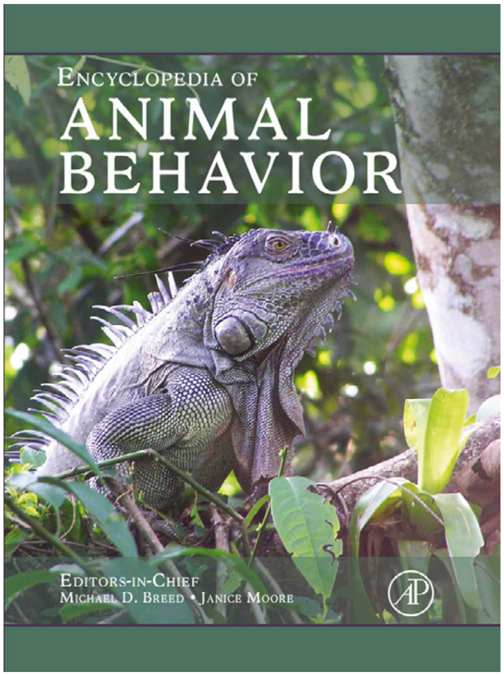

Graham P. (2010) Insect Navigation. In: Breed M.D. and Moore J., (eds.) Encyclopedia of Animal Behavior, volume 2, pp. 167-175 Oxford: Academic Press.

Insect Navigation

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Introduction

The possibility that insects learn the spatial layout of their environment had been dismissed by some as mere 'anthropomorphic delusion,' before experiments by early twentieth century ethologists, such as Jean-Henri Fabre and George Romanes, showed that insects were indeed capable of learning about and navigating around a familiar environment. One elegant example from Romanes involved taking a hive of bees, relocating them to a house, and then allowing them to forage freely from that location. After a period during which bees foraged, he captured a cohort of foragers and transported them ~250 m to a flowerless cliff top. From this location, where bees were unlikely to have foraged, no individuals found their way home. In contrast, all bees released from a flowered garden, also 250 m from the hive, successfully returned. Romanes had shown simply that rather than any arcane 'spatial sense,' it was the experience of places that was necessary for successful homing. When an animal moves to a goal location in this way, it can be classified as true navigation, because the animal must calculate the current location relative to the goal before it can move accordingly. In contrast, equally remarkable spatial behaviors such as long-distance migration or chemotaxis, need only involve the moment-to-moment alignment of an animal's body using sensory feedback and are classified as orientation.

In this article, we focus on the mechanisms that underpin true navigation in insects. We begin with a discussion of path integration, an innate navigational strategy that enables an animal to return to the starting point of a route. We then discuss how insects learn about the landmarks within their environment and use this knowledge to guide complex routes. Insects are capable of impressive feats of navigation using only this simple toolkit of innate behaviors and learned landmark information. Yet, the smooth operation of these navigational strategies requires sophisticated cognitive mechanisms, and we end the article with a discussion of how insects organize the large set of memories required for navigation.

As is evident from this article, our knowledge of navigation in insects is almost exclusively drawn from the study of central place foragers, predominantly, the hymenopteran social insects. Unfortunately, we know much less about the navigation of other insects, but there are strong suggestions that the general mechanisms discussed here are likely widely applicable.

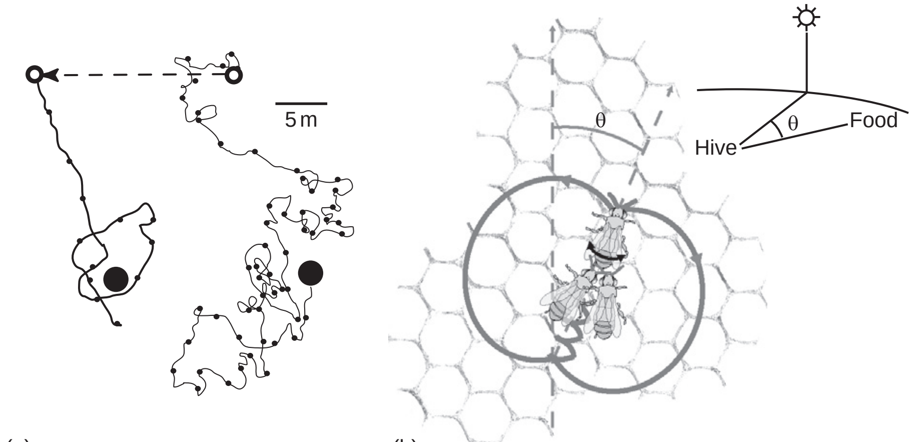
Path Integration

In order to fully exploit environmental resources, an animal must leave her nest and occasionally venture into new territory, from where she must safely return to the starting point of the journey. This is a basic requirement for an animal navigator, and the general mechanism, which is shared by most animals, is called path integration (known to sailors as dead reckoning). Path integration (PI) involves monitoring the orientation and length of journey segments and integrating this information to maintain a continuous estimate of the distance and direction of the direct line back to the starting point of the route (Figure 1(a)). Therefore, at any time, such as when a food item is located or a predator attacks, the animal can take the quickest route home. In addition to guiding a direct route home, information acquired using PI can be used to inform others of the location of a food source. This is seen in the remarkable waggle dance of the honeybee, which is performed by a forager upon returning from a profitable food source. The dances (Figure 1(b)) were decoded by Karl von Frisch, who discovered that the orientation of the waggle runs, relative to gravity, indicates the direction of the goal relative to the azimuthal position of the sun, while the distance to the goal is strongly correlated with the waggle duration. Following von Frisch, scientists were able to read the dance of a returning forager, thus giving an insight into an insect's mind. We will see in subsequent sections how reading the dance has been an important tool for investigations of the mechanisms of navigation.

To perform path integration, an insect needs three things: a compass to measure orientation, an odometer to measure distance or speed, and neural machinery to iteratively perform the path integration calculation. As yet, we know little about how insects' brains perform the PI calculation, though we do know about the compass and odometer mechanisms used by walking and flying insects.

Odometric Mechanisms

There are three possible ways for an insect to measure the distance it has traveled: a proprioceptive mechanism that monitors the movement of the insect's legs or wings; a system that monitors energy usage during a route; or, a sensory mechanism monitoring the consequences of movement, for instance, the optic flow experienced



(a) (b)

Figure 1 (a) Path integration in desert ants. The outward foraging path of a desert ant is shown until she finds food. Before the ant can make a return trip, it is displaced. The homeward path is parallel to the route from food to nest indicating the use of an egocentric estimate of position rather than landmark information. Filled circle denotes nest and fictive nest, open circle food Reproduced from Wehner R, Boyer M, Loertscher F, Sommer S, and Menzi U (2006) Ant navigation: One-way routes rather than maps. *Current Biology* 16(1): 75–79. (b) The waggle dance of the honeybee. A returning forager performs a waggle dance on the vertical honeycomb in order to communicate food location to other bees. The dance is made up of a waggle runs followed by loops of alternating direction. The direction to the food is signaled by the orientation of the waggle run relative to gravity which represents the bearing the recruit should take relative to the current azimuthal position of the sun (inset). Distance to the goal is signaled by the duration of the 'waggling' during the waggle run.

during a route. The most appropriate odometric mechanism for a given species will vary as a consequence of their mode of locomotion.

For a walking insect that is in contact with the ground, a reliable estimate of the distance traveled can be retrieved from monitoring its own leg movements. This 'step-counting' hypothesis was verified for ants by manipulating the lengths of their legs before they were allowed to make a PI guided return to their nest. Foragers were allowed to find a feeder at the end of a long channel and from there they were transported to a test channel. When control ants are released in this channel, they walk the distance that would have ordinarily taken them back to their nest, before starting to search. Two further groups of ants were subjected to a delicate surgery before being placed in the test channel. Ants with shortened legs searched at a reduced distance and ants with their legs lengthened with pig bristle, overshot the fictive nest position. In each of these three conditions, the ants' return journey consisted of approximately the same number of strides. So, we can conclude that ants use a proprioceptive odometer as also used by other terrestrial invertebrates such as spiders and crabs.

For flying insects, the influence of air movement means that the attempts to measure distance in terms of motor output or energy usage may be inaccurate, although, following the ideas of von Frisch for a long time, the predominant theory of odometry for flying insects was one based on energy consumption. It took a simple experiment by Harald Esch and John Burns to overturn the energy hypothesis and suggest an alternative. They trained bees to forage at a feeder in an open field and then recorded the distance signaled by the dances of returning bees. Over time, the feeder was raised above the ground, so bees had to fly further and use more energy flying against gravity. However, the distance signaled in their dances reduced, leading Esch and Burns to suggest that bees' distance estimates may depend on the degree of visual motion generated by their flight. Visual motion, also known as optic flow, is generated by an animal's movement as the images of environmental objects move across the retina. The degree of visual motion depends on the animal's speed and the distance between the animal and environmental objects. As Esch and Burns forced bees to fly higher and higher to the elevated feeder, the amount of perceived visual motion dropped because bees were flying further from the ground. This led to the 'optic flow' hypothesis: that a bee's estimate of distance depends on the amount of perceived visual motion rather than its energy usage.

The optic flow hypothesis has been rigorously tested by Mandyam Srinivasan and colleagues who trained bees to fly in small tunnels with high contrast stripes on the walls. One of their earliest experiments shows the influence of the optic flow on the bees' perception of distance. Bees were trained to find food at a fixed distance along a tunnel which had a radial (perpendicular to the direction of flight) stripe pattern on the walls and floor. Bees were able to learn the food distance and would search persistently at the correct distance when tested in a feederless fresh tunnel. However, when the radial stripes were replaced with axial stripes (aligned with the direction of flight), bees showed no focused search pattern. The axial pattern provides no optic flow relative to the direction of flight, making distance estimation impossible.

The fact that flying insects use optic flow to measure distance creates a problem for our perception of the waggle dance, as the dance cannot signal an absolute distance but only the amount of optic flow experienced along a route. This will depend on the proximity and density of objects along the flight path, so the relationship between the waggle duration and the absolute distance varies as a function of the environment within which a particular colony forages. However, this is not a problem as long as the bee following the dance takes a similar path through the environment as did the dancer.

Compass Mechanisms

For many insects, the sun plays a major role in providing compass information, as is evident from the waggle dance of honeybees. To use the sun as a compass, insects must solve two fundamental issues: Firstly, the sun moves during the day, and secondly, the sun is often hidden by clouds. Insects can compensate for the daily movement of the sun by learning its position relative to the time of day. Insects have some innate knowledge of the sun's movements, they know that the sun's position changes slowly near dawn and dusk and more quickly around noon. Combining this knowledge with observed sun positions relative to stable environmental landmarks allows an insect to learn an accurate function describing how the sun moves throughout the day, We know about the innate knowledge of bees following experiments where new foragers have their experience of sun position restricted to the morning. In orientation tests in the afternoon, the insects show that they have fitted their morning experience of the sun's position to a step-shaped template which includes information about the rapid sun movement around noon and slower sun movement late in the day.

When the sun is obscured by clouds, but portions of blue sky remain, insects are able to derive compass information from the polarization patterns created by the scattering of sunlight in the upper atmosphere. The orientation of polarized light forms concentric circles around the sun's position, and if an insect knows the time of day, she can retrieve compass information from any patch of blue sky. Insects are, therefore, able to use the sun as a compass even when it is not in view. To detect these polarization patterns, most diurnal insects'compound eyes have special dorsal areas that are sensitive to the direction of polarized light. Of course, there will be overcast days when no celestial compass information is available. On such days, bees use the same prominent landmarks they used as references when learning about the movement of the sun. Other insects are able to take a more leisurely approach on overcast days, the desert ant *Cataglyphis* remains inside the nest on those rare days when there is no sun.

Path integration allows insects to explore unfamiliar terrain while being connected to the starting point of their journey by the distance and the direction information required for a direct route back to the start. What is more, insects can store the PI co-ordinates of a profitable location and use PI to guide a subsequent return or signal that location to a nestmate. With such an elegant mechanism to guide insects between important locations, why should they use any other navigational strategy? The answer lies in the fact that PI is an egocentric estimate of position and so, small errors will accumulate throughout a route. Therefore, upon the completion of a PI-guided homeward trajectory, the insect may not be at the goal as expected. An inexperienced animal has no choice but to search systematically for the goal. However, if an insect is familiar with a location, it can use terrestrial landmarks to guide its search and correct for any errors accrued during the path integration process. In the next section, we look at the mechanisms and uses of landmark guidance.

Using Landmarks to Pinpoint a Goal

Terrestrial landmarks provide a stable geocentric reference by which animals can define a location. This was demonstrated by Niko Tinbergen in his famous digger wasp experiment (**Figure 2(a)**). Tinbergen identified a digger wasp nest and placed a ring of pine cones around the entrance. When the digger wasp departed, she inspected the nest surrounds before leaving on her foraging trip. While the wasp was away, Tinbergen relocated the pine cone ring, and on her return, the wasp searched at the center of the relocated pine cone ring even though the real nest entrance was only centimeters away. Tinbergen concluded that the information learned about the nest entrance's position relative to the pine cones dominates over any directly perceptible odor or visual cues from the entrance itself. In natural situations, because landmarks are usually stable, learning how a goal location relates to the surrounding landmarks mitigates the risk that cumulative errors from PI will lead to missing the goal.

View-Based Navigation

We now know much about how insects use visual landmarks to define a goal location. Evidence from ants, flies, and solitary and social bees and wasps suggests that places are represented as 2D retinotopic images of the world as seen from that place. We can illustrate the basic phenomenon with recent data from wood ants (**Figure 2(b)**). Ants were trained to find food at a location defined solely by two cylindrical landmarks. In tests, with no feeder present,

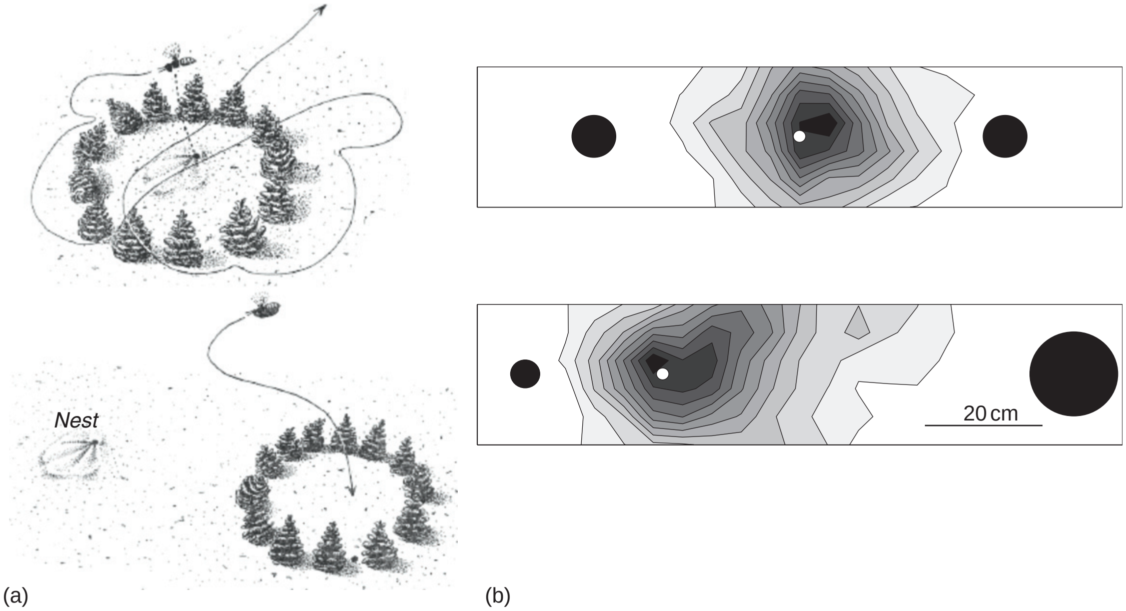


Figure 2 (a) Tinbergen's digger wasp. Upper: Tinbergen placed a circle of pine cones around the nest of a solitary digger wasp. This change in surroundings triggers a period of observation before she finally departs the nest locale. Lower: During the wasp's foraging trip, Tinbergen moved the ring of pine cones, resulting in the wasp searching for the entrance in the wrong location. Reproduced from Tinbergen N (1951) *The Study of Instinct*. Oxford: Clarendon Press. Reprinted with the permission of Oxford University Press. (b) Goal localization using snapshots. Upper: Ants are trained to find food midway between two cylinders (white circle) and their search distribution is concentrated on that spot when the feeder is missing. Darker areas denote the regions where ants spent the most time during search. Lower: Training cylinders are replaced by one cylinder that is smaller (in height and width) and one that is larger. Ants' searches are focused at the location where the cylinders look the same as they did from the feeder in training (white circle). Reproduced from Graham et al. (2004).

ants search mostly at the training location. In further tests, with one small and one large cylinder, ants show a search distribution biased towards the small cylinder. The peak of this new search distribution is at the location where the small and large cylinders have the same apparent size as did the regular cylinders from the food location during training. Using view-based matching to find a goal is an economical navigational strategy as it does not require the computation of the absolute distance to objects.

Stored retinotopic views of the world from goal locations are commonly known as snapshots. Snapshots are made up of the retinal positions of a set of visual features such as apparent size, orientation of high contrast edges, color, and vertical center of gravity. Importantly, snapshots are not only used to identify when an insect is at the goal location. Insects also use the difference between their current view of the world and their stored snapshot to derive a movement direction. Identifying the differences between the current view of the world and the stored snapshot is made easier if the insect faces in the same direction as when the snapshot was stored. Bees and wasps can fly in any direction relative to their line of sight and can therefore fix a body orientation, using their compass mechanisms, thus aligning current view with the stored snapshot before moving to reduce the discrepancy between the two. The process of snapshot alignment is less clear for walking insects because they can only translate in the direction of their body axis and cannot maintain a fixed orientation. There is some evidence that ants align snapshots by fixating conspicuous landmarks or using compass information. However, these mechanisms can align snapshots only temporarily, and it is not yet clear what ants do when the current view and goal snapshot are not aligned.

Learning About a Goal Location

When Tinbergen's Digger wasp left her nest, she initiated a period of observation of the nest locale prompted by the conspicuous change in nest surroundings. This was an example of a learning flight, a type of predictive learning, where insects anticipate what information will be useful in the future and use stereotyped learning behavior to acquire that information. Tinbergen's rough sketch did not capture the detailed structure of this flight, but using film and video technology, further experiments have revealed the fine structure of the similar learning behaviors of other wasp and bee species.

When an individual bee or wasp leaves an important location, be it nest, feeder, or even a parasitized host, she turns to face that location and moves backwards and upwards while flying in arcs of increasing size (Figure 3(a)).

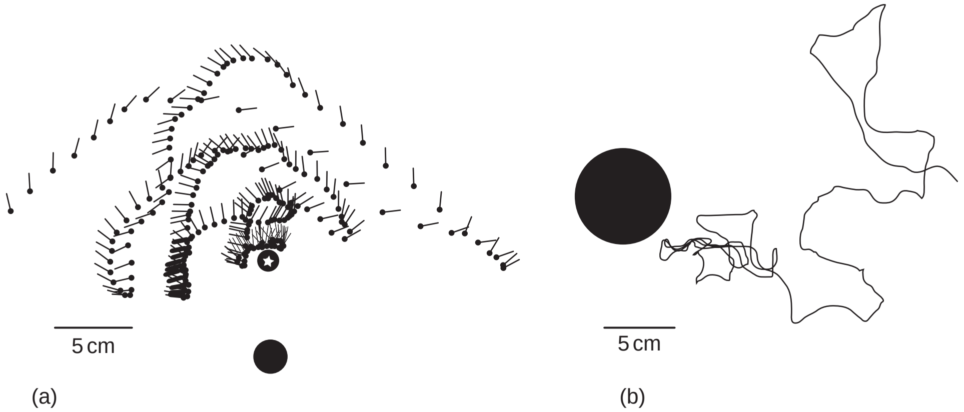


Figure 3 (a) The learning flight of a wasp. Learning flight of a solitary wasp. (*Cerceris rybyensis*) as she leaves the nest Circles with tails denote the wasp's position and orientation every 20 ms. The star shows the nest entrance, and the filled black circle indicates a small cylinder placed nearby. Reproduced from Collett TS and Zeil J (1996) Flights of learning. *Current Directions in Psychological Science* 5(5): 149–155. (b) The learning walk of a wood ant. Departure walk of an ant after visiting a feeder at the base of a black cone. Reproduced from Nicholson et al. (1999).

This provides a prolonged period of observation from the point of view that she will adopt when returning to the goal. Because bees do not have stereoscopic vision, they have to generate 3D depth structure from the motion parallax generated by translatory movements. The arcing structure of the flight is, therefore, suited to determining the relative distance of the landmarks surrounding the goal and identifying those close landmarks which are the most reliable for navigation. The apparent paradox between a snapshot, which does not contain any absolute depth or distance information, and the learning flight, which seems ideally structured to extract depth information, was addressed by Miriam Lehrer and Tom Collett. They trained bees to collect a reward from a feeder that was located in a fixed position relative to a cylinder. Probe tests demonstrated that bees learned both apparent size (a snapshot) and also the absolute distance between the landmark and the feeder. Following further tests, it was shown that the absolute distance provides the primary cue during the initial phase of learning, with the absolute size becoming more important later on. Later, when the close-by landmarks have been reliably identified, the bee can rely on a snapshot which contains only the apparent size of those landmarks. As the insect gains experience, the duration of learning flights drops off and eventually, the insect will fly directly away from the goal. However, flights will recommence at the start of each day, if local landmarks are changed or following a difficult inbound trip.

Early in their foraging careers, bees also gain experience of the large-scale environment around their nest by undertaking a series of flights in which they do not collect nectar or pollen. The so-called survey flights seem to consist of a series of loops with relatively direct trajectories away from and returning to the hive. This structure would seem suited to learning about the routes back to the hive from surrounding areas, and it has been shown that after a single survey flight, bees are able to fly directly home from release sites within a direct line of sight of the hive. The time and effort invested in learning and survey flights highlights the importance of gaining accurate information about local landmarks. This advantage also applies to ants which have been observed performing a similar behavior (Figure 3(b)), referred to as learning walks. These maneuvers are similar to learning flights in terms of inspecting the goal area and surroundings, but as yet, we do not have a functional analysis of learning walk behavior.

Habitual Routes

Insects could theoretically navigate using a toolkit of path integration augmented by snapshot guidance near a goal. However, they do not restrict themselves to this simple procedure, but also build extensive knowledge of their environment by learning sets of instructions that can guide long and complex idiosyncratic routes. As with place learning, route learning depends on the sophisticated interaction of innate behavior and predictive learning. Additionally, the organization of the large sets of memories required for route navigation highlights the cognitive abilities of insects.

The consummation of the route learning process is a set of procedural instructions associated with visual landmark information. Figure 4(a) gives an elegant demonstration of the properties of such a learned route. Martin Kohler and Rudiger Wehner allowed individual Australian desert ants to learn a route between their nest and a food source. Individual foragers showed idiosyncratic and stable routes through the scrub and grass tussocks. Experienced ants were then taken from the feeder or from near their nest and relocated to the midpoint of their habitual route.

In both cases, they accurately reproduce the second half of the route. From this demonstration, we can infer several of the properties of visually guided routes. Firstly, even with its low resolution eyes in a world of similar objects, the ant is able to identify its location. Secondly, this knowledge has to be accessible independently of path integration or sequence information. Finally, the ant knows which way she is going and reproduces the second half of her homeward rather than her foodward route. These properties of routes come about because of the way navigational memories are organized in the insects' brain, and this is discussed in the section 'Organization of Spatial Memories.' In the remainder of this section, we look at the types of procedural information used to guide routes as well as the strategies that insects have for the rapid learning of route information.

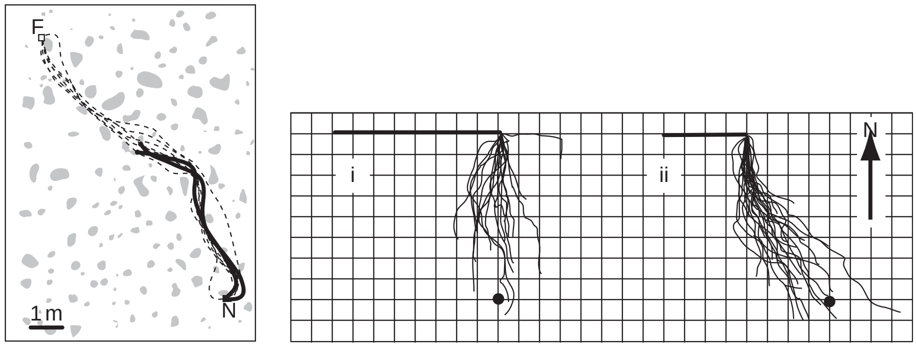
Mechanisms for Route Following

Experienced foragers demonstrate in their habitual routes a variety of ways of utilizing visual landmark information. In the section 'Using Landmarks to Pinpoint a Goal,' we showed how snapshots can be used to navigate to a single goal location, and snapshot guidance can similarly be used to guide insects to subgoals along a route. However, routes do not generally require the same level of precision along their entire length as they do at the end. Therefore, simple procedural instructions, such as taking the correct direction at a recognized location, will ensure that an insect stays on course.

Two simple procedural mechanisms have been identified from the studies of the North African desert ant *Cataglyphis*. Firstly, if navigating in cluttered terrain, routes can be described as a series of detours around recognized landmarks. Studies have shown that ants will learn the appearance of landmarks close to a route. They will then make appropriate detours to put the landmark on the same side of their path as they experienced during route learning, although they do not take a precise route to exactly match the retinotopic appearance of the landmark experienced in training. The second procedural mechanism for route guidance comes from associating compass directions with defined locations. In the experimental example from **Figure 4(b)**, ants were trained to take an L-shaped route from a permanent feeder back to their nest. The first part of the route was along a channel, and from the end of the channel, ants would head due south to the nest. Experienced ants have learned to associate the end of the channel with the southerly direction habitually taken there. This association of a direction with a salient location is called a local vector. If the channel is shortened, ants will have conflicting information at the end of the channel. Their local vector will point due south but their path integration system will point in a south westerly direction. We see that the procedural information 'wins out' and ants follow their local vector, though the path integrator continues to calculate the homeward direction, and after a while, the ants switch to following the direction set by PI.

The Scaffolding of Route Learning

In order to accurately and quickly learn route information, insects should establish a consistent route shape as soon as possible. As the shapes of routes are determined by path integration and an insect's innate responses to objects, innate behaviors play an important role in learning by ensuring that a naïve individual takes similar routes on her early foraging trips. We can thus say that the



(a) (b)

Figure 4 (a) Idiosyncratic foraging routes. Australian desert ants (*Melophorus bagoti*) complete their habitual route when placed at the midpoint after being taken from the feeder (F) or close to the nest (N) Dotted lines show normal homeward trajectories. Black lines show test paths. Gray areas depict grass tussocks Reproduced from Kohler M and Wehner R (2005) Idiosyncratic route-based memories in desert ants, *Melophorus bagoti*: How do they interact with pathintegration vectors? *Neurobiology of Learning and Memory* 83(1): 1–12. Reprinted with the permission of Elsevier. (b) Local vectors. Ants were trained on an L-shaped homeward path consisting of 8 m in an open topped channel (thick line) and 8 m over open ground to the nest (●). i: The trajectories of ants taken from the feeder and placed at the end of a test channel on a novel test ground. ii: Trajectories from ants taken from the feeder to the end of a 4 m channel. Reproduced from Collett M, Collett TS, Bisch S, and Wehner R (1998) Local and global vectors in desert ant navigation. *Nature* 394: 269–271.

innate behaviors act as a scaffold for learning, providing a consistent route shape allowing the insect to confidently learn landmark information from along the route. The key outcome of this process is that experienced foragers can guide their routes independently of the original innate behavior which determined the route shape.

Path integration provides one obvious mechanism for ensuring a consistent route across multiple foraging runs. Another is the innate attraction that some insects show towards conspicuous visual landmarks (beacons). In an illustrative experiment with wood ants, individual foragers were allowed to learn routes with a large landmark placed laterally to the direct path between the start-point and the feeder. Mature routes were biased towards this beacon, which became an intermediate goal on the route to the feeder. In tests, however, experienced ants performed the same routes even when the beacon was removed or displaced, showing that they had learned other visual cues to guide their route. Although the beacon determined the shape of the route, routes were robust to the removal of the beacon.

Organization of Spatial Memories

An insect's navigational repertoire consists of a set of simple behaviors, including path integration, view-based homing, and local vectors. In combination, these simple behaviors enable insects to learn and robustly perform complex foraging routes of many thousands of body lengths. What is more, individuals can learn multiple routes as necessitated by cyclical or seasonal changes in resource availability. Therefore, an individual forager not only has to organize the large set of procedural instructions that define a single route but must also have multiple sets of route instructions that lead to different locations. The efficient organization and accurate recall of route memories is critical for navigation, and the studies of these processes highlight the impressive cognitive performance of an insect's small brain.

Organization of Memories for a Single Route

A single route through cluttered terrain is built from many instructions associated with specific locations or landmarks (route marks) of which accurate identification is essential. Yet, natural landmarks, such as trees, shrubs, bushes, and grass tussocks, may look similar to insects' low-resolution eyes. To lessen the chance of misidentification leading to the recall of an inappropriate route instruction, insects bind together memories of route marks with contextual information from larger and more distant landmarks. As an insect moves along a route, the appearance of distant landmarks changes more gradually than the appearance of local route marks. These distant landmarks can therefore be used as contextual cues, reducing the set of possibilities about the insect's current position and simplifying the task of recalling the appropriate route instruction for the current route mark. The binding together of information about route marks with information from larger landmarks has been shown for both ants and bees when a spatial task requires an individual to treat identical landmarks differently in two contexts.

One alternative mechanism for recalling the appropriate instruction for the currently perceived landmark would be to store route memories as a rigid sequence of instructions where the performance of one action primes the recall of the next instruction in the sequence. An internal mechanism of this type may not be necessary when considering spatial behavior as the route sequence already resides in the external environment. Additionally, we have seen that the Australian desert ant is able to perform her routes independently of a rigid sequence (**Figure 4(a)**). However, experiencing route landmarks in the correct sequence does seem to have some effect. Lars Chittka and colleagues trained bees to fly along a route marked by a series of conspicuous tents. Compressing the distance between the tents prompted bees to search for the feeder after a shorter distance than usual. This showed that the bee's expectation of finding the feeder is not just triggered by landmarks close to the goal but by perceiving those goal landmarks after experiencing the route landmarks in the correct sequence.

Organization of Multiple Route Memories

Although insects show flexibility in their ability to access route memories out of sequence, the individual must ensure that only those memories associated with the current route are available to be accessed. In the simplest instance, a central place forager with experience of its environment will have two routes through it: an outward route to a food source and an inward route back to the central place. An elegant experiment by Rudiger Wehner shows how the information for guiding outward routes is insulated from that for guiding inward routes. Using barriers, Wehner was able to spatially separate outward and inward routes so that ants took a looped route from the nest to the feeder and back. Experienced ants on their inbound route were captured either from the feeder, along the inbound route, or near the nest and then displaced to a point on their habitual outward route. Despite this being a familiar location, ants behaved as if they were lost and only managed to return home if their systematic search led them by chance to discover their familiar inbound route. Further experiments with bees and ants have confirmed that an insect's internal motivational state can act as a contextual cue for priming appropriate memories for outbound or inward routes even in identical spatial contexts.

Other examples of contextual signals that can prime particular route memories are the time of day and odor. Bees will readily learn routes to two locations if nectar is available in one location in the morning and another in the afternoon. Similarly, if bees are trained to forage at two locations with differently scented feeders, simply introducing one of the scents into the hive is enough to motivate bees to recall the route instructions that will take them to the feeder carrying that scent. In summary, we see that the use of multiple contextual cues allows an insect to organize memories for multiple routes. These mechanisms give an insect the flexibility to choose different routes for different purposes and yet ensure that only the instructions for the current route are used.

Cognitive Maps

One of the most persistent debates within navigation research is whether insects are able to organize their large set of spatial memories into a single representation of the world; a so-called 'cognitive map.' In principle, the path integration system would allow co-ordinates to be allocated to key goals and landmarks so that locations would share a common frame of reference. While much energy has been wasted on debates surrounding the definition of the term 'cognitive map,' there is a general consensus that the behavioral signature of such a map would be the ability to take novel shortcuts between familiar locations.

Here, we look at the evidence from ants and bees to determine whether insects construct cognitive maps. For ants, the simple experiment by Rudiger Wehner (section 'Organization of Multiple Route Memories') shows how sets of route instructions are insulated from each other rather than integrated into a single map. Moreover, despite the indirect interaction between landmark learning and path integration (section 'The Scaffolding of Route Learning'), there is no evidence that familiar locations or prominent landmarks can become associated with the metric information acquired from path integration. In contrast, the debate over whether bees might hold a cognitive map has been more intense.

The idea that bees might be able to develop a unitary representation of the world, while ants do not, may be based on the bees' elevated perspective of the world and their ability to cover large distances during foraging trips. This would, in principle, make it easier to integrate information from different locations and routes. So, when James Gould reported that bees did, in fact, build a cognitive map, the finding was not considered controversial. Gould had trained bees to find one feeder (A) located in a wooded area and then proceeded to catch regular foragers as they left the hive and transported them to a new location (B). The ground sloped up from B to A such that bees could not see A from the new location. Yet, bees flew directly from B to A suggesting that they had knowledge of the world, enabling them to take direct paths to important locations; this would satisfy many people of the existence of a cognitive map in bees. However, this finding has proved difficult to replicate. For instance, Fred Dyer reports an experiment similar to Gould's original. Two feeders, A and B, were established at equal distances from a hive. The terrain meant that feeder A was higher than B. Bees departing the hive for either A or B were transported to the other feeder and released; bees familiar with B were able to fly directly to B from A; however, bees familiar with A could not reach it from B. Only when bees from A could see the landmarks surrounding B, could they fly directly there, suggesting that bees were using simple landmark guidance rather than a map-like representation. Dyer's experiment had seemingly quietened the cognitive map debate; yet, recent experiments using radar tracking have shown bees appearing to take novel shortcuts to their hive. So far, the data is inconclusive, but the interest and debate surrounding cognitive maps is sure to continue.

Concluding Remarks

True navigation requires a combination of physical, sensory, and cognitive adaptations, and insects tell a fascinating story in all these three dimensions. The scale over which some insects navigate is astounding, and the mechanisms they use to do this, represent a paradoxical combination of simplicity and sophistication. We have seen how insect navigation is built on the interaction of innate strategies with learned information. Throughout its life, an individual gains experience of the world and thus, develops a reportoire of stored snapshots and procedural vector instructions linked to familiar places. These memories are bound together into contextually labeled routes. Representing knowledge of the world in this way, as a series of routes, may be the limit of an insect's navigational ability. There is no evidence that insects are capable of building a map-like representation of the world as vertebrates appear to do, and perhaps, this is a fundamental limitation of the small brains of insects. Either way, with ever-improving technologies, the continued study of social and solitary insects is sure to reveal more examples of elegant behavioral and cognitive solutions to the problem of navigating through the real-world.

See also: Magnetic Compasses in Insects.

Further Reading

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