

View-based navigation in insects: how wood ants (*Formica rufa* L.) look at and are guided by extended landmarks

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Summary

Bees, wasps and ants learn landmarks as views from particular vantage points, storing the retinal positions of landmark edges. By moving so as to minimise the difference between their stored and current view, they can return to the vantage point from which a view was taken. We have examined what wood ants learn about a laterally placed, extended landmark, a wall, while walking parallel to it to reach a feeder and how they use this stored information to guide their path. Manipulation of the height of the wall and the ant's starting distance from it reveals that ants maintain a desired distance from the wall by keeping the image of the top of the wall at a particular retinal elevation. Ants can thus employ image matching both for returning to a place and for following a fixed route.

Unlike many flying insects, an ant's direction of motion while walking is always along its longitudinal body axis and, perhaps for this reason, it favours its frontal retina

for viewing discrete landmarks. We find that ants also use their frontal retina for viewing a laterally placed wall. On a coarse scale, the ant's path along the wall is straight, but on a finer scale it is roughly sinusoidal, allowing the ant to scan the surrounding landscape with its frontal retina. The ant's side-to-side scanning means that the wall is viewed with its frontal retina for phases of the scanning cycle throughout its trajectory. Details of the scanning pattern depend on the scene. Ants scan further to the side that is empty of the wall than to the side containing the wall, and they scan further into the wall side when the wall is of a lower apparent height. We conclude that frontal retina is employed for image storage and for path control.

Key words: view-based navigation, navigation, image matching, wood ant, *Formica rufa*, landmark.

Introduction

Ants, bees and wasps employ visual landmarks both for specifying the position of their nests and feeding sites and for guiding their path along fixed routes between them (Santschi, 1913; Tinbergen, 1932; Baerends, 1941; Rosengren, 1971; Collett et al., 1992; Wehner et al., 1996). When guided by visual landmarks, insects demonstrate an impressive ability to use long-term visual memories for controlling their movements. Current evidence suggests that landmark memories are stored in the form of views of landmarks seen from defined vantage points (Wehner and Raber, 1979; Cartwright and Collett, 1983; Judd and Collett, 1998). An insect can then return to a site corresponding to such a vantage point by moving until it has regained its stored view. Route guidance, on the face of it, poses a rather different problem in which the insect is not aiming at a site, but sticks faithfully to a narrowly defined path (Santschi, 1913; Baerends, 1941; Collett et al., 1992; Wehner et al., 1996). Little is known about the way in which landmarks help specify such a path. Two recent advances have allowed us to examine the details of ants' paths as they follow a landmark-defined route and to elucidate a possible mechanism of path guidance. The processes of

following a route and finding a place turn out to have several elements in common.

The first advance underpinning this study is the finding that two species of ant, *Cataglyphis fortis* (Collett et al., 2001) and *Leptothorax albipennis* (Pratt et al., 2001), will follow a path that is defined by an extended landmark, such as a wall, that can be parallel or at an oblique angle to the ant's path. For *Cataglyphis fortis*, when the barrier was rotated from the training orientation, the ants' paths rotated by approximately the same amount. This result implies that ants' paths can be governed entirely by visual information derived from the wall independently of compass cues and makes it possible to study landmark guidance in isolation, without complications introduced by other navigational mechanisms. We examine here what visual information the wood ant (*Formica rufa*) obtains from a wall when using it for guidance, how the ant might gain this information, and how this information might serve to correct the ants' path. By rotating the wall on every trial and placing the start position and a sucrose reward at constant positions relative to the wall, we have forced ants to rely exclusively on the wall for guidance.

The second advance is technical. A tracking video camera recorded the paths of individual ants as they walked parallel to the wall. This camera gives images of the ant at high magnification over a large (3 m×2.5 m) indoor arena so that not only the ant's position but also the orientation of its long axis can be monitored throughout its path (Fry et al., 2000). Unlike many flying insects that can fly sideways or even backwards, walking ants are limited to moving parallel to their long axis. This constrained pattern of locomotion may be why they place particular emphasis on viewing features with their frontal retina (Judd and Collett, 1998; Nicholson et al., 1999; Fukushi, 2001). We were particularly interested in the way in which ants look at an object to the side of their route, whether they have a pattern of movements that enables them to scan their environment with their frontal retina and, if so, how their scanning pattern and overall path might be controlled by visual features of the wall.

Materials and methods

The ants

Experiments were performed on foragers from queen-right wood ant (*Formica rufa* L.) colonies housed in large plastic tanks within the laboratory. The temperature was a constant 21 °C, and the laboratory was on a 12 h:12 h light:dark cycle. When the colony was not being used for experiments, it was allowed constant access to sucrose solution, and water and frozen crickets were provided every 2–3 days. At the start of training, the colony's only access to food was through the individuals performing the experiment. After a cohort of 3–4 foragers had been selected as experimental subjects, the colony was allowed a reduced ration of sucrose during the 10 or so days of the experiment.

Experimental apparatus and training configurations

Experiments were performed in a 300 cm×250 cm arena surfaced with white Perspex that was roughened to prevent the ants slipping. The arena was surrounded by a Fluon-coated barrier to prevent escape and a 230 cm high curtain to obscure external cues. The arena was lit from above by four fluorescent strip lights. The walls used as landmarks were made from aluminium sheet sprayed black and bent into an L-shape so as to be free-standing. For all experiments except those with a stepped wall, the wall used in training was 20 cm high. Ants were carried from the nest to the arena on a drinking straw and were placed at the starting point on an upturned polystyrene cup, from which they descended to the floor. A drop of sucrose solution was provided on a microscope slide at a distance that was typically 80 cm from the starting point. Ants were trained in two configurations in which the route from the start to the food was parallel to the wall, either at 20 cm or 30 cm from it. In a third configuration, the route was oblique to the wall, starting 20 cm from the wall and ending with the food 30 cm from the wall. In all three cases, the wall, the start and the food were rotated *en bloc* between each training trial. For comparison, we also trained ants in a fourth situation, again

with the start and the food placed 20 cm from the wall but without rotating the wall.

Two-wall experiment

Some ants were trained to a route defined by two walls. The ants' routes ran down the centre of a corridor composed of two walls 20 cm high and 160 cm long and placed 60 cm apart. The end of the corridor towards which the ants headed was blocked off by a semi-circular piece of card of the same height as the walls. Ants started from a polystyrene cup and walked towards sucrose solution on a microscope slide 100 cm away. Between each training trial, the walls were rotated by 80° about the centre of the arena.

Training

In the early stages of training, 20–30 active ants from the colony were placed on top of the start cup with the sucrose-laden microscope slide placed at the finish. The first 10 ants to reach the slide were caught and marked individually with dots of enamel paint. They were then allowed to feed and to return to the start cup, where they were caught again and returned to the nest. Ants typically emerged from the nest mound a few minutes later and were given another training trial with the wall in a new position. After 20–25 runs (2–3 days), the ants' paths followed a direct line from the start cup to the food, regardless of the wall position. Testing began when the ants had performed three straight runs to the food, all of which had been tracked successfully by the camera. During the testing phase, ants were given three rewarded training runs between non-rewarded tests, with the wall rotated between each training or test run. Between runs, the arena surface was wiped down with ethanol to remove possible pheromone cues.

Tracking

During test runs, ants were tracked by a camera placed 3 m above the centre of the arena. The camera (Sony EVI-D30) has movable optics allowing a high-resolution image to be captured of any part of the arena. The camera is controlled by a PC (Pentium II 233 MHz) running customized software (Fry et al., 2000) that maintains the ant at the centre of the camera's visual field and stores the pan and tilt values of the camera at 50 frames s⁻¹. The orientation of the long axis of the ant is also calculated in real time, and the 180° ambiguity is solved by assuming that the ant always walks forwards. Before analysis, the output was converted to arena coordinates and smoothed by taking a moving average with a window size of nine frames. Trajectories were lost on occasions when the ant entered the shadow created by landmarks or if there were additional high-contrast objects in the camera's field of view.

The Cartesian coordinate system used to superimpose trajectories took the start of the wall as the origin and the wall as the *x*-axis. For instance, in the 20 cm condition, the start was at (20,20) and the food was at (100,20). Throughout this paper, we follow this convention, with *x* distance and *y* distance referring to distance along and perpendicular to the wall respectively.

Table 1. Mean headings with mean angular deviation for test conditions with walls of varying heights and start positions

Run conditions		Angular deviation (degrees)						
Wall height (cm)	Starting y distance (cm)	<i>n</i>	<i>N</i>	<i>x</i> distance from start (cm)				
				10	20	30	40	50
40	40	23	9	0.76±21	7.4±19	1.7±16	2.6±13	3.9±11
20	40	17	8	7.6±27	7.6±25	11±14**	12±12**	11±12**
40	20	23	10	-2.6±23	-11±19**	-8.8±16**	-8.9±10**	-8.8±8**
20	20	50	12	6.0±19*	4.3±11**	2.4±8.3*	2.2±7.4*	0.57±6.4

For each trajectory, the angular deviation from a path parallel to the wall is measured at 10 cm intervals.

0° is parallel to the wall; positive angles represent trajectories directed towards the wall and negative angles those directed away from the wall.

Asterisks indicate whether trajectory directions differ significantly from a course parallel to the wall, using the 99%(**) and 95%(*) confidence intervals of the mean (Batschelet, 1981).

N, number of ants; *n*, number of trials.

Finding endpoints

The endpoint of a trajectory was defined as the first major turn that the ant made. This turn was found by heavily smoothing the tracks (moving average, window size 100) and locating the first maximum in a trace of distance from the start, indicating the point at which the ant first turned back. To make sure that the algorithm picked out an event specific to the start of a search process, rather than a characteristic of an ongoing trajectory, it was applied to the middle 50 cm of 48 trajectories recorded from ants on the way to the food during training. The algorithm found endpoints in only eight of these trajectory sections. When applied to 50 control runs in which no food was present, the algorithm found 39 endpoints clustered around the expected position of the food slide (as in Table 2).

Measuring the wavelength and amplitude of path wiggles

On a fine scale, the ants' paths were roughly sinusoidal. The wavelength of each cycle was taken to be twice the average distance between adjacent zero-crossings, where zero-crossings are the points at which individual trajectories crossed the direct line from the start to the goal. To calculate amplitude, the maximum deviation from the line was measured every half-cycle and summed over each cycle. Amplitude is the mean of these cyclical deviations.

Results

Do ants learn the shortest path?

Individual ants were trained to go from a start point to a food site. The two locations were fixed relative to an extended landmark, a wall, that was shifted and rotated from trial to trial so that it provided the only useful directional cue. After an initial training period of 25–30 runs that lasted for 2–3 days, ants shuttled between the start cup and the food, taking a path that was in all cases approximately direct. Three training conditions were used. In two of them, the line between the start and the finish was parallel to the wall (i.e. in the *x* direction) at a distance of either 20 or 30 cm perpendicular to it (i.e. in

the *y* direction). In the third condition, the line was oblique, from a start point 20 cm from the wall to the food at 30 cm from the wall. In all three cases, the start position was 20 cm along the wall and the food position was 100 cm along the wall in the *x* direction. Sample trajectories from one individual trained to each condition are shown in Fig. 1B,D,F together with mean trajectories for each group of ants trained to that condition (Fig. 1A,C,E). During the early stages of training, ants tend to head towards the wall and then stick close to it, leaving the wall when near the food. The mean trajectories of well-trained animals do not depart significantly from the direct line from start to food at any point along the route. Experienced ants take the shortest route whether it is parallel or oblique to the wall. Further analysis of all three conditions showed that the mean deviation from the shortest route is independent of the orientation of the wall within the arena (Fig. 1G). The distribution of atypical trajectories was also homogeneous across wall orientation (Fig. 1H).

How do ants measure and control their distance from the wall?

A simple means of controlling distance from the wall (*y* distance) is to keep the top edge of the wall at the appropriate vertical position on the retina (see also Pratt et al., 2001). According to this hypothesis, ants trained to follow a route 20 cm from a 20 cm high wall keep the top edge of the wall at an elevation of 45°. The path of an ant trained under these conditions and started at 40 cm from a 40 cm high wall should also be parallel to the wall where the retinal elevation of the top of the wall is 45°. However, an ant started at 20 cm from a 40 cm high wall should tend to move out from the wall, and if started 40 cm from a 20 cm wall should head towards the wall. The outcome of testing ants with these conditions is summarised in Fig. 2 and Table 1.

If the apparent height at the start of the path differs from that experienced during training, correction starts immediately, but progresses slowly (Fig. 2A,C). The mean path of ants displaced to a *y* distance of 40 cm from the normal 20 cm high wall is

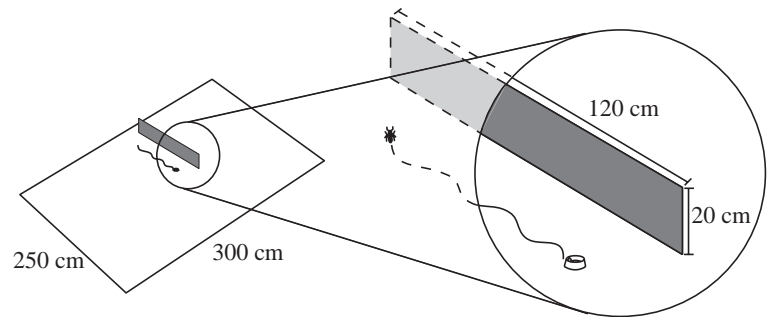
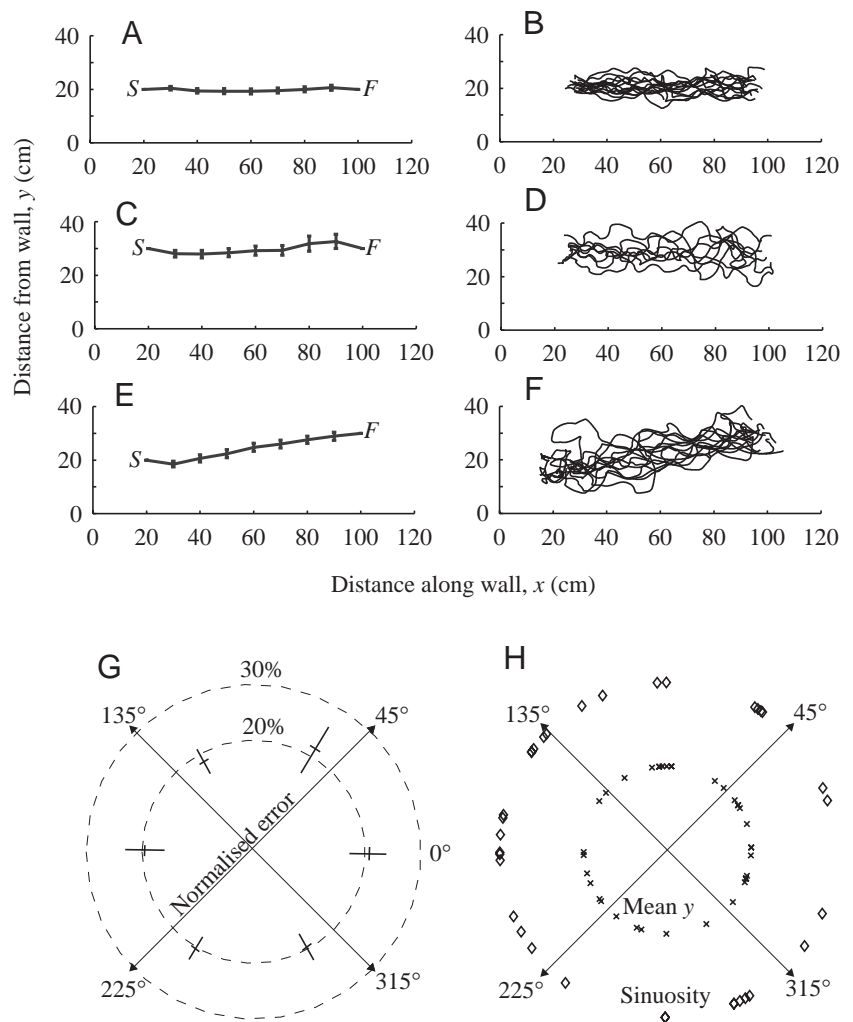


Fig. 1. Routes taken by experienced ants along the wall. Top: sketch of the arena and wall. (A,C,E) Mean path from start (*S*) to food (*F*), with 95% confidence intervals, for the 20 cm, 30 cm and oblique training routes respectively (20 cm route, $n=154$, $N=17$; 30 cm route, $n=65$, $N=6$; oblique route, $n=88$, $N=6$; incompletely recorded paths are excluded. n , number of trajectories; N , number of ants). The mean path was calculated by averaging, over all runs, the perpendicular distance from the wall (y) at 10 cm intervals along the wall (x). (B,D,F) Trajectories from three different ants performing the 20 cm, 30 cm and oblique routes respectively. Data are rotated to align the wall positions. (G) The arena was divided into six sectors, and runs from all conditions were separated into six groups depending on which sector contained the wall. To test whether ants behave uniformly within the arena, we assessed the quality of each run by determining how much each trajectory strayed from the direct route to the goal. This metric, referred to as normalised error, is defined as the mean difference in y value between the actual route and the direct route, normalised by the y value for the direct route. There are no significant differences between the six groups (one-way ANOVA, $F=0.391$, $d.f.=5,286$, $P=0.86$). (H) There is also no significant clustering of bad trajectories. Bad trajectories are defined as those that fall more than 2 s.d. from the mean, for straightness (Sinuosity; outer circle) or mean distance from the wall (Mean y ; inner circle). Neither distribution differed significantly from random (Rayleigh test; mean distance from wall, $r=0.18$, $P>0.3$; straightness, $r=0.18$, $P>0.3$).

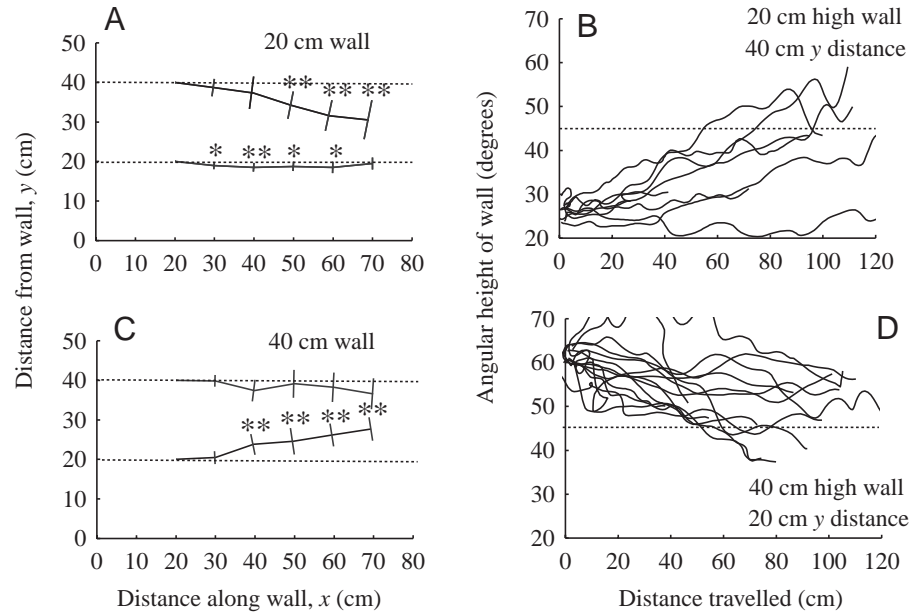


directed towards the wall and differs significantly from the straight-ahead course for all x distances greater than 20 cm. Starting at a y distance of 20 cm from a 40 cm high wall, the mean path heads away from the wall and differs significantly from the parallel course at all x distances along the wall greater than 10 cm. Ants tend to approach the wall when the elevation of the top edge is less than 45° and to veer away from the wall when the elevation is greater than 45° , moving in an appropriate direction to reduce the mismatch between the training and perceived elevation. Compensation for the mismatch (Fig. 2B,D) is rarely complete. Ants trained with a 120 cm long wall were also tested with a longer wall of 155 cm. The ants'

starting position was either 20 cm from a 40 cm wall or 40 cm from a 20 cm high wall. The retinal elevation of the top of the wall *versus* distance travelled for individual runs is plotted in Fig. 2B,D. Ants slowly reduce the 20° discrepancy between the desired and actual elevation. But in only seven out of 21 cases does the elevation reach the 45° experienced in training.

When the vertical elevation of the wall matched that of the training condition, deviations from a parallel course were small. The resultant mean path of ants started at 20 cm y distance from a 20 cm high wall deviates by 1.5 cm at most from a line parallel to the wall. This deviation is, however, significant and comes from a small but consistent bowing of the trajectories towards

Fig. 2. Responses of ants to the angular height of the wall. (A,C) Cumulative plots of mean headings, with 95% confidence intervals, for different wall heights and starting positions. Ants were trained on the 20 cm route with a wall that was 20 cm high and 120 cm long with the food 100 cm in the x direction. They were tested with different starting positions and wall heights. In A, ants were presented with the wall as in training and were released at a point either 20 or 40 cm from the wall. In C, the wall height was increased to 40 cm, and ants were released at 20 or 40 cm from the wall. Asterisks show where the mean path departs significantly ($*P < 0.05$, $**P < 0.005$) from a course parallel to the wall (dashed lines). (B,D) Individual paths plotted in terms of the angular height of the nearest part of the wall to the ant against the ant's distance along the wall. Traces stop at the point where the ant turned back towards the start position. The dotted line at 45° represents the angular height of the wall in the training condition. In B, the wall is 20 cm high, with a start position 40 cm from the wall. In D, the wall is 40 cm high, with a start position 20 cm from the wall.



the wall. When both starting y distance and wall height are set at 40 cm, the mean trajectory does not differ significantly from the parallel course over the first 50 cm. The mean path shows a small kink after 20 cm, which is corrected by 30 cm. After 40 cm, the mean path lies only 1.5 cm from the predicted parallel course. This parallel path suggests that other cues to y distance have at best a small effect on an ant's path. The gradual correction of errors in apparent height (Fig. 2B,D) is likely to occur because of the way that the correction process operates and not because of interference from other cues.

Where do ants look during trajectories?

Earlier studies (Judd and Collett, 1998; Nicholson et al., 1999; Fukushi, 2001) suggested that wood ants tend to look at landmarks with their frontal retina when storing information about the appearance of the landmarks or using them for guidance. Ants need a scanning strategy if they are to view an extended wall with their frontal retina while walking parallel to it. A detailed analysis of the ants' trajectories reveals that their path is sufficiently sinuous to place the wall on their frontal retina approximately 30% of the time. Frequency distributions of where ants look along the wall are shown in Figs 3A,C for the 20 cm and 30 cm training conditions respectively. Ants spend most time looking at a point on the wall approximately 20–30 cm ahead of their current x position. The mean looking points for the 20 and 30 cm conditions are not significantly different (20 cm, 27 ± 6 cm, $N=132$; 30 cm, 28 ± 9 cm, $N=65$; means \pm s.d.; t -test, $t=-0.7$, d.f.=192, $P > 0.4$).

Looking distances of similar lengths for the two conditions arise as a consequence of the ant turning further towards the wall when the route was 30 cm from the wall than when it was 20 cm. It can be seen in Fig. 3B,D that ants trained at 30 cm from the wall spend significantly more time at orientations

further from the straight-ahead course when viewing the wall than do ants trained at 20 cm from the wall (Watson's F -test, $F=13.69$, d.f.=192, $P < 0.001$). We suggest that this increased turning is generated by a scanning system that aims to put large stimuli on the frontal retina. However, the increase in turning is insufficient to equalise the retinal elevation of the top of the wall for the two conditions. At the mean looking points, the retinal elevation for the 20 cm training condition is 36° and that for the 30 cm training condition is 28° .

The conclusion that turning is controlled by what the ant sees on its frontal retina is supported by an asymmetry in the amplitude of the scan to the two sides (Fig. 3B,D). Ants turn significantly further from the direct path when they face away from the wall than when they face towards it. In the 20 cm training condition, this asymmetry occurs in 95 out of 132 runs, and it occurs in 55 out of 65 runs in the 30 cm training condition (binomial test, $P \leq 0.01$ in both cases). These asymmetries and looking patterns are constant along the length of the wall. The same asymmetry (Fig. 3E,F, 56 out of 74 runs, binomial test, $P \leq 0.01$) was found when ants were trained under more natural conditions with the wall always in the same position. However, the distribution of looking distances differed significantly from those of the 20 cm and 30 cm conditions, perhaps because the paths bowed more towards the wall.

Fine structure of trajectories

To analyse these looking patterns further, individual cycles were segmented into four phases (Fig. 4A) on the basis of the ants' looking direction (towards or away from the wall) and turning direction (clockwise or counterclockwise). The mean amplitudes and wavelengths of an average cycle for ants trained at a 20 cm y distance from the wall differed significantly from those of ants trained with a 30 cm y distance

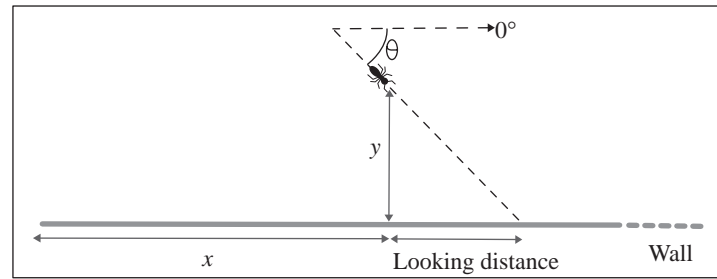
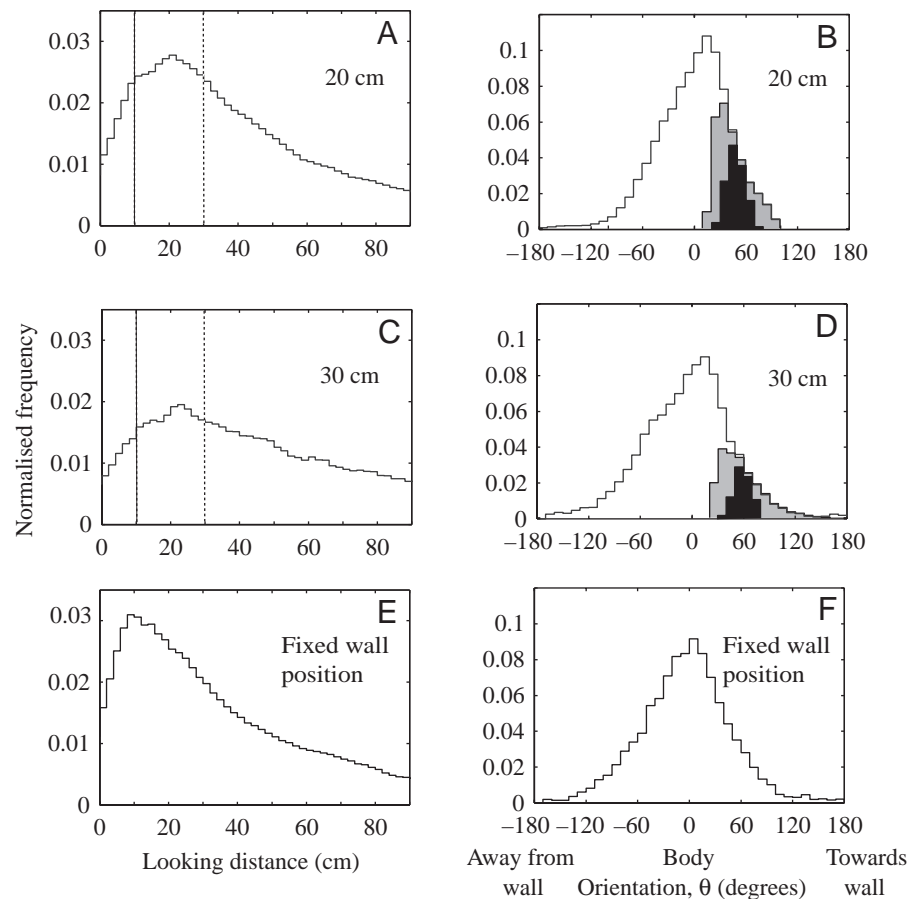


Fig. 3. Looking patterns while travelling along the wall. (A,C,E) Distributions of looking distances, as defined in the top diagram, for ants trained to the 20 cm, 30 cm and fixed routes respectively. Normalised frequency is the number of video frames (frame rate 50 Hz) corresponding to the condition of each bin divided by the total number of frames in the sample. For every 20 ms time step, we calculated the point at which the forward extension of the ant's longitudinal axis intersects the wall. The looking distance is defined as the difference between this intersection point and the current x position of the ant. Bins are 2 cm wide, and the centres of the modal bins are 21 cm for the 20 cm condition, 23 cm for the 30 cm condition and 11 cm for the fixed wall condition. (B,D,F) Distributions of the orientations of body axis for ants in the same conditions as above, again normalised by the total number of frames. At 0° , an ant's longitudinal axis is parallel to the wall and positive angles are clockwise (the ant faces towards the wall). The grey shaded area gives the distribution of orientations for those frames in which the wall is viewed with the frontal retina. The black shaded area gives the subset of this distribution for which looking distance is between 10 and 30 cm (dashed lines on A and C).



from the wall (mean amplitudes, 20 cm, 2.9 ± 2.8 cm, $N=132$; 30 cm, 4.1 ± 4.0 cm, $N=65$; t -test, $t=-2.0$, d.f.=85, $P<0.05$; mean wavelengths, 20 cm, 10.4 ± 4.1 cm; 30 cm, 12.4 ± 5.9 cm; t -test, $t=-2.745$, d.f.=195, $P<0.01$; means \pm s.d.). These differences must be a consequence of the visual input received during the trajectory. If the amplitude of the 'sinusoidal' component of movement is transformed into changes in the apparent height of the wall between the extremes of the sinusoid, the difference between groups ceases to be significant (20 cm, $4.1 \pm 2.7^\circ$, $N=132$; 30 cm, $3.5 \pm 2.3^\circ$, $N=65$; t -test, $t=1.552$, d.f.=179, $P=0.1$; mean \pm s.d.). Ants at 30 cm from the wall deviate more from their straight-ahead course to look at the wall at their favoured point (Fig. 3C), and the amplitude of trajectories in this condition is correspondingly greater. The increased sinuosity in the 30 cm condition is also associated with a slightly reduced velocity along the trajectory

(20 cm, 2.9 ± 0.7 cm s^{-1} , $N=132$; 30 cm, 2.5 ± 0.5 cm s^{-1} , $N=65$; t -test, $t=4.8$, d.f.=168, $P<0.05$; means \pm s.d.).

The asymmetry in the looking patterns (Fig. 3) can be related to the significantly different amplitudes and angular velocities of the four (i-iv) phases of the cycle (Fig. 4D, i versus ii, i versus iii, i versus iv, ii versus iii and ii versus iv all differ in angular velocity, Watson's F -test, $P<0.005$; iii versus iv does not). Ants turn fastest in phase i (rotating clockwise whilst looking away from the wall) and slowest in phase ii (rotating clockwise and looking towards the wall). We suggest that the ant turns to one side until a visual feature that is captured on the frontal retina slows and brings the scan in that direction to a stop. Ants thus turn relatively slowly and less far in the direction of the wall, which increasingly fills their visual field. They turn faster and further when turning away from the wall with no significant visual object to slow them down.

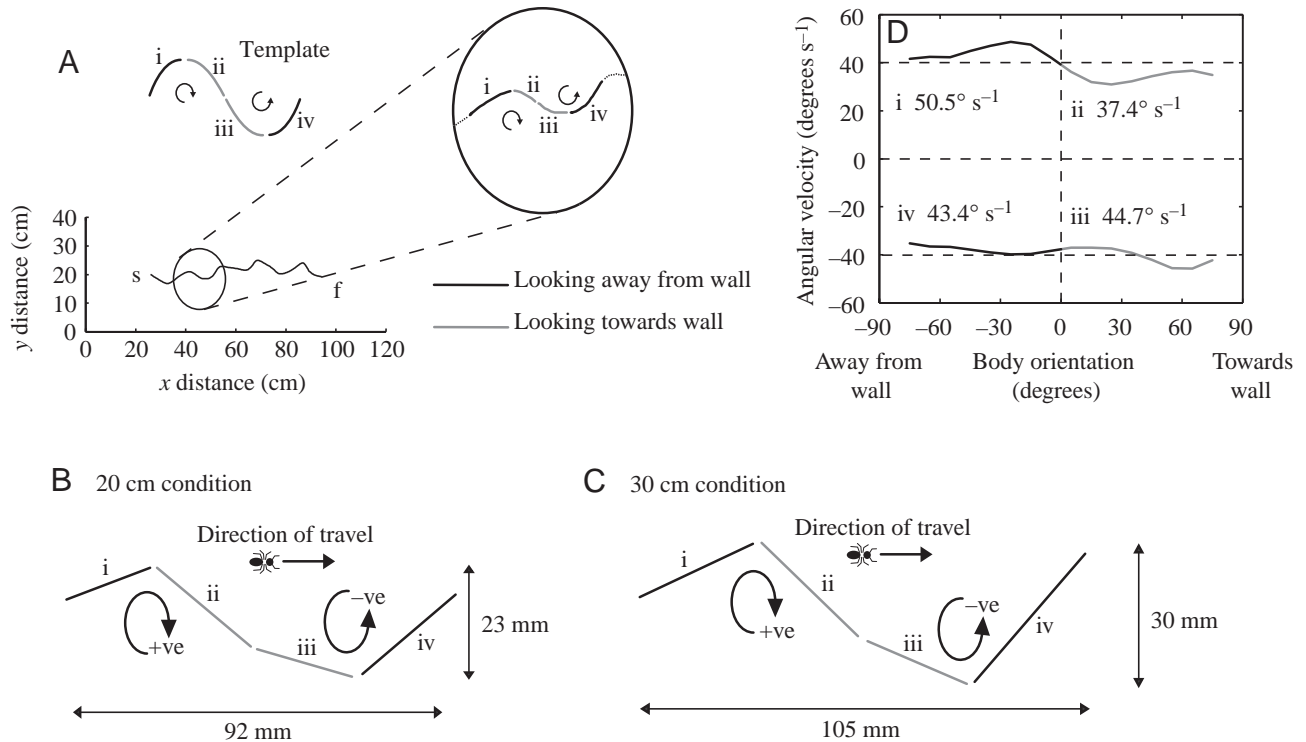


Fig. 4. The fine structure of the ant's wiggly paths. (A) Each cycle of the ants' wiggles was split into quadrants according to the ants' orientation and turning direction. (i) Orientation away from the wall ($-ve$), clockwise turn ($+ve$). (ii) Orientation towards the wall, clockwise turn. (iii) Orientation towards the wall, counterclockwise turn. (iv) Orientation away from the wall, counterclockwise turn. (B,C) The mean distance travelled in each quadrant for the 20 and 30 cm conditions respectively. The large arrow represents the direction of travel. (D) Mean angular velocity in each quadrant plotted against orientation. The data are from 20 cm training routes.

Testing a scanning model of trajectory control

The ant's approximately sinusoidal path and the dependence of the form of the sinusoid on visual input (Fig. 4) led us to test a simple model of course control. According to this model, the ant scans along the wall and learns wall height using its frontal retina at the most extreme position of its scan, when the wall's retinal elevation (for a wall of uniform height) is at a maximum. If the ant is too close to the wall, the learnt elevation will be reached earlier in the scan. If the ant reverses its scan at this point, its trajectory will veer away from the wall, gradually correcting the path over several scanning cycles. Conversely, if the ant is too far from the wall and it scans a little further in the same direction, its overall path will turn towards the wall. The model implies that scanning and correction are a single process that is adjusted by input to the frontal retina. Simulation of the model (Fig. 5A) shows that correction is slow, taking many cycles, corresponding to the ant's behaviour shown in Fig. 2.

To test this model, ants were trained to run down the middle of a 60 cm wide, blindly ending corridor with 20 cm high walls (Fig. 5B). The scanning model predicts that the amplitude of the sinusoid will be smaller when both walls are raised and larger when both walls are lowered. With two walls of equal height, the amplitude of the sinusoid should increase or decrease by the same amount on both sides of the midline, and the ant's path should remain in the middle of the corridor. The

data do not support the model. In tests with trained ants, the walls were either raised to 40 cm or lowered to 15 cm. Neither the amplitude of the sinusoid nor the angles through which the ants turned were altered significantly by these changes to wall height. Fig. 5C–E shows the distributions of orientations at the points where ants finish a scan phase. The distributions have a characteristic bimodal shape with a peak at 0° and another peak at approximately 60° . The peak at 0° may be a consequence of ants paying attention to the semi-circular end segment of the corridor. The position of the second peak does not vary significantly across conditions and certainly does not match the prediction of the scanning model (shown on the distributions as a grey bar).

Where along the wall is height measured?

Throughout their trajectory, ants scan the wall ahead with their frontal retina. Is wall height measured continuously during this cycle or are measurements restricted to particular phases? We have approached this question with a test situation in which the height of the first part of the wall matched the training condition, but the second part was higher than the ants expected. We could then assess how far in advance the ants responded to the unexpected increase in height. Two situations were used. In the first, ants were trained with a wall of uniform height (20 cm) and tested with a wall that was stepped to 40 cm in height after 60 cm (Fig. 6A). Fig. 6B shows mean

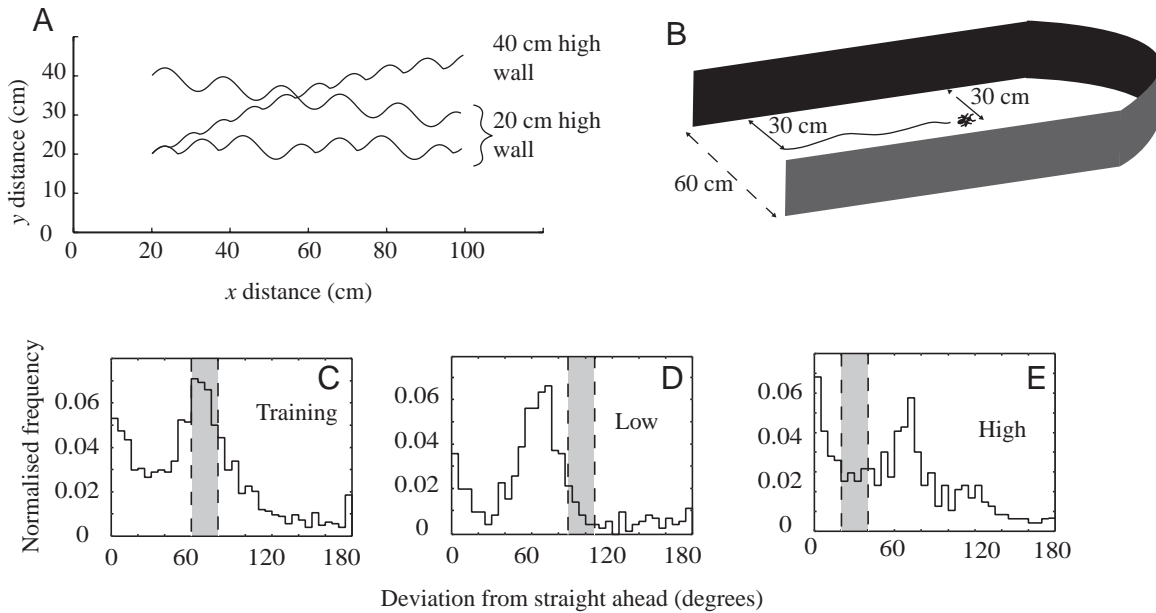


Fig. 5. A model of correction. (A) Model trajectories were generated with a sine function scaled to approximate the characteristics of real trajectories. The tangent to the curve gives the orientation of the model ant, and the apparent height of the wall is defined as the vertical angle subtended by the portion of the wall that is viewed by the frontal retina of the model ant. The clockwise scanning phase, during which the ant turns towards the wall, ends when the apparent height of the wall reaches the stored value, and the counterclockwise scanning phase ends at a set angle. With training conditions, a starting y distance of 20 cm from a 20 cm high wall, the trajectory is parallel to the wall. With a 40 cm high wall and a starting y distance of 20 cm, the view on the frontal retina matches the required retinal height at a reduced deviation from the straight-ahead direction. Since rotation in the counterclockwise phase is unchanged, the trajectory veers away from the wall. Conversely, with a 40 cm y distance from a 20 cm high wall, the model ant rotates further towards the wall to match retinal height, and its course veers towards the wall. (B) The scanning model was tested in experiments in which ants were guided along the middle of a 60 cm wide channel by two 20 cm high walls. (C–E) Plots of the orientation at the end of each scan cycle for the training wall and the low (15 cm) and high (40 cm) test walls. The shaded areas in D and E indicate the predicted mode for the distribution based on the scan model and on the mode of the distribution for training runs in C.

Table 2. Mean length of trajectory with potential stopping cues in conflict

	Predicted trajectory length (cm) using			n	N	Endpoints	Measured trajectory length (cm)
	Idiothetic cues	Room cues	Wall cues				
Control	80	80	80	31	13	24	81.8±13.8
Distance <i>versus</i> visual cues	80	115	115	19	6	15	117±21.6**
	80	45	45	15	6	12	56.9±6.66**
Room cues <i>versus</i> wall cues	80	45	80	22	6	17	61.44±22.3**
	80	80	45	21	10	14	64.6±9.27**
	80	115	80	16	4	7	94.2±27.0**
	80	80	115	17	6	15	84.8±19.1

Columns 2–4 give predicted stopping distance for each of the three potential cues.

n is the number of recorded trials and N is the number of ants tested.

Stopping points from each condition are tested for significance against the control group using a two-tailed t -test (** $P < 0.005$).

Idiothetic, room and wall cues all contribute to the position of the endpoint.

Measured stopping distance is given as the mean±s.d.

trajectories for test and training runs. The means of the difference between each individual's test and training runs are shown in Fig. 6C. Test and training runs have diverged by the time the ant has walked 40 cm in the x direction: i.e. 20 cm

before the increase in wall height. In the second situation, ants were trained with a wall that was stepped in height from 20 to 40 cm at 100 cm and then tested with a wall of a constant 40 cm height (Fig. 6D). The second portion of the test wall again gave

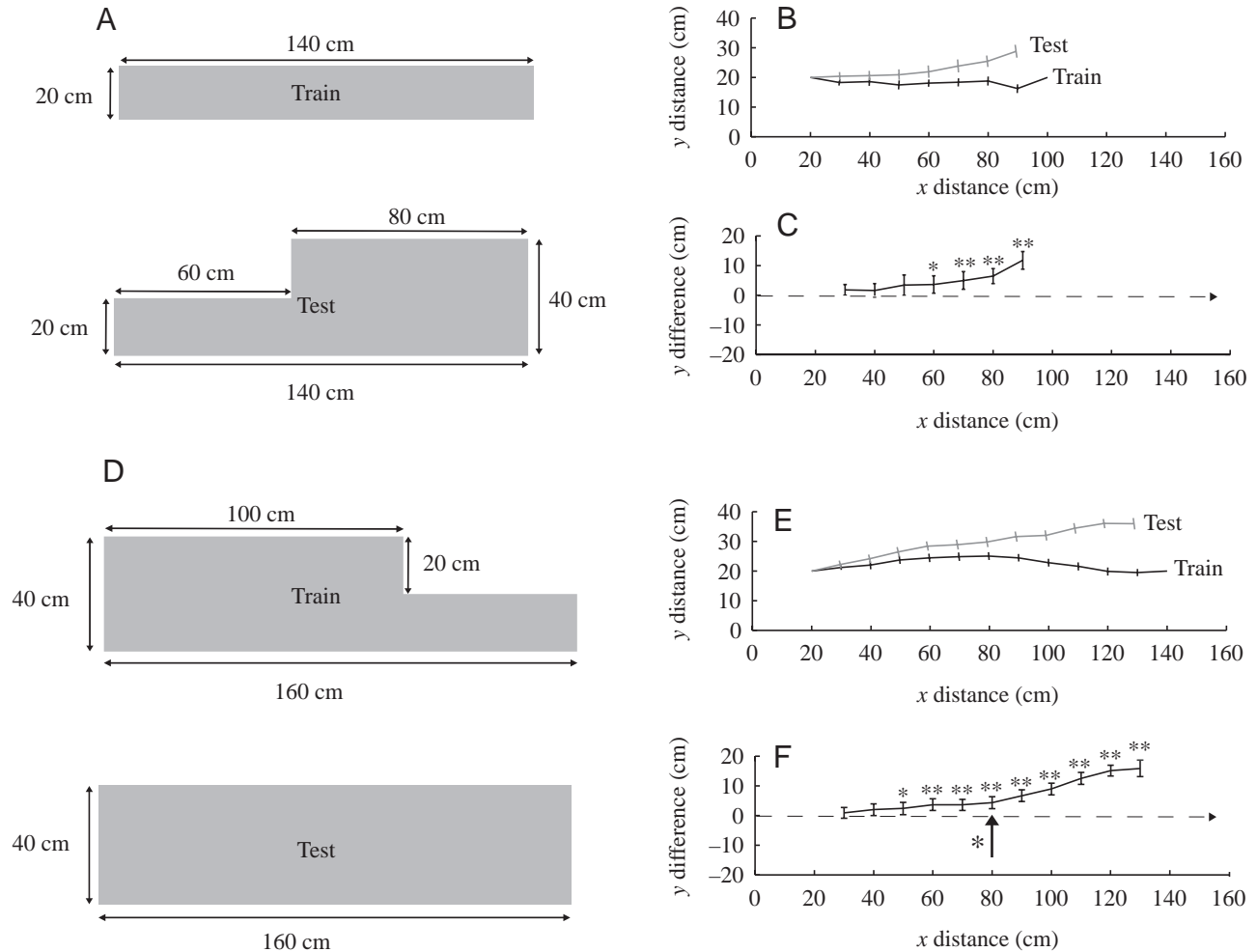


Fig. 6. Responses to stepped walls. (A) The dimensions of the training and test walls from an experiment in which ants were trained to a 20 cm high wall and tested with a stepped wall. (B) Plots of mean headings during training (black lines) and under test conditions (grey lines). (C) Mean differences between test runs and training runs. Each test run is paired with the previous training run from the same ant. Error bars show the 95% confidence interval of the mean. The significance of these differences is calculated using a two-tailed t -test, tested against zero. Significant results are highlighted on the graph; ** $P < 0.005$, * $P < 0.05$. Means are calculated from 22 test and 22 control paths from five ants. (D) In a second experiment, ants were trained to a stepped wall that began at a height of 40 cm and dropped to a height of 20 cm after 100 cm, and they were tested with a uniform 40 cm high wall. (E) Mean trajectories from test and training runs in this condition, and (F) mean difference between a test run and the previous training run by that individual. Means are calculated from 55 test and 55 control paths from seven ants. The arrow in F indicates the only point where the gradients of adjacent sections are significantly different (t -test, $t = 2.4$, d.f. = 108, $P < 0.05$).

an increased retinal elevation in comparison with the training wall. The training and test trajectories diverge from the start and are significantly different after 30 cm, even though the step in the wall is still 50 cm ahead of the ant's current position. This early response suggests that ants either integrate signals from the frontal retina over the entire scanning cycle or measure wall height over a large area of the retina. Weak evidence that the frontal retina may dominate in measuring wall height comes from the increase in the rate of divergence between training and test trajectories 20 cm before the two walls differ in height (Fig. 6F), a distance that matches the position of the peak in the distribution of looking distances (Fig. 3).

What sets trajectory endpoints?

When ants are tested in a cleaned arena with no food present, their trajectories stop at the expected food site (Table 2; Fig. 7A,B). The stopping point could be controlled by visual cues from the wall or from other parts of the room or by self-generated idiothetic cues. One likely cue from the wall is the vertical edge at the food end. Since the rotation of the wall marks out an annulus in the centre of the area, the lighting array and the surrounding curtains may also provide a rough indication of the position of the food site. Ants could also learn the distance that they travel between the start and food from proprioceptive signals or monitors of their motor output (Ronacher et al., 2000) provided that they can abstract distance

across training trials in which trajectory direction is constantly changing.

Table 2 summarises the data from tests in which the signals from different stopping cues conflicted. In all conditions, the ants set a course parallel to the wall and maintained it until search behaviour began (e.g. Fig. 7E).

Visual cues versus distance cues

Ants were tested with walls that were 155 and 85 cm long (approximately 130 and 70% of the length of the training wall). Walls were placed in the arena so that the endpoints specified by the end of the wall and by room cues coincided. In both cases, the mean length of the trajectory differed significantly from the 80 cm travelled in training (mean \pm s.d.; 85 cm wall, 56.9 \pm 6.66 cm; 155 cm wall, 117 \pm 21.6 cm). The stopping points for the longer wall (Fig. 7D) cluster around the endpoint set by visual cues. With the 85 cm wall (Fig. 7C), ants stop significantly earlier than the normal 80 cm distance (Table 2), but their paths are significantly longer than the 45 cm predicted by visual cues (t -test, $t=6.7$, d.f.=11, $P<0.005$).

What is the visual cue?

Table 2 shows that both room cues and wall cues are significant, but the results cannot be summarised neatly. If one of the cues is set at 80 cm and the other at 45 cm, ants stop at an intermediate value, whether room or wall cues signal the longer distance. The results are less clear if one cue is set at 80 cm and the other set beyond the normal distance at 115 cm. When wall cues predict 115 cm and room cues 80 cm, the mean endpoint is approximately 80 cm, but the scatter is large. Some trajectories stop transiently at approximately 80 cm and then continue parallel to the wall until the end, without any searching. When room cues are set to 115 cm and the wall set to 80 cm, ants mostly continue beyond the wall, again without searching. Table 2 gives the mean

value for the seven out of a total of 16 trajectories for which endpoints could be measured. For this subset of trajectories, room cues seem to dominate wall cues in controlling stopping.

In conclusion, we see that room cues, wall cues and idiothetic cues all have a role in determining endpoints. Visual cues override idiothetic cues when the wall and room cues coincide in indicating a distance longer than 80 cm. However, ants are reluctant to stop before they have walked 80 cm and overshoot the 45 cm set by both visual cues. This result indicates that ants can abstract the distance that they travel in the absence of compass cues. It was surprising to find that room cues are as significant as the closer and seemingly better-defined wall cues.

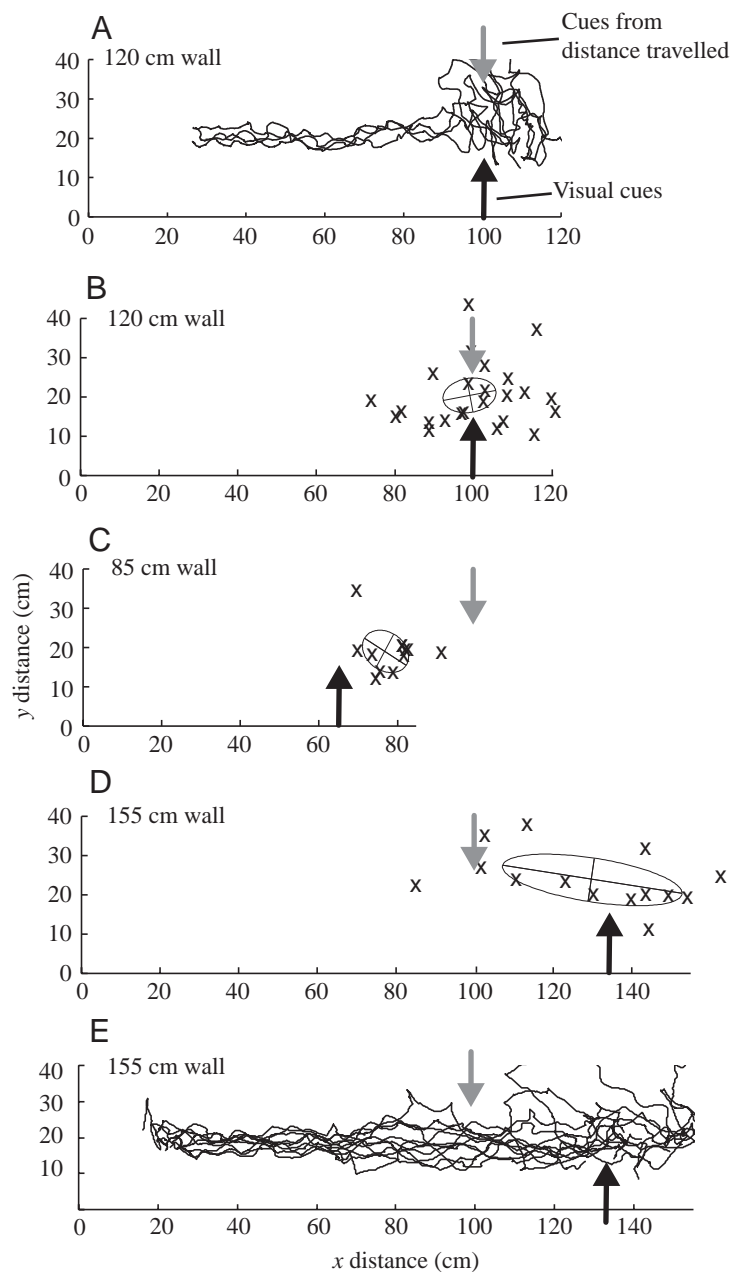


Fig. 7. Stopping points. (A) Example trajectories from the control condition with no food present (food in training is 100 cm along the wall). (B–D) Stopping points from individual runs with walls of different length. The stopping point of a trajectory is taken as the point where the ant turns through more than 90° and heads back towards the start position (see Materials and methods). (B) Control condition with same wall length as in training, (C,D) Tests with an 85 cm long wall and a 155 cm long wall, respectively, putting visual cues and cues from distance walked into conflict. Individual stopping points are shown as crosses. Mean stopping points are shown by the intersection of the major and minor axes of the 95% confidence ellipse of the mean. Large arrows show the predicted stopping points along the x dimension (the predicted stopping points for visual cues are indicated by black arrows, the predicted stopping points for cues from distance walked by grey arrows). (E) Example trajectories from the 155 cm length wall condition. Trajectories remain at 20 cm from the wall until the start of search behaviour.

Discussion

Ants can learn to follow an arbitrary path that is parallel or at an oblique angle to an extended wall. They control their path by learning the retinal elevation of the top of the wall and adjusting their distance from the wall to keep the wall at the learnt elevation. The fact that the path remains parallel to the wall when the wall is extended beyond its usual length (Fig. 7E) implies that the retinal information guiding the ant's path does not depend only on cues supplied by the end of the wall. Ants also rely on visual information extracted along the length of the wall. The ant's ability to take an oblique path relative to a wall of uniform height (Fig. 1F), or a parallel path along a stepped wall (Fig. 6), suggests that the ant stores several elevations and recalls the appropriate one according to its position along the route (see Judd and Collett, 1998). Ants are thus guided by remembered views of landmarks, whether the landmarks are used to guide the search for a goal (Wehner et al., 1996) or, as here, to specify a route.

Since ants always move parallel to their long axis (unlike flying bees and wasps), they can change their direction of motion only by turning. Consequently, if ants relied on the lateral retina for wall-following and moved in a straight line, the wall's position on their retina would change whenever the ant corrected its path – not a good recipe for a stable control system. One consequence of the ant's approximately sinusoidal track (Fig. 4) is that, for some part of the scanning cycle, the important part of the scene is guaranteed to be picked up by frontal retina.

We tested a simple scanning model of trajectory control in which the scan to one side ended when frontal retina encountered a part of the wall that subtended a desired retinal height. The suggestion was that this desired value is set when learning the route and that the value may be the outcome of two opposing tendencies: (i) the ant turning to maximise the informational content on its frontal retina and (ii) the ant's increasing tendency to reverse the direction of the scan as its orientation deviates further from its direct path. The ant would then turn further than usual if the wall were lower than expected and less far if it were higher. Visual control of the scan could then automatically correct the path. The greater turning amplitude found when the ant was trained at 30 cm rather than at 20 cm from the wall fits this model. However, in the two-wall experiment, raising or lowering the wall from the training value did not influence the amplitude of the scan. Consequently, a model that combines scanning and correction into one process must be rejected. Instead, the

data suggest that the result of a mismatch between stored and perceived elevation causes the overall direction of the trajectory to shift. Separating the detection and correction of errors is possibly a more versatile way of using the variety of discrete and extended landmarks that may be encountered along a route. In this case, the gradual correction that is seen in Fig. 2 may be a consequence of an in-built preference to take a straight path, and it may prevent the ant from making large changes in direction that might cause a discrete landmark to fall outside the range of its scanning movements.

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References

- Baerends, G. P. (1941) Fortpflanzungsverhalten und Orientierung der Grabwespe *Ammophila campestris* Jur. *Tijdschr. Entomol.* **84**, 68–275.
- Batschelet, E. (1981). *Circular Statistics in Biology*. London: Academic Press.
- Cartwright, B. A. and Collett, T. S. (1983). Landmark learning in bees: experiments and models. *J. Comp. Physiol.* **151**, 521–543.
- Collett, T. S., Collett, M. and Wehner, R. (2001). The guidance of desert ants by extended landmarks. *J. Exp. Biol.* **204**, 1635–1639.
- Collett, T. S., Dillmann, E., Giger, A. and Wehner, R. (1992). Visual landmarks and route following in desert ants. *J. Comp. Physiol. A* **170**, 435–442.
- Fry, S. N., Bichsel, M., Muller, P. and Robert, D. (2000). Tracking of flying insects using pan-tilt cameras. *J. Neurosci. Meth.* **101**, 59–67.
- Fukushi, T. (2001). Homing in wood ants, *Formica japonica*: use of the skyline panorama. *J. Exp. Biol.* **204**, 2063–2072.
- Judd, P. D. and Collett, T. S. (1998). Multiple stored views and landmark guidance in ants. *Nature* **39**, 710–714.
- Nicholson, D. J., Judd, P. D., Cartwright, B. A. and Collett, T. S. (1999). Learning walks and landmark guidance in wood ants (*Formica rufa*). *J. Exp. Biol.* **202**, 1831–1838.
- Pratt, S., Brooks, S. E. and Franks, N. F. (2001). The use of edges in visual navigation by the ant *Leptothorax albipennis*. *Ethology* **107**, 1125–1136.
- Ronacher, B., Gallizzi, K., Wohlgenuth, S. and Wehner, R. (2000). Lateral optic flow does not influence distance estimation in the desert ant *Cataglyphis fortis*. *J. Exp. Biol.* **203**, 1113–1121.
- Rosengren, R. (1971). Route fidelity, visual memory and recruitment behaviour in foraging wood ants of genus *Formica* (Hymenoptera, Formicidae). *Acta Zool. Fenn.* **133**, 1–106.
- Santschi, F. (1913). Comment s'orientent les fourmis. *Rev. Suisse Zool.* **21**, 347–425.
- Tinbergen, N. (1932). Über die Orientierung des Bienenwolfes (*Philanthus triangulum* Fabr.). *Z. Vergl. Physiol.* **16**, 305–334.
- Wehner, R., Michel, B. and Antonsen, P. (1996). Visual navigation in insects: coupling of egocentric and geocentric information. *J. Exp. Biol.* **199**, 129–140.
- Wehner, R. and Raber, F. (1979). Visual spatial memory in desert ants. *Cataglyphis bicolor* (Hymenoptera: Formicidae). *Experientia* **35**, 1569–1571.