Insect Navigation ☆

Paul Graham, University of Sussex, Brighton, United Kingdom

Glossary

Odometry Odometry is the process of measuring distance traveled. Navigating animals have to use odometric information, combined with compass information to keep track of their location.

Path integration Path Integration (PI) is a process by which odometric and compass information are combined to keep track of one's position relative to the start of a journey. PI enables animals to explore unfamiliar terrain and safely return to familiar territory.

Sky compass Insects can extract information about their current direction from information present in the sky. The sun gives directional information if one knows the time of day, also patterns of polarized light and chromatic gradients can give directional information.

Social insects Social insects are those species that live in colonies and show individual division of labour. Some individuals (e.g., the queen) are responsible for reproduction, whereas others may be specialist foragers. Hymenopteran insects (ants, bees and wasps) make up most of the social insect species.

Abstract

Insects are capable of impressive feats of navigation using an integrated toolkit of simple strategies. Inexperienced foragers rely on path integration where distance and direction estimates are continuously combined in such a way that at any point they can return to the starting point of their journey by a direct path. With increased experience, individuals learn and use a large reportoire of memories about the world that are organized into habitual foraging routes. The smooth integration of these navigational strategies and the rapid learning of environment information require mechanisms that are impressive, given the limited neural resources available to insects.

Keywords

Ants; Bees; Cognitive map; Foraging; Landmarks; Odometry; Path integration; Route learning; Sky compass and snapshot

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 20th century ethologists, showed that insects were indeed capable of learning about and navigating around a familiar environment. One elegant example from Romanes (1885) 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.

In this article, we focus on the mechanisms that underpin 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 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 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 (Fig. 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 (Fig. 1(B)) were decoded by von Frisch (1967), 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. We are only just learning about how insects' brains may perform the PI calculation (Stone et al., 2017), 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 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 (Wittlinger et al., 2006). 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'
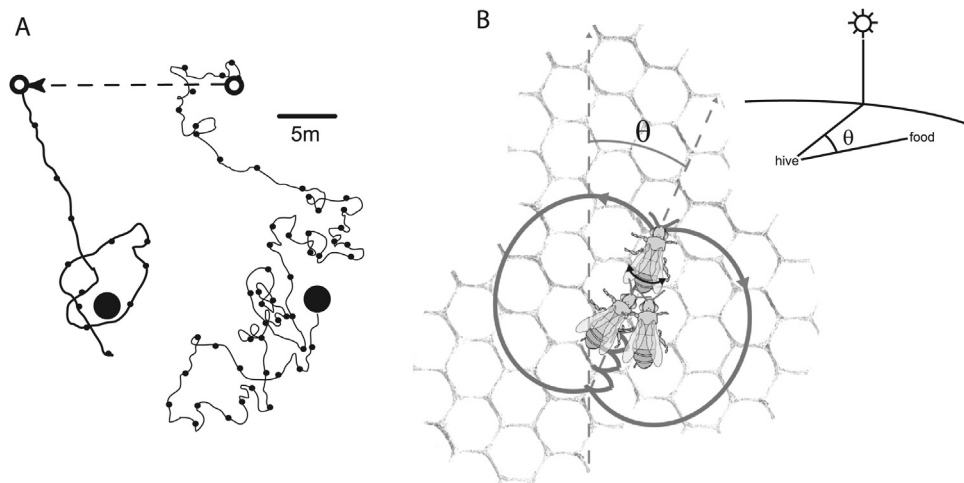
Fig. 1   (A) Path integration in desert ants. The outward foraging path of a desert ant is shown until she finds food. Before the ant can make a return trip, it is displaced. The homeward path is parallel to the route from food to nest indicating the use of an egocentric estimate of position rather than landmark information. Filled circle denotes nest and fictive nest, open circle food. Reproduced with permission from Wehner, R., Wehner, S., 1990. Insect navigation: Use of maps or Ariadne's thread? Ethology Ecology & Evolution 2 (1), 27–48. (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.

return journey consisted of approximately the same number of strides. So, we can conclude that ants use a step-counting 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 Esch and Burns (1996) 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 (Srinivasan et al., 1996).

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 (Dyer and Dickinson, 1994). 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, Cataglyphis desert ants in North Africa remain 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 environmental information 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 specifically visual information from the environment.

Using Visual Cues to Pinpoint a Goal

Terrestrial objects provide a stable geocentric reference by which animals can define a location. This was demonstrated by Niko Tinbergen (Tinbergen, 1951) in his famous digger wasp experiment (Fig. 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 large objects are usually stable, learning how a goal location relates to such 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 data from wood ants (Graham et al., 2004; Fig. 2(B)). Ants were trained to find food at a location defined solely by two cylindrical landmarks. In tests, with no feeder present, ants search mostly at the training location. In further tests, with one small and one large cylinder, ants show a search distribution biased toward 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 (Cartwright and Collett, 1983) and can be used to identify when an insect is at the goal location. Insects can also use the difference between their current view of the world and their stored snapshot to derive a movement direction or rotation. Importantly for small brained animals, snapshots can be used for navigation without the need for lots of visual processing, in fact view-based navigation can be implemented using almost "raw" views of the world, without having to identify the specific objects that make-up a scene.
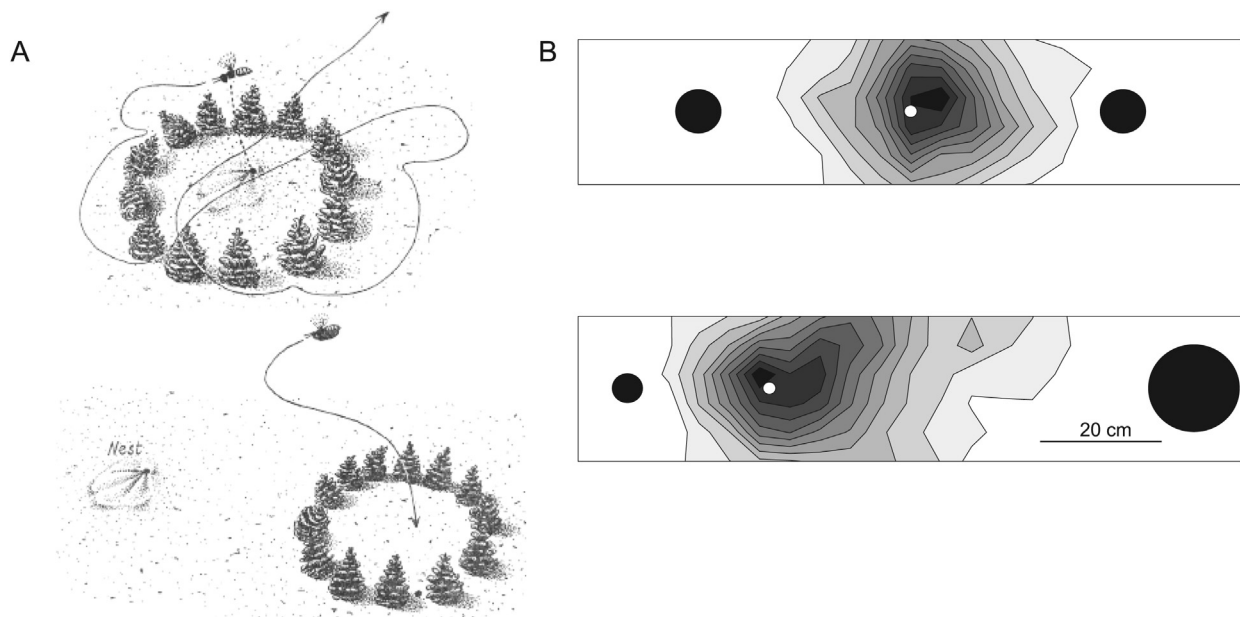

Fig. 2   (A) Tinbergen's digger wasp. Upper: Tinbergen placed a circle of pine cones around the nest of a solitary digger wasp. This change in surroundings triggers a period of observation before she finally departs the nest locale. Lower: During the wasp's foraging trip, Tinbergen moved the ring of pine cones, resulting in the wasp searching for the entrance in the wrong location. Reproduced with permission from Tinbergen, N., 1951. The Study of Instinct. Oxford: Clarendon 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, P., Durier, V., Collett, T.S., 2004. The binding and recall of snapshot memories in wood ants (Formica rufa L.). Journal of Experimental Biology 207 (3), 393–398.

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 such flights, but further experiments have revealed the fine structure of the similar learning behaviors in other wasp, ant and bee species (Fig. 3).

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. This provides a prolonged period of observation from the point of view that she will adopt when returning to the goal. 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 longer 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 (Capaldi et al., 2000). 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 the environment.

Habitual Routes

Insects could theoretically navigate using a toolkit of path integration augmented by view-based guidance near a goal. However, they do not restrict themselves to these simple procedures, but also build extensive knowledge of their environment by learning sets of instructions that can guide idiosyncratic routes (Fig. 4). As with place learning, route learning depends on the interaction of innate behavior and learning. The consummation of this route learning process is a set of procedural instructions associated with locations. Fig. 4(A) gives an elegant demonstration of the properties of such a learned route. Kohler and Wehner (2005) 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. For instance, although mechanisms like PI define the early path of foragers, visual learning rapidly ensures that the procedural instructions needed to guide routes can be used flexibly.
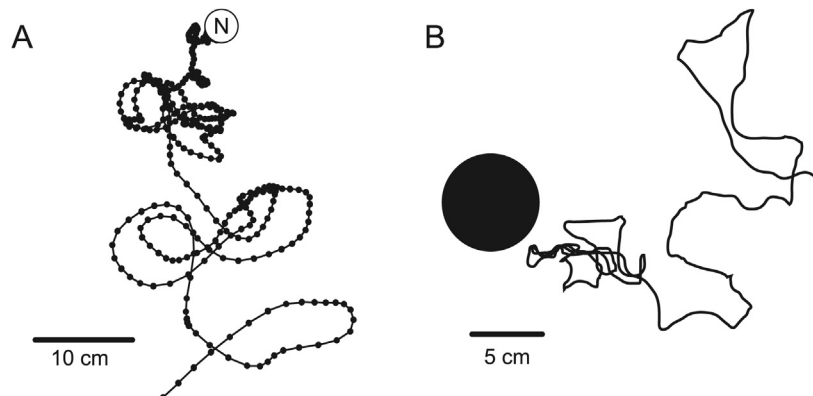

Fig. 3 (A) The learning flight of a bumblebee as she leaves the nest. Figure provided by Andrew Philippides. Adapted from Philippides, A., de Ibarra, N.H., Riabinina, O., Collett, T.S., 2013. Bumblebee calligraphy: The design and control of flight motifs in the learning and return flights of *Bombus terrestris*. Journal of Experimental Biology 216 (6), 1093–1104. (B) The learning walk of a wood ant. Departure walk of an ant after visiting a feeder at the base of a black cone. Adapted from Nicholson, D.J., 1999. Learning walks and landmark guidance in wood ants (*Formica rufa*). Journal of Experimental Biology 202, 1831–1838.
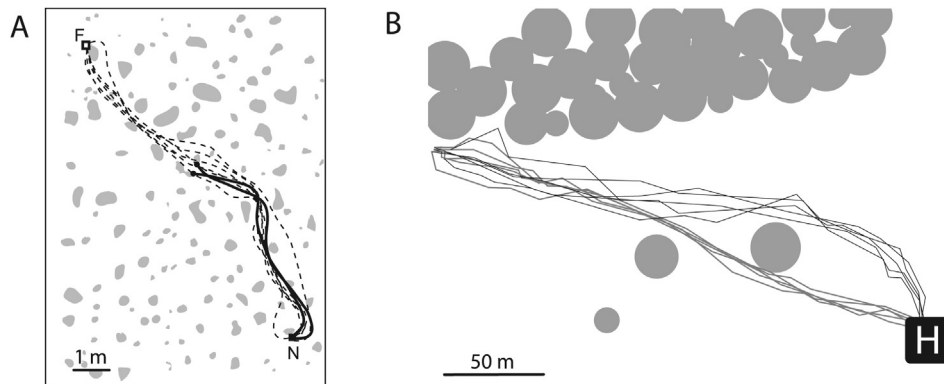
Fig. 4 Idiosyncratic foraging routes. (A) Australian desert ants (Melophorus bagoti) complete their habitual route when placed at the midpoint after being taken from the feeder (F) or close to the nest (N). Dotted lines show normal homeward trajectories. Black lines show test paths. Gray areas depict grass tussocks. Adapted with permission from Kohler, M., Wehner, R., 2005. Idiosyncratic route-based memories in desert ants, *Melophorus bagoti*: How do they interact with path-integration vectors? Neurobiology of Learning and Memory 83 (1), 1–12. (B) An individual bumblebee shows idiosyncratic paths over a series of 5 foraging trips. Outward (gray) and inward (black) paths are shown. Data from Woodgate, J.L., Makinson, J.C., Lim, K.S., Reynolds, A.M., Chittka, L., 2016. Life-long radar tracking of bumblebees. PLOS ONE 11 (8), e0160333.

Organization of Spatial Memories

An insect's navigational repertoire consists of a set of simple behaviors, including path integration and view-based homing. 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 sets of procedural instructions that define a single route, but must also store multiple sets of route instructions that lead to different locations. The efficient organization and accurate recall of route memories is critical for navigation.

Although insects show flexibility in their ability to access route memories out of sequence (Fig. 4(A)), individuals must ensure that only those memories associated with the current route are 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 shows how the information for guiding outward routes is insulated from that for guiding inward routes (Wehner et al., 2006). Using barriers, ants' outward and inward routes were separated, 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 those scents into the hive is enough to motivate bees to recall the route instructions that will take them to the feeder carrying that scent (Reinhard et al., 2004). 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 coordinates to be allocated to key locations, such that they 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. Gould (1986) reported that bees could take such shortcuts, suggesting that they can form cognitive maps. 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, Dyer (1991) 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. Subsequent experiments using radar tracking have re-opened the debate, although the data is inconclusive (Cheeseman *et al.*, 2014; Cheung *et al.*, 2014).

Concluding Remarks

Navigation requires a combination of physical, sensory, and cognitive adaptations, and insects tell a fascinating story in all these regards. 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 procedural 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. However, with ever-improving technologies, the continued study of insect navigation is sure to reveal more examples of elegant behavioral and cognitive solutions to the problem of navigating through the real-world.

> *See also:* **Migration and Orientation:** Insect Migration; Magnetic Orientation in Migratory Songbirds; Maps and Compasses; Magnetic Compasses in Insects.

References

Capaldi, E.A., Smith, A.D., Osborne, J.L., et al., 2000. Ontogeny of orientation flight in the honeybee revealed by harmonic radar. Nature 403 (6769), 537.

Cartwright, B.A., Collett, T.S., 1983. Landmark learning in bees. Journal of Comparative Physiology 151 (4), 521–543.

Cheeseman, J.F., Millar, C.D., Greggers, U., et al., 2014. Way-finding in displaced clock-shifted bees proves bees use a cognitive map. Proceedings of the National Academy of Sciences 111 (24), 8949–8954.

Cheung, A., Collett, M., Collett, T.S., et al., 2014. Still no convincing evidence for cognitive map use by honeybees. Proceedings of the National Academy of Sciences 111 (42), E4396–E4397.

Dyer, F.C., 1991. Bees acquire route-based memories but not cognitive maps in a familiar landscape. Animal Behaviour 41 (2), 239–246.

Dyer, F.C., Dickinson, J.A., 1994. Development of sun compensation by honeybees: How partially experienced bees estimate the sun's course. Proceedings of the National Academy of Sciences 91 (10), 4471–4474.

Esch, H., Burns, J., 1996. Distance estimation by foraging honeybees. Journal of Experimental Biology 199 (1), 155–162.

Gould, J., 1986. The locale map of honey bees: Do insects have cognitive maps? Science 232 (4752), 861–863.

Graham, P., Durier, V., Collett, T.S., 2004. The binding and recall of snapshot memories in wood ants (*Formica rufa* L.). Journal of Experimental Biology 207 (3), 393–398.

Kohler, M., Wehner, R., 2005. Idiosyncratic route-based memories in desert ants, *Melophorus bagoti*: How do they interact with path-integration vectors? Neurobiology of Learning and Memory 83 (1), 1–12.

Reinhard, J., Srinivasan, M.V., Zhang, S., 2004. Olfaction: Scent-triggered navigation in honeybees. Nature 427 (6973), 411.

Romanes, G.J., 1885. Homing faculty of hymenoptera. Nature 32, 630.

Srinivasan, M., Zhang, S., Lehrer, M., Collett, T.S., 1996. Honeybee navigation en route to the goal: Visual flight control and odometry. Journal of Experimental Biology 199 (1), 237–244.

Stone, T., Webb, B., Adden, A., et al., 2017. An anatomically constrained model for path integration in the bee brain. Current Biology 27 (20), 3069–3085.

Tinbergen, N., 1951. The Study of Instinct. Clarendon Press, Oxford.

von Frisch, K., 1967. The Dance Language and Orientation of Bees. Harvard University Press, Cambridge, MA.

Wehner, R., Boyer, M., Loertscher, F., Sommer, S., Menzi, U., 2006. Ant navigation: One-way routes rather than maps. Current Biology 16 (1), 75–79.

Wittlinger, M., Wehner, R., Wolf, H., 2006. The ant odometer: Stepping on stilts and stumps. Science 312 (5782), 1965–1967.

Further Reading

Knaden, M., Graham, P., 2016. The sensory ecology of ant navigation: From natural environments to neural mechanisms. Annual Review of Entomology 61, 63–76.

Wehner, R., 2003. Desert ant navigation: How miniature brains solve complex tasks. Journal of Comparative Physiology A 189 (8), 579–588.

Wystrach, A., Graham, P., 2012. What can we learn from studies of insect navigation? Animal Behaviour 84 (1), 13–20.

Zeil, J., 2012. Visual homing: An insect perspective. Current Opinion in Neurobiology 22 (2), 285–293.