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Navigation without vision: bumblebee orientation in complete darkness

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In flight cages, worker bumblebees (*Bombus impatiens*) spontaneously explored the surroundings of their nest and foraged in complete darkness by walking instead of flying from feeders up to 150 cm away from the nest. This behaviour was wholly unexpected in these classically visual foragers. The finding provides a controlled system for dissecting possible non-visual components of navigation used in daylight. It also allows us to isolate navigation mechanisms used in naturally dark situations, such as in the nest. Using infrared video, we mapped walking trails. We found that bumblebees laid odour marks. When such odour cues were eliminated, bees maintained correct directionality, suggesting a magnetic compass. They were also able to assess travel distance correctly, using an internal, non-visual, measure of path length. Path integration was not employed. Presumably, this complex navigational skill requires visual input in bees.

Keywords: bumblebee; distance estimation; magnet compass; navigation; path integration

1. INTRODUCTION

Bees are known to rely heavily on visual cues when foraging. To estimate direction, a sun compass and the polarization pattern of the sky are used (Rossel & Wehner 1984; Wehner *et al.* 1996), in addition to landmarks (Chittka & Geiger 1995*a*; Chittka *et al.* 1995*a*; Dyer 1996; Menzel *et al.* 1996). To gauge distance, bees evaluate the retinal image flow of the passing landscape as they move (Srinivasan *et al.* 1996; Esch & Burns 1996), and specific familiar landmarks (Chittka & Geiger 1995*b*; Chittka *et al.* 1995*b*). Some species of bees will fly in low light conditions (such as bright moonlit nights), but still rely on visual cues (Roubik 1989; Warrant *et al.* 1996).

We show here that bumblebees will also forage as ambulating, nocturnal workers when offered the opportunity to collect sucrose solution outside the nest in complete darkness. They would forage from feeders more than 1 m away from the nest entrance. As anyone who has ever tried to navigate a novel apartment blindfolded can imagine, this is not a trivial task. How do bees judge distances and directions when they don't see?

The use of odour cues is one possibility. Bumblebees have variously been proposed to mark flowers with attractant (Cameron 1981) or repellent (Stout *et al.* 1998) and use trail marks on the short path between their nest and the entrance of an artificial nestbox (Cederberg 1977). All of these have been assumed to be produced by the tarsal glands (Schmitt 1990; Stout *et al.* 1998). However, whether bumblebees indeed produce more than one tarsal scent or whether the marks are primarily a hydrocarbon glue to make their feet stick on vertical surfaces (Lensky *et al.* 1987) is unclear. In the latter case, the substance may be continuously leaking from the tarsal gland, and so indicates wherever a bumblebee has recently trodden. Bumblebees may simply interpret these marks according to context, i.e. to tell whether a flower has been recently visited and emptied or whether a given mouse hole in the ground is their own.

The question of how bees measure distance has been controversial. It was earlier suspected that bees use the energy consumed during their flight to estimate how far they have already flown (Heran & Wanke 1952). Later research showed that bees use a variety of visual (external) cues to estimate distance (Esch & Burns 1996; Chittka & Geiger 1995*b*; Chittka *et al.* 1995*b*), so that some researchers have suggested discarding the 'energy hypothesis' (Srinivasan *et al.* 1996). Only when visual cues are eliminated altogether (such as here) can this question be answered unambiguously.

To estimate direction, honeybees and other arthropods may use a magnet compass in some conditions (Martin & Lindauer 1973; Schmitt & Esch 1993; Collett & Baron 1994; Wiltschko & Wiltschko 1995; Walker 1997). Here, we exploit the bumblebees' readiness to forage in complete darkness to see if they would be able to orientate in a correct direction by means of a magnet compass or by some ideothetic cues, i.e. based on proprioceptive inputs (Mittelstaedt 1985; Srinivasan *et al.* 1996). The study examines, in addition, the bees' ability to correctly estimate the distance that must be walked to arrive at the goal. Since information on direction and distance constitute the basis of path integration, we also examine whether bees are capable of such integration when visual navigation fails. Path integration is a strategy used by many arthropods (Mittelstaedt 1985; Chittka *et al.* 1995*b*; Menzel *et al.* 1996; Wehner *et al.* 1996). Using this strategy, animals on a search for food away from home continuously update all distances travelled and angles turned to

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keep an update of their home direction. This enables them to head directly home whenever they wish to do so, i.e. when they have captured prey or filled their honey stomach sufficiently in the case of nectarivores.

2. METHODS AND RESULTS

Prior to our experiments, we had observed that bees foraged during the night, from feeders in dark flight arenas. In the present study, we tested bees that had never left the nest before the experimental procedures began. We found that they would spontaneously leave the nestbox in darkness and explore the vicinity of the nest entrance, apparently in search for food. This exploratory activity started rapidly after the nest entrance was connected to the arena (typically within 15 min several individuals had entered the arena). All experiments were performed in an entirely dark basement laboratory. Bumblebee (*Bombus impatiens*) colonies with individually marked workers were kept in a nestbox that was connected to one of two types of arena (see below) by means of a transparent plastic pipe. Manual shutters in the pipe allowed us to control which bees entered the arena. Bees were identified in the pipe using a flashlight in the otherwise dark room. At these times bees were contained in a short segment of the pipe and could not have seen the testing arena or the feeder.

To observe bees in darkness, we used infrared (IR) equipment as bees do see red light (Chittka & Waser 1997). An IR light source (cut-off wavelength 800 nm) was suspended 1.2 m above the arena. To rule out any heat gradient generated by the IR source, we measured temperature across the arenas using a thermometer that evaluated simultaneous temperatures at a pair of points. We found no temperature differences (measured to the nearest 0.05 °C) at any separation distances within the arenas. We recorded behaviour using an IR-sensitive TV camera (RCA, TC 1000) connected to a standard video recorder.

(a) *Estimation of direction*

To test whether bees could assess directionality in the absence of visual cues, we used a circular arena (diameter 96 cm; height 9 cm), in which bees were trained to a feeder south of the central entrance hole. Before the actual tests were started, bees were allowed to forage, as a group, from the feeder for a full day (10.00 to 18.00). To compare performance of naive bees with experienced ones, we randomly picked 20 successful bees (which located the feeder and, later, the arena exit) during the first hour of foraging and 40 during the last two hours. The bees were initially extremely slow at locating the feeder. The median (m) time taken was $m = 9$ min 30 s, with upper (q_u) and lower quartiles (q_l) of $q_u = 22$ min and $q_l = 5$ min 20 s. But performance substantially improved during the day, so that bees took only $m = 30$ s ($q_u = 65$ s; $q_l = 24$ s) during the last two hours of training. Return walks (those from the feeder to the central hole) took about twice that time ($m = 70$ s; $q_u = 140$ s; $q_l = 45$ s). However, even in experienced foragers, the path was never direct, as would have been the case when visual cues are available. Although the distance between entrance and feeder was only 40 cm, the shortest path ever taken by an experienced forager was 120 cm, and the median path length was 152 cm. Return paths were even longer ($m = 188$ cm). Bees never followed one another directly (e.g. by means of antennal contact) and their walking trails never coalesced into a single, direct foraging trial, as known in ants (Deneubourg & Goss 1989). Yet, as there *is* striking improvement from early to late trials, some strategy must be used.

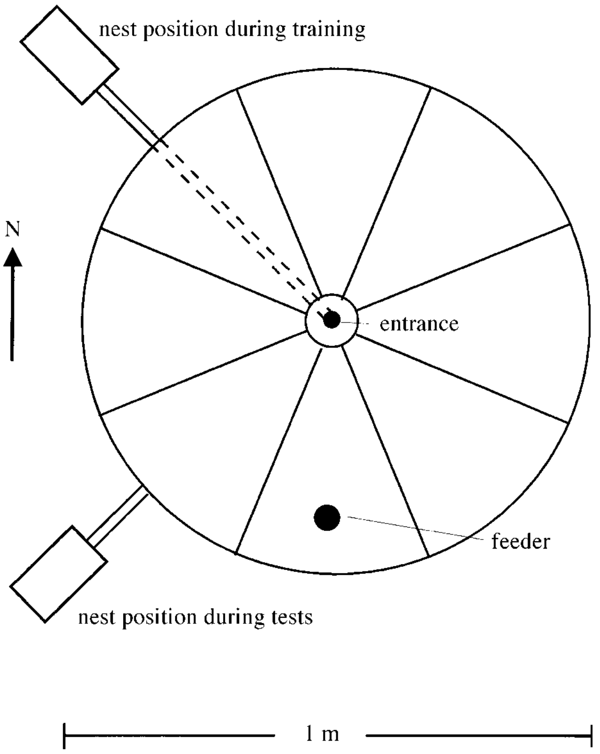

Figure 1. Circular arena set-up. The floor was made of smooth acrylic Plexiglas with a central hole. Bees entered the arena from below through a plastic pipe connected to the nest box. The horizontal pipe was transparent so that we could monitor the identity of the bees entering the arena. The feeder was a Petri dish with holes drilled in the top, containing 50% (by volume) sucrose solution. It was located directly south of the entrance hole, 40 cm from the centre of the arena. The pipe between the nest and the entrance hole ran in a northwest direction, giving a 135° angle between pipe orientation and feeder direction within the arena. The arena was subdivided into eight sectors of 45° width each. During tests, the feeder was removed, the entrance pipe was swung 90° counter-clockwise and the floor rotated 180°.

Tests with individual bees were started on the next day. All bees were first rewarded at the feeder until sufficient traffic had been established. The feeder was then removed so bees were not rewarded during tests. Next, the entrance pipe was moved to a south-east direction (figure 1) so that we could distinguish between the hypotheses that bees use a compass versus that they remember the angle between the entrance pipe and the direction within the arena. In the latter case, we would expect bees to choose an eastward direction, whereas with the use of a compass, bees should move southward. The floor was then manipulated in one of two ways: (i) the floor was rotated by 180° and left uncleaned so that scent marks, if left by the bees, would be available during the tests but would indicate a direction opposite the training direction; (ii) the entire floor was cleaned with ethanol to make unavailable potential odour marks left by bees during training. To be entirely sure that bees would not be able to use any residual odour to find the correct (southward) direction, we again rotated the floor by 180°. Experienced bees were then tested individually for up to 7 min. Each bee was tested only once. To determine the direction that bees preferred, we divided the arena into 45° sectors and recorded the amount of time a bee spent in each. Sectors were

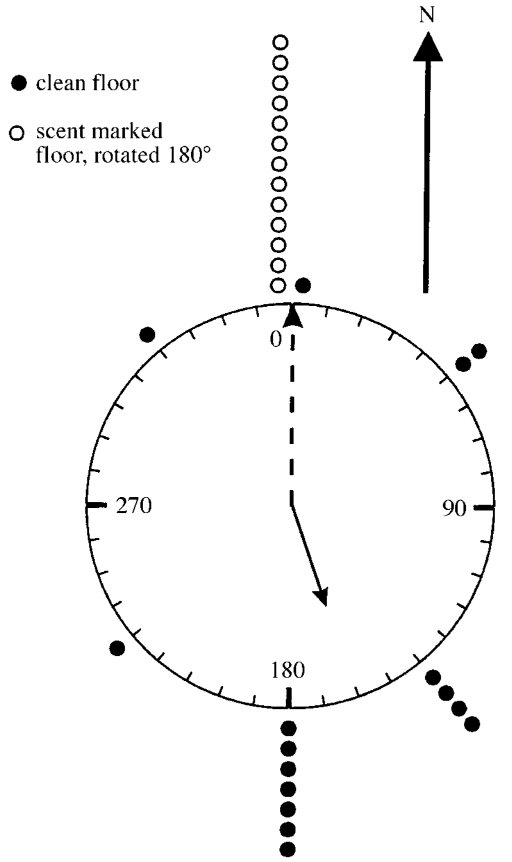

Figure 2. Circular distribution of the sectors in which each bee searching for the feeder spent the greatest amount of time. Arrows within the circle denote the resultant vectors (dashed: unclean floor; continuous: clean floor). Bees on the uncleaned, rotated floor were significantly oriented towards north (mean vector: $\Phi = 0^\circ$, $r = 1$, $n = 13$, $p < 0.01$; Rayleigh test). Thus they orientated towards odour marks left during training. Bees on the clean floor preferred the southern direction (mean vector: $\Phi = 160^\circ$, $r = 0.51$, $n = 16$, $p < 0.05$). The 95% confidence interval extends from 120–200° and thus includes the training direction of 180°.

orientated so that one spanned the displaced area that had contained the feeder, a second one the compass direction to which bees were trained and a third one the angle to the feeder with respect to the entrance pipe.

When the floor was left uncleaned, bees clearly preferred the direction opposite the one they had been trained to (figure 2), i.e. the direction indicated by odour marks. This suggests that odour marks left between the entrance and the feeder outweigh all other directional orientation systems, if they exist. When the floor was clean, however, the majority of bees spent most time on the south sector (figure 2). The sectors chosen by the bees may not be the only good indicator of a compass system. Suppose, for example, that a bee makes an initial error and walks 30 cm east (instead of south) after exiting the central hole. Even if that bee subsequently moves only in the north–south axis for several minutes, we would record that bee only on eastern sectors and so assume that it has no compass. However, strong southward directionality on an eastern (or western) sector is as good an indicator of a compass systems as a southbound movement on the south (training) sector. Therefore, we also recorded the angular direction of forward movement of each bee every second for the first minute of the test period (figure 3). Bees moved generally toward the southern half of the arena, again suggesting that a magnet compass system is employed. The distribution of movement vectors is statistically indistinguishable from the training direction (figure 3). There is no evidence for eastward movement. Thus, a proprioceptively assessed angle between the entrance pipe and the feeder direction within the arena is not used to establish direction in total darkness.

(b) *Estimation of distance*

We used a linear, 'one-dimensional' arena to determine whether bees could assess the distance to which they had previously been trained. This arena was a steel trough, 150 cm long, 6.5 cm wide and 2.5 cm high. We placed a linear scale with ten 15-cm intervals next to the training/test trough, so that the bees' position could be specified as being on one of ten segments. Bees were trained to a feeder at one of four segments from the nest: the second segment (training distance 22.5 cm); the fifth (67.5 cm); the eighth (112.5 cm); and the tenth (142.5 cm). Fresh rails were used in tests to preclude bees from using odour marks deposited during training. Distributions of outbound trips originating at the entrance were significantly different between all training treatments ($p < 0.001$), except 8 and 10 (Kruskal–Wallis, followed by Mann–Whitney U-tests with $\alpha_{\text{adj}} = 0.0085$). As all outbound trips (not just those originating at the arena entrance) are added, the pattern becomes even clearer. These tests unambiguously show that bees aborted their outbound paths most frequently at the distances to which they had been trained (figure 4).

(c) *Path integration*

Had our bees used path integration, they should have headed directly home from the feeder, no matter how tortuous their outbound path. To examine this possibility, we evaluated bees returning from the feeder on the first day of training. To see if they would be correctly orientated towards the centre of the arena, we measured the angle at which they broke an imaginary circle of $\varnothing = 10$ cm around the feeder. These data were collected during the last two hours of foraging, when bees were comparatively efficient at locating the exit hole. Directions taken were statistically indistinguishable from random (figure 5; $r = 0.053$, $n = 40$, $p > 0.6$, Rayleigh test; Batschelet 1981). This early choice of direction may be biased because bees initially circle around the feeder before choosing a defined direction. We therefore also evaluated the points at which bees crossed the boundary of a circle of $\varnothing = 20$ cm around the feeder. Again, bees crossed this circle at randomly distributed points ($r = 0.22$, $n = 40$, $p > 0.1$).

This shows that path integration fails to provide a correct estimate of home direction when bees cannot use visual information. However, these results do not yet show that bees do not, despite considerable imprecision in their assessment of distance and direction, attempt to calculate a home direction from their movements prior to feeding. In that case, homebound bees might choose random directions as a group, but each might initially walk a certain distance along a straight path, because it 'thinks' that it has a correct estimate of home direction. If paths taken by homebound bees were straight, we would expect the points at which bees break the 10-cm circle to be correlated with those at which they break the 20-cm circle. This was not the case: the circular correlation coefficient r (Batschelet 1981) is 0.23; at $n = 40$, this is not significant ($p > 0.1$). The correlation coefficient is similarly low for naive bees during the first hour of training ($r = 0.33$; $n = 20$; $p > 0.1$), indicating that not using

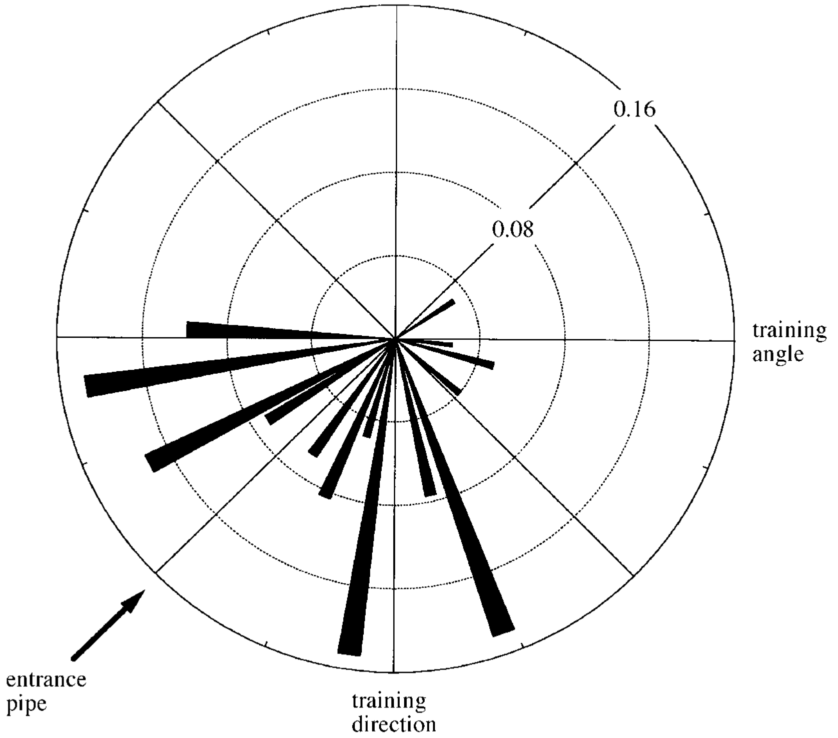

Figure 3. Vectors of mean angular movement over the first 60 s for individual bees searching for the feeder on a clean floor ($n = 16$). The direction of each vector indicates the mean angle, and the vector length (resultant vector) measures the strength of directionality, where unit length would be complete unidirectional movement (mean resultant vector: $\Phi = 206°$; $r = 0.57$; 95% confidence intervals 157–255°). The direction marked 'training angle' would be expected to be chosen if bees memorized the angle between the entrance pipe and the direct path between the central hole and the feeder. The 'training direction' is the compass direction in which the feeder lies from the centre.

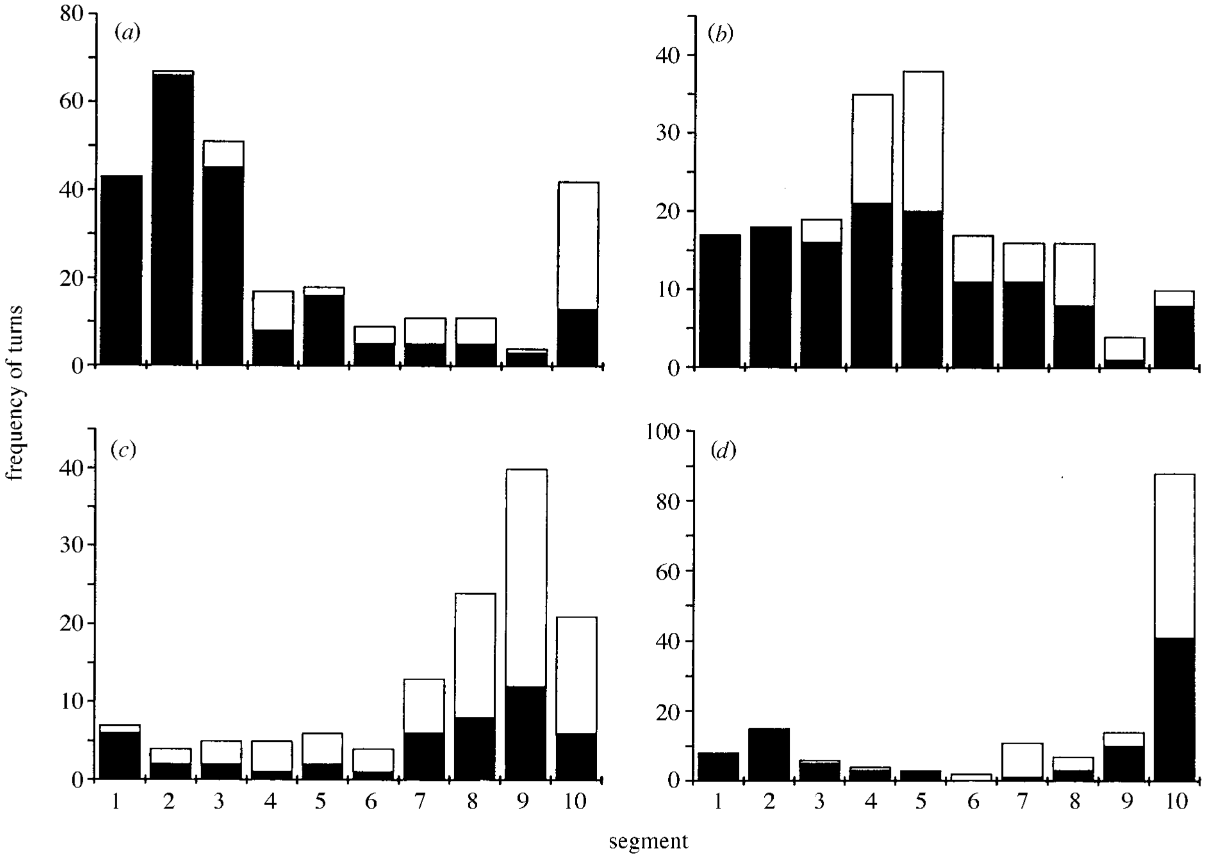

Figure 4. Distance measures of bees in a linear arena, histogram of the distribution of outbound trips terminated on different segments for bees trained to segments (*a*) 2, (*b*) 5, (*c*) 8 or (*d*) 10. Single bees were observed searching for the feeder for up to 10 min. We recorded the segments on which bees aborted their outbound paths and turned back towards the nest. Before returning to the nest, all bees made several outbound trips. Black bars, trips originating at the entrance; white bars, other outbound trips (total bar, all outbound trips).

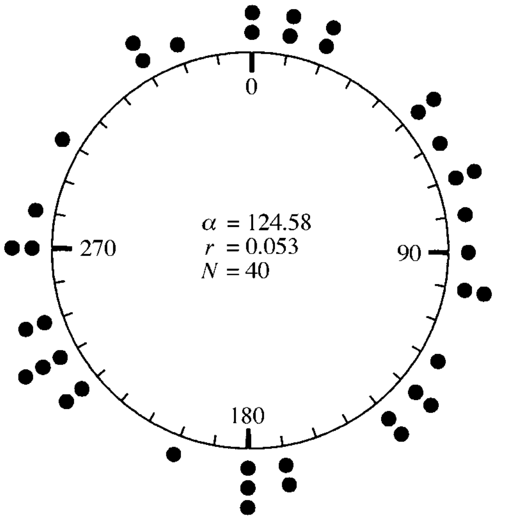

Figure 5. Directions taken by homebound bees leaving the feeder. We recorded the angular position at which bees broke an imaginary circle ($\varnothing = 10\,\mathrm{m}$) around the feeder. Directions were statistically indistinguishable from random ($r = 0.053$, $n = 40, p > 0.1$).

path integration is not a result of learning that it does not work. In summary, bees do not even attempt to use path integration when they search for the arena exit.

3. DISCUSSION

We show here that bumblebees can be transformed into nocturnal workers, when the opportunity to collect sucrose solution near the nest entrance is offered. The readiness of social bees to exploit almost any conditions to increase resource intake, even in completely unnatural situations, is certainly amazing. It can also be informative, however: it may tell us something about what orientation mechanisms are available to bees in more natural situations. Which cues do bees use in our experiments?

We show that scent is indeed the predominant directional cue for bees when their visual sense yields no information. Bees were fooled into walking north instead of south when odour cues were rotated around the centre in the circular arena. How is the feeder marked? We often observed bees circling around the feeder before walking back home, so that the floor is possibly marked with tarsal gland secretions (Schmitt 1990). It is unclear if the scent is actually an attractant (as suspected by Cameron (1981)), or whether the feeder is simply marked as an outstanding location by letting the tarsal glands leak hydrocarbons at a constant rate, but walking more around the feeder than elsewhere. We also sometimes observed bees walking slowly backwards and drumming their abdomen on the floor several times. The significance of this behaviour is elusive, but since we invariably observed it near the feeder, we suspect that it might be associated with recruitment of nestmates, possibly by using an anal substance (Aguilar & Sommeijer 1996), or substrate vibrations (Raub *et al.* 1997). Why walking backwards, however, would be necessary for such recruitment (or any other purpose) is unclear.

Bumblebees do not appear to use trail marks in the way ants do, meaning that the scent marks are organized so that eventually all foragers will march in single file to the marked goal (Deneubourg & Goss 1989). Instead, even the paths of experienced foragers contained numerous twists and turns and were far from direct. Preliminary tests with three foragers that were trained and tested individually (so that no other individual could leave interfering odour marks while a particular bee was trained) showed that bees never followed the same path to the goal twice. These findings support the notion that the feeder location itself is the predominant scent beacon and potential odour marks left along the way are not as effective.

In total darkness and in the absence of any landmarks, when odour cues were made unavailable, the bees' ability to determine direction is less accurate. Nevertheless, there is evidence for the use of a vision-independent compass. Bees spend significantly more time in the area defined by the compass direction in which they were trained and exhibited significant directional movement. We suspect that bumblebees use a magnetic compass for these purposes, as is know from honeybees (Martin & Lindauer 1973; Schmitt & Esch 1993; Collett & Baron 1994) and other arthropods (Wiltschko & Wiltschko 1995; Walker 1997).

Bumblebees were also able to measure distance in darkness, even when scent cues were made unavailable. This result came as a surprise, because recent work on honeybees seemed not to support the notion that distance is measured by anything but visual cues (Srinivasan *et al.* 1996). The 'energy hypothesis' (Heran & Wanke 1956), which suggests that bees evaluate fuel consumption during flight by measuring the tension in their honey stomach, was considered unnecessary, but our results indicate that some such non-visual capability exists, at least in bumblebees. Of course, there are other possibilities than energy: bees might measure time on the outbound path or evaluate the number of steps taken. What is certain, is that bumblebees do have an internal measure of distance that functions independently of any visual information. Interestingly, the precision of distance estimation was greater when all outbound trips were evaluated (not just those originating at the entrance of the arena). This result indicates that bees 'know' the distance of the new starting point relative to the arena entrance. Bees apparently integrate the distances they had previously walked during their search and use the result for calculating the total distance that must be walked. Similarly, bees estimating distance by using visual (optic flow) cues have been shown to be capable of such distance integration (Srinivasan *et al.* 1996).

Thus, bumblebees can measure both distance and direction in darkness. We therefore tested if they might use these measurements for a more complex navigational strategy, path integration. However, correct directionality was not observed by bees returning from the feeder (even if odour was present), so path integration is apparently not used. It may not work for our bees, since both distances and directions are estimated with considerable imprecision. Path integration apparently requires visual input in bumblebees (unlike spiders which are capable of path integration in darkness; Mittelstaedt 1985).

Our results, nonetheless, show that bumblebees have vision-independent navigation systems to gauge distance and direction that might be available as back up cues, to supplement visual assessment of a bee's flight path.

Certainly, bees will not forage outside the nest from natural flowers in complete darkness, as in our study. A single foraging load requires linking hundreds or thousands of natural flowers (Heinrich 1979), and the imprecise orientation strategies described here will surely fail to bring the bee home on such extended paths. Non-visual navigation strategies, however, will become primary in some situations. Social bees must perform a large variety of tasks in complete darkness. With few exceptions, their nests are dark; they are commonly located in underground burrows, tree cavities or arboreous termite nests (Chittka *et al.* 1997), and often have intricate and complex architectures (Roubik 1989). Within these nests, bees must navigate successfully between brood cells, honey pots, pollen stores and the nest entrance, and even pursue intruders through such mazes (Chittka *et al.* 1997). Bumblebees, which commonly nest in mouse holes, have to negotiate extended underground labyrinths which generally have more than a single exit (B. Koenig, personal communication). Heinrich (1979) reports of a nest entrance tunnel of 2 m length and mentions that they are generally several feet long. In view of this, underground navigation without visual input is an essential capacity, and our results show that bees do have the necessary abilities. Whether bumblebees indeed use these abilities inside the nest and its entrance tunnels, or whether they only rely on tactile cues, remains to be examined.

Finally, we wish to mention the curious temporal activity pattern of the bumblebees foraging activity. When food is continuously offered from a feeder in an arena, colony foraging activity (as monitored by IR equipment) follows a bimodal circadian pattern, peaking both at midday and at midnight in a 12L:12D cycle. This pattern persists for more than a week in perpetual darkness, but collapses in permanent daylight conditions. We know from *Drosophila melanogaster* that circadian activity is maintained for some time when animals are kept in darkness and disappears in continuous light (Myers *et al.* 1996), but nocturnal activity peaks in a diurnal animal appear to be a novelty among insects.

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