990; Esch and Burns 1995), and ants (Schäfer and Wehner 1993). In bees, recent results clearly favour the optic flow hypothesis (Esch and Burns 1995). In ants, the evidence is less clear cut. Although the present results show unequivocally that systematic manipulations of optic flow components consistently influence the distances travelled by the ants (Figs. 2 and 4), the experiments in which the ants walked on a featureless platform or had the ventral halves of their eyes covered (Fig. 6) in addition show that optic flow cues are not the only ones that the ants can exploit. Since additional loads, and thus increased energy expenditure, did not influence travel distances (Schäfer and Wehner 1993), the main hypothesis we are left with is distance estimation based on idiothetic cues. Experiments with spiders (Seyfarth and Barth 1972; Seyfarth et al. 1982) demonstrated that arthropods can assess travel distances exclusively on the basis of such idiothetic information. However, the precision of the homing distances decreased with distance (tested up to 0.7 m), and so one wonders how travel distances could be assessed with the precision actually measured up to distances of 10 meters or more solely on the basis of idiothetic cues. In this context, it is worth mentioning that in our *Cataglyphis* experiments the variances were somewhat larger in the reduced optic flow conditions than in the controls (which could experience self-induced visual flow).

There is yet another possibility worth considering: It is conceivable that the ants are able to use all the three cues mentioned above (or still other cues). In that case the experimental manipulation of only one parameter (either energy expenditure or optic flow fields) could possibly be compensated for by exploiting other cues and using other mechanisms. First and foremost, however, our next step must consist in testing the second hypothesis proposed in the Introduction, i.e. in asking whether the ants use kinesthetic information as their main cue for estimating distances travelled. Next, experiments are wanted in which several parameters can be manipulated simultaneously.

References

David CT (1982) Compensation for height in the control of ground-speed by *Drosophila* in a new, 'barber's pole' wind tunnel. J Comp Physiol 147: 485–493

Esch HE, Burns JE (1995) Honey bees use optic flow to measure the distance of a food source. Naturwissenschaften 82: 38–40

Görner P (1958) Die optische und kinästhetische Orientierung der Trichterspinne *Agelena labyrinthica*. Z Vergl Physiol 41: 111–153

Görner P (1966) Über die Koppelung der optischen und kinästhetis-chen Orientierung bei den Trichterspinnen *Agelena labyrinthica* und *Agelena gracilens*. Z Vergl Physiol 53: 253–276

Götz KG (1964) Optomotorische Untersuchung des visuellen Sy-stems einiger Augenmutanten der Fruchtfliege *Drosophila*. Kybernetik 2: 77–92

Goller F, Esch HE (1990) Waggle dances of honey bees: is distance measured through energy expenditure on outward flight? Naturwissenschaften 77: 594–595

Heran H (1956) Ein Beitrag zur Frage nach der Wahrnehmu-ngsgrundlage der Entfernungsweisung der Bienen. Z Vergl Physiol 38: 168–218

Heran H, Wanke L (1952) Beobachtungen über die Entfernungsmel-dung der Sammelbienen. Z Vergl Physiol 34: 383–393

Kunze P (1961) Untersuchung des Bewegungssehens fixiert fliegen-der Bienen. Z Vergl Physiol 44: 656–684

Mittlelstaedt H, Mittelstaedt ML (1973) Mechanismen der Orien-tierung ohne richtende Außenreize. Fortschr Zool 21: 46–58

Müller M, Wehner R (1988) Path integration in desert ants, *Cata-glyphis fortis*. Proc Natl Acad Sci USA 85: 5287–90

Neese V (1988) Die Entfernungsweisung der Sammelbiene: ein ener-getisches und zugleich sensorisches Problem. Biona Report 6: 1–15

Reichardt W (1969) Movement perception in insects. In: Reichardt W (ed) Processing of optical data by organisms and by machin-es. Acad Press, New York, pp 465–493

Sachs L (1984) Angewandte Statistik. Springer, Berlin

Schäfer M, Wehner R (1993) Loading does not affect measurement of walking distance in desert ants, *Cataglyphis fortis*. Verh Dtsch Zool Ges 86.1. G. Fischer, Stuttgart, p 270

Seyfarth EA, Barth FG (1972) Compound slit sense organs on the spider leg: mechanoreceptors involved in kinesthetic orienta-tion. J Comp Physiol 78: 176–191

Seyfarth EA, Hergenröder R, Ebbes H, Barth FG (1982) Idiothetic orientation of a wandering spider: compensation of detours and estimates of goal distance. Behav Ecol Sociobiol 11: 139–148

Sokal RR, Rohlf FJ (1981) Biometry. Freeman, New York

Srinivasan M (1992) How bees exploit optic flow: behavioural ex-periments and neural models. Phil Trans R Soc Lond B 337: 253–259

Srinivasan M, Lehrer M, Kirchner WH, Zhang SW (1991) Range perception through apparent image speed in freely flying honey-bees. Visual Neuroscience 6: 519–535

Srinivasan M, Zhang SW, Chandrashekaran K (1993) Evidence for two distinct movement-detecting mechanisms in insect vision. Naturwissenschaften 80: 38–41

Wehner R (1981) Spatial vision in arthropods. In: Autrum H (ed) Handbook of sensory physiology, vol VII/6C. Springer, Berlin Heidelberg, New York, pp 287–616

Wehner R (1982) Himmelsnavigation bei Insekten. Neuro-physiologie und Verhalten. Neujahrsbl Naturforsch Ges Zürich 184: 1–132

Wehner R (1992) Homing in arthropods. In: Papi F (ed) Animal homing. Chapman and Hall, London, pp 45–144

Wehner R (1994) The polarization vision project: championing or-ganismic biology. In: Schildberger K, Elsner N (eds) Neural basis of behavioural adaptations. Fortschr Zoologie, vol. 39, G. Fischer, Stuttgart, pp 103–143

Wehner R, Müller M (1985) Does interocular transfer occur in visual navigation by ants? Nature 315: 228–229

Wehner R, Srinivasan M (1981) Searching behaviour of desert ants, Genus *Cataglyphis* (Formicidae, Hymenoptera). J Comp Physiol 142: 315–338

Wehner R, Wehner S (1990) Insect navigation: use of maps or Ariadne's thread? Ethol Ecol Evol 2: 27–48