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REVIEW

Where paths meet and cross: navigation by path integration in the desert ant and the honeybee

Mandyam V. Srinivasan[1]

Abstract Animals that travel large distances in search of food need to be equipped with navigation systems that are capable of keeping track of the distance and direction of travel throughout their outbound journey, so that they may return home expeditiously and without losing their way. The challenge of homing is especially acute when the environment is devoid of landmarks. Desert ants and honeybees are able to meet this challenge, despite their minuscule brains and restricted computational capacity. This article reviews some of the processes and mechanisms that underlie the homing abilities of these creatures, which are among the best-understood navigators in the animal kingdom.

Keywords Navigation · Dead reckoning · Odometry · Insect · *Cataglyphis* · *Apis mellifera*

Introduction

Research over the past century has revealed that many insects are surprisingly competent navigators. A foraging honeybee, for example, can travel as much as 10 km away from its nest in search of food, and then return home quickly and unerringly (von Frisch 1993). A desert ant, *Cataglyphis,* measuring a mere centimetre in length, can venture a distance of up to 100 m away from its nest (amounting to more than 10,000 body lengths), before returning home with its booty—not by back-tracing its tortuous outbound route, but by taking the shortest, straight-line return path (Wehner 2003; Wehner and Srinivasan 2003; Wolf 2011). This is illustrated in Fig. 1. If the ant, after having collected its food, is picked up and released at a different location, the ant runs along a straight line parallel to the original return path; and when it does not find the nest after it has travelled the appropriate distance, it begins to search for the nest by performing a series of loops around the expected location (Fig. 1; Wehner and Srinivasan 1981). The displacement experiment demonstrates that a foraging desert ant is fully aware of the distance and the direction of home, even when it has moved a relatively long distance away.

Ants are capable of this impressive navigational feat even in barren desert environments that do not contain any landmarks. How do they achieve this? In principle, the task can be achieved by a process that sailors have termed "dead reckoning", and biologists and engineers have termed "path integration" (Wehner and Srinivasan 2003). This process requires the navigating animal to keep a moment-to-moment record of the incremental translation and rotation that it makes along each step of its outbound trajectory. As we shall describe later, these elementary translations and rotations can then be pieced together mathematically to determine the distance and direction of home. To perform path integration, therefore, an insect must possess an odometer, to record the elementary travel distance, and a compass, to record the instantaneous direction of travel. This article reviews briefly how the desert ant and the honeybee—two superb invertebrate navigators—measure and combine odometric and compass information to achieve path integration that is sufficiently accurate to guide them home. In what follows we consider (1) odometry (2) acquisition of compass information, and (3) path integration, in desert ants and honeybees.

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Fig. 1 Experiment demonstrating the navigational capacity of the desert ant *Cataglyphis*. Modified from Fig. 2a of Wehner (2003). Description in text
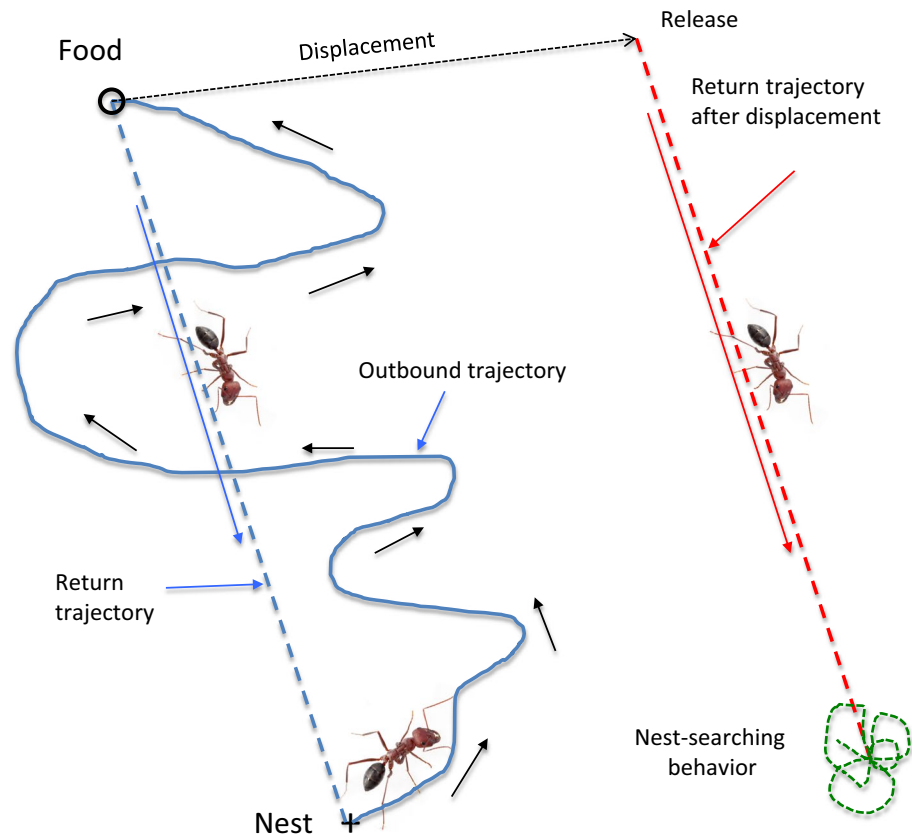
Odometry

The desert ant

Odometry has been investigated comprehensively in the desert ant, *Cataglyphis* (Sommer and Wehner 2004; Wittlinger 2006; Wittlinger et al. 2006). In an early study a tunnel, pointing in a given direction (northwards, for example), was placed at the entrance to a *Cataglyphis* nest, and ants were trained to walk through the tunnel to find food at a particular distance from the entrance. When the ants had completed several foraging trips from the nest to the feeding site, the trained ants were tested by positioning them in a fresh tunnel (termed a test tunnel) immediately after they had picked up the food (Sommer and Wehner 2004). The test tunnel was longer than the training tunnel and was oriented parallel to the training tunnel. When released in the new tunnel, the trained ants ran in the homebound (southward) direction in search of the nest, and when they did not find the nest at the expected location, they began to search for the nest by moving back and forth around the expected nest location in a zig-zag fashion (Sommer and Wehner 2004). The searching location, measured as the average of the turning positions, corresponded closely to the expected location of the nest. In other words, the ants had learnt the distance from the nest to the food source. [However, there

was a small but systematic undershoot, which increased with increasing travel distances (Sommer and Wehner 2004). This may be an adaptation to ensure that, when foraging in natural circumstances, ants returning home begin to search for the nest in a region that was traversed during the outbound journey, rather than in unfamiliar territory on the other side of the nest.]

How were the ants measuring the distance that they had travelled? This was explored by manipulating the legs of the trained ants after they had made several visits to the feeding site (Wittlinger 2006; Wittlinger et al. 2006). When a trained ant arrived at the feeding site, it was treated in one of two ways. In one treatment, the ant's legs were shortened by amputating the tarsomeres, or severing the leg at the mid-tibia level, to reduce their length by about 50 %. In another treatment, the ants' legs were artificially lengthened by using stilts to extend the length of the tarsomeres by about 30 %. When the treated ants were released in the test tunnel (after giving them a piece of food to initiate their homing instinct), the ants with the shortened legs searched consistently at a position in the tunnel that was short of the nest location. In other words, these ants were overestimating the distance that they had travelled. On the other hand, the ants with the extended legs searched at a position that was beyond the nest location. In this case, the treated ants were underestimating their travel distance. In each case, the

treated ants commenced their search after they had made approximately the same number of footsteps on their home-bound journey. But because each stride produced a shorter-than-normal progress in the short-legged ants, and a longer-than-normal progress in the stilted ants, the former group undershot the nest location, whilst the latter group overshot it. These experiments demonstrated clearly and convincingly that the desert ant *Cataglyphis* estimates its travel distance by using a form of 'stride integrator' that computes an approximate product of the average stride angle and the number of strides that are made in traveling from the nest to the food site, and uses this measure, in reverse, to chart its way back home (Wittlinger et al. 2006, 2007). Other experiments, exploring the possible contribution of vision to odometry—specifically, the visual motion of the environment that is experienced by the ant during its journey—have revealed no influence of motion in the lateral visual fields (Ronacher et al. 2000), and a very small effect of motion in the ventral visual field (i.e. the motion of the image of the substrate on which the ant walks) (Ronacher and Wehner 1995). Thus, the ant's odometer is based primarily on a stride integrator, which may be appropriately described as a 'podometer'. More recent experiments have revealed that the ant's podometer is robust to locomotion over a variety of corrugated surfaces—the stride integrator delivers an accurate odometric signal despite the frequent slippage and stumbling that occurs whilst walking on such surfaces, and despite the fact that walking on corrugated surfaces often necessitates changes in stride length, stepping frequency and walking speed. The podometer is even robust to amputation of up to two legs (Steck et al. 2009). Exactly how this impressive level of robustness is achieved is presently unclear, but it must have an important adaptive value, given the varying nature of the terrain and the possibility of frequent predator-evoked injury.

Honeybees

Honeybee odometry studied through food-searching behaviour in flight tunnels

Nearly 20 years ago, honeybees (*Apis mellifera*) were trained to enter a tunnel to visit a sugar-water feeder placed at a certain distance from the entrance. The inside walls were lined with vertical stripes. After training, the bees' behaviour was observed when the feeder was temporarily removed. The trained bees searched for the feeder at the position where it was previously located (Srinivasan et al. 1996, 1997). This finding, backed up by a series of control experiments described in these papers, ensured that the bees were not localising the position of the feeder by (a) using scent marks deposited in the vicinity of the feeder, or (b) counting the number of stripes on the walls on the way

to the feeder. The possibilities that the bees were gauging distance flown by measuring the time of flight to the feeder, or the energy consumed en route, were ruled out by testing the bees in the presence of a headwind or a tailwind, generated by placing a small fan at the end of the tunnel. In a headwind the bees flew slower, took a longer time to get to the feeder location, and searched at a position that was beyond the training location. The opposite was true in a tail wind. These experiments revealed that the bees were not using cues based on travel time or energy consumption because, in the headwind the bees would have consumed a greater amount of energy and travelled for a longer period of time before they began to search for the feeder, compared to the control bees that were tested in still air. Conversely, the bees that were tested in the tailwind would have consumed a lower amount of energy and travelled for a shorter period of time before they began to search for the feeder. These findings also ruled out the possibility that the bees were measuring and integrating their airspeed over time to estimate flight distance, because the airspeed on the way to the feeder would have been higher in the headwind (and the travel time longer), and lower in the tailwind (and the travel time correspondingly shorter).

The only conceivable remaining cue that a bee could have used to infer how far it had flown would be a visually based one; that involves measuring the extent to which the image of the environment moves in the bee's eyes during the journey to the feeder—the longer the journey, the larger this movement would be. This so-called 'optic flow' hypothesis was investigated by training and testing bees in conditions where image motion was eliminated or reduced, using tunnels that carried axially oriented stripes on the walls and floor. Such tunnels provided no information on image motion, because the bees were then flying in a direction parallel to that of the stripes. In these tunnels, the bees' behaviour was strikingly different: they showed no ability to gauge distance travelled. The bees searched uniformly over the entire length of the tunnel, showing no tendency to stop or turn at the former location of the reward. Evidently, when bees are deprived of image-motion cues, they are unable to gauge how far they have flown. This finding provides direct and rather compelling evidence that the honeybee's odometer is driven by image motion (Srinivasan et al. 1996, 1997).

A similar set of studies, conducted subsequently on stingless bees (*Melipona seminigra*), has revealed that that these creatures, too, rely on optic flow cues for gauging foraging distance (Hrncir et al. 2003). Furthermore, these bees also use optic flow information to locate food sources in the vertical plane—which is important, given that they live and forage in forest environments in which the nest and the food source can be separated in three dimensions (Eckles et al. 2012).

Honeybee odometry studied via the waggle dance

When bees return home from an attractive food source, they perform the so-called "waggle" dance to advertise to their nest mates the distance and direction of the goal (von Frisch 1993). In this dance, which is performed on the vertical surface of the honeycomb, the bee moves in a series of double-loops, each shaped roughly like a figure of eight. After completing each loop, the bee enters a so-called 'waggle phase' in which it shakes its abdomen from side to side, in a stereotyped fashion. The duration of the waggle is proportional to the distance of the food source from the hive, and the angle between the axis of the waggle and the vertical direction is equal to the azimuthal angle between the sun and the direction in which a bee should fly in order to find the goal. The information in the dance is decoded and used by the nest mates to locate the food source, and to harvest it efficiently. But the waggle dance has also been useful for the researcher who wishes to unravel the mysteries of the honeybee's odometer, because it provides a window into the bee's perception of how far she 'thinks' she has travelled.

Esch and Burns (1995, 1996) investigated distance measurement by filming the bees' dances in the hive when they returned from an artificial feeder, placed outdoors in an open meadow. They observed how these dances changed when the height of the feeder above the ground was varied systematically, by attaching it to a weather balloon. When the feeder was on the ground, 70 m away from the hive, the bees correctly indicated a distance of 70 m. However, when the altitude of the feeder was increased, the bees did something quite surprising. Instead of signalling a larger distance—as one might expect, since they were now flying a longer route to the feeder, and expending more energy to get to it—they signalled a shorter distance. When the feeder was 90 m above the ground, and at a horizontal distance of 70 m from the hive, the bees indicated a distance of as little as 25 m! In another set of experiments (Esch and Burns 1996), bees were trained to fly from a hive placed on the roof of one tall building (50 m high) to a feeder placed atop another tall building (34 m high). Although the hive and the feeder were horizontally separated by 228 m, the returning bees signalled a distance of only 125 m. From these observations, Esch and Burns inferred that distance flown is gauged in terms of the motion of the image of the ground. The higher the bee flies, the slower the ground beneath her appears to move. This finding is congruent with those of the tunnel experiments: both studies suggest that honeybees gauge the distance that they have distance flown to reach a food site by measuring the extent to which the image of the environment moves in their eyes during their journey.

Srinivasan et al. (2000) and Esch et al. (2001) investigated waggle dances in a different experimental paradigm.

They trained bees to fly directly from their hive into a short, narrow tunnel that was placed very close to the hive entrance (Fig. 2). The tunnel was 6 m long and 11 cm wide. A feeder was placed 6 m from the entrance. The walls and floor of the tunnel were lined with vertical stripes. The dances of bees returning from this feeder were videofilmed. Incredibly, these bees signalled a flight distance of ca. 200 m, despite the fact that they had flown only a small fraction of this distance. Evidently, the bees were overestimating the distance they had flown in the tunnel, because the proximity of the walls and floor of the tunnel greatly magnified the optic flow that they experienced, in comparison with what would normally occur when foraging outdoors. On the other hand, when the bees were flown in a tunnel of the same dimensions, but lined with axial stripes, the bees produced a 'round dance' (Fig. 2), signalling the experience of a very short journey (von Frisch 1993). Evidently, in this case, the absence of optic flow caused the odometer to barely tick over (Srinivasan et al. 2000). These experiments again drive home the point that image motion is the dominant cue that bees use to gauge how far they have travelled.

Determination of travel direction: the celestial compass

There is abundant evidence to indicate that desert ants, as well as bees, rely on the sun to provide a reference compass direction that informs them about the direction of their travel. In desert ants, reversing the sun's apparent position by using a mirror (and using a mask to occlude the sun's real position) causes systematic and predictable changes in the direction of the ants' homing runs (Lanfranconi 1982; Santschi 1913). Experiments in which the sun is occluded, and the homing ants are presented with strips or patches of clear sky reveal that, in the absence of solar cues, ants also rely on the pattern of polarisation, as well as on the pattern of hues that the sun creates in the sky (Wehner 2001). When the sun is not visible, these patterns of polarisation and hue can be used as surrogate compass references because they move with the sun as it transits the sky during the course of the day. In bees, most of the evidence for the use of polarised light-cues for orientation comes from observation of how their waggle dances are affected by systematic changes in the position or the direction of polarisation of an artificial light stimulus that illuminates the interior of the hive (e.g. Rossel and Wehner 1982; von Frisch 1949). Experiments in which ants (or bees) are tested whilst navigating in channels in which the overhead illumination presents only polarised light-cues have revealed that both ants and bees are capable of deriving compass cues purely from polarisation information, although they display the consequences of
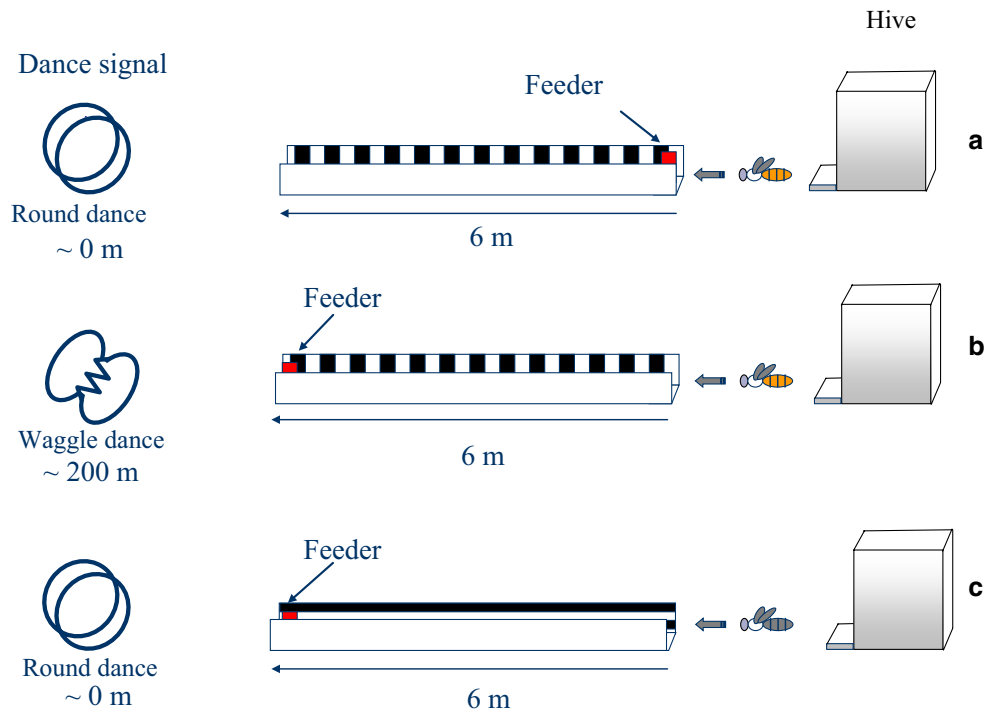
Fig. 2 Honeybee odometry, investigated via the waggle dance. **a** Bees are trained to visit a feeder positioned at the entrance of a short, narrow tunnel near the hive entrance. The returning bees perform a round dance. **b** When the feeder is moved to the end of the tunnel, the returning bees perform a strong waggle dance indicating a travel distance of 200 m, massively overestimating the distance that they have flown in the tunnel. **c** When image-motion cues are eliminated by decorating the tunnel walls with horizontal stripes—rather than vertical stripes as in **a** and **b**—the bees perform a round dance, indicating that their perception of travel distance is based on the extent to which the image of the environment has moved in the eyes during the journey from the hive to the food source. Modified from Fig. 20 of Srinivasan (2011)

the 180° directional ambiguity that is inherent to polarised light (Lebhardt et al. 2012; Evangelista et al. 2014). These experiments will be described in detail later below.

The neural basis of polarisation sensitivity

Work so far is suggesting that the principles that underlie the analysis of polarised light may be conserved across several insect genera (Wehner 1989). Although some of our knowledge about the neural pathways that subserve polarised-light analysis in insect vision comes from *Cataglyphis* (Labhart 2000), most of it comes from crickets and locusts (Labhart and Meyer 2002; Wehner 2003; Homberg 2004), and there is relatively little information, so far, with regard to honeybees. This is because orthoptera seem to be more amenable to electrophysiology of these pathways. The analysis of polarised skylight begins at the polarisation-sensitive photoreceptors in the so-called dorsal rim area (DRA) of the insect eye. There, photoreceptors with orthogonally oriented preferred directions provide antagonistic inputs to second-order neurons, which have small receptive fields and display strong polarisation sensitivity and very low sensitivity to variations in light intensity.

Thus, these neurons, which may be termed "elementary polarisation detector" (EPD) neurons, signal the true local direction of polarisation irrespective of light intensity (Labhart 1988). The small-field EPD neurons feed into interneurons in the medulla, which is the next stage of information processing in the insect visual pathway. These neurons are also polarisation sensitive, but have large visual fields. They can be subdivided into three classes, depending upon their preferred polarisation orientation. The three classes of polarisation-sensitive neurons have preferred directions that differ by approximately 120°, so that they sample the orientation domain uniformly. They constitute the minimum set of polarisation-sensitive channels that would be required to encode a polarisation orientation unambiguously.

In locusts, the responses of neurons to polarised light have also been examined at a much higher level, namely, that of the central complex. At this level, the neurons no longer show just three distinct, preferred e-vector orientations. Rather, each neuron is sharply tuned to a particular orientation, and, collectively, these neurons exhibit a range of preferred orientations that are distributed more or less uniformly over the entire orientation domain, ranging from 0° to 360° (Vitzthum et al. 2002; Homberg 2004; Heinze

and Homberg 2007, 2009). There is evidence to suggest that these neurons combine polarisation orientation information with information about the sun's azimuth to generate a neural celestial compass that can use information based on the position of the sun, on the spectral gradients in the sky, on the polarised-light pattern of the sky, or on all three types of cues, depending upon what the sky offers (Wehner and Mueller 2006; Cheng et al. 2014; el Jundi et al. 2014). Further information on the neural basis of polarisation analysis in the insect visual system can be found in a number of reviews (e.g. Labhart and Meyer 2002; Wehner 2003; Srinivasan 2011; el Jundi et al. 2014).

Other orientational cues

Recent work is beginning to reveal that, in addition to the orientational cues provided by the sky per se—namely, polarisation and hue—desert ants are also capable of using the profile of the skyline produced by the surrounding terrain. Thus, the silhouettes of distant hills trees and buildings provide a position-invariant visual panorama that an ant can use to determine its instantaneous orientation, provided that these silhouettes are not occluded by nearby structures (Graham and Cheng 2009; Philippides et al. 2011; Wystrach et al. 2011). The neural representation of skyline-based orientational information remains to be uncovered.

Path integration

So far, we have reviewed how desert ants and bees determine (1) the distance they have travelled to reach the food source, and (2) the direction of their movement. What remains to be done is to examine how the information on direction and distance are combined to determine the position of the food source in relation to the hive. This process is termed "path integration". If an insect moves in a straight line from its nest to the food site, the distance to the food site is indicated by the odometer, and the direction of the food site is given by the celestial compass. These two items of information define a vector $\overline{V}_1$ that specifies the position of the food source relative to the hive (Fig. 3a). From the food site, the direction of the nest would be obtained by simply reversing the direction of the vector ($-\overline{V}_1$, as shown in Fig. 3a). If an insect sets out on an exploratory journey to seek a food source the outbound path will most likely be a tortuous one, complicating the process of path integration. In this case the curved trajectory of the insect can be approximated by a sequence of short, straight, translatory motions, as illustrated by the vectors in Fig. 3b. The position of the food site with respect to the hive would then be given by a vector $\overline{V}_2$ that is equal to the sum of the vectors
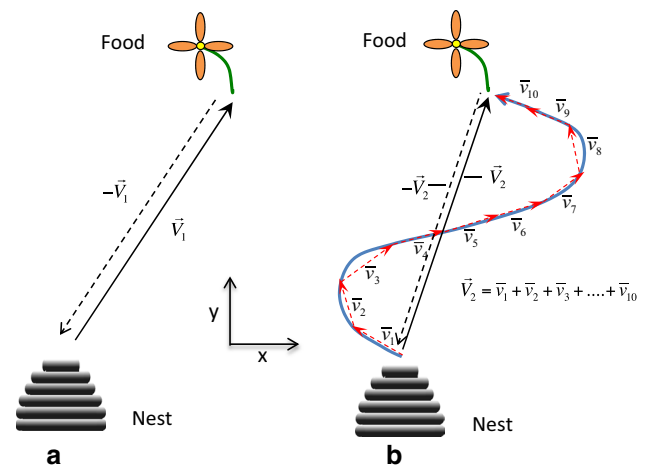

Fig. 3 Path integration. **a** If a bee flies a *straight line* to a source of food, the distance and direction of the food site relative to the nest are specified by the vector $\overline{V}_1$, and the homebound direction and distance are obtained by reversing this vector ($-\overline{V}_1$). **b** If a bee makes a tortuous trajectory before it discovers a food source, the distance and direction of the food site relative to the nest are specified by a vector $\overline{V}_2$ which is the sum of the elementary translational vectors $\overline{v}_1$, $\overline{v}_2$,…, $\overline{v}_{10}$. The homeward vector is $-\overline{V}_2$

$\overline{v}_i$, $\overline{v}_2$,… that represent the elementary translatory motions that the insect has performed on its outward journey, and the distance and direction of home would be obtained by reversing this vector ($-\overline{V}_2$, Fig. 3b).

In principle, one does not need an absolute directional reference (such as the celestial compass) to perform path integration. The insect can instead continuously monitor its turning rate (using proprioceptive or visual motion signals) and integrate this rate to estimate its current direction of travel. But such a scheme is very susceptible to noise in the measurement of the turning rate, which would cause errors in the estimating heading direction to increase rapidly with travel distance, causing it to be impracticable except for very short travel distances (Cheung et al. 2007, 2008). The observation that bees and desert ants can navigate accurately over long distances makes it very likely that they are not measuring and integrating turn rates. Rather, they are using an externally referenced directional compass. Indeed, the work of Lebhardt et al. (2012) provides direct evidence that desert ants do not use idiothetic cues to estimate their orientation.

Path integration in desert ants

As we have seen in the "Introduction", there is clear evidence that desert ants perform path integration. If a desert ant is displaced to a new, unfamiliar location immediately after it has found food, it will run a homing course parallel to the original direction, and when it has travelled a distance that approaches the length of the expected homing
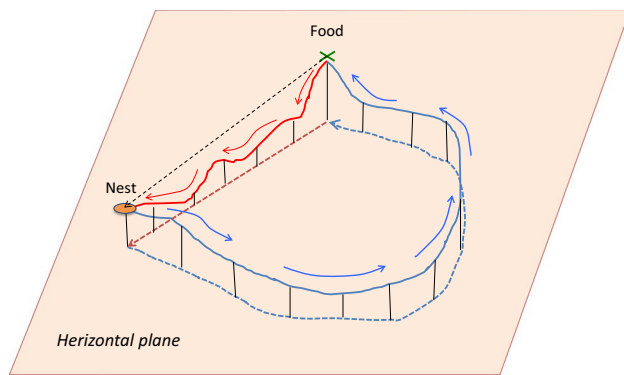
Fig. 4 Illustration of the problem of navigation and path integration in three dimensions. Description in text

vector it will begin to look for the (missing) nest in a stereotyped searching pattern (Fig. 1). This demonstrates that the ant's path integration system has evaluated the distance as well as the direction of home in rough accordance with the scheme illustrated in Fig. 3b. Exactly how this computation is accomplished will be discussed later below.

How do ants cope with the problem of navigation when walking on the undulating terrain that is common in the sand dunes of deserts? In such situations they would be moving in three dimensions rather than two, and in all likelihood the outbound and inbound journeys would cover different regions of the environment, with differently undulating terrain, as illustrated in Fig. 4. How do ants deal with the challenge of navigation under these circumstances? One solution would be to perform path integration in three dimensions. Thus, the path-integrated 3D vector, when reversed in direction, will provide a homing vector that should direct the ant back to its nest accurately (dashed black arrow, Fig. 4). The ant would simply have to run along the azimuthal direction specified by the homing vector until it has fully played out the 3D vector. An alternative strategy would be to measure only the horizontal component of travel by projecting all of the ant's motions on to the horizontal plane, as illustrated by the dashed curves in Fig. 4. Path integration would then be reduced to a two-dimensional problem, and the accuracy of homing would be unaffected by the undulations in height of the outbound and the inbound paths.

Do ants indeed deal with the problem of 3D path integration in this way? A possible answer to this question has been provided by a series of elegant experiments designed to examine how 'podometry' works when ants move on uneven terrain (Wohlgemuth et al. 2001, 2002; Grah et al. 2005). Ants were trained to visit a feeding site by walking along a specially designed channel that had a sawtooth profile, consisting of ramps that sloped alternately upward and downward (Fig. 5). When these trained ants were tested

on their homing runs in a long, straight channel (Fig. 5), they searched at a location that did not correspond to the total 3D distance that they had travelled to reach the feeding site during the training. Rather, they searched at a position that corresponded to a travel distance that was equal to the length of the projection of the undulating trajectory on the horizontal plane. This finding was confirmed by additional experiments in which various channel profiles were used: for example, steeper upward ramps and shallower downward ramps, and vice versa (Wohlgemuth et al. 2002), as well as other configurations (Grah et al. 2005). In all of these experiments, the ants behaved as if they were measuring only the horizontal component of the total distance that they had traversed. Further studies have suggested that navigating ants estimate the local variations in the slopes of the terrain in terms of the variations in the reactive forces that they experience in their legs during locomotion, although the precise nature of the underlying sensing mechanisms is yet to be clarified (Seidl and Wehner 2008). Be that as it may, the above experiments provide strong evidence that *Cataglyphis* deals with the problem of navigation in undulating terrain by projecting its 3D motions on to the horizontal plane.

Path integration in honeybees

Bees, too, appear to perform path integration, although the analogous experiments are more difficult to perform because they fly long distances in three dimensions, making it difficult to record their movements. Recent advances in harmonic radar tracking technology (e.g. Capaldi et al. 2000; Riley et al. 2005) are making it feasible to begin to investigate path integration in flying insects. A harmonic-radar study in which trained bees were displaced from a feeding site and released at a new, unfamiliar location indicated that they, too, showed a homing behaviour similar to the displaced desert ants (Riley et al. 2005), although these experiments do not shed direct light on the underlying path integration strategy.

In the meantime, the bulk of our knowledge about path integration in flying honey bees has come from observing the waggle dance, which provides an excellent readout of the bee's path integration system. The waggle dance opens a window into the bee's mind to reveal how far, and in which direction, the bee thinks it has travelled. Dancing bees always signal the bee-line direction to a food source even if they have to circumvent a large obstacle to reach it (von Frisch 1993). Interestingly, however, the distance signalled by these dancing bees is not the length of the resultant (short cut) vector, but the total length of the circuitous path that they are forced to take as a result of the detour—a much larger distance. Thus, when bees are trained to fly around a hill to find a feeder on the other side, by moving

Fig. 5 Experiment investigating odometry on undulating terrain. Ants are trained to leave their nest and walk through a sawtooth-profiled channel to receive a food reward at the far end. The trained ants are then tested by releasing them at the end of a straight tunnel oriented in the same direction. The homing ants search for their nest at a point along the tunnel at a distance that corresponds to the projected distance of the outbound journey on the horizontal plane, although the actual 3D distance traversed by the ants on their outbound journey is much longer
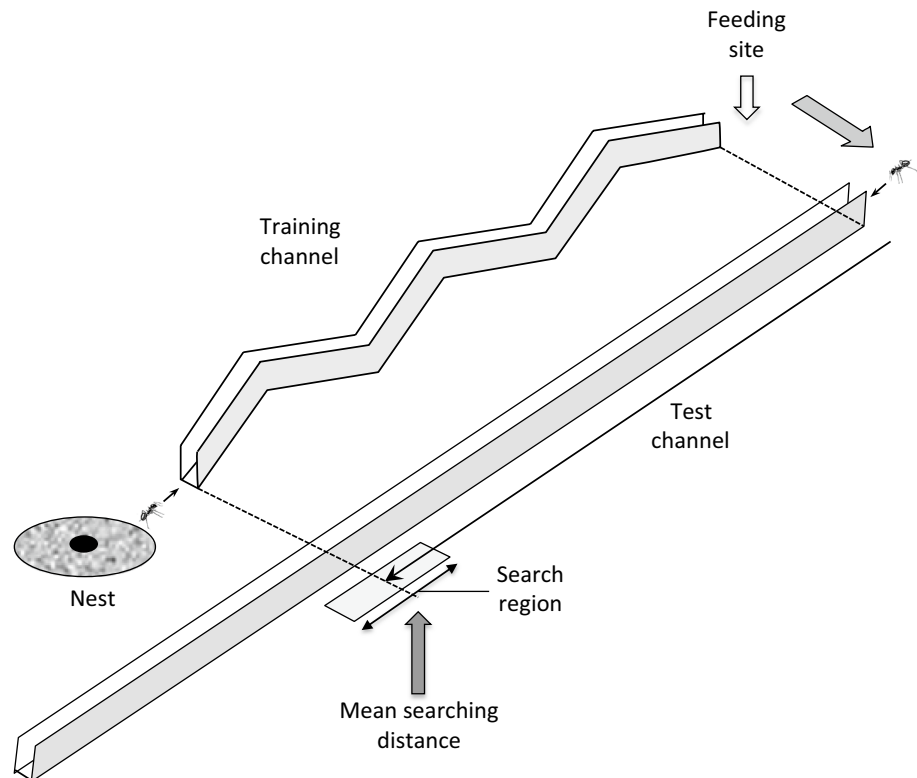
the feeder step by step around the perimeter of the hill—thus making a large detour on the way to the food—they signal in their waggle dances the vector direction of the food source from the nest, but the perimeter length of the circuitous journey, rather than the vector distance [(von Frisch 1993), pp. 174–180]. However, the bees that are recruited by the dance never take the detour—they heed the dancer's instructions and take the short cut over the hill, rather than fly around it [von Frisch (1993), pp. 178–80; Gould and Gould (1988), p. 64].

When bees are forced to make detours, why do they signal the total path length to the target rather than the direct vector distance, given that the recruits take the short cut? One reason may be that even the short-cut route over the hill is likely to be longer than the direct distance between the hive and the nest in the horizontal plane, because the short-cut actually involves flying up and down the hill. In one such detour experiment conducted by von Frisch and Lindauer in 1950, the route around the hill was 133 m, the length of the short-cut vector in the horizontal plane was 80 m, and the length of the actual flight along the short-cut route that the recruits took (up and down the hill) was 150 m [(von Frisch 1993), p. 177].

Signalling of the perimeter distance in dances is also observed when bees fly journeys in the vertical plane. In one investigation, bees were trained to fly through an L-shaped tunnel that required them to fly initially through

a vertical section (during which their eyes experienced vertically directed optic flow) and then through a horizontal section (during which the eyes experienced horizontally directed optic flow). The distance that the bees then signalled in their waggle dances corresponded to the optic flow that was experienced over the total distance flown in the tunnel, rather than the distance corresponding to the hypotenuse (Dacke and Srinivasan 2007).

In a more recent study, bees were flown along a straight tunnel that simulated flight through an L-shaped tunnel, by rotating the artificial overhead compass cues by 90° halfway down the tunnel (Evangelista et al. 2014). This was accomplished by providing polarised overhead illumination that was oriented perpendicular to the tunnel axis in the first half of the tunnel, and parallel to the tunnel axis in the second half. Because of the 180° ambiguity in the compass directions that were inherent to each direction of polarisation, there are four possible directions in which the feeding site could have been located—oriented at 45°, 135°, 225°, and 315° with respect to the forward direction of the tunnel axis. Interestingly, bees returning from the tunnel signalled precisely these four directions in their dances, fully reflecting the directional ambiguity that was inherent in the polarised illumination that they had experienced on their outbound journey. Indeed, some individuals indicated all four directions within a single dance (Evangelista et al. 2014). However, the bees did not indicate the apparent vector

distance to the destination, which would have been ($d/\sqrt{2}$), where d is the tunnel length. Rather, they signalled a distance that corresponded to the full length (d) of the tunnel (which is the perimeter length of the virtual L-shaped tunnel). In a sense, this finding can be viewed as a scaled-down, laboratory-based confirmation of von Frisch's hill-detour experiment described above.

The results obtained in these polarised-light experiments are very similar to those obtained in an earlier, analogous study of the homing behaviour in *Cataglyphis* (Lebhardt et al. 2012). There, ants were released to return home under an open sky after having been trained to forage at a feeding site at the end of a tunnel in which the overhead illumination was polarised in a direction parallel to the tunnel axis in the first half of the tunnel and perpendicular to the tunnel in the second half, or vice versa. Individual home-bound ants ran along one of the four different directions as mentioned above. However, the ants searched for the nest after traveling a distance that corresponded to the apparent *vector distance* ($d/\sqrt{2}$), and not the full length of the tunnel (d).

In summary, when performing path integration along real (or virtual) detours, both bees and ants appear to extract the vector direction of the food site. However, while ants also extract and use the vector distance of the food site in performing their homing runs, bees seem to extract and signal the total (perimeter) distance in their dances. Why are bees different from desert ants with respect to estimating the distances in a journey that involves a detour? Further work is required to answer this question. However, one reason could be that bees, as discussed above, may need to signal the total flight distance to their nest mates in their dances, in order to convey accurate information on the actual length of the journey. Desert ants, on the other hand, do not necessarily require information about the total length of the meandering path that they took to find their food. One reason is that their environment is usually barren and devoid of obstacles that necessitate large detours. Furthermore, these ants do not recruit their nest mates to feeding sites. In the desert, naturally occurring food items (such as dead insects) are small and sparsely distributed. Given these conditions, there is no need for recruitment, and thus desert ants appear well adapted to using the vector distance to get home. After all, it is the linear vector connecting the feeder to the nest that defines the true spatial relationship between these locations.

Interaction of path integration with landmark information

This review has been confined to a description of the navigational strategies that are used by desert ants and honeybees in terrains that are devoid of landmarks. In such circumstances, they can rely only on path integration to establish were they are in relation to home or to a food source. However, it is now well known that both ants and bees can also use information derived from prominent landmarks—if present in the environment—to augment, or even substitute for the information that is available from path integration. For example, landmarks that are learned during repeated visits to a food source can be used as beacons that signal the direction of the food source, or be used as known 'waypoints' en route to the feeder. Such waypoints can serve to correct for errors in odometry and path integration (Srinivasan et al. 1997). Indeed, path integration can even be eschewed in favour of landmark-based navigation in areas that carry an abundance of landmarks. It is also known that bees and ants acquire and use visual 'snapshots' of the nest and the feeding site for the purpose of homing in on their destination, toward the end of the journey. There is a rich and extensive body of research documenting the interactions between path integration and landmarks during navigation in desert ants as well as honeybees. A detailed discussion of these studies is beyond the scope of the present article and the interested reader is referred to some of the excellent reviews that exist in the literature, for example (Wehner 1981, 1992; Collett and Zeil 1998; Judd and Collett 1998; Collett and Collett 2002; Collett et al. 2003; Wehner et al. 2006; Collett 2009).
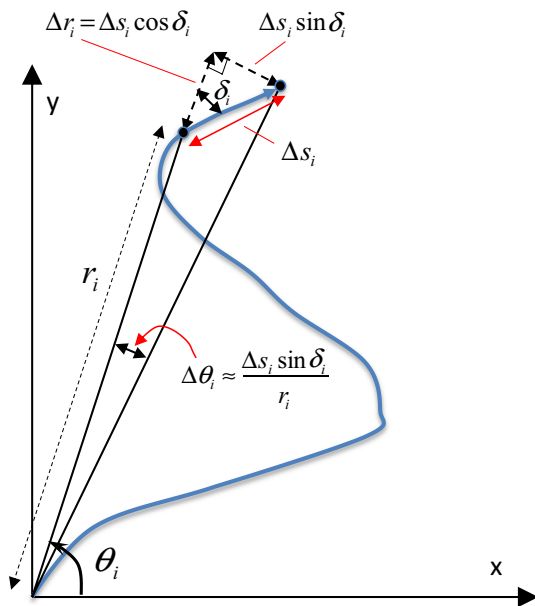
Models of path integration

Given the relative ease with which experimenters can follow relatively short, two-dimensional trajectories of desert ants—as opposed to the long and three-dimensional trajectories of bees—the former have led to the development of quantitative models of path integration, some of which are outlined briefly below.

The simplest and most direct model of path integration is one in which the ant's position at any point along its outbound trajectory is estimated by considering the trajectory to be composed of a number of short, linear segments, as illustrated in Fig. 3. The position of the ant relative to its nest ($\overline{V}_i$) at the end of the nth segment is then specified by a vector that is the sum of the vectors $\overline{v}_i$ that represent the individual segments:

$$\overline{V}_i = \sum_1^n \overline{v}_i.$$

One way to obtain this vector sum would be to separately sense and sum the components of motion along two orthogonal axes, x and y, in an external geocentric frame of reference as shown in Fig. 3 [see, for example, (Mittelstaedt and Mittelstaedt 1982)]. Thus, the x and y components of

Fig. 6 Illustration of a model that performs approximate path integration, as proposed by Mueller and Wehner (1988), based on the study of navigation in the desert ant. Modified from Fig. 2c of Mueller and Wehner (1988). Details in text

the position of the ant relative to its nest at the end of the ith step, V_i^x and V_i^y, are given by $V_i^x = \sum_{i=1}^{n} v_i \cos \theta_i$ and $V_i^y = \sum_{i=1}^{n} v_i \sin \theta_i$, where v_i is the size of the ith step, θ_i is the direction of the ant's movement during this step, and $v_i \cos \theta_i$ and $v_i \sin \theta_i$ represent the x and y components of motion, respectively, during the ith step. The sizes of the individual steps would be provided by the odometer, and the directions of the individual steps would be provided by the celestial compass. While this is obviously an accurate mathematical solution to the problem of path integration, it is not clear if this is indeed the way in which the problem of path integration is solved by the ant's nervous system, and whether the ant's motions are indeed sensed along two mutually orthogonal directions in an external frame of reference.

An alterative model that represents a 'quick and dirty' solution to the problem of summing vector components has been proposed by (Mueller and Wehner 1988). Their model is based on the observation that at the end of each step i on the outbound journey (see Fig. 6), the change Δr_i in the ant's distance to the nest and the change $\Delta \theta_i$ in the ant's bearing relative to the nest can be approximated by $\Delta s_i \cos \delta_i$, and $\frac{\Delta s_i \sin \delta_i}{r_i}$, respectively, if the ant is sufficiently far away from the nest that the step size (Δs_i) is small compared to the current nest distance (r_i). The ant's distance (r_n) and bearing (θ_n) relative to the nest at the end of the nth step are then given approximately by $r_n = \sum_{i=1}^{n} r_i$, and $\theta_n = \sum_{i=1}^{n} \Delta \theta_i$, respectively.

How does the ant perform the requisite computations at the neural level? Although the answer is not yet clear, Mueller and Wehner (1988) and Hartmann and Wehner (1995) have proposed an ingenious neural architecture that could provide a starting point for neurophysiological investigations. In this scheme Δr_i and $\Delta \theta_i$ are approximated by the following functions:

$$\Delta \theta_i \sim k \frac{\delta_i (180° + \delta_i)(180° - \delta_i)}{r_i} \tag{1}$$

and

$$\Delta r_i \sim 1 - \frac{|\delta_i|}{90°}. \tag{2}$$

The variable δ_i is monitored by keeping track of the ant's present orientation (via the celestial compass), and subtracting from it the current bearing of the ant relative to the nest (see Fig. 6). The angles θ_i and δ_i are encoded as activities in two circular arrays of neurons, each arranged in the form of a ring. Subtractions and additions are performed by representing the results in a third circular array that receives appropriate excitatory or inhibitory inputs from the two input arrays. Multiplication (as required in Eq. 1, for example) is performed by representing each of the factors (δ_i), $(180° + \delta_i)$ and $(180° - \delta_i)$ in three separate circular arrays, and performing 'and-like' gating operations across the outputs of corresponding neurons in these arrays. The final result is represented as the number of neurons that are active in an output array that carries the result of this gating operation. Details of the model are given in Hartmann and Wehner (1995). An interesting feature of the model is that it predicts some of the systematic errors that the real ants display in their path integration performance. Specifically, if the ant makes a sharp backward turn on its outbound trajectory before arriving at its goal, then it invariably undershoots the nest on its return journey (Mueller and Wehner 1988). This apparent imperfection in the real ant's path integration system is faithfully reproduced by the model (Hartmann and Wehner 1995), making it an attractive starting hypothesis for investigating the neural basis of path integration in the desert ant, and/or the bee.

Haferlach et al. (2007) present another scheme for path integration, also based on a neural network that features a circular array of neurons. However, in this case the network is evolved using a genetic algorithm approach, and the resulting network represents the homing vector as population code over a set of memory neurons that integrate the input during the outbound journey from a set of direction-encoding neurons. While these are attractive models with plausible neural correlates, it remains to be seen whether the brains of these creatures indeed work with navigational variables by representing them as activities in circular arrays of neurons.

Fig. 7 Model of path integration based on an array of neurons analogous to "place cells" in the vertebrate hippocampus. **a** Motion in a fixed direction toward a feeder, under an open sky that offers unambiguous directional cues, causes sequential activation of place cells along the route. **b** Motion in a tunnel illuminated with transversely polarised light causes place cell activity to proceed in two opposite directions, one towards a fictive sun and the other away from it, reflecting the 180° directional ambiguity that is inherent to polarised light
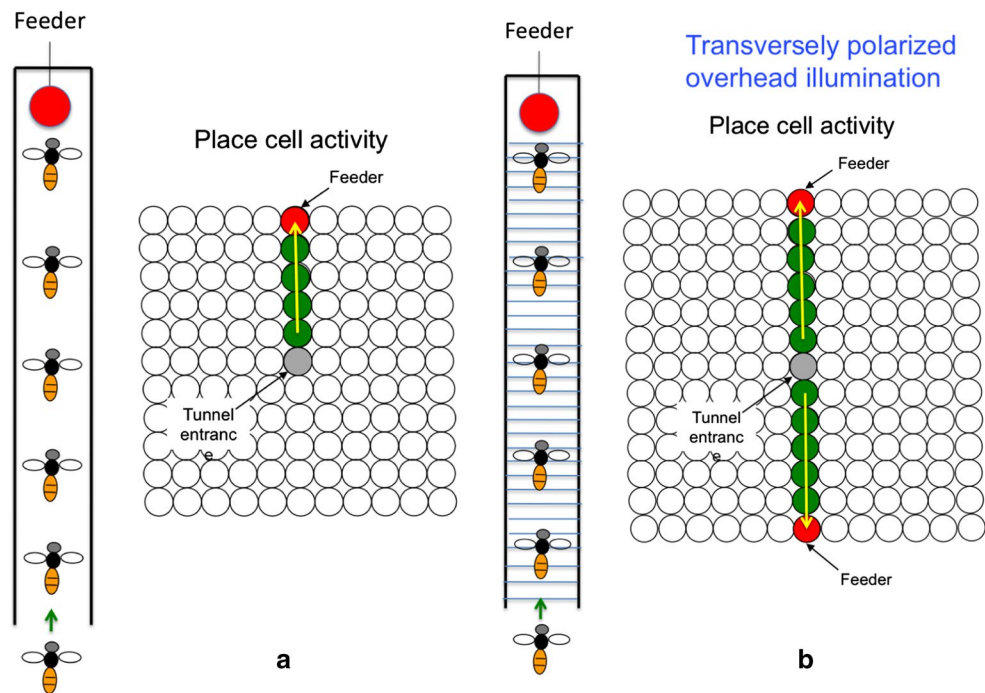
Another model (Evangelista et al. 2014) posits that the insect's spatial location is represented by the activity of an ensemble of "place neurons" located in the mushroom body complex, (Mizumani et al. 1998a, b), analogous to the "place neurons" that exist in the hippocampus of rodents and primates (O'Keefe and Nadel 1978; Ekstrom et al. 2003). If this were the case, the bee's flight toward its destination would induce transient activity in a succession of place neurons that would register the passage through successive locations along the journey, as illustrated in Fig. 7a. The place neuron that is active at the end of the journey would represent the location of the food source, as well as the distance of the food source from the hive. In this scheme, there would be no need to accumulate spike counts over the entire journey—it would only be necessary to shift the activity from one place neuron to the next, every time the incremental odometric signal that has accumulated since activating the most recent place neuron, has reached a prescribed threshold magnitude.

If an ant or a bee is trained to find food at the end of a tunnel with the transversely oriented e-vector illumination, for example, the two possible locations of the food source would be represented by the firing of two place cells, one corresponding to a location at the appropriate distance from the hive in the direction of the sun, and the other to a location at the same distance, but in the opposite direction, as shown in Fig. 7b (Evangelista et al. 2014). Training in a tunnel that provides axial e-vector illumination would lead to activity in two other place cells, again representing two locations equidistant from the hive, but which would be reached by flying in directions that are 90° to the left or the right of the sun (Fig. 8a). Extending this reasoning one step further, training in a tunnel with transverse e-vector illumination in the first half and axial e-vector illumination in the second half would lead to activity in four different place cells, each positioned at the vertex of a square and representing a location of the food source along one of the diagonal directions (Fig. 8b).

One of the attractive features of such a scheme is that it not only performs path integration, but is also capable of representing multiple target locations simultaneously, within the mushroom body complex of an individual bee. Whether this is indeed how the brain represents ambiguous locations, remains to be explored.

This review has only considered navigation by means of path integration, and has not included a discussion of the various ways in which insects use landmarks and other prominent features to increase navigational accuracy. It is known, for example, that bees can learn salient landmarks en route to a goal and use them to restrict the inevitable accumulation of odometric errors that accompany increasingly long journeys (Srinivasan et al. 1997). There are many other ways in which landmark information is combined with, or used interchangeably with the path integration process, to enhance the accuracy of navigation. For details, the reader is referred to some of the numerous papers and reviews on the subject, for example (Collett and Graham 2004; Kohler and Wehner 2005; Cheng et al. 2009; Collett et al. 2013; Cheng et al. 2014).
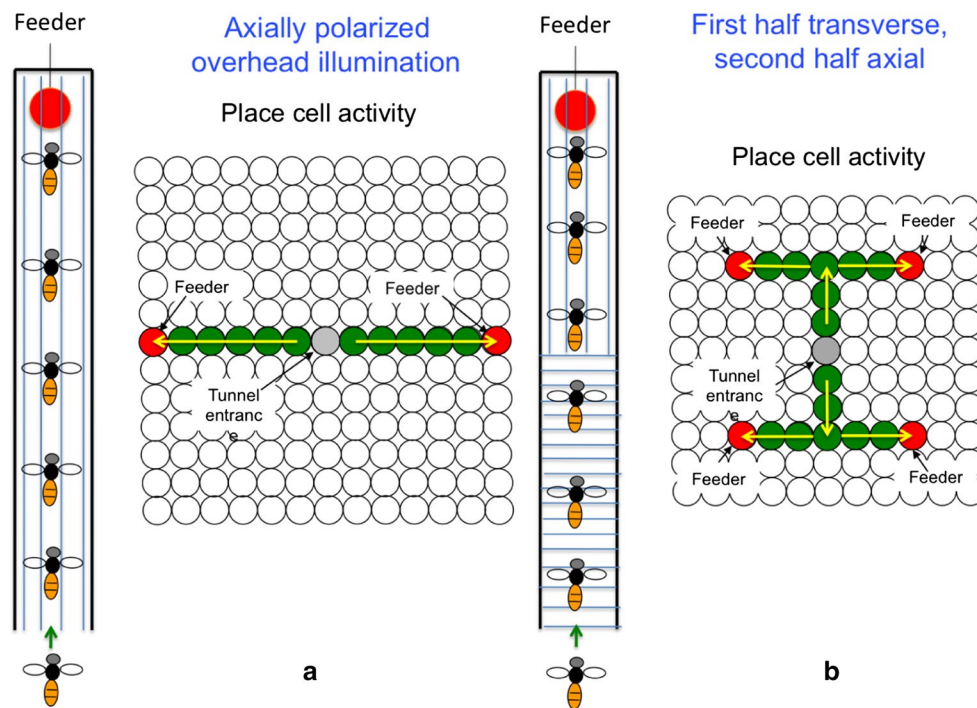
Fig. 8 Model of path integration based on an array of neurons analogous to "place cells" in the vertebrate hippocampus (continued). **a** Motion in a tunnel illuminated with transversely polarised light causes place cell activity to proceed in two opposite directions, 190° to the *left* of a fictive sun and the other 90° to the *right* of it, reflecting the 180° directional ambiguity that is inherent to polarised light.

b Motion in a tunnel in which the first half is illuminated with transversely polarised light and the second half with axially polarised light causes place cell activity to propagate towards and against the fictive sun during the first half of the journey, and along directions 90° to the *left* or *right* of the sun during the second half, reflecting the fourfold ambiguity in the location of the food source

A comprehensive model that characterises path integration, interaction with landmarks and visual panoramas, and incorporates a desert ant's various navigational and motivational states is described in (Cruse and Wehner 2011; Wehner et al. 2014).

Future directions

One of the exciting future challenges is to uncover the neural circuits that underlie odometry and path integration, and to understand how they carry out the requisite computations. Although neurons sensitive to visual motion have been documented and characterised in the honeybee (e.g. Kaiser and Bishop 1970; Paulk et al. 2009) and in many other insects including the fly (e.g. Egelhaaf et al. 2005; Borst 2009), we do not know whether, and if so which of these neurons or neural pathways plays a role in odometry. Furthermore, although we are beginning to obtain a picture of where and how compass directions are represented in the brain (as outlined earlier in this article), we have little knowledge of how information on the current direction of motion is combined with information about the current incremental distance

travelled—in a moment-to-moment fashion—to perform path integration. The models of path integration outlined briefly above offer a few starting points for investigation. Promising recent technological developments are the use of virtual-reality arenas within which an insect is tethered and allowed to walk on a light sphere supported by an air cushion, while it views a panoramic visual scene (e.g. Moore et al. 2014). Optoelectronic sensors viewing the surface of the sphere, or a video camera viewing the sphere from a distance, are used to monitor the sphere's rotations about three orthogonal axes, and to thus infer the insect's translations and rotations in a moment-to-moment fashion. The inferred movements of the insect are used to modify the panorama to simulate the changes in the visual scene that the insect would experience as it moves through its simulated world. If walking ants or bees can be persuaded to forage in virtual environments of this kind, one can record neural responses from various brain regions while the insect learns to navigate to a virtual feeding site where it receives a reward. Indeed, it is now technically feasible to record the electrophysiological responses of neurons in various brain regions while an insect walks in such a virtual-reality arena (e.g. Chiappe et al. 2010; Seelig et al. 2010; Paulk et al. 2014).

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