Navigation by Honey Bees

Naïla Even[1], Olivier Bertrand[2] and
Mathieu Lihoreau[3]
[1]Institut National Polytechnique, Ecole Nationale Superieure d'Ingénieur en Art Chimique et Technologique (ENSIACET), Toulouse, France
[2]Neurobiology and Center of Cognitive Interaction Technology (CITEC), Bielefeld University, Bielefeld, Germany
[3]Research Center on Animal Cognition (CRCA), Center for Integrative Biology (CBI), CNRS, University Paul Sabatier, Toulouse, France

Definition

Navigation by honey bees refers to the cognitive and behavioral mechanisms bees of the genus *Apis* use to move between a location and one or multiple goals. These involve the evaluation and integration of direction and distance cues as well as the learning of specific places. For honey bees, goals can be as diverse as the colony nest, a foraging site, a new nesting site, or an open-air mating area.

Introduction

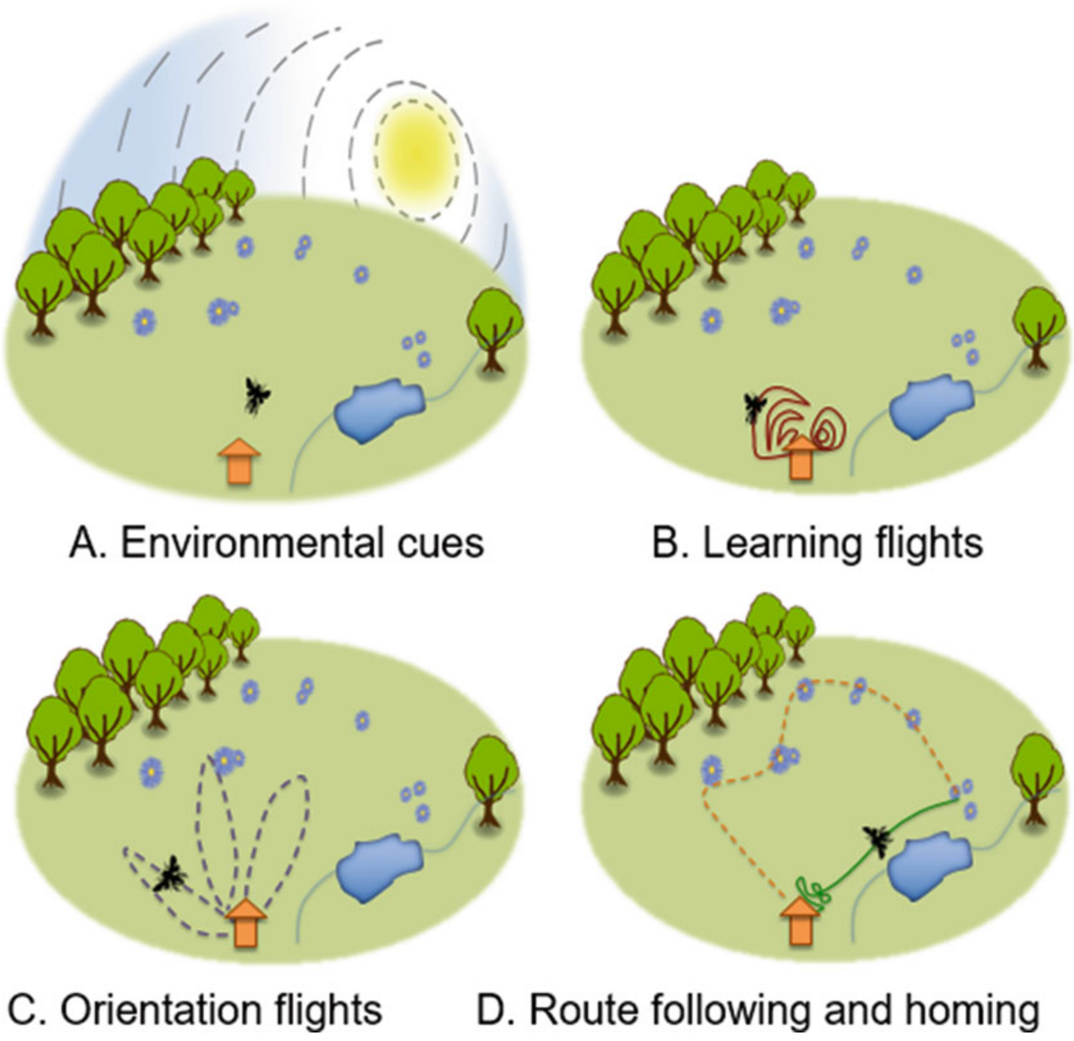
The vast majority of the about 20,000 known bee species are central place foragers: adults collect and bring back resources (flower nectar and pollen, water, resins) in a stable nest where they raise their progeny (Michener 2007). Foraging requires navigation skills to locate resources, travel between them, and return to the nest. Many bees must also navigate at some point in their life to find mating partners, a new suitable nesting site, or even to orient inside their dark nests.

About a century of research on insect navigation, starting with pioneering work of Turner (1908) and von Frisch (1967), shows that these navigation behaviors are sustained by a cognitive "toolkit" (Wehner 2009) involving celestial cues (typically a **sun compass**), a distance estimator (**odometer**), a system for integrating both information (**path integrator**), and the ability to learn **visual landmarks** and specific places (see Fig. 1a and Glossary). For bees, these mechanisms sustain the expression of different types of spatial behaviors that change as individuals learn and gain experience with their environment.

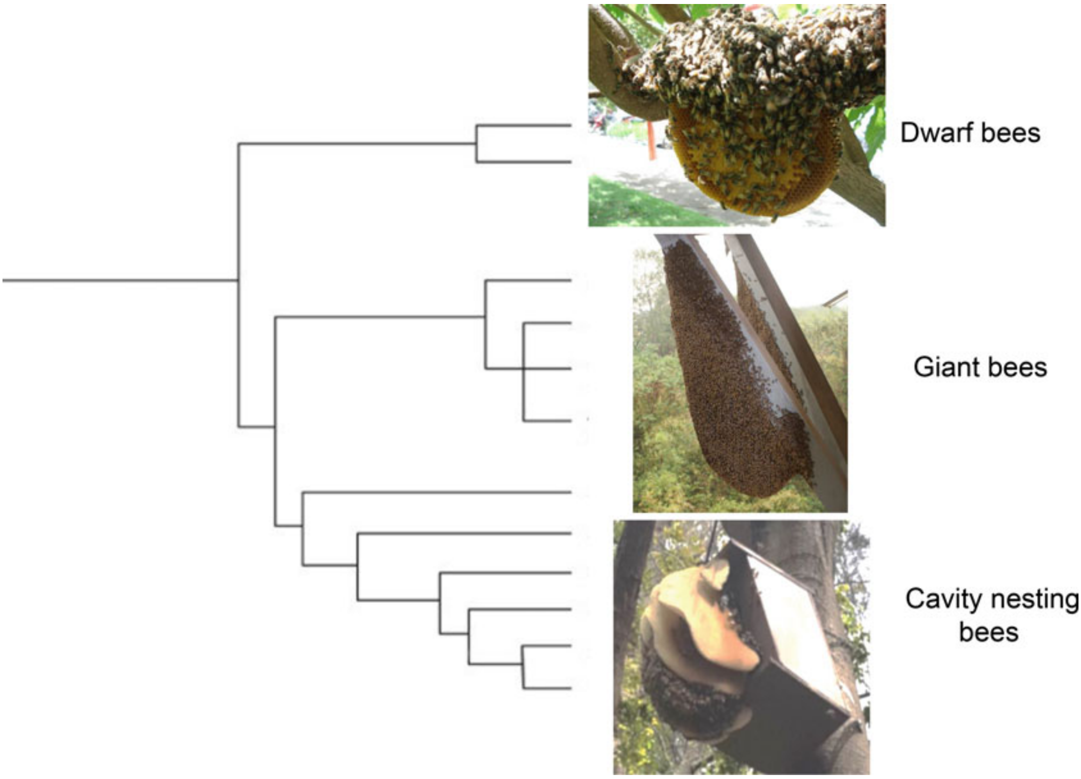
In this entry we describe these spatial behaviors in honey bees (Fig. 2), a group of 11 species

J. Vonk, T. K. Shackelford (eds.), *Encyclopedia of Animal Cognition and Behavior*,
https://doi.org/10.1007/978-3-319-47829-6_623-1

and 44 subspecies (Lo et al. 2010) exhibiting some of the most advanced levels of social forms in the animal kingdom, characterized by a reproductive division of labor (fertile queens and drones, sterile workers), cooperative breeding, and overlapping generations of adults. Navigation skills are required by individuals of the different castes (Seeley 2010). The foragers collect food,



Navigation by Honey Bees, Fig. 1 (**a**) Environmental cues used by honey bees to navigate. Bees use the position of the sun in the sky (or polarized light dashed lines under cloudy conditions, dashed lines) as compass. They learn visual landmarks (e.g., trees, rivers, paths) and views of broader visual cues like panoramas and skyline (i.e., snaphots). When closer to the goal, bees use local available information to pinpoint the goal (e.g., shape, color, odors). (**b**, **c**, **d**) Hypothetical examples of flight sequences performed by a forager as it gains experience. (**b**) Learning flights: during its first excursions outside the hive the bee learns the visual scene characterizing the nest entrance using concentric circles increasing in size (red plain lines). (**c**) Orientation flights: after a few trips, the bee starts exhibiting sequential exploration of sectors around the nest (orange dashed line) to find flower patches. (**d**) Route following and homing: once experienced, the bee follows a multi-destination route (trapline) learnt from previous foraging trips (dashed orange line). The bee returns home following a home vector computed through path integration (inbound in green). At the end of this homing flight the bee corrects eventual path integration errors through small search loops to precisely locate the nest entrance



Navigation by Honey Bees, Fig. 2 Honey bees contain 11 species. Dwarf open nesting honey bees like *Apis florea* are the most basal group and live mostly in Asia and Middle East. The open nesting giant honey bees like *Apis dorsata* are found only in Asia. The most recently derived group are the cavity nesting honey bees represented by six species: five of which are distributed in Asia. *Apis mellifera* has a natural distribution in Africa, Europe, and the Middle East, but has been domesticated and distributed throughout the world. It is now found in the wild on all continents except Antarctica. Photo credits: Dwarf and cavity bees from Naïla Even, giant bees from Benjamin Oldroyd. Phylogeny modified from Lo et al. (2010)

water, and resins from plants. The scouts must find new nesting sites. The reproductives must find mating partners for reproduction. And the in-hive workers move between important places in the nest, such as brood cells, honeycombs and the nest entrance. All these tasks require the ability to explore the environment, identify and learn places of interest, and sometimes communicate spatial information to nestmates.

Here we focus in particular on the Western honey bee (*Apis mellifera*) as this species has a long history of domestication for honey production and crop pollination and is a model for the study of insect navigation. We discuss the different types of flights exhibited by foragers because they have been best described, especially since the development of automated tracking systems that record bee movements over several hundred meters (e.g., harmonic radar: Riley et al. 1996). However similar behaviors are expected by scout and reproductive bees. In-hive navigation has been less studied and is therefore not discussed.

Exploration Flights

Western honey bees hatch in a dark nest, visually isolated from the outside environment. After about 2 weeks, they become foragers, which mean that they collect plant resources, sometimes scattered over several kilometers around the nest, to provision the colony. While foraging, the bee engages in different types of exploration flights during which it acquires visual memories of salient features of its environment, presumably in the form of **snapshot memories** (Collett et al. 2013), to guide future foraging trips.

On its first few excurions outside the colony nest, a bee engages in peculiar flight sequences known as "learning flights" (Fig. 1b), during which the bee learns the skyline **panorama** and **visual landmarks** associated with its nest location (Zeil 2012). Learning flights are composed of many convoluted maneuvers, loops, arcs, and zigzags facing the nest. During the initial learning flight, the bee slowly increases the radii of the loops and arcs, distancing itself from the colony nest until a point when it returns home without bringing back any resources. On the next few flights, the bee flies a bit further, slowly gaining experience with the outside environment.

Once a visual memory of the nest location is acquired, the bee engages in "orientation flights" (Fig. 1c), this time turning back to the nest. The bee flies along extended loops anchored at the nest location and covering a narrow angular sector in a given direction. Successive orientation flights are longer loops covering other sectors of the environment until every direction has been covered (Capaldi et al. 2000). During this process, the bee orients itself and searches for flower sites. If the bee is caught and released at an unfamiliar location outside the area covered by its previous flights, it engages in an extended search for its nest. By contrast, if the bee is released at a familiar location, it flies straight back home (Degen et al. 2016). Drones (males) have also been shown to be faster to relocate the colony nest after several exploration flights, allowing them to come back home from the drone congregation area if they failed to mate a queen.

Exploration flights are not exclusive to first trips outside the nest, but also occur during the foraging process. For instance, once a food resource is found, a forager may exhibit learning flights to learn the visual scene surrounding this new site so that it can more easily return to this site on subsequent foraging trips (Robert et al. 2018). When a resource is depleted, the bee searches for an alternative site through longer flights centered at the familiar depleted location. These exploration flights, composed of straight segments and turns, have Lévy characteristics, meaning that there is a larger proportion of long flight segments than one would expect from a normal distribution (i.e., a Brownian search) (Reynolds 2008). This type of random search pattern is expected to be optimal to locate patchily distributed food sources, like plants, for animals with little knowledge of their environment.

Homing Flights

At the end of every foraging trip, a forager must navigate back to its nest to unload its crop and feed the colony. "Homing flights" are composed of two phases: a straight line flight to return to the nest area, and a convoluted flight to pinpoint the nest entrance (Fig. 1d).

To return home, the bee uses its estimation of directions and distances of the often tortuous inbound path toward a goal (e.g., feeding site) and integrates both information using a **path integrator**. In honey bees, directions are primarily estimated through the position of sun in the sky, constituting a **sun compass**. When the sun is not directly visible (e.g., during cloudy days), this information can be retrieved from the pattern of **polarized light**. Distances are estimated using an **odometer** through the quantity of visual information perceived on the retina of the compound eye while flying. It is possible to study this mechanism in bees by making them fly in narrow tunnels with black and white strips of different widths, thereby making them under- or overevaluate their real flight distances (Srinivasan 2011).

When the crop (stomach) of the bee is full of nectar or its tarses are packed with pollen grains, its motivation to return home sets a new directional aim: the nest. A straight line return (also called "beeline") is then indicated by the opposite of the integrated vector during the inbound journey. During the homing flight, the bee also integrates the distance and direction traveled, shrinking the integrated vector pointing to the nest. A central part of the bee brain, called the "central complex," receives and integrates inputs of directions and distances from diverse internal senses like eyes, body hair, wing muscles, and other brain parts, and allows all these neural computations (Stone et al. 2017). The integration process is subject to noise accumulation during the journey of the bee. To reduce this error, foragers also refer to **visual landmarks** learned during previous flights to pinpoint directions and goals (Srinivasan 2011). Anything salient in the environment can be used as visual landmarks, even elongated structures on the ground such as rivers, edges, and paths (Menzel et al. 2019).

The last bit of the homing flight (also known as "view-based homing") is guided by visual landscape cues. Since the seminal experiments of Bouvier (1900), showing that bees locate their nest entrance with surrounding visual cues, bees have been challenged to pinpoint their home in a plethora of scenarios. Objects may be displaced closer to or further away from their nest, displaced to a new location, replaced with smaller or differently colored one, or even camouflaged (Dittmar et al. 2010). Based on these studies, we know that bees learn relations between a myriad of visual cues and their nest entrance. These relations are not necessarily explicit. Indeed, the use of **panoramic skyline snapshots** around the nest entrance is sufficient to guide a simulated bee toward its home (Towne et al. 2017).

Two navigational routines, **path integration** and visual guidance, jointly lead a bee home (Hoinville et al. 2018), but the importance of the routines depends on the context, such as the foraging experience of an individual bee. For instance, **path integration** tends to be preferred over **visual landmarks** in a novel environment. However when both navigational routines are conflicting, **visual landmarks** are favored (Kheradmand and Nieh 2019).

Route Following

After several foraging trips, foragers tend to develop routes to efficiently return to known profitable feeding sites. Bees can famously be trained to learn straight line outbound paths between the nest and a feeder providing large amounts of sucrose solution (von Frisch 1967). However, in many natural conditions, bees may visit hundreds of flowers, sometimes dispersed over several kilometers, to fill their crop with nectar (honey bees have been observed homing after being released 11 km from their nest (Pahl et al. 2011)). When this is the case, foragers therefore need to develop more complex circuits between multiple goals, a routing challenge analogous to the well-known Traveling Salesman Problem (TSP) in mathematics.

A naive honey bee forager first visits flowers in an unorderly sequence as it discovers them. However with experience, the bee can develop a stable route linking multiple flowers, a behavior described in many other pollinators (e.g., bumblebees, bats, hummingbirds) and known as **trapline** foraging (an analogy of the routes used by trappers to check their traps; Fig. 1d). This behavior was discovered by observing individual bees foraging in small arrays of artificial flowers within 100 m from the hive (Buatois and Lihoreau 2016). As long as the artificial flowers were regularly replenished with a sucrose reward, the bees learned to revisit them and adjusted their visitation sequence in order to minimize overall travel distances, ultimately selecting the shortest possible route (i.e., thus solving the TSP).

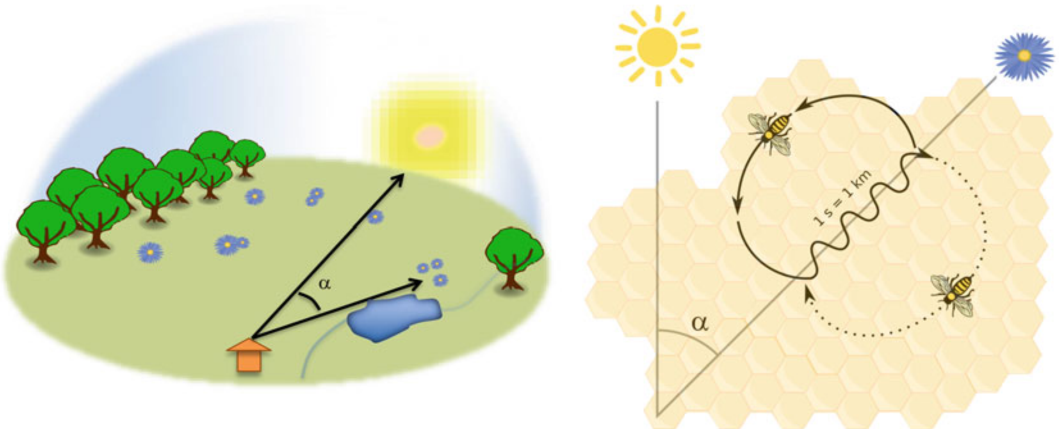
Computational models attempting to decipher the cognitive mechanisms underpinning this navigational feat show that trapline development and optimization can emerge based on the ability of bees to learn sequences of places using visual memories (Collett et al. 1993) and estimate travel distances with **path integration** (Srinivasan 2011). According to these models, at the end of its foraging trip the bee may sum the straight line distances between successively visited flowers and derive the net length of the entire route. By comparing successive routes, the bee could thus increase its probability of reusing the vectors composing the shortest experienced route (Lihoreau et al. 2012). Through trial and error, this simple learning process may enable the development of good (if not optimal) routes in environments with different numbers and spatial configurations of feeding sites (Reynolds et al. 2013).

Place Communication

Once back in the hive, the honey bee forager can communicate the direction, distance, and quality of a discovered feeding site via a sequence of movements known as the "waggle dance" (von Frisch 1967; Fig. 3). Scout bees also use this communication system to indicate the location of a suitable nesting site (e.g., cavity, hive) to reach a consensus about the best available site before swarming (Seeley 2010).

While this ability to recruit nestmates for profitable places was discovered by naturalists long ago (e.g., Aristotle), the symbolic meaning of the dance was finally decoded by Karl von Frisch. In 1919, von Frisch trained bees to forage on feeders containing sucrose solution placed around the hive. He observed that the foragers returning to the hive performed energetic rounds and were occasionally followed by other bees who would then fly to the communicated feeder. von Frisch described two types of behaviors referring to them as "dances" depending on the distance of the food source to the hive. For feeders within 90 m the hive, foragers performed a round movement, where for longer distances they performed a waggled movement following an eight-shaped figure. It is now acccepted that both dances are in fact a single behavior, whose precision varies with the distance of the food source to the hive (Griffin et al. 2012).

During the waggle dance, the forager waggles its abdomen and moves toward the direction of the food relative to the sun. In cavity nesting honey bees, like the Western honey bee, the invisible sun in the dark hive is encoded by the vertical vector facing up (i.e., against gravity). Therefore, the angle between the waggle trajectory and the vertical of the comb represents the angle of the food source and the sun. In open nesting honey bees, however, the dance occurs horizontally on the top of the single frame and the dancing bee faces directly the direction of the food or the future nest. In both open nesting and cavity nesting honey bees, the distance of the food source is communicated via the duration of the waggle movement that correlates with a distance in meters. This correlation and the precision of the duration slightly varies between species and subspecies of honey bees (Beekman et al. 2015). The



Navigation by Honey Bees, Fig. 3 The waggle dance. Upon returning to the colony nest following a successful foraging trip, a honey bee forager can communicate the location of the discovered food site to its nestmates by performing a waggle dance. The bee communicates the direction of the resource by waggling in the direction of the resource relative to its angle with the sun (α). The duration of the waggling movement is proportional to the distance of the food. The bee repeats the waggling movement coming back from the left and then from the right drawing the figure height. The more the dance is repeated the higher the quality of the resource. Any bee following the dance can thus integrate the information and leave the hive using the instruction from the dance. The waggle dance is also performed by scout honey bees to communicate the location of a new nest site before swarming. Modified from Emmanuel Boutet (CC BY-SA 2.5) rewarding value of the resource is communicated by the total duration that the bee performs repeating the eight-shape dance. Dancing for a longer time increases the probability to recruit foragers susceptible to be interested by the navigation instructions for a new resource (Seeley 2010).

Migration

Several *Apis* species from tropical Asia, such as the cavity nesting honey bee (e.g., *Apis cerana*), the giant honey bee (*Apis dorsata*), or the dwarf honey bee (*Apis florea*), do not remain in a stable nest but can abandon the nest or migrate over long distances to respond to local food shortage (Oldroyd and Wongsiri 2009, Fig. 2). Giant honey bees, for instance, have been reported to migrate to destinations up to 200 km away, stopping over in bivouac congregations to rest and forage. These bees can even sometimes return to the exact same tree after the migration period. During migration, Asian honey bees use dance communication to orient the swarm departure in the correct direction toward a new nest. In the case of long distance migrations, especially in open nesting giant honey bees, the direction is communicated but the distance is only indicated by a very long waggle signaling (Dyer and Seeley 1994). Sensory mechanisms used to migrate to a new location are similar to those used by honey bee foragers, including the **sun compass**, the **optic flow**, and the learning of visual landscape cues.

Concluding Remarks

Honey bees show a unique diversity of spatial behaviours but share numerous sensory abilities and navigational strategies with other insects (see Glossary). Thus, they are key model species to study insect navigation. Understanding how a tiny brain, with about one million neurons, uses computations to navigate efficiently in three dimensions over large spatial scales, finds direct applications in algorithmic and robotics and may help understand how these mechanisms evolved in the more complex brains of vertebrates (Chittka and Niven 2009). Some features described in mammal navigation studies, like the hypothesis of the representation of the global surrounding in a single mental map (i.e., cognitive map), influence debates about mental representations of space in insects (Menzel 2019). Even though no consensus has been yet reached, most studies show that **path integration** and visual guidance are sufficient to explain the complex spatial behavior exhibited by honey bees and other insects (Webb 2019).

The study of the neural mechanisms underlying navigation in the insect brain may address this important knowledge gap and clarify whether honey bees use cognitive maps. Deep brain structures start to be linked to navigational functions such as the central complex for **path integration** and the mushroom bodies for visual memories (Webb and Wystrach 2016). Exploring brain function in vivo in a flying insect in its natural environment is still out of reach. However, recent advances in virtual reality setups (e.g., Buatois et al. 2018) and onboard neuron-stimulator or recorders (e.g., Sato et al. 2015) increase the possibilities to study navigation under tightly controlled, yet ecologically relevant, conditions while exploring brain function.

Cross-References

- ▶ Central Place Foraging
- ▶ Cognitive Map
- ▶ Dead Reckoning
- ▶ Foraging by Honeybees
- ▶ Insect Navigation
- ▶ Travel Salesman
- ▶ View-Based Homing

Glossary

Central place foraging Foraging behavior consisting in collecting resources in the environment and carrying them back home. In the case of honey bees, foragers make back and forth trips between resource sites (food, water, resin) and their nest to feed the colony.

Odometer Mechanism enabling animals to estimate travel distances. In honey bees, distance estimation is mediated by the apparent motion of surrounding objects on the retina of the compound eye, also called "optic flow."

Panorama Piece of visual information corresponding to a global visual cue, such as a landscape or a skyline. A panorama can also correspond to a combination of several visual landmarks (e.g., trees, buildings, rivers). Honey bees use panoramas for learning places such the location of their colony nest or a profitable food site.

Path integration Method used by an animal for knowing its current position from a reference point, also known as "dead reckoning". Honey bees integrate odometry cues (distances) and sun compass (directions) to compute the vector pointing to a reference point (e.g., the nest) from their current position. This computation allows a honey bee to come back to the nest in a straight line.

Polarized light patterns Rayleigh scattering creates patterns of polarized sunlight, which are distributed in the sphere of the sky following concentric circles with the sun as a center (see Fig. 1a). With photoreceptors located in the dorsal area of their compound eyes, honey bees can detect direct sunlight as being the unpolarized area of the sky and can sense that polarization increases when the e-Vectors (electric vectors of light) are further away from the sun along the concentric circles.

Snapshot Learning of a 2D image at one point in time. For a honey bee, the memorized view corresponds to a specific orientation of the bee relative to the image, similar to a camera objective taking a snapshot from a specific angle.

Sun compass Utilization of the sun's position in the sky as a directional guide. For honey bees, the position of the sun can be perceived directly (when the sun is visible) or indirectly through the pattern polarized light (when the sun is not visible). To orient when the sun is visible, bees can use the light intensity (higher closer to the sun) and the chromatic gradients (toward green in solar region to UV in the antisolar region).

Trapline Repeatable sequence of flower visits, starting and ending at the nest. With experience, honey bee foragers tend to develop traplines minimizing overall travel distances between familiar feeding sites. These routes are based on individual experience.

Visual landmark Salient feature in the visual scene. Honey bees can use many types of landmarks spanning from 3D trees or buildings to 2D elongated patterns on the ground (e.g., paths, edges, rivers, roads).

References

Beekman, M., Makinson, J. C., Couvillon, M. J., Preece, K., & Schaerf, T. M. (2015). Honeybee linguistics – A comparative analysis of the waggle dance among species of *Apis*. *Frontiers in Ecology and Evolution, 3*, 11.

Bouvier, E.-L. (1900). I. Les habitudes des Bembex (monographie biologique). *L'année Psychologique, 7*(1), 1–68. https://doi.org/10.3406/psy.1900.3183

Buatois, A., & Lihoreau, M. (2016). Evidence of trapline foraging in honeybees. *The Journal of Experimental Biology, 219*, 2426–2429.

Buatois, A., Flumian, C., Schultheiss, P., Avarguès-Weber, A., & Giurfa, M. (2018). Transfer of visual learning between a virtual and a real environment in honey bees: The role of active vision. *Frontiers in Behavioral Neuroscience, 12*, 139.

Capaldi, E. A., Smith, A. D., Osborne, J. L., Fahrbach, S. E., Farris, S. M., Reynolds, D. R., Edwards, A. S., Martin, A., Robinson, G. E., Poppy, G. M., & Riley, J. R. (2000). Ontogeny of orientation flight in the honeybee revealed by harmonic radar. *Nature, 403*, 537–540.

Chittka, L., & Niven, J. (2009). Are bigger brains better ? *Current Biology, 19*, R995–R1008.

Collett, T. S., Fry, S. N., & Wehner, R. (1993). Sequence learning by honeybees. *Journal of Comparative Physiology. A, 172*, 693–706.

Collett, M., Chittka, L., & Collett, T. S. (2013). Spatial memory in insect navigation. *Current Biology, 23*, R789–R800.

Degen, J., Kirbach, A., Reiter, L., Lehmann, K., Norton, P., Storms, M., Koblofsky, M., Winter, S., Georgieva, P. B., Nguyen, H., Chamki, H., Meyer, H., Singh, P. K., Manz, G., Greggers, U., & Menzel, R. (2016). Honeybees learn landscape features during exploratory orientation flights. *Current Biology, 26*, 2800–2804.

Dittmar, L., Stürzl, W., Baird, E., Boeddeker, N., & Egelhaaf, M. (2010). Goal seeking in honeybees:

Matching of optic flow snapshots? *The Journal of Experimental Biology, 213*, 2913–2923.

Dyer, F. C., & Seeley, T. D. (1994). Colony migration in the tropical honey bee *Apis dorsata* f. (Hymenoptera: Apidae). *Insectes Sociaux, 41*, 129–140.

Griffin, S. R., Smith, M. L., & Seeley, T. D. (2012). Do honeybees use the directional information in round dances to find nearby food sources? *Animal Behaviour, 83*, 1319–1324.

Hoinville, T., & Wehner, R. (2018). Optimal multiguidance integration in insect navigation. *Proceedings of the National Academy of Sciences, 115*(11), 2824–2829. https://doi.org/10.1073/pnas.1721668115

Kheradmand, B., & Nieh, J. C. (2019). The role of landscapes and landmarks in bee navigation: A review. *Insects, 10*, 342.

Lihoreau, M., Raine, N. E., Reynolds, A. M., Stelzer, R. J., Lim, K. S., Smith, A. D., Osborne, J. L., & Chittka, L. (2012). Radar tracking and motion-sensitive cameras on flowers reveal the development of pollinator multi-destination routes over large spatial scales. *PLoS Biology, 10*, e100139.

Lo, N., Gloag, R. S., Anderson, D. L., & Oldroyd, B. P. (2010). A molecular phylogeny of the genus *Apis* suggests that the Giant Honey Bee of the Philippines, *A. breviligula Maa*, and the Plains Honey Bee of southern India, *A. indica Fabricius*, are valid species. *Systematic Entomology, 35*, 226–233.

Menzel, R. (2019). The waggle dance as an intended flight: A cognitive perspective. *Insects, 10*, 424.

Menzel, R., Tison, L., Fischer-Nakai, J., Cheeseman, J. F., Sol Balbuena, M., Chen, X., landgraf, T., Petrasch, J., Polster, J., & Greggers, U. (2019). Guidance of navigating honeybees by learned elongated ground structures. *Frontiers in Behavioral Neuroscience, 12*, 322.

Michener, C. D. (2007). *The bees of the world*. Balitmore: The Johns Hopkins University Press.

Oldroyd, B. P., & Wongsiri, S. (2009). *Asian honey bees: Biology, conservation, and human interactions*. Cambridge, Massasuchetts, and London, England: Harvard University Press.

Pahl, M., Zhu, H., Tautz, J., & Zhang, S. (2011). Large scale homing in honeybees. *PLoS One, 6*, e19669.

Reynolds, A. M. (2008). Optimal random Lévy-loop searching: New insights into the searching behaviours of central-place foragers. *Europhysics Letters, 82*, 20001.

Reynolds, A. M., Lihoreau, M., & Chittka, L. (2013). A simple iterative model accurately captures trapline formation by bumblebees across spatial scales and flower arrangements. *PLoS Computational Biology, 9*, e1002938.

Riley, J. R., Smith, A. D., Reynolds, D. R., Ewards, A. S., Osborne, J. L., Williams, I. H., Carreck, N. L., & Poppy, G. M. (1996). Tracking bees with harmonic radar. *Nature, 379*, 29–30.

Robert, T., Frasnelli, E., Hempel de Ibarra, N., & Collett, T. S. (2018). Variations on a theme: Bumblebee learning flights from the nest and from flowers. *The Journal of Experimental Biology, 221*, jeb172601.

Sato, H., Vo Doan, T. T., Kolev, S., Huynh, N. A., Zhang, C., Massey, T. L., van Kleef, J., Ikeda, K., Abbeel, P., & Maharbiz, M. M. (2015). Deciphering the role of a coleopteran steering muscle via free flight stimulation. *Current Biology, 25*, 798–803.

Seeley, T. D. (2010). *Honeybee democracy*. Princeton, NJ: Princeton University Press.

Srinivasan, M. V. (2011). Honeybees as a model for the study of visually guided flight, navigation, and biologically inspired robotics. *Physiological Reviews, 91*(2), 413–460. https://doi.org/10.1152/physrev.00005.2010

Stone, T., Webb, B., Adden, A., Ben Weddig, N., Honkanen, A., Templin, R., Wcislo, W. T., Scimeca, L., Warrant, E., & Heinze, S. (2017). An anatomically constrained model for path integration in the bee brain. *Current Biology, 27*, 3069–3085.

Tinbergen, N. (1932). Über die orientierung des bienenwolfes (*Philanthus triangulum* Fabr.). *Zeitschrift für Vergleichende Physiologie, 16*, 305–334.

Towne, W. F., Ritrovato, A. E., Esposto, A., & Brown, D. F. (2017). Honeybees use the skyline in orientation. *The Journal of Experimental Biology, 220*, 2476–2485.

Turner C. H. (1908) The homing of the burrowing-bees (Anthophoridae). *Biol. Bull., 15*, 247–258.

von Frisch, K. (1967). *The dance language and orientation of bees*. Cambridge, MA: Harvard University Press.

Webb, B. (2019). The internal maps of insects. *The Journal of Experimental Biology, 222*, jeb188094.

Webb, B., & Wystrach, A. (2016). Neural mechanisms of insect navigation. *Current Opinion in Insect Science, 15*, 27–39.

Wehner, R. (2009). The architecture of the desert ant's navigational toolkit. *Myrmec News, 12*, 85–96.

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