

# Path integration in insects

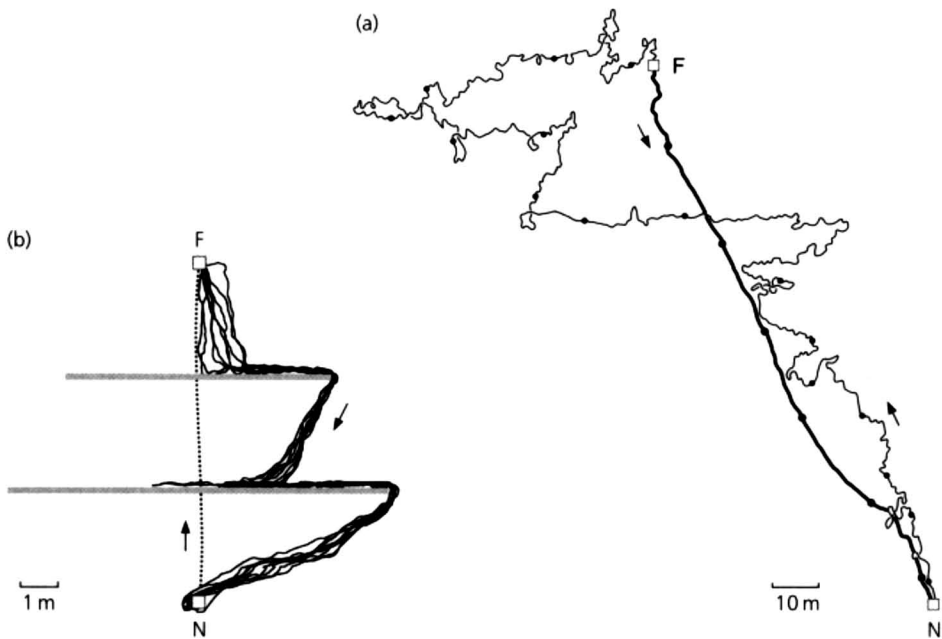
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### Introduction

The most highly advanced social insects such as bees and ants are impressive, long-distance navigators. They forage over distances of hundreds of metres (ants: Wehner 1987) or even kilometres (bees: Visscher and Seeley 1982) from their home base, thus routinely travelling over unfamiliar territory for distances of several thousand times their body lengths. During these foraging journeys they integrate circuitous outbound paths into straight inbound vectors, enabling them to return to their point of departure along the shortest route. Later, during the next foraging trip, they can use the 180° reversal of this 'home vector' in order to return directly to the previously visited feeding site (Fig. 1.1). In human navigation this feat of navigation—continuously keeping track of one's own position relative to the point of departure—was historically called 'dead reckoning'. In animals, the terms 'path integration' (Mittelstaedt 1983) and 'vector navigation' (Wehner 1983) have been introduced.

How do animals accomplish this dead reckoning (path integration) task? In principle, they must continuously record the rotational and translational components of their movement and integrate these angular and linear data into their current home vector. They may obtain the necessary information by relying exclusively on motion cues: that is on various signals derived from the animal's own locomotor activities. A good example of such a system is the inertial navigation system used in aeronautics, where the angular and linear accelerations experienced by the navigator, during all the twists and turns, are recorded and double-integrated over time (Barlow 1964; Mayne 1974; Wiener and Berthoz 1993). Similarly, when foraging at night, rodents such as mice and gerbils depend on inertial navigation by using signals from angular (vestibular) and linear (otolithic) acceleration sensors. This information is supplemented by somatosensory information and stored motor commands (Mittelstaedt and Mittelstaedt 1980, 1982; Mittelstaedt and Glasauer 1991; Etienne *et al.* 1996). Wandering spiders, *Cupiennius salei*, also active at night, integrate their paths by drawing upon proprioceptive information from cuticular strain receptors, the so-called lyriform slit-sense organs, which are located near the joints of the spider's legs. If these organs are experimentally destroyed, the homing abilities of the spiders are abolished (Seyfarth and Barth 1972; Seyfarth *et al.* 1982).

Path integration systems that depend exclusively on self-generated motion signals have one great disadvantage: they are severely constrained by the rapid accumulation of errors (for experimental demonstration see Etienne *et al.* 1988, for theoretical arguments see Benhamou *et al.* 1990). The problem of error accumulation is exacerbated by the fact that path integration systems, operating without reference to any external guides, must run



**Fig. 1.1** Path integration in desert ants, *Cataglyphis fortis*. (a) Path integration during foraging: vector summation results in a continually updated home vector. The 592-m and 18.8-min outward run (thin line) and the 140-m and 6.5-min homeward run were recorded in a North African salt pan. Time marks (small black dots) are given every 60 s. (b) Vector subtraction during enforced detours. An individually marked ant having performed straight outbound runs (dotted line) was forced away from its direct homeward route by two barriers. Each time it recovered from the imposed detour, it reoriented directly towards the goal. N and F denote the nesting and feeding site, respectively. Modified from Wehner and Wehner (1990), and Andel and Wehner (unpubl.).

continuously and cannot be shut off even if the animal is exploring the local vicinity of a feeding site. It is no surprise, then, that path integration systems operating purely on the basis of self-generated signals are used primarily by nocturnal animals during short-range foraging endeavours.

Diurnal long-distance foragers, such as bees and ants—the supreme navigators of the insect world—are able to employ external systems of reference in order to determine their angular (and to a certain degree also linear) components of movement. The angular movements are monitored by a visual compass that relies on cues emanating from the sky: the direct light from the sun (Santschi 1911) and the scattered light from the sky (von Frisch 1949). The latter generates marked spectral and polarization (so-called electric vector or ‘e-vector’) gradients extending across the entire celestial hemisphere. In general, cues from skylight are the ones that are most appropriate for taking compass readings. As the sky is virtually at infinity, it will produce image motion in the retina only when the animal rotates, and not when it translates. This greatly simplifies the animal’s task of disentangling these two kinds of motion as it proceeds with path integration.

In contrast to the sky, objects on the ground are located at finite distances from the animal. Hence, such objects induce retinal image motion even when the animal translates. Consider an animal that is moving along a straight path. The retinal image flow it experiences while moving should provide it with some means of monitoring distance travelled. Of course, the use of this flow-field information as an accurate odometric cue is somewhat confounded by the fact that the induced image velocity depends not only on the animal's speed of locomotion but also on the bearing and distance of the object: the image velocity is higher when the object is closer or located more laterally to the direction of locomotion. Nevertheless, as we shall see later, flying insects (such as bees) do exploit retinal image motion induced by the ground and by terrestrial objects, such as trees and bushes, for inferring how far they have travelled. Interestingly, the systems for measuring rotation and translation reside in different parts of the insect's eye and brain, providing a striking example of parallel coding.

In the chapter that follows, we first discuss how the insect's compass and odometer work as well as the manner in which their outputs are combined. Then we shall return to the path integration system in general and examine how central place foragers such as bees and ants make use of the results of the path integration process. It will become apparent that the path integration system provides vectors that guide the animal to nesting and feeding sites, or from one waypoint to another, and endows the animal with a framework for acquiring and using spatial knowledge about its environment. In solving these navigational problems in an *ad hoc* rather than *ab initio* way, the insect accomplishes high-level tasks by context-dependent low-level means.

## Compass orientation

### Use of the sun

Santschi (1911) observed that harvester ants, *Messor barbarus*, changed their homeward courses by 180° when the ants' view of the sun was obscured by a screen and the image of the sun was mirrored towards the ants from the opposite side. This was the first demonstration that an animal could use the sun as a compass cue. Four decades had to pass until the sun compass was discovered in another group of animals as well—birds (Kramer 1951). More recent mirror experiments performed in desert ants, *Cataglyphis bicolor*, have shown that it is only the horizontal component of the position of the sun (solar azimuth) rather than the vertical component (solar elevation) that provides the animal with compass information (Lanfranconi 1982). This is a sensible strategy, because during the course of the day any particular azimuthal position of the sun occurs only once, but any particular elevation occurs twice: in the morning as well as in the afternoon.

However, using a point-light source such as the sun as a compass cue has snags. First, a point-light source can easily vanish from an animal's field of view if it is obscured by clouds or vegetation. Second, the accuracy with which the solar azimuth can be read from the sky deteriorates rapidly with increasing elevation of the sun (Wehner 1994). Any compass mechanism is relieved from such constraints if it is based on extended celestial patterns such as the large-scale polarization and spectral gradients that result from the scattering of sunlight by the air molecules within the earth's atmosphere. Indeed, it is from these patterns, especially from the former, that bees and ants derive their most powerful compass information. Note, however, that these skylight cues change their position during the course of the day. As we shall see later, insects can accommodate this change with a time compensation mechanism.

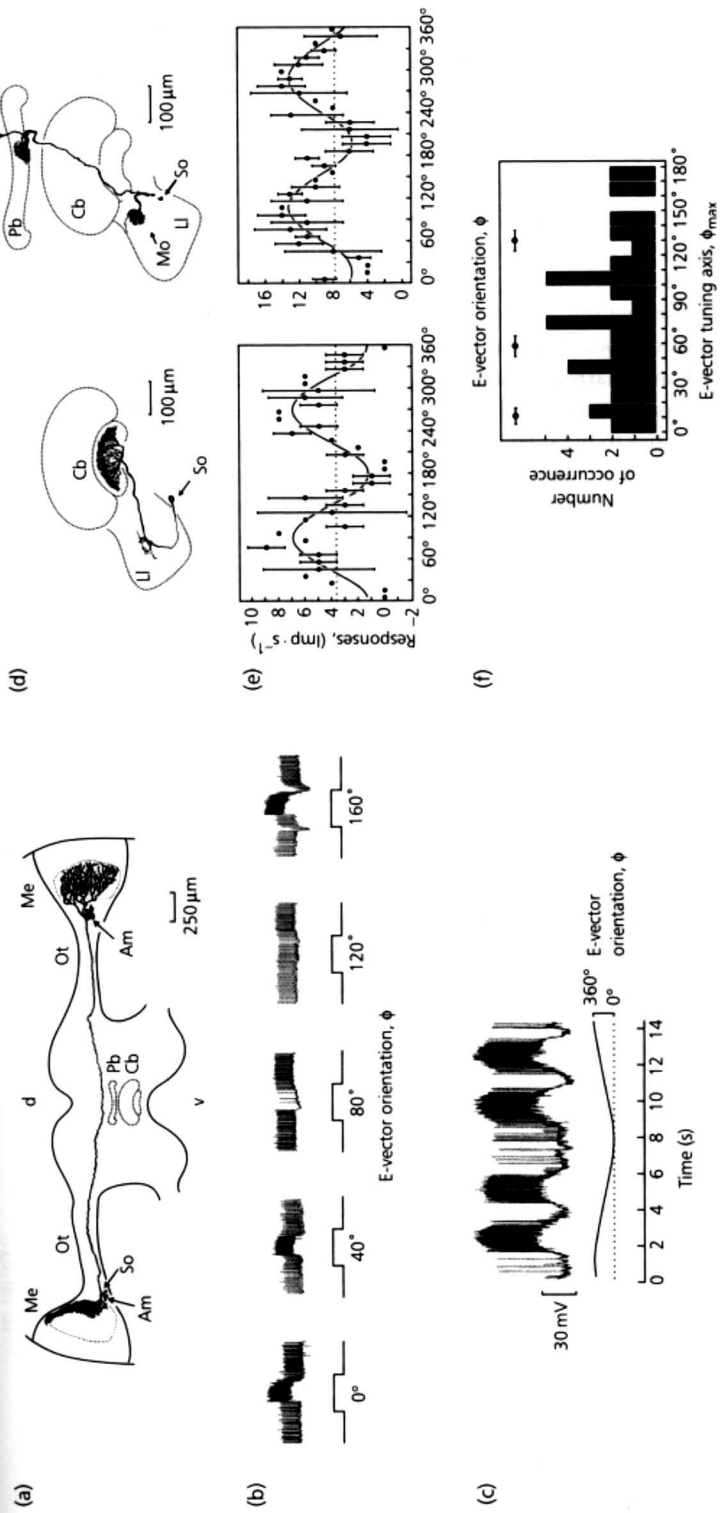
## Use of polarization cues

Unlike humans, insects are able to perceive a striking optical phenomenon in the sky: the pattern of polarized light (e-vector pattern). In each pixel of sky the plane within which the electric vector (e-vector) of light oscillates is oriented in a particular way (the angle of polarization or e-vector orientation). The distribution of e-vectors varies with the elevation of the sun. However, one geometrical feature is common to all of the resulting e-vector patterns: along the solar and the antisolar meridians, the skylight is invariably polarized parallel to the horizon (horizontal e-vector orientation). At all other points in the sky, the direction of polarization changes as the sun migrates in the sky during the course of the day.

The first to show that insects can use skylight for navigation was von Frisch (1949). He presented honeybees with the view of a small patch of sky while they were performing their recruitment dances on a horizontal comb. When he positioned a sheet of polarizer above a dancing bee and then rotated the polarizer, the bee changed the direction of its dance accordingly. Since the time of that classic experiment, extensive further work has shown that bees and ants can deduce any compass course—say,  $30^\circ$  to the left of the solar meridian—by viewing any particular patch of any e-vector pattern in the sky, even if this patch is only  $5\text{--}10^\circ$  wide (see Wehner 1994, 1997 for reviews).

As we now know from a combined behavioural and neurobiological approach, in ants and bees this demanding task is accomplished by an amazingly small part of the insect's visual system which receives its input from a tiny fraction of the photoreceptors of the eye (6.6 per cent in *Cataglyphis bicolor*: Wehner 1982; Fent 1985, and 2.5 per cent in *Apis mellifera*: Wehner *et al.* 1975; Wehner and Strasser 1985). It is only in this uppermost dorsal part of the eye (POL area) that molecular and cellular specializations render the photoreceptors highly sensitive to polarized light, whereas in the remainder of the eye polarization sensitivity is markedly reduced or even completely abolished (Wehner *et al.* 1975; Labhart 1980, 1986; Meyer and Domanico 1999). Furthermore, in both ants (Duelli and Wehner 1973) and bees (v. Helversen and Edrich 1974) the polarization compass uses only information provided by the ultraviolet (UV) receptors. Within each detector unit (ommatidium) of the POL area there are two sets of UV receptors that have their microvilli, and hence their e-vector tuning axes, oriented in mutually perpendicular directions (Labhart and Meyer 1999). Signals from these two sets of receptors interact antagonistically at the first synaptic level (Fig. 1.2) These specializations amplify the polarization signal and, more importantly, render the system insensitive to the intensity fluctuations that inevitably occur in the sky during the course of the day.

Populations of many such small-field e-vector detectors converge on to a small number (probably only three) of large-field integrator neurons in the medulla of the insect's visual lobes (Fig. 1.2a–c). These integrator neurons have been characterized best in the visual system of crickets, which due to their relatively large size are more readily amenable to electrophysiological analysis than are bees or ants (Labhart 1988; Labhart and Petzold 1993; Petzold 2001). Nevertheless, similar neurons have been found in *Cataglyphis* too (Labhart 2000). Since each integrator neuron is served by a different population of local e-vector detectors, the e-vector tuning axes of the three integrator neurons are different. In fact, they are separated by about  $60^\circ$  from one another, thus sampling the sky more or less uniformly in azimuth. Each integrator neuron has contralateral arborizations (Petzold 2001), and binocular, polarization sensitive neurons have been found further upstream in the central complex of locusts (Vitzthum 1997; Fig. 1.2d, e). Thus, it is likely that the



**Fig. 1.2** Polarization-sensitive interneurons in the insect's brain. (a) Integrator neuron in the visual lobes of the cricket, *Gryllus campestris*. Left, ipsilateral (input) side; right, contralateral side. (b) Intracellularly recorded e-vector responses of an integrator neuron as shown in (a). Antagonistic interactions between orthogonally arranged sets of retinal analysers. Vertical e-vectors (0°) cause depolarization and an increase of the spontaneous firing rate, while horizontal e-vectors (90°) result in hyperpolarization and a decrease in spike frequency. (c) Integrator responses as shown in (b), but resulting from stimulation with a beam of light, in which the e-vector was rotating (through two full cycles). (d) Polarization sensitive neurons in the central complex of the brain of the locust, *Schistocerca gregaria*: left, tangential neuron TL2; right, columnar neuron CP1. (e) E-vector responses of the neurons shown in (d). Means  $\pm$  SD. Dotted lines, spontaneous firing rate; thick solid lines,  $\sin^2$  fitting curves revealing e-vector tuning axes ( $\phi_{\text{max}}$  values) of 88° (left) and 113° (right). (f) Distribution of  $\phi_{\text{max}}$  values (orientation of e-vector tuning axes) of polarization-sensitive neurons in the medulla (upper part of figure: means  $\pm$  SD) and the central complex (black-bar histogram). 0° (–180°) marks the longitudinal body axis. Am, accessory medulla; Cb, central body; d, dorsal; Li, lateral accessory lobe; Me, medulla; Mo, median olive; Ot, optic tract; Pb, protocerebral bridge; So, soma (cell body); v, ventral. Combined and modified from Labhart and Petzold (1993), Petzold (2001), and Vitzthum et al. (2002).

polarization compass contains three binocular integration neurons with largely overlapping visual fields, and e-vector tuning axes separated by about 60° from one another.

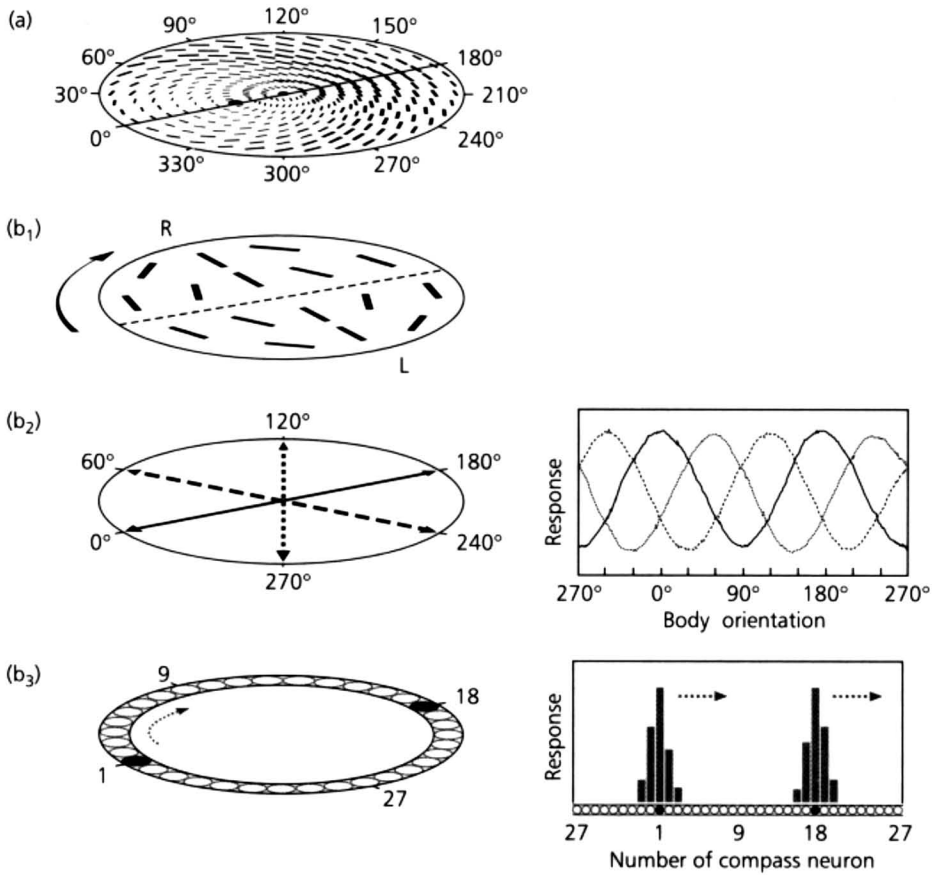
On the basis of these neurophysiological findings, one could propose the following hypothesis about how the compass might work (Fig. 1.3; for a simple means by which the insect could determine the position of the solar vertical see Rossel and Wehner 1984a, 1986; Wehner and Rossel 1985). Each point of the compass—that is, each direction in which the animal could be facing—is characterized by a specific pattern of responses of the three wide-field integrator neurons (for an opto-electronic simulation and robotics implementation of this model see Lambrinos *et al.* 1997). Following an assumption made by Hartmann and Wehner (1995), one could propose that the response patterns of the integrator neurons are neurally transformed into a position code and that the broad-band responses of the integrator neurons are transformed into narrowly tuned responses of an array of ‘compass neurons’. Each compass neuron would be activated maximally when the animal is heading in a particular compass direction relative to the solar azimuth (Wehner 1998; Fig. 1.3). Recently Labhart and Lambrinos (2001) have proposed a feed-forward neural network, with excitatory and inhibitory connections between layers of neurons, that could accomplish this task: i.e. lead to the selective activation of compass neurons as shown in Fig. 1.3b<sub>3</sub> (right figure).

It might well be that such direction-coding compass neurons are found among the polarization sensitive neurons described by Homberg and his co-workers for the central complex of the locust brain (Fig. 1.2d–f; Vitzthum *et al.* 2002). The e-vector tuning axes of these neurons are spread over the entire compass scale (Fig. 1.2f). This is an important prerequisite that must be met by any set of compass neurons. Furthermore, it is worth mentioning that the central complex, a highly stratified and distinctly layered neuropil within the insect brain (Homberg 1991), is considered to play a decisive role in the coordination of motor programmes. This is borne out especially by a number of *Drosophila* mutants, which exhibit structural defects in the central complex and concomitantly show behavioural defects in locomotor tasks, mainly in performing turning manoeuvres (Strauss and Heisenberg 1993).

Note that in the compass system described above, the information about individual e-vectors in individual pixels of sky gets buried in the integrated overall responses of the wide-field integrator neurons. Yet, this is more of an advantage than a drawback. If skylight conditions vary on a short-term basis—e.g. due to changes in cloud cover during an animal’s foraging trip—a large-field compass system will be able to balance the effects of such local changes (for real-sky demonstrations see Labhart 1999; Pomozi *et al.* 2001) and hence render the system robust to local atmospheric disturbances.

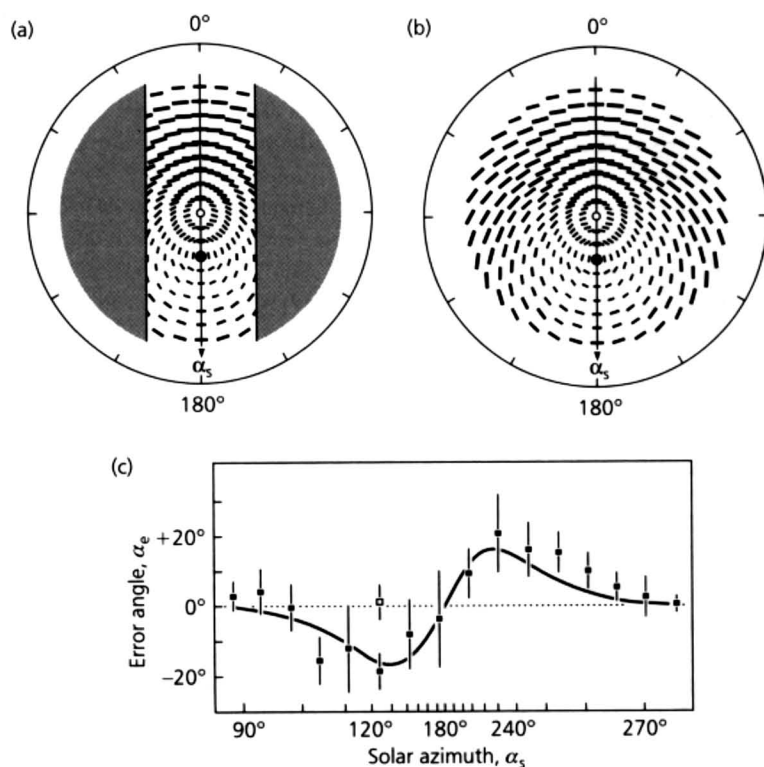
Errors in direction coding will occur only if the animal is confronted with highly asymmetric parts of the e-vector pattern, as, for example, patches of skylight that lie exclusively to the left or right of the vertical plane of symmetry that passes through the solar and the antisolar meridians. Then, a particular compass neuron that would normally be activated whenever the animal was facing, say, the solar azimuth in a clear sky, might now signal a different direction. For example, experiments have been performed in which *Cataglyphis* ants were presented with different e-vector patterns during the outbound and inbound runs. If the ants were, for example, trained under the full e-vector pattern and later tested under a partial e-vector pattern, or vice versa, systematic navigational errors occurred exactly as expected (Wehner 1982, 1997; Fent 1985; for bees see Rossel and Wehner 1984a; Wehner and Rossel 1985).

This shift within the activity pattern of the array of compass neurons (Fig. 1.3d) need not be disadvantageous as long as the asymmetric e-vector pattern in the sky does not change



**Fig. 1.3** Schematic representation of the insect's e-vector compass (hypothesis). (a) Celestial e-vector pattern. Filled circle, sun; open circle, zenith. The thick line represents the symmetry plane of the e-vector pattern ( $0^\circ$ , solar azimuth;  $180^\circ$ , antisolar azimuth). (b<sub>1</sub>) Array of e-vector tuning axes of retinal analysers. L, R, left and right visual field; dashed line, longitudinal body axis. The fan array of analysers is highly schematized and symmetric not only about the longitudinal body axis but also (and unlike the situation in *Cataglyphis*) about the transverse one. (b<sub>2</sub>) E-vector tuning axes (left) and response functions (right) of large-field integrator neurons in the insect's medulla.  $0^\circ$ , solar azimuth. Abscissa: Body orientation with respect to solar azimuth ( $0^\circ$ ). (b<sub>3</sub>) Annular array of hypothetical compass neurons (left) and their responses (right) when the animal is facing the solar azimuth. The  $180^\circ$  ambiguity results from the fact that the fan array used here (see B<sub>1</sub>) is symmetrical about the transverse body axis. As the animal alters its orientation with respect to the solar azimuth, i.e. rotates about its vertical body axis, the peak response moves along the array of compass neurons. Modified from Wehner (1998).

during an animal's entire round trip. In *Cataglyphis*, for example, the foraging journeys last for tens of minutes rather than hours (Wehner 1987), so that this condition is usually met. The errors induced in the experiment described above did not occur if the ants tested under the partial e-vector pattern had previously been trained under the very same partial pattern (Fig. 1.4). It is as if a human navigator used a magnetic compass that pointed, say, due east



**Fig. 1.4** (a, b) Experimental paradigm, in which desert ants were trained to perform their outward paths under a partial e-vector pattern (a, strip-like celestial window) and their homeward runs under the full e-vector pattern (b). Filled circle, sun;  $\alpha_s$ , solar azimuth. (c) Angular deviations,  $\alpha_e$ , of the ants from the true homeward course: means (filled squares)  $\pm$  SD. The experiments were performed at different times of day, so that the ants could be presented with different orientations of the solar azimuth relative to the long axis of the strip-like celestial window (see abscissa;  $0^\circ$ , north). The thick line depicts the errors to be expected theoretically (based on errors induced by e-vectors in isolated pixels of sky). No errors occur (open square), if the ants are trained and tested under the same partial skylight pattern. Adapted from Wehner (1997).

rather than north. In spite of this misalignment, the instrument can be used as a reliable direction indicator as long as its needle points east *consistently*.

## Use of spectral cues

In addition to polarization gradients, scattered skylight provides another source of directional information: spectral gradients. The ratio of long- to short-wavelength radiation increases from the antisolar towards the solar half of the sky. In particular, the sun is the point in the sky that is characterized by the highest relative content of long-wavelength radiation, and by zero polarization. If bees are presented with an artificial source of unpolarized light, they interpret this source as the sun if  $\lambda > 410$  nm, but as part of the antisolar half of the sky if  $\lambda < 410$  nm (Edrich *et al.* 1979). That bees and ants can deduce compass information



from spectral cues can be shown by painting out the POL areas of both eyes and preventing the animals from seeing the sun (Rossel and Wehner 1984*b*; Wehner 1997) or by presenting the animals with unpolarized beams of light (Brines and Gould 1979; Edrich *et al.* 1979). As the spectral gradients are coarser than the polarization gradients and more easily affected by clouds, compass information is more precise and robust if derived from the latter. Under natural conditions, spectral cues are used, for instance, to resolve ambiguities encountered by the polarization compass if the sun is close to the horizon.

Information about polarization and spectral gradients in the sky is processed by different visual modules that are already separated at the level of the retina. The 'polarization compass', which receives its input from the POL area, is monochromatic and hence colour-blind whereas the 'spectral compass', receiving its input from the remainder of the dorsal retina, contains polarization-insensitive photoreceptors and hence is polarization-blind. If the dorsal halves of both eyes are fully painted out, *Cataglyphis* performs strong roll and pitch movements of its head, attempting to look at the sky with the ventral halves of its eyes, but behaves as though it were lost. Evidently, the ventral part of the ant's visual system lacks the neural machinery that mediates compass orientation.

### Time compensation

If skylight cues are to be used as a compass, the animal must solve yet another fundamental problem. Owing to the westward movement of the sun during the course of the day, the sun's azimuth, and, with it, all polarization and spectral gradients in the sky, rotate about the zenith, and do so with non-uniform speed. Hence, any animal that derives compass information from skylight cues must use an internal circadian clock to correlate time-linked azimuthal positions of the sun with an earthbound system of reference. As shown in bees, the latter is provided by the horizon skyline of landmarks (Dyer and Gould 1981).

However, as the function correlating the solar azimuth with the time of day (the 'ephemeris function') varies with time of year and geographical latitude, the calibration task is by no means trivial. Therefore, it has even been assumed that bees do not use any long-term knowledge about the sun's rate of movement but merely extrapolate linearly from the most recently observed rate of movement (Gould 1980) computed by a running-average processing system (Gould 1984). Even though it was soon shown that bees (Dyer 1987) and ants (Wehner and Lanfranconi 1981) used more detailed knowledge about the solar ephemeris function than assumed by the extrapolation hypothesis, the question of how the insect acquired this knowledge remained to be answered.

Part of the answer came from experiments in which bees (Dyer and Dickinson 1994) and ants (Wehner and Müller 1993) were tested at times during the day at which they had never previously seen the sky. For example, incubator-reared bees were allowed to see only a small portion of the sun's course during the late afternoon each day. When these bees were subsequently tested at various times in the morning, they invariably assumed the solar azimuth to be  $180^\circ$  from the azimuth they had learned on previous afternoons. Hence, bees—and *Cataglyphis* ants as well—come innately programmed with an approximative ephemeris function—a  $180^\circ$  step-function—in which the azimuthal position of the sun abruptly shifts by  $180^\circ$  at noon.

When bees and ants acquire experience with the sky at other times of day, they transform this innate step-function into a representation that more closely conforms to the true, sigmoidal ephemeris function as it applies to any latitude and any season. This transformation

seems to rely on linear interpolations between successive memorized positions of the sun. For example, if diurnal desert ants trained during daytime hours are tested at night with either the moon or an artificial light source mimicking the sun, they behave as if they had time-compensated the sun's movement at a linear rate between the solar azimuths at sunset and sunrise (Wehner and Lanfranconi 1981; Wehner 1982).

## Odometry

If an insect is to navigate successfully to a food source and back, it needs to know not only about the direction in which it is travelling, but also about how far it has travelled. In other words, the animal's 'path integration' system must combine information on the direction and rate of travel, moment by moment, to determine where its owner is in relation to the starting point or the destination. We have already described above how bees and ants use their 'celestial compass' to determine the direction in which they are heading. How do they establish how far they have travelled? In other words, what is the nature of their 'odometer'?

Let us begin by considering flying insects. In principle, there are a number of ways in which a flying insect could keep track of how far it has progressed. For example, it could (a) monitor the duration of flight, (b) count wingbeats, (c) measure energy consumption, (d) sense and integrate airspeed, (e) measure the apparent motion of the environment in the eye, or (f) use some form of inertial navigation involving sensing and integrating the animal's accelerations.

Odometry in flying insects has been studied most intensely in the honeybee. The reason for this probably arises from the famous 'waggle' dance that bees perform after returning home from an attractive food source, to advertise to their nestmates the distance and direction of the goal (von Frisch 1993). The dance 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. Towards the end of each loop, the bee waggles her abdomen from side to side. 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 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 nestmates to locate the food source, and to harvest it efficiently. But the waggle dance is also 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.

Early studies of the waggle dance suggested that distance travelled is measured in terms of the total energy expended during flight (Heran and Wanke 1952; Heran 1956; von Frisch 1993). The evidence for this was twofold. First, if a foraging bee was made to carry an extra load, by attaching a small steel ball to her thorax, she signalled a greater flight distance in her dances. Second, bees signalled larger distances when they flew to food sites located uphill from the hive, than when they flew to food sites positioned downhill at the same distance. However, recent findings question this hypothesis (Neese 1988; Goller and Esch 1990; Esch *et al.* 1994) and suggest that an important odometric cue is the extent to which the image of the environment moves in the eye as the bee wings her way to the target (Esch and Burns 1995, 1996; Schöne 1996; Srinivasan *et al.* 1996, 1997, 2000; Esch *et al.* 2001). In other words, the odometer is driven by a visual, rather than an energy-based signal. Here we shall describe some of the new work that led to this insight.

About five years ago, researchers in Canberra trained bees to find a food reward placed in a tunnel, and then explored the cues by which they inferred how far they had flown to get to the food (Srinivasan *et al.* 1996, 1997). The walls and floor of the tunnel were lined with

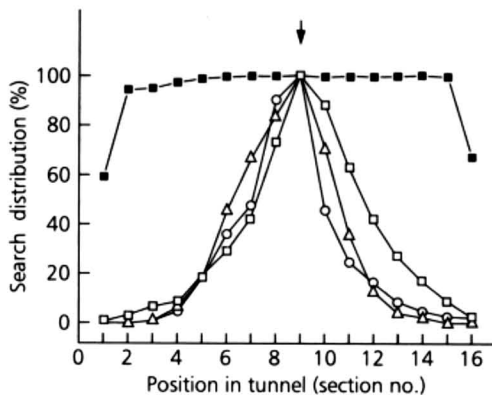
black-and-white stripes, usually perpendicular to the tunnel's axis. The reward consisted of sugar solution offered by a feeder placed in the tunnel at a fixed distance from the entrance. During training, the position and orientation of the tunnel were changed frequently to prevent the bees from using any external landmarks to gauge their position relative to the tunnel entrance. The bees were then tested by recording their searching behaviour in a fresh tunnel, which carried no reward and was devoid of any scent cues (details are given in the figure legend and in Srinivasan *et al.* 1996, 1997).

Bees trained in this way showed a clear ability to search for the reward at the correct distance, indicated by Fig. 1.5 (open squares). How were the bees gauging the distance flown? A number of hypotheses were examined, as described below.

Were the bees learning the position of the feeder by counting the stripes *en route* to the goal? To examine this possibility, bees were trained in a tunnel lined with stripes of a particular spatial period and tested in a tunnel lined with stripes of a different period. The test bees searched at the correct distance from the tunnel entrance, regardless of stripe period (Fig. 5, open circles and triangles). Therefore, distance is not gauged by counting the number of stripes or other features passed whilst flying through the tunnel (Srinivasan *et al.* 1996, 1997).

Were the bees measuring distance flown in terms of the time required to reach the goal? This possibility was examined by training bees as above and testing them in a tunnel that presented a headwind or a tailwind, generated by a fan at the far end of the tunnel. In a headwind, bees flew slower and took longer to reach the estimated location of the reward. The opposite was true in a tailwind (Srinivasan *et al.* 1997). Therefore, distance is not estimated in terms of time of flight, or other correlated parameters such as number of wingbeats. In a headwind, bees overshot the location of the reward; in a tailwind, they undershot it. Therefore, distance flown is not measured in terms of energy consumption.

Were the bees measuring distance flown by gauging the extent of motion of the image of the surrounding panorama as they flew to the goal? To investigate this possibility, bees were



**Fig. 1.5** Comparison of searching distributions of bees that have been trained and tested in tunnels lined with either vertical stripes (open symbols) or axial stripes (filled symbols) after having been trained to forage from a feeder positioned in section 9 as indicated by the arrow. The experiments with vertical stripes resulted in searching distributions with peaks and mean values positioned very close to the position of the feeder during training, regardless of whether the patterns had the same period as in the training (open squares), half the period (circles), or double the period (triangles). Using axial stripes (filled squares) completely disrupts the bees' ability to learn the position of the feeder. Combined from Srinivasan *et al.* (1996, 1997).

trained and tested in tunnels that carried axially oriented stripes on the walls and floor. Such tunnels provided no information on image motion, because the bee's flights in them were parallel to the direction of the stripes. In these experiments, 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 (Fig. 1.5, filled squares). Evidently, when bees are deprived of image-motion cues, they are unable to gauge how far they have flown. This finding provides rather compelling evidence that the honeybee's odometer is driven by image motion (Srinivasan *et al.* 1996, 1997).

The above results indicate that image motion is critical to odometry in bees, and suggest that distance flown is measured by integrating the amount of image motion that is experienced over time. These conclusions are consistent with those of Ugolini (1987), who transported wasps passively in transparent containers from their nests to various sites, then released them and observed their homing trajectories. He found that the wasps headed accurately towards their homes when they had been taken to the release site in a transparent container—and could thus observe their passage through the environment—but not when they were transported in an opaque container. Thus wasps, like bees, infer the direction and distance of their travel by observing the apparent motion of the visual panorama.

Esch and Burns (1995, 1996) investigated distance measurement by honeybees through a different experimental approach. They filmed the bees' dances in the hive when they returned from an artificial feeder, placed outdoors in an open meadow. They investigated 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! From this observation, 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 conclusion is completely consistent with the results of the tunnel experiments. Evidently, then, visual odometry is used not only in short-range navigation—as in the tunnel experiments—but also in situations that typify natural, outdoor foraging.

The above findings may partly explain why the early studies erroneously concluded that the honeybee's odometer uses energy consumption as the primary cue. Burdening a bee with a steel ball would tend to make her fly closer to the ground, thereby increasing the image motion that she experiences from the ground and causing her to report a larger distance in her dance (Esch and Burns 1996). Similarly, when a bee flies in a headwind she may fly closer to the ground, either to maintain the same image velocity as she would in still air, or simply to 'duck the breeze'. This would, again, increase the image motion, and therefore the odometric reading. While these explanations are presently only speculations that need to be checked, they illustrate, rather disturbingly, how easily one can be led to false conclusions about mechanisms.

The balloon experiment caused bees to underestimate the distance they had flown, because they experienced an optic flow that was weaker than what they would normally experience during normal, level flight. What happens when bees encounter the opposite situation, namely, one in which image motion cues are artificially exaggerated? Srinivasan *et al.* (2000) and Si *et al.* (2003) explored this question by training bees to fly directly from their hive into a short, narrow tunnel that was placed very close to the hive entrance. 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 a random visual texture. The dances of bees returning from this feeder were video-filmed. Incredibly, these bees signalled a flight distance of ca. 200 m, despite the fact that they had flown only 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. This experiment again drives home the point that image motion is the dominant cue that bees use to gauge how far they have travelled.

Do hive mates pay attention to the 'erroneous' dances made by bees returning from the tunnel, and if so, how do they respond? It turns out that the dances indeed recruit other foragers (Esch *et al.* 2001). Furthermore, the foragers do not fly into the tunnel in search of the advertised food: they search at the distance indicated by the dance, that is, almost 200 m away! This finding reveals that the dance does not signal an 'absolute' distance to potential recruits: rather, it specifies the amount of image motion that they should experience en route to the food. The recruits simply fly outdoors, in the appropriate direction, until they have 'played out' the prescribed amount of image motion.

What are the advantages and disadvantages of a visually based odometer? Unlike an energy-based odometer, for example, a visually driven odometer would not be affected by wind or by the load of nectar that the bee carries. It would also provide a reading that is independent of the speed at which the bees fly to the destination, because the reading depends only upon the total amount of image motion that is registered by the eye, and not upon the speed at which the image moves. However, as we have seen above, a visual odometer would work accurately only if the bee followed a fixed route each time it flew to its destination (or if a follower bee adhered to the same route as a dancing scout bee). This is because the total amount of image motion that is experienced during the trip would depend upon the distances to the various objects that are passed *en route*. Indeed, the dances of bees from a given colony exhibit substantially different distance-calibration curves, when they are made to forage in different environments (Esch *et al.* 2001). The strong waggle dances of bees returning from a short, narrow tunnel illustrate this point even more dramatically. However, the unavoidable dependence of the dance on the environment may not be a problem in many natural situations, because bees flying repeatedly to an attractive food source tend to remain faithful to the route that they have discovered (e.g. Collett 1996). Since the dance indicates the direction of the food source as well as its distance, there is a reasonably good chance that the new recruits, which fly in the same direction as the scout that initially discovered the source, will experience the same environment, and therefore fly the same distance.

There is another complication, however. Even if all bees take the same route to a food source, they may not necessarily fly at the same height. And if they derive their odometric signal from the motion of the image of the ground, the signal will vary substantially, depending upon the height of flight. Indeed, this is precisely what the balloon experiment suggests (Esch and Burns 1995, 1996). Further study is required to investigate whether bees tend to maintain a more or less fixed height above the ground whilst flying to a food source, or whether the odometric system is capable of estimating and partially compensating for variations in altitude.

Let us now turn to walking insects. How do insects measure how far they have travelled when they walk? Schöne (1996) encouraged honeybees, returning from a foraging flight, to walk through a short channel before entering their hive via one of three holes located on one of the side walls. The three holes were positioned at different distances from the channel entrance. Behind the transparent walls of the channel were textured patterns that could be moved in or against the bees' walking direction. A movable pattern was also visible beneath the transparent floor. Schöne found that moving the patterns with the bees tended to make the bees choose the

hole farthest from the channel entrance; moving the patterns against them, on the other hand, made the bees choose the closest hole. In other words, the bees walked a longer or a shorter distance, depending upon whether the patterns were moved with or against them. This observation suggests that image motion could play a role in assessing walking distance. The effect, however, is small and therefore suggests that non-visual cues, such as kinaesthetic signals, may be more important. Ronacher and Wehner (1995) and Ronacher *et al.* (2000) investigated the basis of odometry in the desert ant, *Cataglyphis*, again using patterned channels. They found that, while motion of a visual pattern under the floor had a small effect on distance estimation, image motion in the lateral field of view played no apparent role. They concluded that, in desert ants, odometry is carried out primarily through non-visual cues, possibly originating from movements of the legs. Interestingly, the ant's odometer is not affected by the burden that the ant carries, suggesting that there, too, energy consumption may not be the dominant distance-indicating cue (Schäfer and Wehner 1993). Chittka *et al.* (1999) report that walking bumblebees can learn the location of a feeder in complete darkness, indicating that they, too, can use non-visual information to gauge distance travelled.

The message emerging from these studies appears to be that walking insects gauge how far they have travelled by relying primarily on non-visual signals, probably originating from movements of the legs. Flying insects, on the other hand, seem to rely mainly on image motion. At least, this seems to be the case with honeybees, the only flying insect that has been investigated in this context so far.

What are the neural mechanisms by which the distance signal is computed? Where, in the insect's brain, is the odometer located? How is the odometric information combined with directional information, at the neural level, to perform path integration? At present we have no answers to these questions. The visual systems of flying insects, in particular, flies (Egelhaaf and Borst 1993) and bees (DeVoe *et al.* 1982), contain neurons that respond strongly to image motion, although they do not specifically encode the velocity of the image. Ibbotson (1991, 2001) has reported the existence of spiking visual interneurons in the bee that respond to the movement of patterns in the front-to-back direction in each eye. The spike frequencies of these neurons increase approximately linearly with pattern velocity. The output of such a neuron, integrated over the time of flight, would provide a signal that indicates how far the bee has flown, independently of the speed at which the bee flies to the destination. In other words, the total number of spikes fired by the neuron would be a robust representation of the distance covered. However, such a mechanism would require a means of counting spikes over the rather long time that is characteristic of a bee's outdoor flights—typically, at least a minute. How the bee's nervous system counts spikes—if this is indeed what it does—remains a mystery. If this were indeed how the flying honeybee's odometer works, it would not be very different from da Vinci's (1500) original odometer, conceived at the turn of the sixteenth century. This device measured how far a cart had travelled by gearing a road wheel to a system of other wheels that ultimately caused a pebble to drop into a chamber each time the road wheel had completed enough rotations to cover one Roman mile.

## Integration

Let us now turn to the problem of path integration *per se*. How does the insect put together the moment-to-moment information on distance and direction of travel, to estimate its current position in relation to home? In other words, how far away is home, and in what direction?

It is immediately apparent from the ants' performances, as illustrated in Fig. 1.1 that these animals integrate their paths with surprising accuracy. General models of path integration have been designed since the days of biological cybernetics (e.g. Mittelstaedt 1983), but the question remained how accurately the path-integration system actually worked under various experimental conditions. Quite surprisingly, when *Cataglyphis* ants were trained to forage along angular trajectories (enforced detours) and were then tested in open terrain, their homeward courses deviated systematically from the true home direction (Müller and Wehner 1988). In the two-leg experimental paradigm depicted in Fig. 1.6 the error angle  $\varepsilon$  is a function of the turning angle  $\alpha$  and (not shown here) the ratio of the lengths of the two legs.

The ants' behaviour can be fully described by applying a distance-weighted arithmetic-mean computational strategy, described as follows. The ant, while proceeding on its foraging journey, adds some measure of the angle  $\delta$  between its  $n$ th step and the direction of the home vector pertaining to its  $(n - 1)$ th step to this previous vector (Fig. 1.6c), and in so doing scales down all successive angular contributions  $\delta$  in proportion to the distance  $l$  it has already moved away from the nest (Müller and Wehner 1988; Hartmann and Wehner 1995).

As approximate as this rule of thumb may appear, under natural conditions it works sufficiently well. We note that in the experimental paradigm in which the systematic errors occurred, the ants performed a one-sided turn (to the right in Fig. 1.6a). We also note that errors induced by left- and right-hand turns of the same angular magnitude would cancel each other out. And this is exactly what occurs in the ant's natural foraging life. The frequency distribution of the angular movements  $\delta$  performed during foraging is symmetrical in shape (Fig. 1.6d), so that under natural conditions no systematic errors will build up. Hence, while foraging, *Cataglyphis* applies a locomotor programme that is adapted to the computational strategy of its path-integration system.

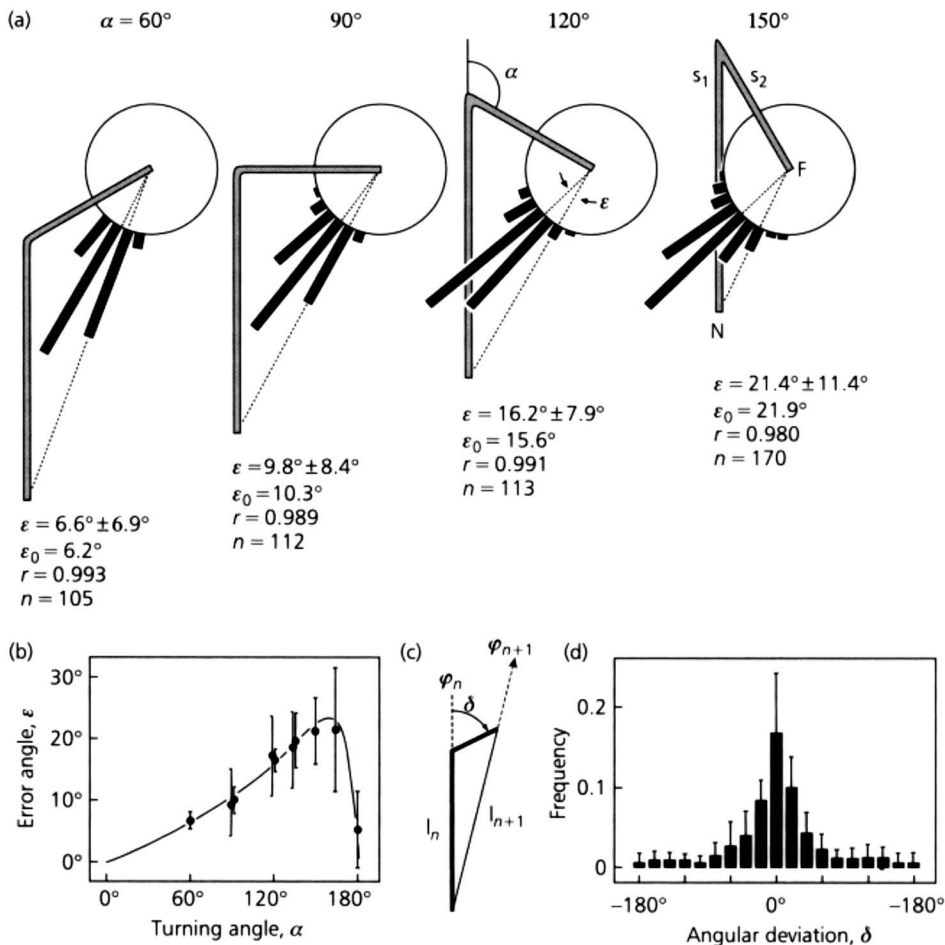
Glancing through the literature reveals some isolated cases in which bees (Bisetzky 1957; von Frisch 1965: 184) and some other animals (revs. Wehner 1992; Etienne *et al.* 1998) have been tested under conditions of enforced one-sided detours. In all these cases the same type of navigational error has been observed, so that what has been described here for desert ants might apply to other path integrators as well.

## Path integration within familiar territory

In unfamiliar territory, bees and ants—like sailors venturing to explore the unknown sea—use path integration as their only means of acquiring positional information. However, the more familiar a forager becomes with its environment, the more likely that information on landmarks is included in its navigational routine; and it is within the framework of path integration that this additional information is acquired and used.

First, the home (inbound) vector, which the animal has acquired while foraging, is reeled off, so to speak, during the animal's homeward journey. Once the animal has returned to its point of departure, the vector has reached its zero-state (within some kind of working memory). Nevertheless, it is fully stored at some higher memory stage, from which it can be loaded down again during the animal's next foraging trip. Reversed in sign by  $180^\circ$ , it will then be used as an outbound vector to guide the animal back to its previously visited feeding site. Hence, inbound and outbound vectors are  $180^\circ$  reversals of each other.

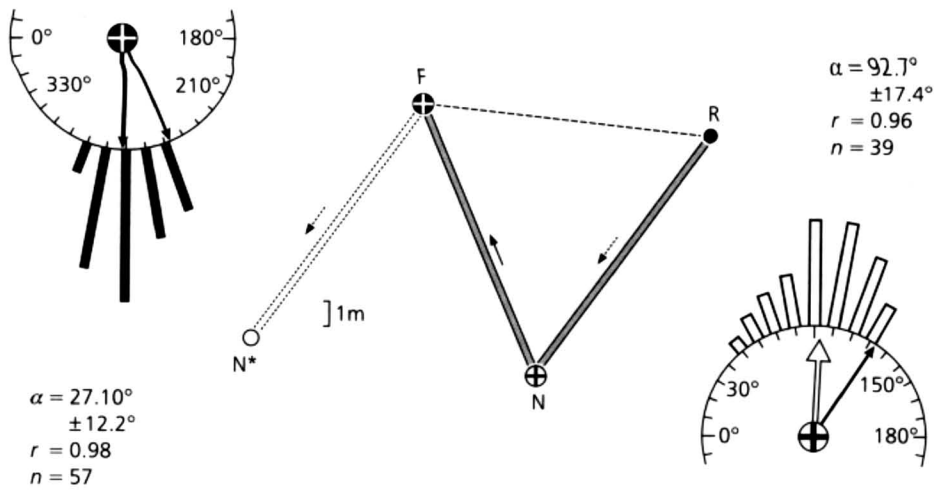
In a particular displacement paradigm, bees (Otto 1959) and ants (Collett *et al.* 1999; Collett and Collett 2000) were forced to move to a feeder in one direction and to return to the nest in a different direction, i.e. in a direction that was not the  $180^\circ$  reversal of the



**Fig. 1.6** Path integration in desert ants, *Cataglyphis fortis*. (a) Angular deviations (error angles,  $\epsilon$ ) from the home vector as occurring in a forced-detour two-leg training paradigm.  $s_1$ ,  $s_2$ , training channels ( $s_1 = 10$  m,  $s_2 = 5$  m);  $\alpha$ , turning angle;  $\epsilon$ , error angle exhibited by the ants;  $\epsilon_0$ , error angle as predicted by the algorithm described in the text; dotted line, true homeward course; F, feeder; N, nest. (b) Error angles,  $\epsilon$ , as a function of the turning angle,  $\alpha$ . Confidence limits are given for  $P = 0.99$ .  $N = 1412$ . (c) A unit step in the ant's path integration process.  $\varphi_n$ ,  $l_n$  and  $\varphi_{n+1}$ ,  $l_{n+1}$ , directions and lengths of the vectors after the ant's  $n$ th and  $(n + 1)$ th step.  $\delta$ , angular difference between the ant's  $(n + 1)$ th step and the vector acquired after the ant's  $n$ th step. (d) Frequency distribution of  $\delta$  (for definition see c) as recorded in the foraging paths of 19 ants. Means + SD. Modified from Müller and Wehner (1988), and Wehner and Wehner (1990).

outbound course (Fig. 1.7). When after several repetitions of this 'training around the circuit' the animals were tested under unconstrained conditions, they selected directions that were intermediate between the experimentally enforced foraging and homing directions. Obviously, the animals had recalibrated their vector every time they had reached the nest and the feeder. Since the outbound and homebound directions were not mutually consistent, the result of calibration at both sites was to produce the intermediate directions observed in





**Fig. 1.7** Vector recalibration. Ants were trained within a two-channel array to follow different outward (from N to F) and homeward paths (from R to N). Due to the passive displacement of the ants along the dashed line (from F to R) the ants had virtually travelled along the dotted double-line leading to N\* rather than to N. When later tested in unconstrained conditions, the ants' outward and homeward trajectories had directions that were intermediate between the ants' outward and homeward training directions and opposite to each other (see data at lower right and upper left, respectively; mean directions,  $\alpha$ , are depicted by the heavy black and white arrows). The ants did not choose directions that were the 180° reversals of the immediately preceding foraging and return paths (thin black arrows). F, feeder; N, nest; R, point of release. Computed from data in Collett *et al.* (1999).

Fig. 1.7. However, depending on the experimental paradigm, the calibration may be asymmetrical, that is it may be stronger at either the feeding or the nesting site, and can occur very rapidly whenever the ant at the nest and at the feeder experiences a mismatch between the current and the stored state of the integrator (Wehner *et al.* 2002). While *Cataglyphis* is evidently able to strike a compromise, so to speak, between discordant outbound and homebound directions, it always ensures that the outbound trajectory that it eventually adopts is directly opposed to the homebound trajectory, as shown in Fig. 1.7.

Second, besides these *global* vectors connecting nesting and feeding sites, in cluttered environments desert ants have been shown to use *local* vectors associated with particular landmark configurations (Bisch and Wehner 1998; Collett *et al.* 1998). These local vectors are recalled independently of the state of the global vector (Bisch and Wehner 2001) every time a particular configuration of landmarks reappears. They can temporarily override navigation governed by the global vector, which may point in a different direction. However, even in these cases the path-integration system is not shut off but continues to update the global vector (Sassi and Wehner 1987).

Third, long-term recordings of *Cataglyphis* foragers have shown that individual ants keep to familiar territory when searching for new feeding sites (sector fidelity: Wehner *et al.* 1983; Schmid-Hempel 1984; Wehner 1987). Hence, the path integration system may be calibrated not only at the nesting and feeding sites, but also at intermediate sites along a frequently travelled route. For example, harvester ants, *Messor semirufus*, calibrate their path integration system every time they leave the scent-marked trunk trail (Wehner 1992), and bees can link

visual scenes to distances flown (Srinivasan *et al.* 1999). Taken together, the path integration system provides a basic framework within which information about visual and chemical signposts is acquired and used. If ants and bees attach coordinates to particular sites, these coordinates are components of a path-integration rather than a map-based system of navigation.

As path integration results in vector information, it has conveniently been called *vector navigation* (Wehner 1983). In the study of bird navigation, however, this term is used in a somewhat different context (Schmidt-Koenig 1973; Berthold 1991; Mouritsen 1998). Recent research on inexperienced hand-raised songbirds has shown that first-year migrants are innately endowed with vector programmes that inform the birds about the direction and the duration for which they should fly in order to reach their goal (e.g. Helbig 1996). In this case, young birds evidently inherit an evolutionary 'blueprint' of large-scale vector routes from their parents, which they modify, as required, in their subsequent migrations. That this might not be completely beyond an insect's ken, is illustrated by the migration pattern of monarch butterflies (Brower 1996; Mouritsen and Frost 2002; Froy *et al.* 2003).

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