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The Use of Edges in Visual Navigation by the Ant *Leptothorax albipennis*

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Abstract

Certain navigating insects home in on their goal by moving so that currently viewed images of landmarks fall on the same retinal locations memorized during previous visits. Here we show that ants can use similar retinotopic learning to guide lengthy routes, by memorizing and walking parallel to a distinct visual edge. We induced workers of the ant *Leptothorax albipennis* to travel parallel to a prominent wall. When the wall's height was changed, the ants' paths consistently shifted toward a lowered wall and away from a raised wall, as would be expected if they attempt to keep the wall's image at a constant retinal position. These path shifts were smaller than would be expected if the wall was the only guide to navigation, suggesting that other cues are also important. Significantly larger shifts were seen when edge guidance was enhanced by using two walls, one on each side of the path.

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Introduction

Many insects are adept navigators, repeatedly travelling routes thousands of times their own body length to arrive at a pinpoint goal (Collett & Zeil 1998). These performances rely in part on visual landmarks. Abundant experimental evidence suggests that insects near the goal recall retinotopically learned images of local landmarks, moving so that currently viewed images fall on the same retinal locations memorized during previous visits (Wehner & R aber 1979; Cartwright & Collett 1983; Collett 1992; Collett 1996). It is less clear how insects use landmarks when traversing the long routes between destinations. Memorization of local views clearly plays a role, and evidence has been found for several strategies.

These include: (1) detouring in a preferred direction around a landmark (Collett et al. 1992); (2) memorizing retinotopic images of a series of objects along the path (Chaméron et al. 1998; Judd & Collett 1998); and (3) associating a given landmark with a particular trajectory (Collett et al. 1998).

Another possible strategy is to use retinotopic learning to follow a route parallel to a prominent visual edge. If a tree line, a fallen branch, or a similar edge lies alongside all or part of the path from nest to goal, then the insect could plot a parallel course simply by holding the edge's image at a constant retinal position. Longer journeys could be assembled out of several segments, each one guided by its own edge. Foraging bees and wasps have long been known to follow tree lines to reach a nest or feeding station (Collett & Zeil 1997), but the underlying mechanism has not been analysed. We undertook to discover whether retinotopic learning underlies similar edge-following during colony emigration by the ant *Leptothorax albipennis*.

Most studies of orientation by social insects have examined foraging, but emigration similarly requires repeated journeys between precise destinations. In *L. albipennis*, a given emigration is carried out by a subset of ants making up 15–50% of the worker population (S. C. Pratt, unpubl. data). These ants either discover the new nest independently on exploration trips, or are recruited to it by successful scouts. Once they have evaluated the nest and found it suitable, the active ants repeatedly travel between the old and new nests, carrying the bulk of the colony to its new home. On average, each transporter makes five to ten round trips, with a few especially active ants making 15 or more (Mallon et al. 2001).

Little is known about how the ants navigate on these journeys. Foragers of other *Leptothorax* species use individual-specific pheromone trails to guide themselves along previously travelled routes (Maschwitz et al. 1986; Aron et al. 1988). Evidence for visual orientation has been found in foraging workers of *L. unifasciatus*, which can be trained to orient with respect to an artificial light source (Aron et al. 1988). In laboratory emigrations of *L. albipennis*, we noted that transporters often follow routes parallel to the walls of the experimental arena. The ants remain several centimetres from the wall, ruling out tactile guidance. We tested the hypothesis that they instead use visual cues to maintain a constant distance from the wall.

Methods

We conducted two experiments. In the first, ants were induced to emigrate such that their paths ran parallel to a prominent wall. Midway through the move, the wall was replaced by one of a different height, creating the visual illusion that it was now closer or farther away. The second experiment was similar, except that the emigration route passed between two parallel walls of different height. Midway through the move, the walls were switched, so that one now appeared closer and the other farther away. In both experiments, we compared paths taken by the ants before and after the switch, to determine whether they shifted location so as to restore their original view of the walls.

Emigration Along a Single Wall

Colonies of *Leptothorax albipennis*, each with 150–300 workers, were collected in Oct. 1999 at Portland Bill in the United Kingdom (50°32' N, 2°27' W). In the laboratory, ants were housed in artificial nests consisting of thin cardboard strips sandwiched between microscope slides (75 × 50 mm). A hole cut in the centre of the cardboard provided a nest cavity similar to the thin rock crevices these ants normally inhabit.

Experiments were conducted in a circular arena 1 m in diameter and 40 cm high, designed to present a minimum of visual landmarks (Fig. 1). The arena walls were constructed of translucent white Plexiglas, and the base of transparent Plexiglas underlain with white poster board. The arena was centred immediately below a fluorescent ceiling lamp to eliminate light gradients to the left or right. A single wall, 84 cm long and either 5 or 20 cm high, ran parallel to and 20 cm away from the axis linking the centres of the old and new nests. The wall was free-standing and supported by 3-cm braces at either end, so that it could be swiftly removed and replaced. Accurate placement of the walls was achieved with the help of a faint grid of 2-cm squares drawn on the poster board underlying the arena floor. This grid also guided placement of the old and new nests in each emigration, to ensure consistent positioning across replicates.

Emigrations were provoked by removing the top slide of the nest. An intact new nest was provided nearby, and made more attractive by moistening the

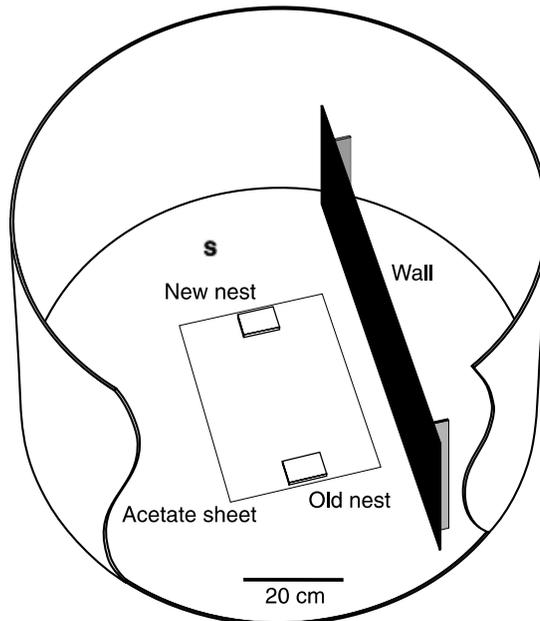


Fig. 1: Experimental arena. The side is partially cut away to show the old and new nests, the wall provided as a landmark, and the acetate sheets used to control for pheromone deposition

cardboard and darkening the interior with a cover of red acetate. The move began once scouts discovered the new nest and recruited nestmates to it. In pilot runs, recruitment was greatly retarded in comparison with previously observed emigrations in visually richer surroundings. To hasten the process, the new nest was at first placed only 4 cm from the old nest, where it was rapidly discovered. After two successful recruitments, the new nest was moved back a further 4 cm. After two more recruitments, it was shifted another 4 cm, and so on, until the distance between the nests had reached 30 cm.

Mapping of the paths taken by emigrating ants began immediately after the nests reached their final separation. One ant at a time was observed and her path traced on a sheet of paper marked with a smaller-scale version of the grid squares on the arena floor. 24 paths were traced before and after the walls were switched. Paths were traced only for ants carrying brood or nestmates from the old nest to the new. Unladen ants leaving either nest were not necessarily participating in the emigration; hence it could not be assumed that they were navigating from one nest to the other.

Because the ants may navigate in part through pheromone trails, steps were taken to eliminate trails laid before the walls were switched. At the start of the experiment, sheets of clear acetate film were placed on the floor of the arena, between the old nest and the final location of the new nest. When the walls were switched, the sheets were removed, so that trails laid in the first part of the emigration could not guide the ants along their old path, potentially overriding any effects of the changed visual scene. After removing the sheets, we waited until a transporting ant successfully travelled all the way from the old to the new nest before tracing any new paths. This typically occurred about 15 min after removal of the sheets.

We did not mark ants individually, because the large size of the arena kept the observer at too great a distance to detect marks on these small ants. As a result, paths could not be treated as independent data points, because any single ant may have been observed more than once in each sample. We instead compared the mean path positions before and after the landmark change. Each of nine colonies received two treatments, one in which the high wall was presented first, and one in which the low wall was presented first. Under the edge-following hypothesis, paths should shift toward the wall in the first treatment, and away from the wall in the second treatment. We used the binomial distribution to calculate the probability of the observed pattern of shift directions, under the null hypothesis that shift directions were randomly distributed across treatments. All other conditions were identical in the two treatments, allowing them to serve as controls for one another.

For each emigration, we also assayed the variation among paths by measuring the width of the zone in which the paths lay. This width was estimated as the interquartile range of path locations. Unless otherwise noted, path locations and path widths were measured at the midpoint between the nests. All values are reported as mean \pm SD.

Emigration Between Two Walls

Methods were identical to those for the one-wall experiment, except that two walls of different height lay on either side of the nest axis, parallel to it and 20 cm away. The walls were exchanged halfway through the emigration, and the mean positions of the ants' paths before and after the switch were compared. The left-right arrangement of the walls was randomized to account for any directional biases of the ants. We used the same nine colonies tested in the one-wall experiment, plus a tenth colony added to achieve an equal number of replicates in each of the left-right arrangements. To determine whether changing two walls provokes a larger path shift than changing only one wall, a paired t-test compared the mean shift to that observed in the first experiment. To provide a control datum for the tenth colony, we induced it to make one additional emigration along a single wall, using the same methods described above for the one-wall experiment.

Results

Emigration Along a Single Wall

Once an emigration was well under way, the paths of transporting ants extended quite directly from the old to the new nest. Paths were by no means identical, but they were restricted to a relatively narrow zone (Mean path zone width: 4.7 ± 1.4 cm). Ants walked well away from the wall (Mean distance: 21.2 ± 1.2 cm), and few if any of them touched it during the journey.

The ants' behaviour changed noticeably when the wall was replaced and the acetate sheets on the floor were removed. At first the ants appeared confused, walking in winding paths over the arena floor between the nests. Within 15 min, however, they re-established routes to the new nest and continued transporting as before. The new paths were fairly direct, but they showed a consistent shift away from their former locations. In every case ($n = 9$), the mean path positions moved toward a lowered wall, and in every case but one, they moved away from a raised wall (Fig. 2). These are the deviations expected if the ants attempt to bring the image of the wall's edge closer to the retinal position it projected when they first learned the route.

An alternative explanation is that the ants always prefer to walk closer to a low wall and farther from a high one, without regard to retinal image positions learned during navigation. Indeed, mean path position was significantly farther from the high wall (21.3 ± 1.3 cm) than the low wall (20.7 ± 1.4 cm), even before wall heights were changed (paired t-test, one-tailed; $n = 9$; $t = 2.04$; $p < 0.05$). However, this tiny difference (mean difference: 0.9 ± 1.4 cm) cannot account for the far greater shifts induced by raising or lowering the walls (mean shift: 7.0 ± 3.5 cm).

On the other hand, the width of routes taken before the walls were changed supports the hypothesis of visual guidance by retinotopic learning. The ants did not all follow the same route; rather their paths fell into a zone whose width was

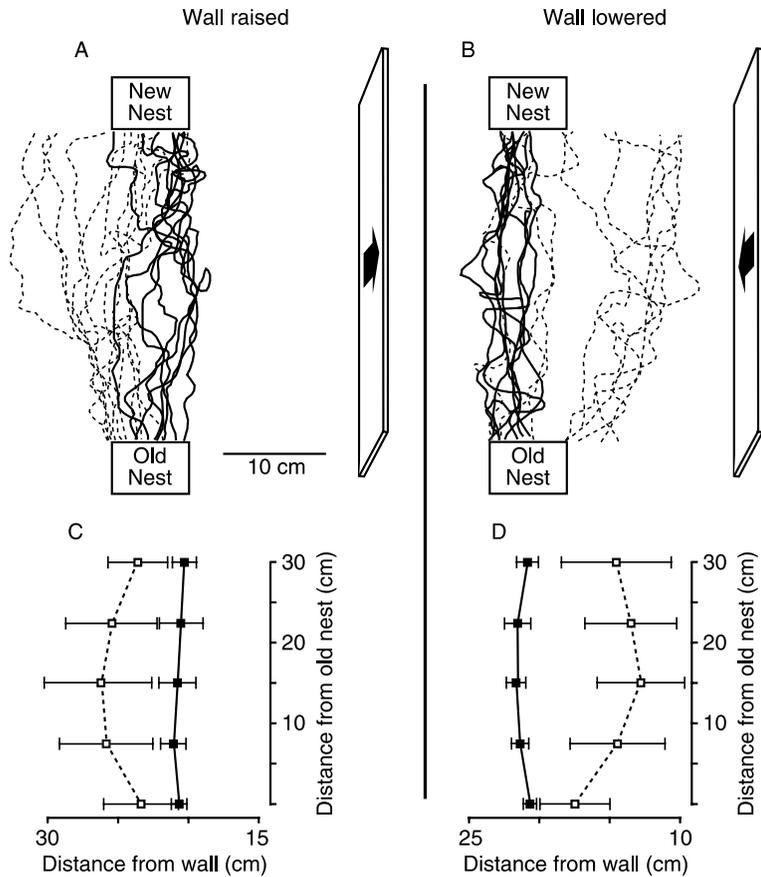


Fig. 2. Ants' paths shift when the height of a wall parallel to their route is changed. (A, B) Samples of paths traced for one colony before (solid lines) and after (dashed lines) the wall was lowered from 20 to 5 cm, or raised from 5 to 20 cm (C, D) Mean path positions for nine colonies before and after the wall was lowered or raised. Brackets show standard deviations. Lowering and raising the wall were significantly associated with shifts toward and away from the wall, respectively, at each of five points along the route (binomial test, $p < 0.0001$)

significantly greater for the low than for the high wall (Fig. 3A). If each ant attempts to visually maintain a fixed distance from the wall, then some of the variation in path position will arise from the ants' limited ability to detect changes in the wall's retinal image caused by movement toward or away from the wall. The image's location on the retina is determined by the angle subtended by the wall at the ant's position. This angle changes as the ant moves laterally, but the movement required to change it by a given amount varies with the size of the angle itself, and thus with wall height (Fig. 3B). The smallest angular change that these ants can detect is not known, but with only 60 ommatidia per eye, it is likely to be large. If we assume a value of 7° , at the high end of published estimates for a broad range of insects (Land 1997), ants along the low wall can stray over a zone 11 cm wide

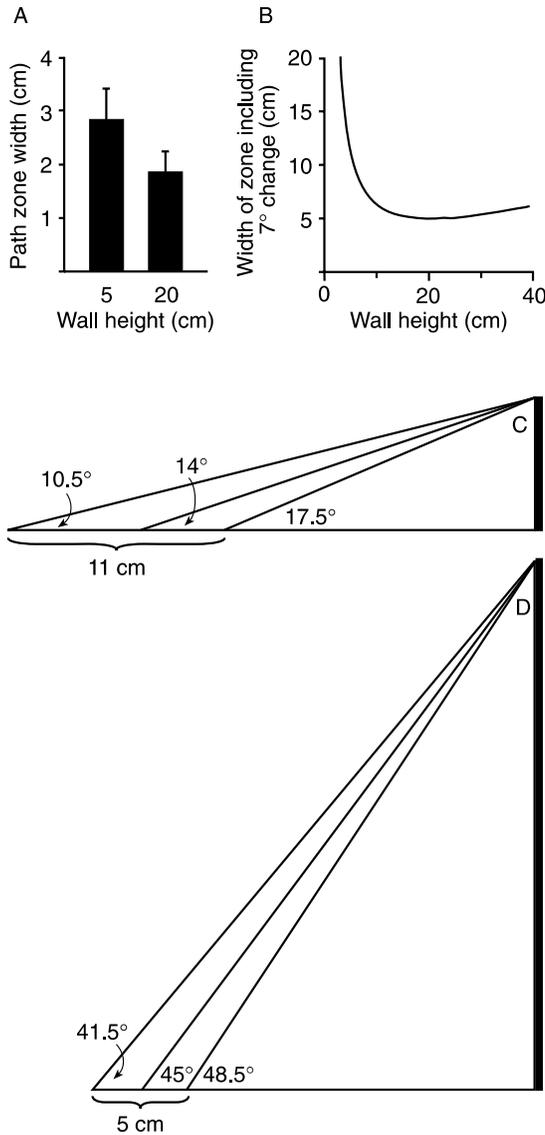


Fig. 3: Path widths depend on wall height. (A) Mean width of traversed zone was significantly higher when colonies used a low wall vs. a high wall (paired t-test; $n = 9$; $t = 4.21$; $p < 0.05$). Brackets show standard deviations. (B) Estimated lateral movement required to produce a detectable change in the angle subtended by the wall at the ant's position, as a function of wall height. As the ants shift toward or away from the wall, the subtended angle increases or decreases, respectively. The y-axis gives the width of a zone encompassing a total angular change of 7°.

(C, D) Illustrations of this zone for walls 5 and 20 cm in height without detecting a change in the wall's image (Fig. 3C). The corresponding zone for ants using the high wall is only 5 cm (Fig. 3D). This difference could contribute to the greater variance in path position observed for the low wall.

If retinotopic mapping of the wall is the only guide to navigation, then the fourfold change in wall height imposed on the ants should cause a corresponding fourfold change in their distance from the wall. That is, the new paths would be expected to lie about 80 cm from the raised wall and about 5 cm from the lowered wall. The observed shifts were in fact much smaller, suggesting that the ants also use other navigational cues. One possibility is that the nests themselves act as beacons when the ants draw near. Assuming a spatial resolution of 7° , the ants should be able to detect a 5-mm tall nest once they draw within 4 cm of it. Similarly, the humidity of the dampened nest, or the colony odour of other ants in the nest, may attract the ants at short range. Nest-based cues are consistent with the generally bowed appearance of the paths after the walls were switched, with the greatest deviation seen in the centre of the route, farthest from the possible influence of the nests (Figs 2C, D).

Emigration Between Two Walls

We hypothesised that two landmarks that change in a consistent manner would diminish the relative influence of competing cues and increase the magnitude of path shifts. Indeed, when we simultaneously changed the heights of two walls, not only did the ants' paths move away from the raised wall and toward the lowered one, but the shift was significantly larger than that seen in emigrations with only one wall (Fig. 4).

Discussion

Our results show that ants can use retinotopic learning to navigate a route parallel to a prominent edge. Although edge-following by navigating insects has long been recognized, the behavioural strategies underlying it have not previously been analysed. When we changed the height of a wall running parallel to the ants' route, their paths shifted in the direction expected if they navigate via retinotopic

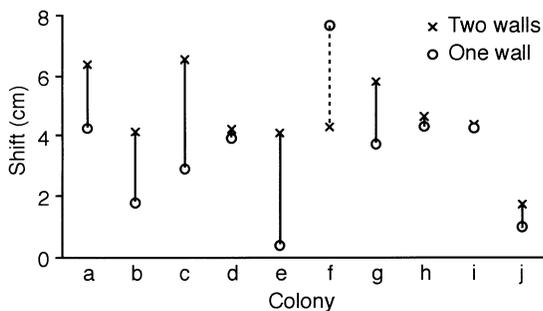


Fig. 4: Two walls are more effective than one. The path shift was larger for all but one colony when two walls were present, rather than just one (paired t-test, one-tailed; $n = 10$; $t = 1.92$; $p < 0.05$)

mapping of the wall. The ants moved closer to the wall when its height was lowered, and farther from it when its height was raised. Mere avoidance of, or attraction to, a disturbance cannot explain this consistent difference in the direction of the shifts. Nor can the difference be explained by other cues in the arena, because these were identical in the wall-lowering and wall-raising treatments. Moreover, the ants' wide separation from the wall rules out mechanosensory orientation by physical contact with a guiding edge, common in many insects (Schöne 1984; Klotz et al. 1985).

The ants' behaviour resembles that previously demonstrated for insects returning to a specific point near a landmark (Collett & Zeil 1998). In these cases, the distance to the object is marked by its apparent size on the retina. Honey bees trained to a food source near a large square will shift their search toward or away from the landmark if it is replaced by a smaller or larger square, respectively (Cartwright & Collett 1979). Experiments on both honey bees and desert ants further show that they pinpoint the location of a feeder or nest entrance by moving so that the retinal images of nearby landmarks match those memorized on earlier visits (Wehner & Räber 1979; Cartwright & Collett 1983). In a similar use of retinal images that does not involve learning, desert ants (*Cataglyphis fortis*) centre their route between two objects by choosing a path that balances the angular heights of the left and right objects (Heusser & Wehner, pers. comm.).

In the present case, the ants use landmarks to guide much of their journey, rather than to pinpoint their destination or to avoid obstacles. Their strategy is similar to route guidance by successive aiming at a series of local landmarks, each one recognized through memorized retinotopic images (Wehner et al. 1996; Judd & Collett 1998). Guidance by edges, however, offers potential advantages in economy of memory usage. Because the appearance of a beacon changes as the ant draws near, she must memorize several such images for each landmark. On longer routes guided by several local landmarks, this might create a significant memory burden. A guiding parallel edge, in contrast, projects a constant image as the ant progresses, potentially allowing a single stored image to govern a lengthy portion of the route.

These ants live in close-cropped grasslands studded with boulders and smaller rocks; the ants themselves typically nest in crevices within these rocks. Thus their visual environment is full of distinct rock and leaf edges that could serve as guides. Although it is unlikely that a single edge could steer an entire route from origin to destination, an ant could successively follow several edges, switching from one to another after travelling the appropriate distance.

In nature, edges are unlikely to have the perfect straightness and uniform height of the artificial walls used here. An irregular edge could nonetheless function as a guide—it would simply yield a more sinuous path, if the ants navigate by keeping it at a constant retinal position. Likewise, an edge need not be parallel to the shortest route between origin and destination, although an oblique edge would cause the ants to adopt an oblique path for the portion of its route guided by that edge. Such indirect paths have been reported for bees using beacon

landmarks (von Frisch 1967; Chittka et al. 1995), but it is not known if ants following edges behave similarly.

At 30 cm, the distance over which the ants had to emigrate was relatively short, as was the 20-cm separation between the wall and the ants' paths. Still, this scale is likely to be quite relevant to a small ant (2–3 mm long) emigrating over tens to hundreds of centimetres in an environment cluttered with stones. Crossing a 30-cm gap clearly challenged the ants' navigational abilities, judging by the difficulty we observed in our initial attempts to provoke emigrations over this distance. Colonies failed to emigrate even after 24 h, unless the separation between the nests was gradually extended from an initial distance of 4 cm. In more visually complex laboratory environments, emigrations over twice this length are typically complete within four hours (Mallon et al. 2001). We attribute the slowness seen here to the difficulty of orienting in an arena with so few distinct visual landmarks.

Nonetheless, the ants probably depended in part on visual cues other than the walls. The relatively small size of the shift in path, and the fact that it was enhanced by using two walls rather than one, suggests competition from other cues. Likely candidates include the nests and the arena itself, despite its relatively featureless appearance. In nature, these ants might also rely on path integration implemented with a celestial compass. If so, appropriate celestial cues were not available in the laboratory, but it is possible that other cues, such as the overhead light, could have partially substituted. Path integration might also be guided idiothetically, using internal cues that indicate turning angle and distance travelled.

The ants' obvious confusion when the acetate sheets were removed suggests that they missed some associated cue, most likely a pheromone deposited earlier in the emigration. Indeed it is possible that only a subset of the transporters actually used the wall to orient, with the others blindly following pheromone trails laid by scouts. Without individually marking the ants, we cannot rule out this possibility, but it does not seem consistent with the ants' behaviour or with previous reports of pheromone use in this genus. *Leptothorax* are not known to lay trails that rouse naïve nestmates to follow the trail to a food source or nest site. Instead, some species produce individual-specific orientation trails used by the scouts themselves to guide their subsequent trips along a familiar route (Maschwitz et al. 1986; Aron et al. 1988). Scouts of *L. albipennis* deposit individual-specific marks in the interior of potential nest sites (Mallon & Franks 2000). It is possible that workers similarly mark repeatedly travelled routes. In our emigrations, transporters did not follow exactly the same path, as might be expected if they used a common recruitment trail. Their wide zone of travel is more consistent with several, individually marked orientation trails.

Competition between the wall and other cues might explain the greater shift seen when the wall was lowered than when it was raised (Fig. 2). Ants trained to the more powerful cue presented by the large wall may depend on it more heavily relative to other cues, and thus respond more strongly to changes in its height. The higher wall may also be more salient because of limitations imposed by the

ants' visual acuity. The resolution of their spatial vision determines not only how large a change in wall height they can detect, but also how far they must drift from the original path before noticing a change in the wall's appearance. This is reflected in the tighter distribution of paths along the higher wall than the lower one. Ants using the higher wall can better detect a departure from the path, because the 45° angle subtended by the higher wall changes more for a given departure than does the 14° angle subtended by the lower wall. It would be interesting to discover if there are circumstances in which ants following edges choose their routes so as to keep the subtended angle near the maximally sensitive value of 45° (Fig. 3B).

Much previous research on visual navigation in insects has focussed on species with large eyes and relatively acute vision, such as desert ants and honey bees (Wehner et al. 1996). The results presented here show that even insects with small eyes and low visual acuity may rely on landmarks, and thus may offer broader insight into the role of vision in insect navigation.

Acknowledgements

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