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Navigation: Cognition, learning, and memory

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What is navigation for a bee?

Discussions about bee foraging are often centered around the final interaction between the bee and a flower, when the insect obtains food and the plant is pollinated. However, they often ignore the fundamental behavioral and cognitive mechanisms that brought the bee to that flower: navigation. Honey bees are "[central-place-foragers](#)," which means they exploit food resources from a stable location, their colony nest ([Orion and Pearson, 1979](#)). While foraging is a collective task shared by hundreds of bees from the same colony, individual foragers need to successfully find resources and bring them back to the hive. Thus, for a bee, knowing how to go from the nest (i.e., location A) to a food source (i.e., location B) is a critical task. Since the identity and the number of food sources that need to be visited may greatly vary during the lifetime of the bee, navigation involves various forms of learning and memories allowing for highly flexible behaviors.

When a bee leaves its nest for the first time, it has no a priori knowledge of where it is. Therefore, it must learn to recognize the visual surroundings of its nest location in order to know how its home looks from the outside and come back. The next challenge for the bee is to know what to collect, find resources, and choose which one is best. While honey bees mostly forage for nectar (the main source of carbohydrates) and pollen (the main source of proteins and lipids) on flowers, they also collect materials such as plant resins, mineral salts, or water according to their colony needs ([Metz et al., 2010](#); [Ohlinger et al., 2022](#)). All these resources can vary in abundance, type, and distribution across the landscape and through time ([Visscher and Seeley, 1982](#)). A honey bee forager, for instance, is expected to visit hundreds of flowers to collect enough nectar or pollen in a single trip ([Schmid-Hempel et al., 1985](#); [von Frisch, 1967](#)). Once the required resources have been located, or when the bee is exhausted, it has to find its way back home using visual information stored on its way out. A complete foraging trip, starting and ending at the nest location, thus requires the bee to solve additional cognitive operations with a measurable impact at a large timescale, such as learning visual information ([Zeil, 2012](#)) or following a "celestial compass" ([Kraft et al., 2011](#)) along familiar routes. But, it also requires abilities with a short-term impact such as learning to avoid collisions with obstacles ([Ravi et al., 2020](#)), crossing gaps through the vegetation ([Ravi et al., 2018](#)), or controlling altitude ([Portelli et al., 2017](#)). Honey bees also tend to optimize route geometry ([Buatois and Lihoreau, 2016](#)) and take shortcuts between known locations ([Müller et al., 2018](#); [Paffhausen et al., 2021](#)). In this chapter we review how some of these navigational abilities are studied and expressed during foraging.

A long history of research

Bees are exceptionally good navigators and their orientation feats have been the focus of detailed observations by naturalists and early ethologists. As early as 1903, Charles Henry Turner performed homing experiments in *Melissodes* bees, showing how foragers follow displaced visual landmarks (cap of a soda bottle) to find the entrance of their underground nest. Later, John Eckert reported the use of an automobile as a landmark to find food by honey bees (Eckert, 1933). Research on bee navigation took a new direction in 1967, after the Austrian Nobel Prize laureate Karl von Frisch, wrote his book on the history of animal behavior (von Frisch, 1967). For the first time, an understanding of an essential mechanism behind honey bee navigation was reported: the "waggle dance," a communication system described in a few species of the genus *Apis*. While the dancing behavior is long known, the discovery of the symbolic nature of this communication system by which bees indicate the location of food sources or nest sites to their nestmates, has enabled us to "read in the mind" of bees and study the spatial learning and memory of foragers (Esch and Burns, 1995; Menzel, 2019). Since the 1990s, technological advances have further advanced this research through the quantification of navigational behaviors in the field. For instance, long-distance tracking systems based on harmonic radar were developed to record the 2D flight paths of flying bees carrying a transponder, which returns a specific signal at double the tracking frequency, eliminating interference from other objects that reflect radar frequencies. The range is approximately 900 m and the transponder weighs under 15 mg, depending on how robustly it is made and attached (Riley et al., 1996). Radio frequency identification (RFID) has been used to monitor the foraging frequency and efficiency of individual bees by recording the traffic of tagged foragers at the hive entrance, and the weights of the tagged individuals can be recorded with precision balances as they leave or return (Klein et al., 2019). Video tracking technologies are also useful to investigate the hive behavior and analyze honey bee dances using machine learning tools (Bozek et al., 2021). These technological and conceptual developments have seen the emergence of other model species, including ants and bumblebees, for navigation research in social insects. Bumblebees are particularly useful. For instance they can be more easily tested under artificial conditions and are more robust to carrying tags required for radar and radio tracking than honey bees (Lihoreau et al., 2012). Their foraging behavior differs in many aspects from that of honey bees, e.g., bumblebee foragers are indifferent to each other; they do not perform waggle dance communication and have simpler forms of communication about colony needs (Brian, 1952; Dornhaus and Chittka, 2005; Minahan and Brunet, 2018). Nonetheless, many navigational aspects observed in these insects are similar to that of honey bees and therefore it is informative to compare their navigational abilities. In what follows, we discuss knowledge about bee navigation focusing on honey bees, but some results were primarily obtained in other social insects like bumblebees but also ants.

The navigational toolkit

Honey bees use their sensory inputs and cognitive capabilities to form a motivation for what to seek and use their sense of time along with vision and olfaction to know when to go out and find it. They can choose to fly beyond their memory record without losing track of the direction to the hive, and they can communicate the distance, direction, identity, and quality of the resources they find. Their navigation behavior is sufficiently variable to support stochastic optimization but not too variable to be successful. The earliest insects were likely capable of body orientation, taking-off and landing, avoiding objects, and flying to a target based on attraction and sensory signals, but honey bees, as central place foragers, need to integrate these basic capabilities with a memory of the nest in the landscape and a cognitive motivational state of activity, including the identity of resource to collect, and outbound or homebound direction (see Chapter 1). There is an overall regulatory process: foragers know what to look for (pol-

len, nectar, nest site, etc.) to meet colony needs, and sense the time of day. Honey bees begin with an extensive innate set of navigational behaviors or capabilities. This includes the physical abilities but also the motivation to explore and undertake intentional learning activities; dancing and following dances; attraction to flowers and other resources; attraction to the home hive; interaction with nestmates, e.g., dance communication and provisioning prior to foraging flight (Harano and Nakamura, 2016). The innate and learned capabilities that a bee can choose from can be compared to a navigational “toolkit.” This analogy was first used to describe desert ants’ navigation skills by Rüdiger Wehner and extended since to other insects (Wehner, 2009). Some of the differences between honey bees and bumblebees can be seen as differences in their toolkits (Townsend-Mehler et al., 2011). Bees use many senses and cues to navigate. Idiothetic cues yield information about the self and include senses like the apparent motion of the scenery on the eye retinae (i.e., the optic flow), as well as proprioceptive cues about the configuration, orientation, and movement of the body. Allothetic cues, by contrast, yield information that is not centered around the self but on anything external to it, such as the position of the sun in the sky or a visual landmark. Throughout life, they combine the innate and learned behaviors and choose what they need from their navigational toolkit to satisfy their motivational urges, based on the interplay of idiothetic and allothetic sensory cues.

Path integration

Path integration is a basic navigational mechanism for central place foraging shared by insects (e.g., bees, ants, crickets, beetles) and virtually all other animals (Mittelstaedt and Mittelstaedt, 1980). Path integration combines an external (allothetic) compass, like the pattern of polarized light in the sky perceived through the dorsal region of the honey bee’s compound eyes (Kraft et al., 2011; Wehner, 1989), and an idiothetic cue like the optic flow (apparent motion of the visual world that is experienced *en route*) (Fig. 4.1). For a honey bee, the position of the sun in the sky indicates the orientation in space of the individual, while optic flow yields information about the distance traveled (Collett and Collett, 2000) (Fig. 4.1C). Optic flow thus acts as the “odometer” (Srinivasan et al., 2000). It is dependent on the distance from the object, the altitude of the flight, the landscape topography, and locomotion velocity (Esch and Burns, 1996; Koenderink and van Doorn, 1987). Assuming a constant velocity and altitude, the honey bee can determine its current position relative to the origin of its journey (i.e., the colony nest) based on optic flow. Therefore, by continually integrating its often-tortuous path toward the current position, the honey bee can return to the place of departure in a relatively straight line (bee-line). Path integration gives the animal access to a “homing vector” memory that indicates the direction and distance of the colony nest at each new step until it is eventually zeroed when the navigator reaches its goal. In the brain of the bee, central areas called the mushroom bodies record route memories (Ardin et al., 2016) and the central complex, a small area in the center of the brain receiving motor and visual inputs, is advocated to be the structure enabling path integration [See the illustration in the section on how bees encode space (Heinze and Homberg, 2007; Stone et al., 2017)].

The derivation of the distance flown from the optic flow requires assumptions about altitude, the texture of the environment, and velocity (Bergantin et al., 2021). Indeed, the recorded response in an insect brain of motion-sensitive neurons to translational movements, such as forward flight, can be modeled approximately using a 2D map-like representation of the visual field encoding for contrast information (which is itself dependent on texture) weighted by landmarks’ distance, which correlates to the altitude as well (Schwegmann et al., 2014). Unfortunately, all these parameters are not likely to remain constant during a foraging trip, for example when flying over water (Tautz et al., 2004), or varying altitude when landing on

flowers, thus leading to conflicting sensory inputs (cue conflicts). Hence, given all these ambiguities, the bee odometer is imprecise, leading to an increase in the positional error of the path integration with distance. Moreover, the longer the journey, the more positional uncertainty accumulates when estimating the goal location (Wystrach et al., 2015). Therefore, honey bees and other flying hymenopterans not only rely to a large extent on terrestrial visual cues to reach their nest (Collett et al., 2013) but can also count on other sources of information, when needed, for cue conflict resolution (Hoinville and Wehner, 2018).

Allothetic cues

Bees have senses that are more varied than those of mammalian species. For instance, they can use and learn floral electric fields (Clarke et al., 2013), the odors left by other bees on flowers (Stout and Goulson, 2001), the smell of a flower (Reinhard et al., 2004), their own scent passively placed at their nest entrance (Eckel et al., 2023), the UV light (Primack, 1982), etc. All information derived from these senses is stored in memory in the mushroom bodies (Plath et al., 2017) and is used during foraging, especially in the task of flower detection. Some of these cues, mainly odors, might also be used to detect the nest entrance (Blum, 1992) or enable route following while walking inside the nest (Chittka et al., 1999). A perceived cue will be associated with a concept, e.g., the nest location, for later cue matching. This variety of cues enables multimodal guidance and resolves uncertainty, notably when there is ambiguity about where to go (Buehlmann et al., 2020). Despite this diversity of sensory cues, vision is the primary source of information used by bees to navigate. Honey bees possess an eye that is almost omnidirectional with a resolution of approximately 2 degrees and can see colors ranging from 300nm (including UV) to 650nm (dark orange) (Srinivasan, 2010). The visual celestial compass is primary in most cases, but there is a landscape-based backup system (Dovey et al., 2013). Landscapes in which honey bees live are rarely barren and offer a variety of potential visual landmarks to support this. Yet, there is no consensus on how this information might be used and what is learned during natural foraging behavior. Indeed, depending on the behavioral context, different means of visual guidance could come into play. In fact, from leaving the hive to finding a rewarding flower until the way back home, various cognitive operations happen, including place recognition, route following, and flower discrimination.

Motivation and selective attention

In all of its activities, the individual forager is constantly making decisions about not just what to do, but whether or not to do it. Some progress has been made in understanding the drivers of these decisions. For instance, Lindauer (1952) showed that this is largely a process of individual bees reacting to stimuli relative to their response thresholds, but bees do not always respond to stimuli above the threshold. There is not only a set of “stop” signals (Kietzman and Visscher, 2015), but also a motivational input to these decisions that makes honey bees more than just predictable automata. They are known to express individual preferences in foraging (Arenas and Kohlmaier, 2019). In fact, honey bees are sufficiently intentional to prepare for foraging bouts by taking in the amount of food they might need for the round trip before departure (Harano and Nakamura, 2016). See the provisioning discussion in Chapter 5 on energetics. The bee must decide to fly out and scout or to follow a dance when it senses the need to forage. It also needs to remember that it is outbound or homebound and behaves differently in response to visual stimuli in a repeated sequence (Menzel, 2019). Since the bee tends to retain a memory of its motivation long enough not only to complete an action, but also to repeatedly do the same task over a period of days; this cognitive condition has been called a motivational state (Dyer, 2002; Nunez and Giurfa, 1996). The idea of a selective memory was proposed as a mechanism

for the expression of this motivational state. Thus, in the outbound state the bee has cognitive access to an appropriate set of memories for image matching, and in the homebound state it has access to a different set of memories (Perry et al., 2017). It is this cognitive level of the bee's navigational toolkit that enables the bee to choose which input signals to accept and how to respond (Menzel, 2019; Zhang et al., 2000). This cognitive mechanism provides adaptability and resilience essential for the survival of the bee and the colony.

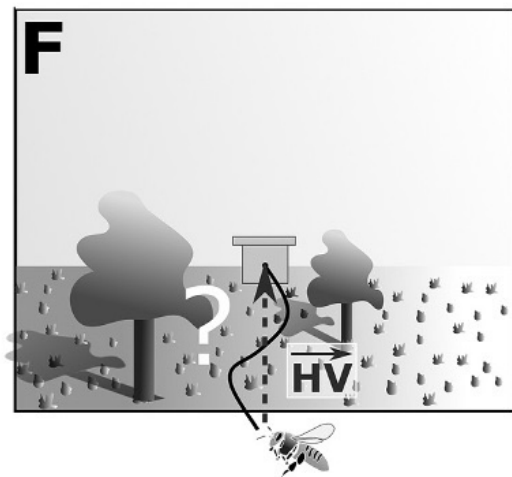
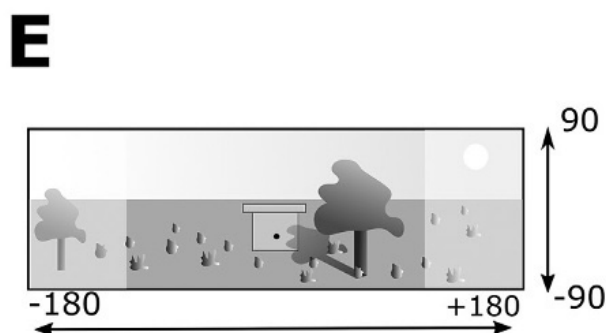
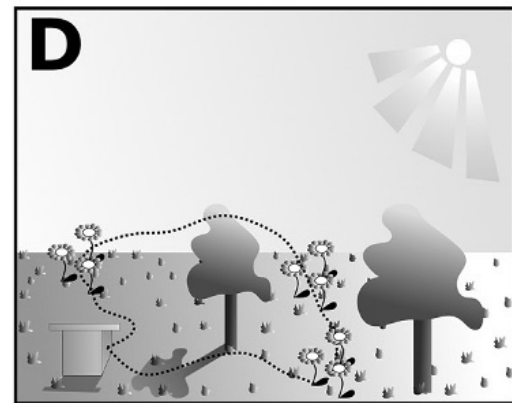
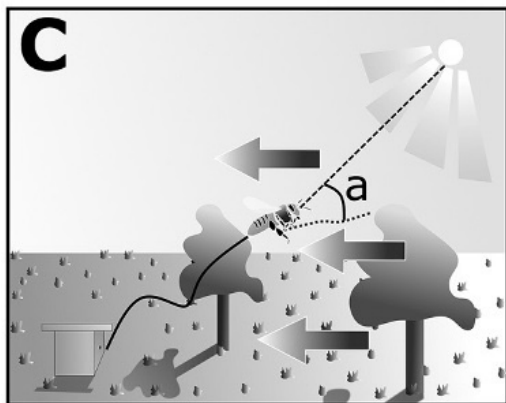
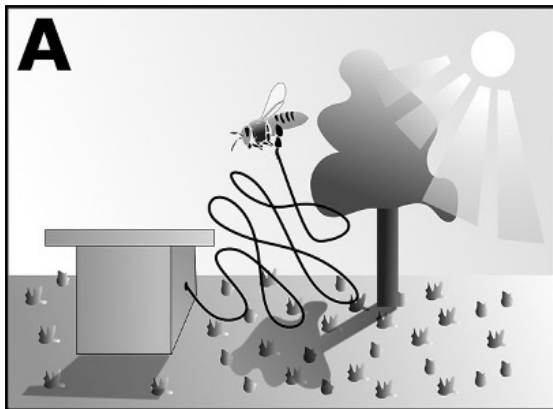


FIG. 4.1 Visual guidance in honey bee forager navigation. (A) Learning flight. A bee performs loops facing the colony nest entrance (hive), with increasing altitude and radii. Learning flights are believed to enable the memorization of panoramic snapshots (images) around the nest. (B) Panoramic snapshot. During the learning flight, the bee memorizes views in the form of a panoramic snapshot directed to the hive entrance. In this hypothetical bee snapshot, shaded areas are the areas of the view, which is behind the bee, due to the assumed panoramic eye. (C) Exploration flight. These flights are used to discover food sources. At each new exit from the hive, the bee investigates a new sector of the landscape, so that all areas can progressively be covered if no food is discovered in the meantime. (D) Path integration. During exploration, the bee integrates the distance flown through the apparent movement of the landscape (optic flow; *gray arrows*) and the angle toward a celestial compass (position of the sun in the sky). (E) Route following. With experience, the bee can exploit resources using routes linking different known feeding sites (traplines). Bees tend to optimize their foraging efficiency by minimizing overall travel distances between the different sites (route optimization). (F) Homing flight. The bee returns home (colony nest) by accessing its homing vector (HV) obtained from its path integration (D). The homing vector would lead it, at first, close to its nest surroundings. In the nest vicinity, by comparing its current view with the ones stored in memory (snapshots), the bee can find the nest entrance by flying in the direction that produces the least mismatch between the two views.

Visual guidance during a foraging trip

Leaving home

Honey bees take their first flights only a few days after emergence from the pupae and before their flight muscles are fully developed. However, they do not begin to forage until approximately 3 weeks of adult age. These early, preforaging, flights are important for learning and orientation (Prado et al., 2020). Specifically, when exiting their home for the first time, bees perform a series of short flights around the colony nest entrance (Fig. 4.1A). Young bees start their learning flights by hovering at the flight entrance and slowly increasing altitude and distance. While doing so, they execute complex flight maneuvers shaped in loops and arcs, during which bees tend to visually fixate on their nest (Fig. 4.1A). This looping behavior is referred to as a “turn-back-and-look” behavior (Lehrer, 1993). Because this type of flight can be triggered when the visual information is experimentally changed around the nest (e.g., displacement of visual landmarks), it is commonly assumed that it is during these flights that they gather information about their visual surroundings and likely memorize it; we call them learning flights (Collett and Zeil, 1996, 2018; Zeil et al., 1996), but what do bees exactly learn?

As humans, we might extract some predilected visual features when wanting to return to our home. This can be a street number or the color of a door. Bees, however, with their small brain, are not expected to understand any of these concepts. A parsimonious approach is that, when a naïve bee leaves its nest, it has no a priori knowledge of what is likely to be a relevant environmental feature. Feature extraction and even attaching concepts to them may not be necessary. In fact, recording a **panoramic snapshot** (i.e., view) of the nest and its surroundings, thanks to bee’s wide field of view, may not require any prior expectations (Fig. 4.1B) (Doussot et al., 2020; Mangan and Webb, 2009; Zeil, 2012). In these panoramic snapshots, there is no segregation between a visual landmark and the rest of the visual scene. Everything is considered, including the background, the skyline, and even local landmarks located directly at the nest entrance. A process of sparse sampling of the visual neural signals has been suggested, given the small size of the bee brain (Horridge, 2005). Several of these snapshots are potentially remembered by the bee, constituting its memory of the nest location (Dewar et al., 2014). Alternately, the integration of multiple flight records could form or modify a memory of the nest and its location. After several trips outside the nest, the bee does not need to perform

learning flights anymore and can fly further away to explore the landscape, unless the hive is moved (Degen et al., 2018).

Exploration of landscape and Searching food

After completing the initial short-range learning flights, bees engage in “**orientation flights**,” displaying extended loops anchored at the nest location and covering a sector of the surrounding landscape in each direction. The distance of these orientation flights is gradually increased, covering other sectors of the environment until each angle has been covered (Capaldi et al., 2000; Capaldi and Dyer, 1999) (Fig. 4.1C). During this process, the bee searches for resources, learns the visual surroundings (Degen et al., 2015), and can return directly to the nest using vector navigation (homing) from an unfamiliar territory with a high probability (Sun et al., 2020; Waiker et al., 2019). Scout bees continue to discover new resources if familiar ones are depleted or disappear. They use a combination of approximately straight flight segments and significant directional changes sometimes described as random Lévy-flights (Reynolds et al., 2007a,b). Once a resource is found and upon leaving it, the bee also performs a learning flight in order to remember the views (snapshots) characteristics of the location of that specific resource. From the colony perspective, there is an ongoing parallel activity of specialists in random exploration and in the exploitation of the best sites that are found (Lemanski et al., 2021).

Communicating a location

A returning honey bee forager that has discovered a highly rewarding food source can communicate the location of that feeding site to other bees in the colony through symbolic behavioral sequences (a dance) consisting of turns and vibrations (l’Anson Price and Grüter, 2015; von Frisch, 1967) (Fig. 4.2).

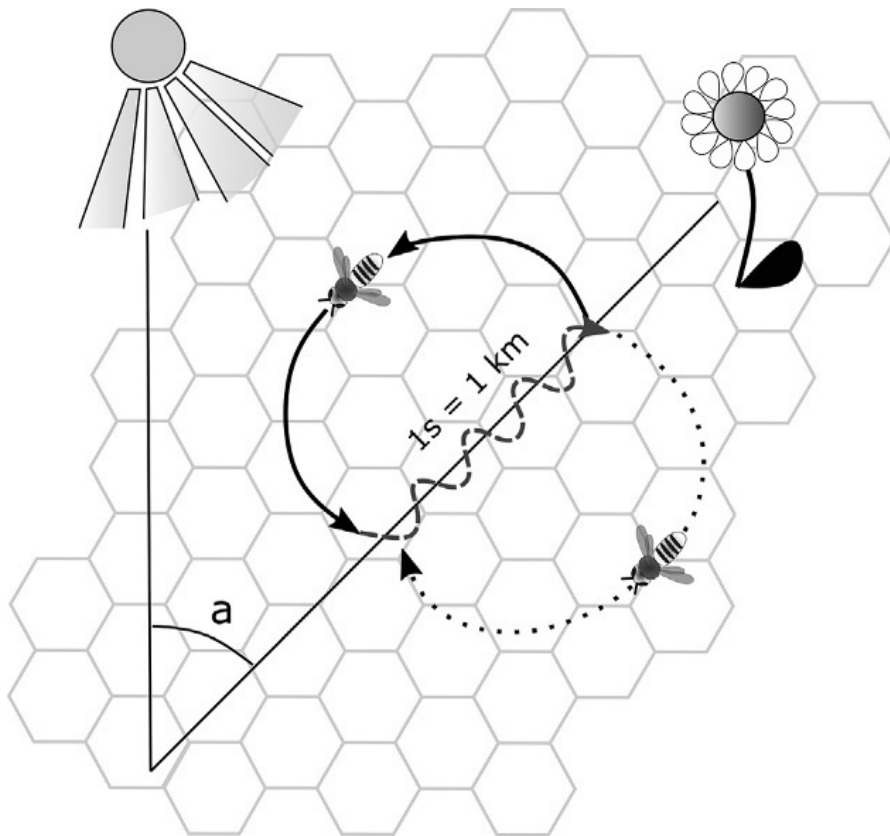


FIG. 4.2 The waggle dance of honey bees. A honey bee forager communicates the location of the newly discovered food resource to its nestmates in the colony nest, by wagging on the comb surface so that the angle from the vertical is the angle of the direction to the resource relative to the azimuth of the sun. The duration of the wagging movements is proportional to the distance between the nest and the food source. The bee repeats the wagging movements coming back from the left and then from the right drawing approximately the figure eight. The more the dance is repeated the higher the quality of the resource. The waggle dance is also performed by scout honeybees to communicate the location of new potential nest sites before swarming.

This behavior communicates the location of a resource not just through pheromones, odor, and food reserves, but through explicit symbolic communication (l'Anson Price and Grüter, 2015; Menzel, 2019; Müller et al., 2018) (see additional discussion in Chapter 3).

Dance communication recruits some of the other bees to begin foraging at the site and can be seen as an evolutionary advantage in the exploitation phase of foraging (Lemanski et al., 2021). For sites that are located nearby the nest (within 100 m range), foragers display a round pattern called a “round dance,” indicating the presence of food outside without precise locational information. But, for more distant sites (beyond 100m from the nest), foragers display a “waggle dance” that contains information about both distance and direction. In this process, the dancer waggles its abdomen and moves in the direction of the food in relation to the sun compass (Fig. 4.2). When the dance is performed in complete darkness on a vertical comb surface, the vertical gravity vector is used to represent the sun’s position, and the direction to the food or other resource is expressed relative to it (Edrich, 1977). The distance of the food source to the nest is communicated through the duration of the waggle movements after which the bee circles back to the starting point alternately to the right or left to complete one cycle (Fig. 4.2). The overall dance duration and a number of times the circuit is repeated indicate the quality of the food source so that the more dance cycles performed, the more profitable the

source advertised (Seeley et al., 2000). Similarly, returning bees may dance to recruit foragers to other resources or to a new nest site for a reproductive swarm.

Foragers that follow these dances must also cope with multiple choices and the variability of the cues received. For recruitment, the dance followers do not compare different dancers; they might be advocating different locations. But, they do follow multiple cycles of the dancer they are following and obtain an average indication of the distance and direction (Preece and Beekman, 2014; Tanner and Visscher, 2008). Averaging multiple inputs is also seen in orientation and learning flights, and honey bee foragers can solve multichoice foraging tasks by probability matching (MaBouDi et al., 2020). At the colony level, quorum sensing is used to resolve selection among multiple nest sites (Sumpter and Pratt, 2009), and collective averaging has been demonstrated by showing that the average of trajectories of dance followers is close to the location indicated by the dancer (Riley et al., 2005).

While such an elaborate communication system can dramatically increase the collective foraging efficiency of bees in most ecological conditions, it is not perfect. Typically, it allows the naïve foragers to arrive in the vicinity of a resource after following a dance, after which they must do a short-range search (Reynolds et al., 2007a) or follow local visual and olfactory cues for the final approach (Fry and Wehner, 2005). Indeed, many bee recruits might get lost despite the indications given by the dancer and must either return to the hive or engage in a more extensive search (Grüter and Farina, 2009; Tautz and Sandeman, 2003). Such failures are both temporally and energetically expensive; hence, there might be environmental conditions where the dance is more effective than other foraging strategies, which do not involve recruitment but only individual-based behavior (like memory and search). When resources are abundant, the dance routines are not profitable; but, when resources are scarce and scattered, or when preferred sources are mixed among nonpreferred, the dance communication gives honey bees a clear advantage in regulating and optimizing exploration and exploitation of food or other resources (Dornhaus et al., 2006; Kohl and Rutschmann, 2021; Robinson et al., 2022). Empirical and theoretical findings suggest that this “symbolic communication” through dances likely evolved in a tropical habitat due to the clustered spatial distribution of food patches and the great diversity of food sources (Dornhaus et al., 2006; Sherman and Visscher, 2002). Despite the dance being not always the optimal strategy to find a location, it is found in 6–10 highly social honey bee species of the genus *Apis* (Beekman et al., 2015; Dyer, 2002; Engel and Schultz, 1997; Lo et al., 2010). Interestingly, the waggle dance is also used by honey bees during reproductive swarming, when bees need to find a new nest site to host the old queen and about half of the colony, while a new queen and the remaining workers inherit the old nest site. In this case, scout bees advertise for potential nesting sites and engage in a quorum-based, collective, decision-making process (Lindauer, 1971; Seeley, 2012).

Route following

Route following is another aspect of resource exploitation. A honey bee forager can store up to 60 μL of nectar in its crop (typically 10–40 μL). Since individual flowers typically provide no more than a few microliters of nectar, it is expected that a nectar-foraging bee must visit hundreds of flowers per foraging trip to fill its crop (von Frisch, 1967). This is probably why the bee dance is only accurate enough to guide the forager to the vicinity of the resource to be exploited. A recruit bee arrives near the target and explores to find its own way among the flowers, gaining efficiency with each repeated trip. In environments where resources are patchily distributed, such as a forest with blooming trees, this means the bee must travel from its hive to a single abundant feeding site. However, when flowers are evenly distributed across

the landscape, such as in a meadow, the bee must move from visiting two locations to visiting many of them (multiple flower patches). In doing so, foragers tend to develop familiar routes to visit the different food patches they have previously discovered (Buatois and Lihoreau, 2016). Such foraging circuits, sometimes called "traplines" (Fig. 4.1E), have been best described in bumblebees (Lihoreau, 2013; Lihoreau et al., 2012; Ohashi and Thomson, 2009). In these primitively eusocial bees, individual foragers must explore, find resources, and optimize a route to exploit them (Kembro et al., 2019); however, in honey bees, most of the exploration is done by scouts (Beekman et al., 2007). Individual bees trained to forage in an array of artificial flowers that were regularly replenished with sucrose solution tend to optimize their foraging routes, gradually minimizing the overall travel distance to visit all flowers once and return to their nest (Ohashi and Thomson, 2009). In doing so, bees behave as if they are solving a mathematical path optimization problem akin to the well known "traveling salesman problem" for which there is no simple solution (Lihoreau, 2013). Unlike mathematicians, bees do not try to solve this problem by brute force: computing and comparing the lengths of all possible routes between all flowers to select the shortest one. Instead, they appear to use a trial-and-error approach to approximate the optimal path. This requires minimal computation power (Reynolds et al., 2013). Route following by bees has been modeled as a set of locations or "nodes" (flowers) and vectors (distance and direction of movement between flowers); bees can use different tools present in their toolkit to optimize their resource collection routes in this representation. Simple iterative learning algorithms in the model predict that, once vectors are learned between flowers (based on path integration and place memories), bees may simply increase or decrease their probability to reuse each vector in future foraging bouts based on the reward obtained at the end of each vector, thereby updating their spatial memory (Dubois et al., 2021). Hence, rewarding vectors are more likely to be reused than unrewarding ones. Since vectors linking two close feeding sites are more likely to be used at any point in space, this simple rule led to increasingly efficient (if not optimal) trapline formation. Such a simple model could explain the behavior of bumblebees (Reynolds et al., 2013) and honey bees (Buatois and Lihoreau, 2016) under many experimental conditions. This model, however, assumes that bees combine and compute the length of several vectors, which is not supported by data. Recently, an anatomically constrained modeling analysis based solely on path integration reproduced trapline formation by honey bees (Le Moël et al., 2019). Nevertheless, the experimental results were quite variable from the model predictions, indicating that path integration interacts with other guidance systems to a greater extent in honey bees. Together, these modeling results compare favorably to the radar tracked flights of bees (Reynolds et al., 2013). There is also an interindividual variation that could explain some of this variance (Lemanski et al., 2021). Indeed, when deciding where to go next, bees may try to follow a movement executed previously at this flower (i.e., a motor memory (Bertrand et al., 2021; Collett et al., 1993)), or instead rely on the visual surroundings. Bees might also use and learn panoramic views on the path between two nodes of the trapline. This resembles the behavior of ants that form a one-way route and follow the learned sequence of views (Mangan and Webb, 2012), or views from the ground (Stankiewicz and Webb, 2021). Route following and optimization are still not fully understood, and there are many possibilities on how the different tools are used by honey bees during this process; but, it likely involves a multimodal integration of cues. While both honey bees and bumblebees develop traplines based on individual experience, data suggest honey bees are less efficient in optimizing routes (Pasquaretta et al., 2017). Presumably, honey bees invest less in individual route learning and optimization than bumblebees because they can also benefit from social information including the role of scout bees and communication through the waggle dance to locate food resources, which is not the case for bumblebees (Buatois and Lihoreau, 2016).

Homing

At some point during its trip, the bee switches its motivational state from foraging to homebound and navigates back to its nest. This may be because it is low in energy or because it has collected the intended load of nectar, pollen, or other resources (Schmid-Hempel et al., 1985). When homing, the bee typically flies back to its nest following its homing vector (Fig. 4.1F). At the beginning of the return trip, information about where to go is precise due to the integration of the outbound path (Wystrach et al., 2015). By following its path integrator, and landscape cues from its orientation flight, the bee can arrive close to its nest. At that point, the bee relies on the visual memories (i.e., panoramic snapshots) from its learning flights to pinpoint the nest entrance. There are several hypotheses on what is remembered in these snapshots. Data suggest they encode the "brightness value" of the setting for each ommatidium (Zeil et al., 2003), the optic flow pattern (Dittmar, 2011; Doussot et al., 2020) (bees can find a location even with camouflaged objects only distinguishable during movement), or the skyline formed by the UV contrast (Graham and Cheng, 2009; Stone et al., 2014). The memory snapshots are compared with the current view experienced by the insect's eyes. The bee uses this image-matching information as a visual compass. The bee moves in the direction that minimizes the mismatch (Doussot et al., 2020; Philippides et al., 2011; Zeil, 2012). The implied image rotation along the azimuthal axis can be a mental rotation or instead, the bee might perform an active scanning of the surroundings such like ants do. Other cues can also be used. When close to the nest a significant object, or the hive itself can be used as a **beacon** to direct their flight, and the bee flies directly to the colony nest entrance (Fry and Wehner, 2005).

Both the homing vector and the bee dance communication are imprecise and require a final approach based on local sensory cues or exploration (Fry and Wehner, 2005; Reynolds et al., 2007b). Some authors consider this variability to be an advantage that both reduces the need for precision and contributes to the ruggedness with regard to changes in the environment around the navigational goal (nest or flower patch) (De Marco et al., 2008; Fry and Wehner, 2005; Riley et al., 2005; Schürch et al., 2013), in addition to the previously mentioned need to direct bees to multiple flowers.

How do bees encode space?

As we have seen above, honey bees use several environmental cues such as the position of the sun, the pattern of polarized light, odor from their nest entrance or from flowers, distance flown, and visual landmarks (Buehlmann et al., 2020). These cues, and their combination, sustain the expression of different types of spatial behaviors that change as individuals learn and gain experience with their habitat. For bees, the toolkit provides an individual with several navigation strategies enabling them to resolve the ambiguity about their orientation and the direction in which to go. However, despite much research, it is not yet clear how these strategies work together to guide the animal home or to a food source. Consequently, the question remains on how space is represented in the brain of an insect.

Space can be represented in many different ways. Two main models have been proposed. The “**map-like**” representation, such as we may build in our brain, is a topological representation where mostly routes and connected nodes are presented. The simpler “**vector-like**” representation is set in an egocentric reference frame, meaning its origin is the self, where an approximate idea of distance and direction is known. In insects, there is still a debate on which representation might be used (Cheeseman et al., 2014; Cheung et al., 2014).

It has been shown several times that bees can link two points in space despite never having made this connection before (i.e., shortcutting). For instance, forager bees trained to fly from their hive to two different feeders can travel directly from one feeder to the other, despite not having flown that path before (Menzel et al., 2005). This ability to use shortcuts has been used to argue in favor of a map-like representation, or “**cognitive map**” (Gould, 1986). However, recent models show shortcuts can also emerge from a decentralized cognitive system combining the interactions between different components of the insect toolkit, i.e., the vector-like representation (Cruse and Wehner, 2011; Sun et al., 2020). There may be other ways to measure the process of integrating cues and motivation. This combination could be based on the “certainty” of each strategy, i.e., the expression of the animal’s judgment on the reliability of this strategy, but also be mediated by its motivational state relative to its thresholds for changes in behavior, i.e., empty versus full crop. Thus, at any one time, the animal can know where to go rather than where it is on some kind of cognitive map (Hoinville and Wehner, 2018).

One strong aspect of this more parsimonious hypothesis is that the guidance systems present in the toolkit can be used concurrently at different instances of the bee journey and not individually. This is an advantage as it helps to resolve a situation of cue conflict or ambiguity, for example when visual cues have been displaced or when the path integrator got compromised due to a passive displacement. The model of Hoinville and Wehner (2018) successfully predicted the results of cue conflict experiments in honey bees where the insects reached a compromise location between the associated guidance goals.

There exist hypotheses on how the brain structures involved in navigation might be the basis for such a decentralized system (Fig. 4.3). By combining results from electrophysiology and modeling analysis, scientists may now describe what is likely happening in the **central complex**, which may be the neural substrate enabling navigation in insects. In the central complex information from speed, compass, visual memories, motivational state, and other modalities can be combined in a cognitive process to generate output signals and enable the insect to steer a course toward its desired goal location (Fig. 4.2) (Heinze, 2017; Le Moël et al., 2019; Sun et al., 2021). The use of vector memories formed by the path integrator between visits to multiple feeding sites could explain shortcutting, making the internal map of insects centered around their nest rather than anchored to the world (Stone et al., 2017; Webb, 2019). This is contrary to the cognitive map in which the nest is just one location in the landscape (Le Moël et al., 2019; Webb, 2019).

As an alternative to the idea of a cognitive map of the landscape, Müller et al. (2018) studied the neurological representation of visual landscape images in the bee brain and proposed a one-dimensional metric of familiarity that represents how closely the current view matches a selected memory from among memories accessible in the current motivational state of the bee. This concept supports image matching mentioned earlier and would support neural output signals for motor control.

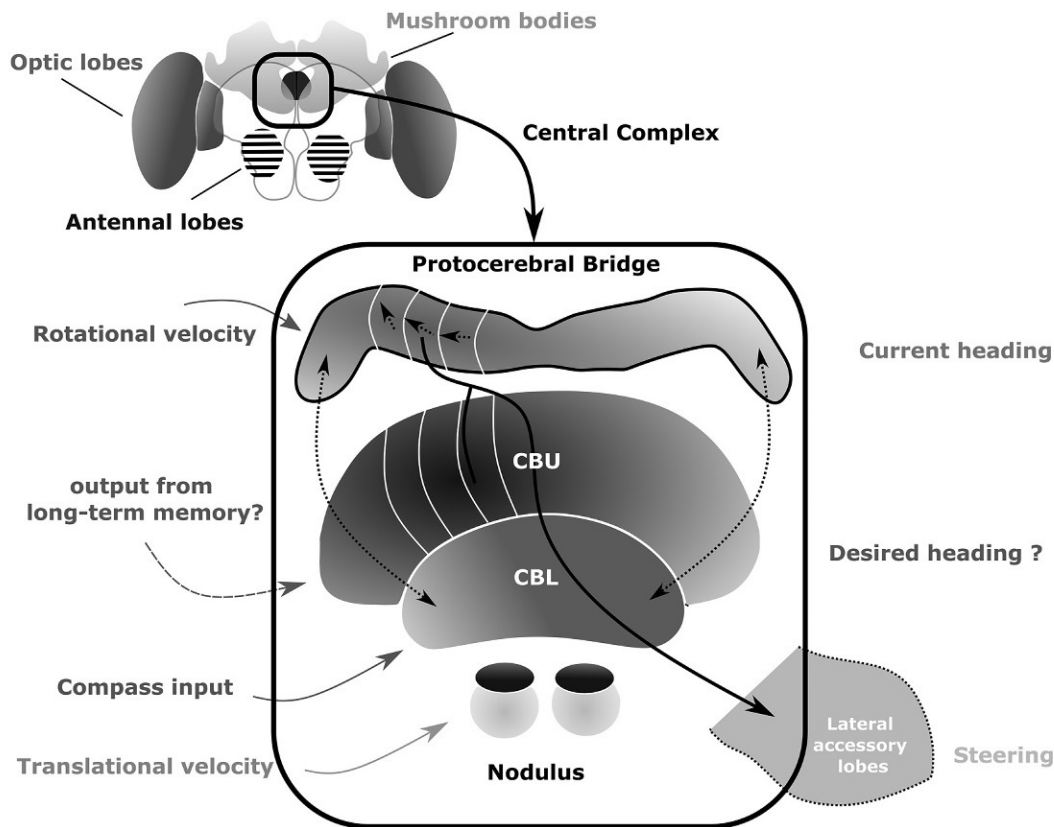


FIG. 4.3 The honey bee brain with details of the **central complex**. The central complex is a small region located in the middle of the honey bee brain. Its size is small in comparison to bigger structures such as the mushroom bodies and the optic lobes (top panel). Its central localization makes it the receptor of the different inputs going through the other brain regions. The central complex is constituted of several parts playing different roles in the navigation abilities of the bee. From top to bottom, the **protocerebral bridge (PB)** cells likely represent the bee's current heading direction. Below, we find the upper division of the central body (**CBU**). Hypothetically, this part could encode the "desired" heading, for example, the home vector obtained from the path integrator. The lower division of the central body (**CBL**) with its columnar cells is thought to integrate information from the protocerebral bridge (rotational optic-flow) and the **noduli** small unit (translational optic-flow), both involved in direction encoding (*black dotted arrows*). The CBL also receives compass inputs, for example, it is connected to neurons responding to polarized light. Finally, neurons projecting in the lateral accessory lobes and receiving input in both the PB and the CBU are suited to compare a current heading with the desired heading and initiate steering (*black arrow*, proposed direction of information flow in the central complex). Inputs are written on the left and outputs are on the right. Modified from Heinz, S., 2017. Unraveling the neural basis of insect navigation. *Curr. Opin. Insect Sci.* 24, 58–67. <https://doi.org/10.1016/j.cois.2017.09.001>.

Concluding remarks

More than a century of research on bee navigation, first based on naturalistic observations and later well-thought-out behavioral experiments and modeling, has yielded solid knowledge on how bees learn to orient, find food sources, and exploit familiar sites in complex natural environments. Yet, many questions remain open and may soon be addressed thanks to technological developments to quantify bee navigational behavior more precisely and results from experimental ethology. For example, current methods for long-distance tracking limit the behavioral investigations of bee movements at the individual level. For that reason, very little is known about how social and competitive interactions influence bee movements and foraging decisions in the field. Furthermore, while most navigation studies have been constrained to recording 2D movements, bees fly and may extract critical information from 3D

movements, as for instance, large visual landmarks on the ground (Brebner et al., 2021). Developments of new tracking systems to record multiple bees in 3D will allow for such studies. The development of virtual reality setups in which every aspect of the visual environment of bees can be controlled will also open new opportunities to test the influence of specific navigational cues in combination at every stage of route formation (Frasnelli et al., 2018). Finally, recent studies reveal the impressive cognitive abilities of honey bees in terms of visual learning, like solving a maze based on symbolism (Zhang et al., 2000) and learning abstract concepts (Howard et al., 2018). So far, these studies have been conducted in artificial contexts in the lab. However, very little is known about whether and how these cognitive abilities help navigation. Given that bees heavily rely on vision for navigation, it is very likely that these visual cognitive feats are involved in orientation and foraging. Bridging the gap between lab and field work is therefore a major and urgent challenge for future research on bee navigation.

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