REVIEW

Odometry and insect navigation

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Summary

Animals have needed to find their way about almost since a free-living life style evolved. Particularly, if an animal has a home – shelter or nesting site – true navigation becomes necessary to shuttle between this home and areas of other activities, such as feeding. As old as navigation is in the animal kingdom, as diverse are its mechanisms and implementations, depending on an organism's ecology and its endowment with sensors and actuators. The use of landmarks for piloting or the use of trail pheromones for route following have been examined in great detail and in a variety of animal species. The same is true for senses of direction – the compasses for navigation – and the construction of vectors for navigation from compass and distance cues. The measurement of distance itself – odometry – has received much less attention. The present review addresses some recent progress in the understanding of odometers in invertebrates, after outlining general principles of navigation to put odometry in its proper context. Finally, a number of refinements that increase navigation accuracy and safety are addressed.

Introduction

Orientation and navigation are almost as ancient as non-sessile animal life. Locomotion through the environment creates the need to orient, with regard to hospitable or dangerous places, with regard to food sources, predators and mates. Navigation becomes necessary when an animal returns to a particular place on an episodic or regular basis. This may be a shelter, a nest or a feeding site. Navigation thus requires a particular location to be remembered and tied into some form of spatial memory. Orientation and memory capabilities for navigation have evolved several times, and probably independently, at least for more complex forms of navigation. Capable navigators occur among the chordates, especially in higher vertebrates, molluscs, especially the cephalopods, and in all major arthropod groups, including insects, crustaceans and chelicerates.

In keeping with the ancient origins of animal navigation, there has been much time for evolutionary refinement. Consequently, even in seemingly simple animals, navigation feats may be complex and consist of many sensory and behavioural components (for reviews, see Collett and Collett, 2009b; Wehner, 1992; Wehner, 1998; Wehner, 2003). One might expect, therefore, that an animal has evolved a number of idiosyncratic solutions to deal with the navigation problems present in its ecological niche (as is the case with other demands associated with such a niche). Any analysis should thus consider such idiosyncrasies as well as the more general strategies used by an animal group (Wehner, 1998). Although such idiosyncrasies may restrict direct comparison, in particular to more distantly related organisms, unexpected similarities may elucidate principles where functional necessity has dictated general features and strategies.

According to complexity and level of abstraction, navigation strategies can be sorted into three broad categories. Although other modes of categorisation are possible and useful depending on the task at hand, the distinction of route following, path integration and map use serves the present purpose (Fig. 1).

Route following

Route following is perhaps the most straightforward mode of navigation, even if the route that is followed by an animal will usually not be straight at all. A limpet, for example, spends the time of low tide on its 'home scar'. This is the particular spot on a rock its shell is moulded to and fits snugly to protect the animal from both desiccation and predators. The limpet leaves its home scar to graze algae, leaving behind a trail of mucus. After feeding, the mollusc returns to enjoy the protection of the home scar. The limpet navigates along the route it had laid out with its mucus on the outbound journey, and is thus safely guided home, even if not on the shortest possible trajectory (Cook, 1971). This is the typical situation of route following which is applied by many animals that have to return to a home, be it a shelter or a nest. Ants are no exception, and indeed ant trails that lead from the nest to a food source and back are well known even among non-biologists. These routes are marked by trail pheromones, which are the only orientation cues available when a route is first established, but may be complemented by visual and mechanical cues once a trail has become firmly established as a major road, and cleared and perhaps straightened out. The broad roads of leaf cutter ants are a good example here (Hubbell et al., 1980; Hölldobler and Wilson, 1990).

How is route following accomplished physiologically? In the case of ant pheromone trails, the immediately obvious mechanism would be a comparison of odour concentrations on the right and the left sides of the animal. A decline in pheromone concentrations towards one side would indicate that the animal is close to the trail edge and should steer more towards the centre. This mechanism appears indeed to be used, certainly by ants (Hangartner, 1967; Steck et al., 2010), but probably by all animals that navigate along
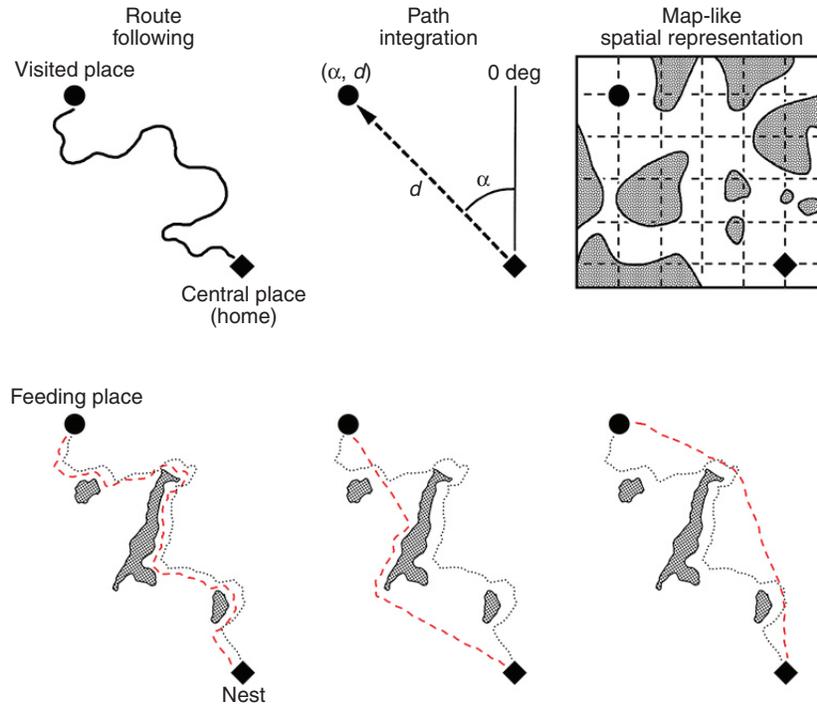
Fig. 1. The three different, though not mutually exclusive, modes of navigation presented here. (Left) Route following; (middle) path integration; and (right) map-like spatial representation. The top diagrams illustrate the principles underlying navigation [modified from Wehner and Wehner (Wehner and Wehner, 1990)], and the bottom diagrams show how these may translate into concrete homing performances. Labelling is given for left column: central place, e.g. home or nest, is indicated as a black diamond; visited site, e.g. feeder, as a filled circle. In the bottom diagrams, outbound paths in search of food are indicated as black dotted lines, homebound paths after a successful visit to a food source are shown as red dashed lines. In route following, the outbound path is retraced when returning home from the visit to a distant goal. In path integration, the homebound vector is incrementally updated by monitoring angles steered (α) and distances covered (d) during outbound travel; the home vector is played out when returning to the nest, and the straight path indicated by the home vector may be interrupted (with the vector still being continuously updated) when obstacles need to be got round (indicated by hatched areas; see also Fig. 5). When using a map-like spatial representation, the animals are informed about the spatial layout of their surroundings, including obstacles; when homing, they should select the shortest (or otherwise preferred, e.g. sheltered) route back home. These different homing performances can be used to distinguish between navigation strategies, in particular, when designing appropriate homing experiments.

a narrow trail of a trace substance (e.g. Duistermars et al., 2009; Rajan et al., 2006). A note of caution is warranted here because this mechanism of trail navigation differs significantly from the chemosensory orientation in open flow fields (see below, localisation of small food sources by odour cues). This more common mode of olfactory orientation in animals is actually through the combined perception of two cues. The first is an olfactory cue, which elicits orientation behaviour, and the second is an air or water current, which provides the directional cue (reviewed by Cardé and Willis, 2008). Such a strategy is necessary since on a macroscopic scale, odour cues are not distributed primarily by diffusion but rather by turbulent flow, resulting in filaments and pockets of odorous in an otherwise odour-free environment (as visualised by the smoke of a cigarette forming filament coils in the air). Therefore orientation directly into the flow will usually not lead the animal safely to the odour source. Instead, an animal normally follows a slightly slanted course with regard to the direction of flow. When the animal has not encountered odour filaments for a while, indicating that it has left the range of the plume, it makes a turn into the direction of flow to regain contact to the odour plume. This behaviour results in the typical zigzagging orientation trajectories observed in odour-tracking animals. Well-studied examples are male moths orienting towards female pheromones (e.g. Kaissling and Kramer, 1990; Cardé and Willis, 2008), but the behaviour is in fact common, even

to such situations as sea gulls and albatrosses orienting towards the smell of a dead fish floating on the water surface (Nevitt et al., 2008).

Routes for navigation may not just be marked by pheromones, however. The complementation of ant pheromone trails by visual and mechanical cues, possibly just collaterally, in cleared and firmly established ant roads has already been mentioned. Another common strategy in ants and other insects is the navigation along memorised sequences of visual 'snapshots' that define a trajectory for navigation (Collett et al., 1998; Macquart et al., 2005; Wehner et al., 1996) (for reviews, see Collett et al., 2003; Collett et al., 2006). A possible disadvantage is that such a visually based path has to be learned individually and cannot be followed by novice ants, as can a pheromone trail. A possible advantage is that navigation safety may be increased. If a pheromone trail is interrupted accidentally, a lengthy search may be necessary to recover the open trail end. A series of snapshots or a memorised panorama or skyline course, by contrast, is more robust against local changes, such as a broken branch on a tree's silhouette, or even a more distant toppled-over tree (e.g. Graham and Cheng, 2009a; Graham and Cheng, 2009b; Basten and Mallot, 2010; Zeil et al., 2003). A small interruption would probably not compromise navigation along the trail because the remaining memorised structures, even if distant, would attract the navigator into the original path (Basten and Mallot, 2010).
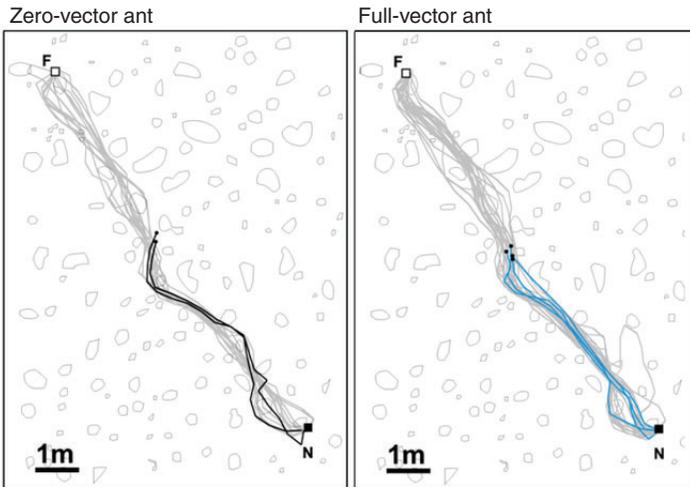
Fig. 2. Route following by a series of visual snapshots or panoramic views. Habitual routes of two individual (left and right diagrams) Australian desert ants (*Melophorus bagoti*) between nest and feeder are shown as grey paths . Solid lines show the paths taken after the individuals had been captured on their return journeys with a food item and released at the points indicated by dots. Ants were captured just before entering the nest, N (left, 'zero vector' ants), or when leaving the feeder, F (right, full 'vector ants'). Reproduced with permission from Kohler and Wehner (Kohler and Wehner, 2005); their fig. 6B (left) and fig. 7B (right).

This is borne out by the foraging paths of the Australian desert ant *Melophorus bagoti* (Kohler and Wehner, 2005; Sommer et al., 2008). This species usually lives in habitats where grass tussocks and small shrubs provide abundant landmarks – although somewhat uniformly shaped and distributed. The landmarks along the whole length of a repeatedly used foraging trail are memorised, such that the ant is always informed about its present position along the trail. This route memory is remarkably robust and dominates other navigation cues. The ant may be intercepted at any time, for instance, just before starting its return journey to the nest after it has collected a food item at a feeder [Fig. 2, right: full-vector ant; feeder (F) established 10 m from the nest (N)], or just before entering the nest with its food morsel (Fig. 2, left: zero-vector ant). If the animal is placed anywhere along the memorised path between nest and feeder, it resumes its homebound journey immediately and is well oriented. This is indeed surprising because the ant was just a moment earlier confronted with the appropriate panorama and possible other stimuli signifying feeder or nest positions, respectively. Furthermore, this visual mode of route following is not the only means of navigation for *Melophorus*. The species also

has a path integrator that constantly updates the animal's position relative to the nest, quite independent of any visual input. However, the visual mode of orientation completely overrides path integration in the above experiments, and path integration is evident only when the animals have to orient in an environment devoid of landmarks (similar to the situation depicted in Fig. 3, right).

Path integration

Path integration, or dead reckoning, makes a navigator independent of a particular idiosyncratic route. It keeps an animal constantly informed about both direction and distance to a goal, and it may further allow optimisation of search and foraging strategies, independent of local orientation marks. Path integration has been studied in many animals, but with particular success in arthropods and, again, in ants (reviewed by Wehner, 1992; Wehner and Srinivasan, 2003). During an excursion from a home base, such as a foraging trip of an ant leaving its nest, direction and distance cues are constantly monitored. The animal has to combine the momentary progress along its trajectory with the total distance and direction to the nest reached so far, its 'home vector'. This is
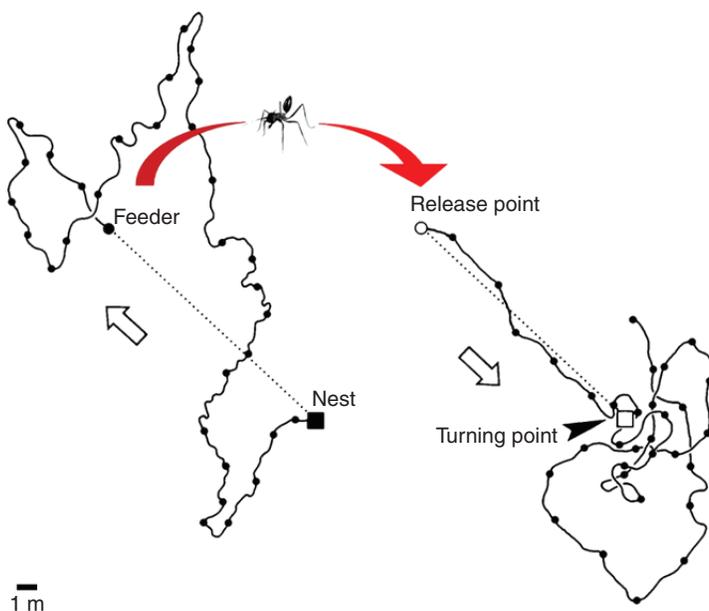

Fig. 3. Path integration and experimental protocol. Sample path of an individual desert ant (*Cataglyphis fortis*). The outbound search path on the left (solid black line; dots mark 10 s intervals) ends with successful arrival at a feeder; (outbound) travel direction is indicated by open arrow. The individual was captured at the feeder and transferred to a (distant) test area where, after being released, it played out its home vector (dotted lines indicate straight paths between nest and feeder). The position of the nest assumed by the transferred ant is indicated by the termination of the straight home run and the beginning of search loops (turning point, arrowhead). Adapted from fig. 3 in Wehner and Wehner (Wehner and Wehner, 1986).
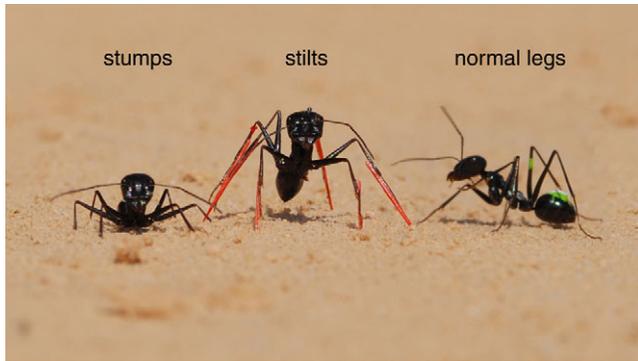
Fig. 4. Odometry by stride integration. Stride integration in desert ant odometry. *Cataglyphis fortis* ants were trained to collect food at a feeder located 10 m from the nest. The animals were captured once they had collected a food item, and their leg lengths were manipulated. Their legs were either severed half way down the tibia, reducing stride length by approximately 30% ('stumps' on the left) (see Wittlinger et al., 2007a). Or the legs were extended by gluing stilts made from pig bristles to the tibiae, increasing stride length by more than 30% ('stilts' in the middle). A control group was handled but kept their normal leg lengths ('normal legs' on the right). The animals were supplied with a food item after the operation and released in a test channel to examine their homing distance, the end of which is reliably indicated by the start of nest searching behaviour (similar to Fig. 3, right). If they relied on a stride counter (and with possible other means of distance measurement eliminated) one would thus expect the ants returning on stumps to underestimate the distance to the nest by approximately 30%. By the same token, the ants on stilts should overestimate homing distance by more than 30%. At the same time, they would disprove the argument that the ants on stumps ran short just because they were disabled; stilts actually impair walking behaviour more than do stumps. And the control ants should home reliably over 10 m before searching for the nest. And this is indeed close to what was observed in the experiments. However, one has to consider that stride length changes also under normal circumstances, in conjunction with stride frequency. If an insect carries a load or walks slowly for any other reason it takes shorter strides, and strides are longer in fast running, and stride frequency changes accordingly (as is true for virtually all animals walking on legs) (Taylor and Heglund, 1982; Full and Tu, 1991). And the above manipulations of leg lengths, and in particular the additional load of the stilts, as well as the food items to be carried, indeed reduced walking speed and thus stride frequency. It is therefore not stride number that is counted; rather, the strides an animals takes are summed considering both their length and their number – they are integrated, hence the term stride integrator. This can be verified when normalising the stride lengths actually observed in the manipulated ants (*via* high-speed video recording) with the changes in stride frequency brought about by the load that is carried. Photograph courtesy of, and copyright, Matthias Wittlinger.

achieved by incremental vector summation of the previous home vector with the present increment in locomotion (Müller and Wehner, 1988). The summed increments in vector integration may correspond to the single strides of an animal (see below, and also Fig. 4). Path integration thus makes an animal truly independent of external orientation cues, such as pheromone trails, landmarks, or terrain structure.

Vector summation is approximate (ants do not know analytic geometry) but this approximate solution is fully functional, although it requires strategies to cope with encroaching errors (Hartmann and Wehner, 1995). For example, turns to the right and to the left are usually statistically balanced to avoid the accumulation of directional errors (Wehner and Wehner, 1990; Müller and Wehner, 1988) (also see below, Error compensation strategy).

The independence of external cues, so-called egocentric navigation, was nicely demonstrated by the standard experiment with desert ants more than three decades ago (Fig. 3; still, the origin of the integrated path, the nest, is a geocentric reference). An ant is observed during its outbound foraging trip, and its tortuous walking trajectory in search of food (usually carcasses of insects that have succumbed to the desert heat) is recorded (Fig. 3, left trace). Once the ant has found a prey item, taken it into its mandibles, and is about to start its homebound journey, the animal is captured gently and put into a dark container that prevents any perception of the transport to a distant test area. The ant is released in the test field and its homebound trajectory is again recorded. Owing to the displacement, all local cues of the nest surrounds are eliminated, such as pheromones, landmarks, soil structure (Seidl and Wehner, 2006) and any others. Nonetheless, the ant resumes its homebound travel immediately, running off its home vector into the correct direction and for the correct distance. Once the ant has run off the home vector, it starts to search for the nest entrance (Fig. 3, right trace).

The density distribution of this search is a good measure for the navigation accuracy perceived by the ant. Ants that are less certain about nest location, for instance, because they have strayed farther from the nest on their foraging trip, exhibit broader search density distributions (Merkle and Wehner, 2010). To maintain navigation accuracy over time, it is of course necessary for the animal to reset the path integrator once in a while, otherwise navigation errors would accumulate infinitely. The most sensible location for such a reset is the central place in a navigator's life, in the case of desert ants, the nest. Although this reset of path integration is still poorly understood, recent experiments demonstrate that the home vector is indeed reset inside the ants' nest (Knaden and Wehner, 2006). However, anecdotal evidence indicates that such reset may also occur at some distance from the nest, for instance, at a place where a given forager regularly passes its prey items on to worker ants shuttling to the nest entrance. What further remains enigmatic are the stimuli that bring about the reset. Are these unloading of food, nest odour, darkness inside the nest, antennal contact to nest mates, or combinations thereof?

Sensory inputs for path integration

What mechanisms might be used to measure distances and directions? Vertebrate animals possess position and acceleration sensors in their inner ears that can be employed for deriving courses steered and distances travelled, for example, by integrating directional and rotational accelerations (for a review, see Rozhok, 2008). And at least some spiders are obviously able to derive both the distance and the direction of travel exclusively from sense organs that monitor the animals' own leg movements (for reviews, see Görner and Claas, 1985; Seyfarth et al., 1982; Barth, 2002; Wehner, 1992). This has been demonstrated by classical experiments using *Cupiennius* and *Agelena* species, with *Cupiennius* providing the most unequivocal data so far. For instance, an animal will return to a prey item that it had abandoned earlier, because of a disturbance, even in complete darkness and without olfactory orientation cues. Under similar conditions, these spiders return to their home shelter after foraging excursions of a few hours (Seyfarth, 1980). These orientation feats can be achieved on the basis of purely idiothetic signals, in this case information provided by proprioceptors associated with the legs (even though visual cues are used if present). These proprioceptors are cuticular strain receptors, the lyriform slit sense organs, located near the joints of the spider's legs. If these organs are destroyed

experimentally, the homing abilities of *Cupiennius* are eliminated, or at least strongly reduced (Seyfarth and Barth, 1972; Seyfarth et al., 1982). *Agelena* appears to use idiothetic information in similar ways, although the situation is complicated by orientation cues provided by the animal's web that serves as the substrate for locomotion. Therefore, definite proof has, as yet, been hard to come by (Görner, 1988).

The slit sense organs are not only exquisitely sensitive to cuticular strain but they are also located in those positions on the leg that exhibit the largest amount of deformation during walking (Barth, 1986), making them suitable candidates for close monitoring of stride length and turning angles. Moreover, stride length is the most constant feature in walking salticid spiders (Land, 1972), and short bouts of straight locomotion are usually interspersed with brief turns into new directions. This would appear to suggest that the spiders' path integrator combines some form of stride counter as a distance gauge with the assessments of angular movement during the turning phases of locomotion.

Insects possess proprioceptive strain sensors in their legs (and elsewhere), the campaniform sensillae. These are strikingly similar in both physiology and arrangement in the leg cuticle (reviewed by Barth, 1981) to the spider lyriform slit sense organs. It is an intriguing possibility that the insect campaniform sensillae are used for path integration in ways comparable to the role of the lyriform organs in spiders, particularly with regard to stride integration (see below, Distance cues).

Such purely idiothetic navigation, although making the animal independent from all external cues, is, however, rather error-prone. Imagine that the proprioceptors used to determine and update the homing distance have a systematic error of 0.1%, which is probably a conservative estimate (Merkle and Wehner, 2010). After 1000 strides, the maximum possible distance error reaches one stride length, which would appear acceptable. It would appear acceptable because this estimate assumes that the error is always in the same direction, whereas, more realistically, it would be expected to fluctuate in magnitude around a mean value that the animal may take as the basis for distance integration. The situation is much worse with regard to angular deviations. Depending on the tortuousness of the path and possible errors in vector summation, a navigation error of 180° – leading the animal in the direction opposite of home – may be reached after 1000 strides with a miniscule systematic angular error of 0.18 deg per stride, which is well below any reasonable angular resolution of proprioceptors (e.g. Seyfarth et al., 1982). Again, this is the maximum error for consistent deviations to one side, but it highlights the basic problem. Moreover, minor asymmetries in leg motor control are quite common, for instance, as a result of minor injuries, potentially leading to such systematic deviations to one side. And 1000 strides is no large distance for an animal to travel. For a desert ant, a moderate distance between nest and feeder is 10 m, amounting to just 1000 strides of approximately 1 cm length. The animals are, however, quite capable of travelling several 100 m on a foraging trip, amounting to several tens of thousands of strides (e.g. Wehner, 1987).

Compass cues

Therefore, reliable external directional cues, so-called compass cues, would appear highly desirable to achieve good navigation accuracy. This is certainly one reason why many animals use the sun as a compass (e.g. Wiltschko and Wiltschko, 1980; Wiltschko et al., 2000), or the skylight's polarisation pattern produced by scattering of the sun's light in the atmosphere (Wehner, 1997) (reviewed by Wehner and Labhardt, 2006). The sun is an almost

ideal compass because it reliably indicates a particular direction, regardless of the trajectory of travel. This holds even if the sun itself is rendered invisible, by clouds or other objects, if the polarisation pattern in the sky, concentric around the sun, is used instead. In nocturnal travellers, moon or stars can be acceptable replacements for the sun (Dacke et al., 2003; Dacke et al., 2004; Nørgaard et al., 2008) (reviewed by Papi, 2001), although light sensitivity of the eyes may be a limiting factor, particularly in compound eyes (reviewed by Kirschfeld, 1984). The only disadvantage for navigation over more extended time periods is the movement of the sun across the sky. Although this movement is relatively slow and perhaps negligible for brief outings, the movement of the solar azimuth has to be taken into account if travel exceeds several minutes or even lasts the whole day, as in diurnal bird migration (reviewed by Berthold, 2001). Appropriate compensation of the movement of the sun has been observed in almost all diurnal navigators, from honey bees (Towne, 2008; Wehner and Müller, 1993) to pigeons (Wiltschko et al., 2000). Details of the sensory physiology underlying celestial compasses, and the use of sun compasses by animals are often reviewed topics (e.g. Wehner and Müller, 2006; Wiltschko et al., 2000). The same is true for magnetic compasses, which do not need the time compensation, which is essential for sun compasses. However, the physiology and transduction mechanisms of magnetic compasses in animals remain enigmatic to this day, despite clear demonstrations of the compass *per se* (Gould, 2010; Lohmann, 2010).

Distance cues: energy consumption and time lapse

As indicated above, accuracy in distance estimation is perhaps not quite as crucial as in direction, at least for dead reckoning – although good accuracy is always advantageous, of course. The only reliable reference with regard to distance is the solid surface of the earth. The fluids covering that surface, bodies of water or the air, provide only relative measures and the possibility of drift has to be accounted for. Thus, distance gauges, or odometers, always have to rely on the relative movements of the body against the environment, and preferably against the ground, whichever parameter indicative of movement distance happens to be used. In bees, classical proposals have invoked energy consumption, for example, the fuel needed by a bee to fly a certain distance, beyond basic metabolism at rest (Heran and Wanke, 1952) (see also Heran, 1956; von Frisch, 1965). A time-lapse integrator might also function as an odometer, provided the speed of travel is relatively constant. In this latter case, distance covered is proportional to time of travel. Also, accurate time measurement would appear quite possible, considering the fact that most animals have internal clocks, even though these are known from their use for different purposes, such as time compensation of the sun compass mentioned above. However, both hypotheses suffer from the same basic problem, the fact that outbound and inbound travels are often performed under rather different conditions. Of particular importance is load, either prey, nesting material or similar items when returning home, or excavation material or refuse when leaving home. Travel in the respective opposite direction is usually performed without load, thus allowing for higher speed of locomotion and lower energy consumption. Similarly, tail or head winds would compromise energy expenditure as a reliable means of distance measurement with regard to both absolute energy costs needed to cover a given distance and relative costs of inbound and outbound travel that would normally encounter different, and often even opposite, wind conditions. The two parameters, energy expenditure and time lapse would thus appear ill suited to serve as

bases for reliable distance measurement. And indeed, neither of the above hypotheses regarding odometry has received lasting experimental support, so far (Collet et al., 2006).

Distance cues: optic flow and stride integration

Another parameter that might be used for odometry is optic flow, which avoids the problem introduced by varying loads. Optic flow, the movement of the external world across the retina of the eye during self motion, is a reliable indicator of the direction, the velocity and, after integration over time, of the distance of travel. Odometry by optic flow has been demonstrated by a set of elegant experiments in honey bees (Esch and Burns, 1995; Srinivasan et al., 1996; Srinivasan et al., 1997; Esch et al., 2001; Tautz et al., 2004), refuting the then prevailing idea of odometry by energy consumption. Two aspects, however, may present problems with this odometer mechanism.

First, optic flow is distributed unevenly across the retina, regarding both velocity and direction of movement. Close objects move faster than distant ones, and lateral ones move faster than objects in front or behind. This fact is familiar to anyone who has looked through the windows of a moving car. Objects close by on the roadside are indistinguishable because of their fast movement, whereas distant objects, the sun as an extreme, do not show any apparent movement. And a side view out of the window blurs at least the closer objects, while the point the vehicle is aimed at does not move at all. That uneven structure of the flow field is readily allowed for by appropriate weighing in the respective areas of the retina (Franz et al., 2004), a property that has been reliably observed in studies on insect eyes, particularly in the context of flight steering (Franz and Krapp, 2000), and object–background distinction (Lehrer, 1994; Egelhaaf and Borst, 1993). An area of the retina that normally looks frontally at distant objects cannot be used to extract useful optic flow cues. An area that looks at surfaces close to the animal and in a direction perpendicular to the direction of travel provides the largest optic flow input. Areas of the retina in between have to be weighed according to their viewing direction. Such local evaluation, and in the context of odometry, integration, of optic flow is not at all surprising, considering the fact that motion cues have to be extracted from the retinal image by local mechanisms (e.g. Egelhaaf and Borst, 1993; Clifford et al., 1997). In dipteran flies these locally and differently weighted inputs are genetically fixed in a manner that reflects optic flow input during normal flight situations, producing so-called matched filters (Franz and Krapp, 2000).

Second, and in line with the first argument, optic flow is dependent on the distance of the moving animal from the visual background, most importantly the ground. In honey bees, this confounding factor has been studied to some extent, and it appears to be compensated by the animals' tendency to fly at a particular height that provides a preferred optic flow input (Esch et al., 2001). If this preference is similar across individuals, distance measurements along a particular path will be similar in the different animals. This adjustment of flight height according to optic flow input is illustrated by observations of the Lindauer and Esch groups (Heran and Lindauer, 1963; Esch and Burns, 1995). When honey bees fly across areas with extremely low contrast and lacking texture, which for a bee are typically lakes, the animals fly very low, apparently in search for stronger optic flow input. They may fly so low that they touch the water surface and drown. In walking animals, the legs provide a relatively constant ground distance for the eyes and thus eliminate this problem (see also Ronacher and Wehner, 1995).

Optic flow is the almost perfect parameter for an experimental biologist to test hypotheses regarding odometry (and other visually guided behaviour). Honeybee foragers, for example, are easily trained to commute between the nest and a feeder established at a distance of up to a few kilometres. Although in classical experiments on bee orientation (for reviews, see von Frisch, 1965; von Frisch, 1967) the trained bees usually commute across open terrain, they can also be trained to fly through narrow tunnels connecting nest and feeder. Inside the flight tunnels, optic flow cues can be manipulated by appropriate textures of the channel lining (Esch et al., 2001). This allows quantitative assessments of how optic flow is translated into distance estimates and of the relevant flow parameters used by the bees (Si et al., 2003). A narrow tunnel of approximately 8 cm in width provides a strongly increased optic flow for the bees, leading to massive overestimation of travel distance, by factors of more than eightfold. One striking result of such experiments is the suggestion that there are two odometers in honey bees, one used for communicating the distance of food sources to nest mates, and the other, a personal one, used by the individual to find its way about (Dacke and Srinivasan, 2008).

In their community odometer, that is, in the waggle dances used to indicate to the nest mates the distance and direction of a food source, the animals consider the total distance flown to the feeder. That is, the distance estimate is independent of the particular conditions during the foraging trip, such as an obscured sky. This makes sense, considering the fact that a bee usually makes a beeline for home after having filled its crop. The personal odometer, by contrast, considers only those segments of the flight path where compass cues were available in the form of a clear view of the sky. Portions of the flight channel that had been covered with opaque lids were not fed into the personal distance estimate. This is in striking agreement with findings in desert ants (Ronacher et al., 2006; Sommer and Wehner, 2005). As strictly individual foragers, these animals may not exhibit a community odometer. The personal odometer, however, feeds into distance estimation, and thus path integration, only during those segments of travel where both distance cues and compass cues are available. With regard to path integration this makes particularly good sense. If the direction of travel is unknown, the error introduced into the home vector estimate may be smaller if the respective path segment is disregarded, rather than considered with, say, the last known heading. This holds at least for tortuous search paths. Considering all these observations, it is perhaps more adequate to speak of community and personal (path) integrators, rather than odometers. The mechanism of odometry would appear to be the same in each situation after all, and it is the odometer input into the integrator that can or cannot be gated. These observations further highlight the fact that in the course of evolution, if a particular mechanism becomes available to an animal, such as odometry by optic flow, it may be employed for a number of different purposes, depending on the species' necessities and evolutionary history.

In animals walking on the earth's surface, such as desert ants, which have been studied in some detail in this regard (Wittlinger et al., 2006; Wittlinger et al., 2007a), but also in fiddler crabs (Walls and Layne, 2009), another mechanism would appear suitable for odometry, namely, stride integration. In any animal walking without aerial phases, i.e. not in a gallop, the number and length of the strides taken during a journey reliably reflect walking distance. And even in galloping, a good approximation of distance covered can be derived with appropriate scaling that considers the average length of aerial travel. Colloquially, stride integration is often referred to as stride counting, which is correct only if stride length

is constant, at least on average. However, as noted above for energy consumption, stride length, too, is dependent on the load carried by the animal. Furthermore, and even without changes in load, stride length depends strongly on walking speed. This is an everyday experience for all legged animals, including humans. If we walk faster, we increase, in conjunction, both frequency and length of our strides (before we start to run by introducing aerial phases; see above) [for a review of vertebrates, see Taylor and Heglund (Taylor and Heglund, 1982); for insects, see Full and Tu (Full and Tu, 1990; Full and Tu, 1991); and ants in particular, see Zollikofer (Zollikofer, 1994a; Zollikofer, 1994b)]. Thus, both stride length and stride number have to be considered for reliable odometry.

This is indeed what North African desert ants, *Cataglyphis fortis*, do (Wittlinger et al., 2007a). Odometry by stride counting, or pedometry, was initially proposed more than a century ago (Pieron, 1904), and a number of later findings further suggested some mode of stride integration. First, the independence of distance estimation from carried prey loads, or from experimentally applied loads (Schäfer and Wehner, 1993), refuted the 'energy hypothesis'. Second, experiments that showed correct assessment of travelling distance even in complete darkness or featureless terrain, or with the ventral halves of the compound eyes covered, all eliminated optic flow as an essential means of distance estimation (Ronacher et al., 2000; Thiélin-Bescond and Beugnon, 2005). Definite proof for stride integration was provided by direct manipulation of stride length (Fig. 4) (Wittlinger et al., 2006). Ants that had reached a feeding site walking normally were captured and had their leg lengths manipulated. This was done either by clipping the most distal leg segments, thus shortening leg and stride length by approximately 30%, or by gluing stilts to the legs, thus extending leg and stride length by more than 30%. The actual changes in stride lengths brought about by these manipulations had to be verified with high-speed video analysis, of course. On their homebound journey the ants misjudged distance in keeping with the changes in stride length, thus establishing the idea of stride integration in odometry. This misjudgement of distance was independent of walking parameters such as load and walking speed (Wittlinger et al., 2007a).

In fiddler crabs (Walls and Layne, 2009), an experimentally introduced slick surface can cause homing animals to slip, which induces accordant errors in distance assessment. The stride integrator of the fiddler crab thus apparently sums up the strides taken regardless of whether the ground contact is slippery or with good grip. The stride integrator of ants is not subject to that sort of error, apparently accounting for irregularities such as slipping and stumbling (Steck et al., 2009a). This surprising error-resistance certainly puts constraints on the sensory mechanisms that could be used for stride integration, which may inform future experiments concerned with stride integration. The discrepancy found between crabs and ants in their ability to account for disturbances in their (idiothetic) stride integration could be examined by experiments with the wandering spider *Cupiennius* (Barth, 2002) because the sensory basis for path integration has been identified in this species (see section 3.1. above) (Seyfarth and Barth, 1972; Seyfarth et al., 1982), and so the mechanisms that convey error resistance may be easier to identify.

Nonetheless, optic flow appears to make a small contribution to the desert ant odometer. This is true for the ventral portion of the ant eye, that is, the part looking at the desert floor and thus predestined to monitor optic flow during locomotion, whereas lateral optic flow is apparently without influence on distance estimation. Ventral optic flow can be manipulated by putting the ants on a Perspex floor during travel and moving a patterned band

underneath this translucent floor, either in the direction of travel or against it. This actually influences the animals' estimation of walking distance, although only to a small extent, apparently less than 10% of the total distance estimate (Ronacher and Wehner, 1995). Manipulation of lateral optic flow has no effect at all (Ronacher et al., 2000). Intriguingly, in the above experiments examining the odometer hypothesis by manipulations of leg length, there were small but consistent deviations in the homing distances predicted from a pure stride integration mechanism. These deviations consistently pointed in the direction of the nest, regardless of experimentally shortened or extended homing distances, and would thus be consistent with a small contribution of another odometer mechanism, in addition to a main contribution of stride integration (Wittlinger et al., 2006). Such an interpretation, namely, identification of optic flow as the second odometer mechanism, as well as the possible functions of such dual mode of odometry, have to await future experimental scrutiny. Results from such a study would be highly significant because they should advance our understanding of both the physiological mechanisms underlying stride integration and the possible interaction of different modes of odometry and its uses. Improvement of navigation accuracy is one evident advantage that might arise from combining different odometer mechanisms.

In summary, neither sensory mechanisms nor functional contexts of odometry are as yet adequately understood. Particularly intriguing features are the possible existence of different odometers in honey bees, as noted above (Dacke and Srinivasan, 2008), and the contribution of ventral optic flow to distance measurement in desert ants *Cataglyphis* (Ronacher and Wehner, 1995). The odometers in ants and bees may well be consist of different and hierarchically organised mechanisms, much like the insect sky compass consists of a skylight polarisation compass, a sun azimuth compass (Wehner and Müller, 2006) and a compass relying on spectral light distribution across the sky (Wehner, 1997).

A further orientation feat of desert ants is extension of path integration into the third dimension. Desert ants that have walked over steep hills on their foraging trip to a nearby feeder but return across flat terrain, or *vice versa*, will experience very different walking distances on their outbound and inbound journeys. Nonetheless, the animals exhibit the correct homing distances, attesting to their ability to judge ground distance when walking over hilly terrain. This is true not just for odometry along a straight, though hilly, line (Wohlgemuth et al., 2001) but holds for truly three-dimensional trajectories (Grah et al., 2005). Sophisticated orientation in branches has been reported for other animals, particularly salticid spiders (Land, 1972) but the sensory bases of these feats are mostly unclear. Unfortunately, this is also true for assessment of the third dimension in desert ants. To date, it is only clear which parameters are *not* used in this context. For example, the fields of sensory hairs typically associated with graviception in ants (Markl, 1962) have been excluded as a means of three-dimensional orientation through ablation experiments (Wittlinger et al., 2007b). Again, the data from spiders [as described above (review by Barth, 2002)] would suggest leg mechanoreceptors as a possible means of three-dimensional orientation; however, at present this is purely speculative.

Levels of sophistication: enriched spatial memories, association between different orientation cues, and the question of map-like representation

The safety of navigation performance may be improved by enriching the spatial memory that is established during route
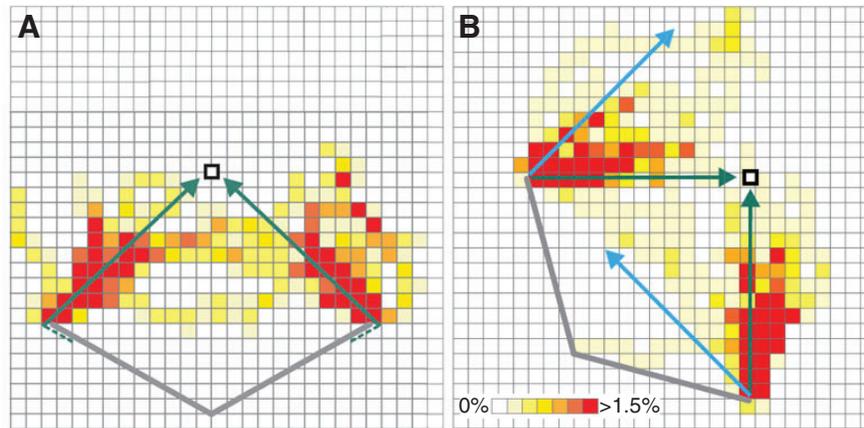
Fig. 5. Motor routines help desert ants in negotiating familiar obstacles. Desert ants (*Cataglyphis fortis*) were trained to collect food at a feeder (not shown, 4.5 m below bottom of figure). To reach the nest (black rectangle) during their homebound travel, the ants had to deviate along a symmetrically arranged (with regard to the straight homebound course) V-shaped barrier (grey bars). Individuals settled for consistent and unhesitant deviations around the barrier either to the left or to the right in the course of training. In the test situation, ants were captured just before entering the nest, to avoid association of local vectors with a particular state of the path integrator, and they were released in front of the barrier (A, dark green paths with arrowheads pointing towards fictive nest position). Path densities cumulated over all tested individuals (>20) are shown as colour coding (white, not visited by ants; darkest red, highest path density). When the ants were tested with the barrier rotated by 45 deg to the right (shown in B) or the left (not shown, but symmetrically identical results), their subsequent turns were with respect to the barrier (dark green paths and path density plot), rather than with regard to the appropriate global direction followed in training runs after passing the barrier (light blue arrows). Reproduced with permission from Bisch-Knaden and Wehner: parts of their fig. 2B (left) and fig. 4B (right) (Bisch-Knaden and Wehner, 2001).

following and path integration. A common strategy has already been noted above for the Australian desert ant *Melophorus bagoti*. This species, as well as the North African desert ant *Cataglyphis fortis*, combines route-defining landmarks and panoramas with path integration. Landmarks may be stored as snapshots (Cartwright and Collett, 1983) in a fixed relationship in the animal's retina (Wehner et al., 1996) and can be used to define the position of the nest entrance or food sources (Wehner, 1992; Wehner et al., 2006; Knaden and Wehner, 2005). *Melophorus* lives in landmark-rich habitats, and in its navigation system guidance by path-defining visual cues dominates path integration (Cheng et al., 2009). *Cataglyphis*, by contrast, inhabits flat and often completely featureless salt pans, and consequently path integration is usually the more important mode of navigation in this animal. Landmarks are still important, however, and landmark information is used according to context. For example, nest-defining landmarks are considered only in the vicinity of the nest (Bisch-Knaden and Wehner, 2003; Bregy et al., 2008), route-defining landmarks may be associated with local vectors (below), and landmarks close to a food source are considered only in that context (e.g. Wolf and Wehner, 2000). This is a useful strategy, considering the fact that an ant will always pass landmarks close to the nest when leaving for or returning from a foraging trip, whereas landmarks far away from the nest may be encountered just once in an ant's lifetime. Orientation with regard to landmarks and the interaction of landmark information with other orientation cues has been reviewed in detail elsewhere (e.g. Wehner, 2003) (see also Wehner et al., 1996).

There are additional cues that are employed for orientation and navigation by desert ants and other insects, if they happen to be available. If the sun and polarisation compasses fail because of an overcast sky or at night, desert ants will use ambient wind direction as a compass cue instead (Müller and Wehner, 2007; Wehner and Duelli, 1971). Considering the fairly constant wind conditions in the desert habitat of *Cataglyphis*, this appears as a useful backup strategy. In addition, landmarks need not be visually recognisable structures, as is usually implied. Instead, the structure of the walking substrate, such as its graininess and texture, may serve a similar purpose if there are consistent local variations in the habitat (Seidl and Wehner, 2006). Likewise, local smells may be used as landmarks, as has been demonstrated just recently (Steck et al., 2009b; Steck et al., 2010).

Path integration, local vectors and motor routines
Path integration provides a so-called global vector that points from the animal's present position to a goal, for instance, the nest or a feeding site known from previous visits. This vector navigation may be supplemented not only by landmarks and panoramas as outlined above, but also by so-called site-based vectors (Bisch and Wehner, 1998) or local vectors (Collett et al., 1998). These are distinguished from global vectors by the fact that they are tied to a particular place, and point into a certain direction from that place, without necessarily implying a certain distance for further locomotion. Such local vectors may be associated with prominent landmarks or guide an animal safely around obstacles (Bisch-Knaden and Wehner, 2001; Collett et al., 2001; Collett and Collett, 2009a) (for reviews, see Collett et al., 2006; Collett, 2009) (Fig. 5) that have been encountered previously. In the course of repeated excursions to a food source, landmark-based route information gains in importance, and experienced foragers often acquire idiosyncratic paths that are used invariably (Wehner et al., 1996; Kohler and Wehner, 2005). In this situation, local vectors may actually dominate the global vector provided by path integration in individuals that have had plenty of experience with a particular route or landmark, and have thus formed strong associations between particular sets of landmarks or panoramas, local vectors and states of the path integrator. A dramatic demonstration of this phenomenon was provided by Andel and Wehner who captured the

same ant repeatedly just when it was about to enter the nest, and replaced it further back along its homing path (Andel and Wehner, 2004). In this way, the animal walked off its original home vector several times, thus accumulating a very long negative homing distance in its path integrator. Provided with the proper set of landmarks, the ant nonetheless unerringly took up its homebound journey along the trail marked by the landmarks. In an area without landmarks, the animal started off into the opposite direction, according to the state of its path integrator.

Cataglyphis ants can also be trained to follow certain motor routines when exposed to well-known situations along a habitual route (Bisch-Knaden and Wehner, 2001). These motor routines are reminiscent of, and may be related to, the local vectors just mentioned. For example, *Cataglyphis* ants can be trained to negotiate a V-shaped barrier across their homebound path by running around it on the right- or the left-hand side (or rather, front-leg side). Each ant stuck to one side once it had performed a few (training) foraging runs (not shown, but similar to data in Fig. 5A). Important for the distinction from a local vector associated with a landmark, this barrier was inconspicuous and vanished from the ant's view after having been passed, thus providing minimal visual orientation cues. To further avoid association of a local vector with a particular state of the path integrator, experienced ants used for testing were captured just before entering their nest, that is, with their path integrator in a zero state. These animals nevertheless accepted the barrier as a cue, followed the barriers right or left leg, and turned by the habitual 120 deg after passing the barrier (Fig. 5A). If, in such a test situation, the barrier was rotated by 45 deg to one side, the ants still stuck to their usual routine of passing the barrier on the right or on the left. And at the end of the barrier the animals did not continue with regard to the global home vector that would have been appropriate after passing the barrier during their normal homing trajectory. Instead, they continued in a direction that would have been correct with respect to the V-shaped barrier in its original position (Fig. 5B). Apparently, the ants had learned during training to turn by approximately 120 deg into the nest direction at the end of the barrier, and they stuck to this (motor) routine even after the barrier had been rotated. This behaviour might be interpreted as a form of motor learning (e.g. Lent et al., 2009) (see also Knaden et al., 2006). At any rate, the local vector clearly dominates global orientation in this experimental situation, an observation that highlights the fact that desert ants use combinations of different cues for navigation, and that the respective weighing of these cues is strongly dependent on experience and context.

Under normal circumstances, that is, without experimental biologists who smartly change selected aspects of orientation cues, such rich and interconnected spatial memories allow safe and rapid navigation with a small error margin. This advantage becomes more distinct with more experience of a forager and the resulting consolidation and connection of memory aspects, ranging from global path vectors to detailed associations between different orientation cues. It also leads to changes in the relative importance of the different navigation cues. The above examples, where a local vector or a motor routine elicited by a familiar landmark or barrier dominates the global homing vector from path integration, are observed only in ants thoroughly familiar with the barrier and its surroundings. Novice ants orient true to their global home vector.

Active pursuit of such enrichment has been observed in several navigators, and certain aspects have received particular attention under the topic of 'active sensing' (e.g. Schuster, 2008; Zeil et al., 2008). Prominent are observations in flying hymenopterans, especially honey bees and solitary wasps. When leaving their nest, these animals exhibit a behaviour termed turn-back-and-look (TBL) (Collett and Zeil, 1996; Judd and Collett, 1998; Lehrer, 1991; Nicholson et al., 1999). As the name suggests, this behaviour consists of turning back towards the nest during the initial part of departure, and scanning the nest entrance and its surroundings with semi-circular flight loops, with the body, and in particular head and eyes, oriented towards the nest. Apparently, landmark information is stored during this behaviour and used during the return journey for the final approach to the nest. In keeping with this idea, experienced bees and wasps maintain rather stereotypical flight trajectories during the final parts of their return flights (Collett and Zeil, 1996). These flight trajectories are related to surrounding landmarks, and can be moved through experimentally shifting these landmarks, as has been shown by Tinbergen in his classical experiments (Tinbergen, 1932). Desert ants, too, appear to show such orientation behaviour close to their nest entrance. *Cataglyphis* perform orientation walks when taking up their role as foragers (Wehner et al., 2004), and *Ocymyrmex* of the Namib desert show similar behaviours (Wehner and Müller, 2010). This behaviour has not yet been examined in physiological detail, but it is certainly reminiscent of TBL behaviour.

Error compensation strategy

As mentioned above, desert ants, *Cataglyphis fortis*, do not just rely on path integration and landmarks during foraging trips. They also use olfactory cues, especially when approaching a familiar, though inconspicuous food source that is easily missed when attempting a direct approach. When wind is blowing from a constant direction, as is usually the case in their desert habitat during daytime, the ants do not approach the food directly. Instead, they steer downwind of the food source to pick up odour filaments emanating from the food. They follow this odour trail upwind, and in this way find the source quickly and reliably. The odour-guided final approach is zigzagging against the wind, in keeping with the chemosensory orientation strategy outlined above (Cardé and Willis, 2008).

This approach behaviour entails a small (downwind) deviation from the shortest route to the food source, but it obviously increases the reliability of finding the source directly and on the first approach. If the ants attempted a direct approach guided by their path integration system, they would often miss their goal, at least small sites without identifying marks. Depending on the accuracy of their vector navigation, they might actually miss it most of the time, since desert ants are often observed to pass a food item just a few centimetres on the upwind side, where no odour cues are available. Missing the food source on the downwind side would not matter because there the animals encounter the food odour. In general terms, such situations are referred to as polarisation of search space (Fig. 6) (Biegler, 2000). That is, almost half of the approaches (the ones leading upwind of the food) might necessitate search behaviour after the ants have passed the food source. On average, these searches far exceed the investment in time and deviation from the shortest route necessitated by a habitual downwind approach (Wolf, 2007).

How should the deviation be adjusted, from the direct approach into the downwind side, to achieve safe encounter of the food odour but avoid excessive detours? It would appear that a downwind distance just exceeding the animals' maximum navigation error is best. If an estimate of the maximum navigation error is available, either from previous foraging experience or perhaps through behaviours such as TBL, this downwind distance would safely lead the animal downwind of the food but avoid unnecessary detours.
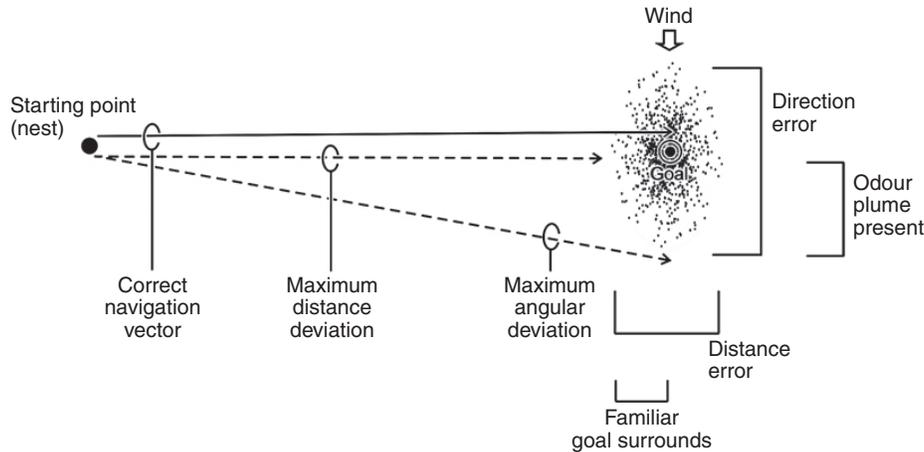
Fig. 6. Error compensation strategies. Search space is often polarised, allowing for strategies that deal with navigation errors in productive ways. In the present example, wind blows perpendicular to the nest–goal axis, i.e. the nest–feeder axis, in desert ant foraging. Downwind of the feeder the odour plume emanating from the food can be used by the ants to localise even very small food sources successfully and without lengthy searches. Attempting a direct approach to the feeder would often result in missing of the goal because of inevitable navigation errors; and missing the feeder on the upwind side would necessitate lengthy searches (Wolf, 2007). A successful compensation strategy consists of steering downwind of the assumed direction to the feeder by an angle just exceeding the maximum navigation error, thus leading the ant safely into the odour plume of the food. The ranges of distance and angular errors are indicated, as well as polarisations of search space by, respectively, familiarity of the goal surrounds on the approach side, and wind carrying goal odours downwind. Scattered dots indicate goal locations associated with errors. Adapted from fig. 6 in Wolf and Wehner (Wolf and Wehner, 2005).

And this is indeed what the desert ants do (Wolf and Wehner, 2005). The distance steered downwind of a familiar feeding site increases with the distance from the nest in a linear fashion, resulting in a relatively constant downwind angle of 5–8 deg. Of course, there is individual variation and dependence on an animal's experience (Wolf, 2007), but desert ants are evidently informed about their own navigation accuracy.

By the same token, ants often start searching slightly before they have played out their full home vector (Müller and Wehner, 1988; Sommer and Wehner, 2004), especially if they are forced to travel home across unfamiliar terrain. Such an earlier search would normally lead the animals into terrain familiar from the outbound journey, and allow a safe return through piloting. This provides an example of search space polarisation with regard to distance, rather than angular deviation.

Map-like spatial representations?

Maps are familiar to humans from everyday use, be it hiking or long distance travel. These maps provide a bird eye's view of the terrain, based on the cartographic concept of representing points and routes in a primarily two-dimensional space. Biologists refer to this idea of maps, although there is no common terminology in detail. The term 'map' is often used to imply that the animals under study, including humans, possess a spatial representation similar to a cartographic map.

First, though, the mode of representation may differ substantially from the bird's eye view. In humans at least, it appears that spatial knowledge that is acquired not from looking at a map but, more naturally, from their own navigation, is represented in a ground level perspective (Thorndyke and Hayes-Roth, 1982). This perspective allows mental access to distant places by seeing through 'translucent' closer objects and places, which may serve as intervening points of access and orientation. This is also borne out in traditional ways of human navigation, for instance, by Polynesian seafarers (Lewis, 1994; Gladwin, 1975).

Second, spatial representations in animals may be much sparser than in an ordinary human map, although a two-dimensional representation that preserves the spatial relationships of places is understood as a basic feature of maps. Therefore, the observation that a navigator takes a novel shortcut while being well-oriented is still considered *the* key proof of map-like representation of space in an animal. The notions of 'novel' and 'well-oriented' are essential criteria to distinguish such feats from just another learned route however rich its endowment with memorised features such as landmarks and local vectors. Proper orientation during the shortcut rules out chance encounters during search-like behaviour, and the novelty provides proof that the shortcut has been derived from knowledge of the spatial relationship of the two places connected by the shortcut. Maps in that sense have not been demonstrated very often, even in mammals (Tolman, 1948).

The assembly of landmarks and local and global vectors into a two-dimensional spatial arrangement would thus yield a map-like orientation capacity – as opposed to the mere local association of landmarks, snapshot sequences and local vectors along a route or along a global vector path. The use of such true maps has been suggested in honey bees (Menzel et al., 2005). Further scrutiny is certainly warranted, though, since alternative interpretations may be adequate for these observations. It is difficult, for instance, to clearly distinguish the recall of local vectors by previously encountered landmarks from the use of a true map if an animal, captured on its foraging trip and released at a different place, first 'looks around' and samples the test environment, and then takes up a well-oriented homebound trajectory (Menzel et al., 2005). Recall of local vectors for proper orientation has been documented in comparable circumstances, and appears not too surprising considering the above-described enriched spatial memory that involves the association between several complementary orientation cues (Collett and Collett, 2006; Wehner et al., 2006). A definitive distinction between path integration or route following supported by enriched spatial memory, on the one hand, and true maps, on the other hand, will be difficult indeed for such sophisticated navigation performance.

Although most literature on invertebrate navigation is concerned with the behavioural level, recent advances have ventured into the

neurobiological domain. Although the location and mode of memory storage in navigation remains elusive, the insect central body seems to emerge as an important substrate for spatial representation (Heinze and Homberg, 2007; Strausfeld, 1999). For example, the polarisation plane of incident light is represented in a regular fashion in a medial structure of the insect brain, the central complex. Orientation of the animal with regard to its celestial compass is mapped across the columns of the central complex, specifically, the protocerebral bridge. Another portion of the central complex, the fan-shaped body, has been implicated in visual landmark and pattern recognition in the fruit fly (Liu et al., 2006). Finally, the central complex appears to be involved in general aspects of locomotor control (Strauss, 2002). The central complex in insects may thus be a higher level centre for locomotor control, orientation and navigation in these animals.

Glossary

Celestial compass

This term subsumes the compass cues available in the sky, namely sun compass, polarization compass and possible spectral and intensity gradients in the sky (Wehner, 1997).

Global vectors

In navigation such vectors are independent of a particular place. They point from the navigator into a particular direction and indicate a certain distance. The home vector produced by path integration is a typical example.

Idiothetic navigation

This form of navigation relies exclusively on sensors monitoring internal states of the animal, such as joint angles, to determine distance and direction of travel.

Local, or site-based vectors

Local vectors are tied to particular points in space that are familiar to the navigator. Ample experience with navigation along such a point (often defined by more or less extended landmarks) has formed a memory association between that particular point in space and the route segment to be followed in its vicinity and immediately afterwards.

Odometer

An odometer is a distance gauge, independent of the mechanism used to determine distance. The term is derived from the Greek 'hodos', for path or distance, and 'meter' as a common generic suffix for measuring devices.

Optic flow

Movement of the visual background across the retina of the eye. Such motion of the visual background, as opposed to the movement of small objects, is usually caused by the motion of the eye itself, or of the organism carrying the eye. Optic flow may thus serve as a useful measure of self-motion with respect to the surrounding environment.

Path integration

An animal performing path integration keeps constant track of progress along its trajectory in terms of distance increments covered and angles steered. Distance increments and corresponding angles are added to the previous positional fix by, usually approximate, vector summation. The term path integration is often used synonymously with the terms vector navigation and dead reckoning.

Polarization(-based) compass

Insects and other arthropods are able to determine possible polarization of incident light because of the particular structure of the photosensitive layers in their eyes (reviewed by Wehner and Labhart, 2006). Given that the blue skylight is polarised with respect to the sun, this polarisation pattern may be used instead of, or complementary to, a sun compass.

Polarization of search space

If an animal searches for a goal in a homogenous area without landmarks, or in completely unfamiliar territory, this search would normally be centred on the assumed position of the goal – as derived from vector navigation, for instance. More profitable search strategies exist, however, if there are directional cues that polarise the search space. Typical examples are wind or water currents that carry odour or other cues emanating from the goal, for example, food items. In such cases centring the search downwind of the goal and sampling the air or water current on cross wind paths should accelerate arrival at the goal.

Sun compass

Many animals, including insects, use the sun as a compass to determine their direction of travel. Such sun compasses use the sun azimuth, that is, the direction the sun indicated on the horizon (i.e. when dropping a perpendicular on the horizon).

Time-lapse integration

Time-lapse integration is a potential alternative means of distance measurement. Integrating the time elapsed since the start, for a navigating animal (typically the start of its outbound trip from home) may provide a good approximation of distance covered. This is true if the speed of travel is constant, as is approximately the case under certain conditions in outbound foraging desert ants and in spiders. However, speed on the homebound journey may be slower, depending on prey load.

Turn-back-and-look (TBL)

Upon leaving their nests for the first time, and occasionally also later on, many insects perform so-called turn-back-and-look behaviour (TBL) (Lehrer, 1991). This behaviour consists of an interruption of the outbound path at a short distance from the nest, a turning back of the body orientation towards the nest, such that the nest and its surroundings are clearly visible with the eyes, and slightly undulating scanning movements along approximate circle segments centred on the nest entrance. During this turn back and look behaviour, usually repeated a few times at increasing distances, the insect acquires knowledge of landmarks and spatial layout surrounding the nest entrance.

Zero-vector animal

When an animal has returned to the origin of its journey, to the point where vector integration started, its vector integrator should have reached the value 'zero'.

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