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Navigation by honey bees

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Definition

Navigation by honey bees refers to the cognitive and behavioural 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 potential 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 the Nobel Prize recipient Karl von Frisch (von Frisch, 1967), shows that these navigation behaviours 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 Figure 1A and Glossary). For bees, these mechanisms sustain the expression of different types of spatial behaviours that change as individuals learn and gain experience with their environment.

In this chapter we describe these spatial behaviours in honey bees (Figure 2), a group of 11 species and 44 subspecies (Lo et al., 2010) exhibiting some of the most advanced levels of social forms in the animal kingdom characterised by a reproductive division of labour (fertile queens and drones, sterile workers), cooperative breeding and overlapping generations of adults. Navigation skills are required by individuals of the different castes (Seeley, 2012). The foragers collect food, water and resins from

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

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

57

58 **Exploration flights**

59

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

67 On its first few excursions outside the colony nest, a bee engages in peculiar
68 flight sequences known as 'learning flights' (Figure 1B), during which the bee learns
69 the skyline **panorama** and **visual landmarks** associated with its nest location (Zeil,
70 2012). Learning flights are composed of many convoluted manoeuvres, loops, arcs,
71 and zigzags during which the bee faces the nest. During the initial learning flight, the
72 bee slowly increases the radii of the loops and arcs, distancing itself from the colony
73 nest until a point when it returns home without bringing back any resources. On the
74 next few flights, the bee flies a bit further, slowly gaining experience with the outside
75 environment.

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

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

99 100 **Homing flights**

101
102 At the end of every foraging trip, a forager must navigate back to its nest to unload its
103 crop and feed the colony. ‘Homing flights’ are composed of two phases : a straight line
104 flight to return to the nest area, and a convoluted flight to pinpoint of the nest entrance
105 (Figure 1D).

106 To return home, the bee uses its estimation of directions and distances of the
107 often turtuous inbound path toward a goal (e.g. feeding site) and integrates both
108 information using a **path integrator**. In honey bees, directions are primarily estimated
109 through the position of sun in the sky, constituting a **sun compass**. When the sun is
110 not directly visible (e.g. during cloudy days), this information can be retrieved from the
111 pattern of **polarized light**. Distances are estimated using an **odometer** through the
112 quantity of visual information perceived on the retina of the compound eye while flying.
113 It is possible to study this mechanism in bees by making them fly in narrow tunnels
114 with black and white strips of different widths, thereby making them under- or over-
115 evaluate their real flight distances (Srinivasan et al., 2012).

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

130 The last bit of the homing flight (also known as ‘view-based homing’) is guided
131 by visual landscape cues. Since the seminal experiment of Niko Tinbergen (another

132 Nobel Prize recipient) showing that digger wasps locate their nest entrance with
133 surrounding visual cues (Tinbergen 1932), bees have been challenged to pinpoint their
134 home in a plethora of scenarios. Objects may be displaced closer to or further away
135 from their nest, displaced to a new location, replaced with smaller or differently
136 coloured one, or even camouflaged (Dittmar et al., 2010). Based on these studies, we
137 know that bees learn relations between a myriad of visual cues and their nest entrance.
138 These relations are not necessarily explicit. Indeed, the use of **panoramic skyline**
139 **snapshots** around the nest entrance is sufficient to guide a simulated bee toward its
140 home (Towne et al., 2017).

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

147

148 **Route following**

149

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

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

169 Computational models attempting to decipher the cognitive mechanisms
170 underpinning this navigational feat show that trapline development and optimisation
171 can emerge based on the ability of bees to learn sequences of places using visual
172 memories (Collett et al., 1993) and estimate travel distances with **path integration**
173 (Srinivasan, 2011). According to these models, at the end of its foraging trip the bee
174 may sum the straight line distances between successively visited flowers and derive
175 the net length of the entire route. By comparing successive routes, the bee could thus

176 increase its probability of re-using the vectors composing the shortest experienced
177 route (Lihoreau et al., 2012). Through trial and error, this simple learning process may
178 enable the development of good (if not optimal) routes in environments with different
179 numbers and spatial configurations of feeding sites (Reynolds et al., 2013).

180

181 **Place communication**

182

183 Once back in the hive, the honey bee forager can communicate the direction, distance
184 and quality of a discovered feeding site via a sequence of movements known as the
185 'waggle dance' (von Frisch, 1967; Figure 3). Scout bees also use this communication
186 system to indicate the location of a suitable nesting site (e.g. cavity, hive) to reach a
187 consensus about the best available site before swarming (Seeley, 2012).

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

200 During the waggle dance, the forager waggles its abdomen and moves towards
201 the direction of the food relative to the sun. In cavity nesting honey bees, like the
202 Western honey bee, the invisible sun in the dark hive is encoded by the vertical vector
203 facing up (i.e. against gravity). Therefore, the angle between the waggle trajectory and
204 the vertical of the comb represents the angle of the food source and the sun. In open
205 nesting honey bees, however, the dance occurs horizontally on the top of the single
206 frame and the dancing bee faces directly the direction of the food or the future nest. In
207 both open nesting and cavity nesting honey bees, the distance of the food source is
208 communicated via the duration of the waggle movement that correlates with a distance
209 in meters. This correlation and the precision of the duration slightly varies between
210 species and subspecies of honey bees (Beekman et al. 2015). The rewarding value of
211 the resource is communicated by the total duration that the bee performs repeating the
212 eight-shape dance. Dancing for a longer time increases the probability to recruit
213 foragers susceptible to be interested by the navigation instructions for a new resource
214 (Seeley 2012).

215

216 **Migration**

217

218 Several *Apis* species from tropical Asia, such as the cavity nesting honey bee (e.g.
219 *Apis cerana*), the giant honey bee (*Apis dorsata*) or the dwarf honey bee (*Apis florea*),

220 do not remain in a stable nest but can abandon the nest or migrate over long distances
221 to respond to local food shortage (Oldroyd 2009, Figure 2). Giant honey bees, for
222 instance, have been reported to migrate to destinations up to 200 km away, stopping
223 over in bivouac congregations to rest and forage. These bees can even sometimes
224 return to the exact same tree after the migration period. During migration, Asian honey
225 bees use dance communication to orient the swarm departure in the correct direction
226 towards a new nest. In the case of long distance migrations, especially in open nesting
227 giant honey bees, the direction is communicated but the distance is only indicated by
228 a very long waggle signaling (Dyer and Seeley 1994). Sensory mechanisms used to
229 migrate to a new location are similar to those used by honey bee foragers, including
230 the **sun compass**, the **optic flow**, and the learning of visual landscape cues.

231

232 **Concluding remarks**

233

234 Honey bees share with other insects numerous sensory abilities and navigational
235 strategies (see Glossary). Thus, they are key model species to study insect navigation.
236 Understanding how a tiny brain, with about one million neurons, uses computations to
237 navigate efficiently in three dimensions over large spatial scales, finds direct
238 applications in algorithmic and robotics and may help understand how these
239 mechanisms evolved in the more complex brains of vertebrates (Chittka and Niven,
240 2009). Some features described in mammal navigation studies, like the hypothesis of
241 the representation of the global surrounding in a single mental map (i.e. cognitive map),
242 influence debates about mental representations of space in insects (Menzel 2019).
243 Even though no consensus has been yet reached, most studies show that **path**
244 **integration** and visual guidance are sufficient to explain the complex spatial behaviour
245 exhibited by honey bees and other insects (Webb 2019).

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

255

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341

342

343 **Glossary: The honey bee navigation ‘toolkit’.** Concepts defined below are
344 highlighted in bold in the main text.

345

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

350

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

354

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

359

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

365

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

372

373 Snapshot: Learning of a 2D image at one point in time. For a honey bee, the
374 memorised view corresponds to a specific orientation of the bee relative to the image,
375 similarly to a camera objective taking a snapshot from a specific angle.

376

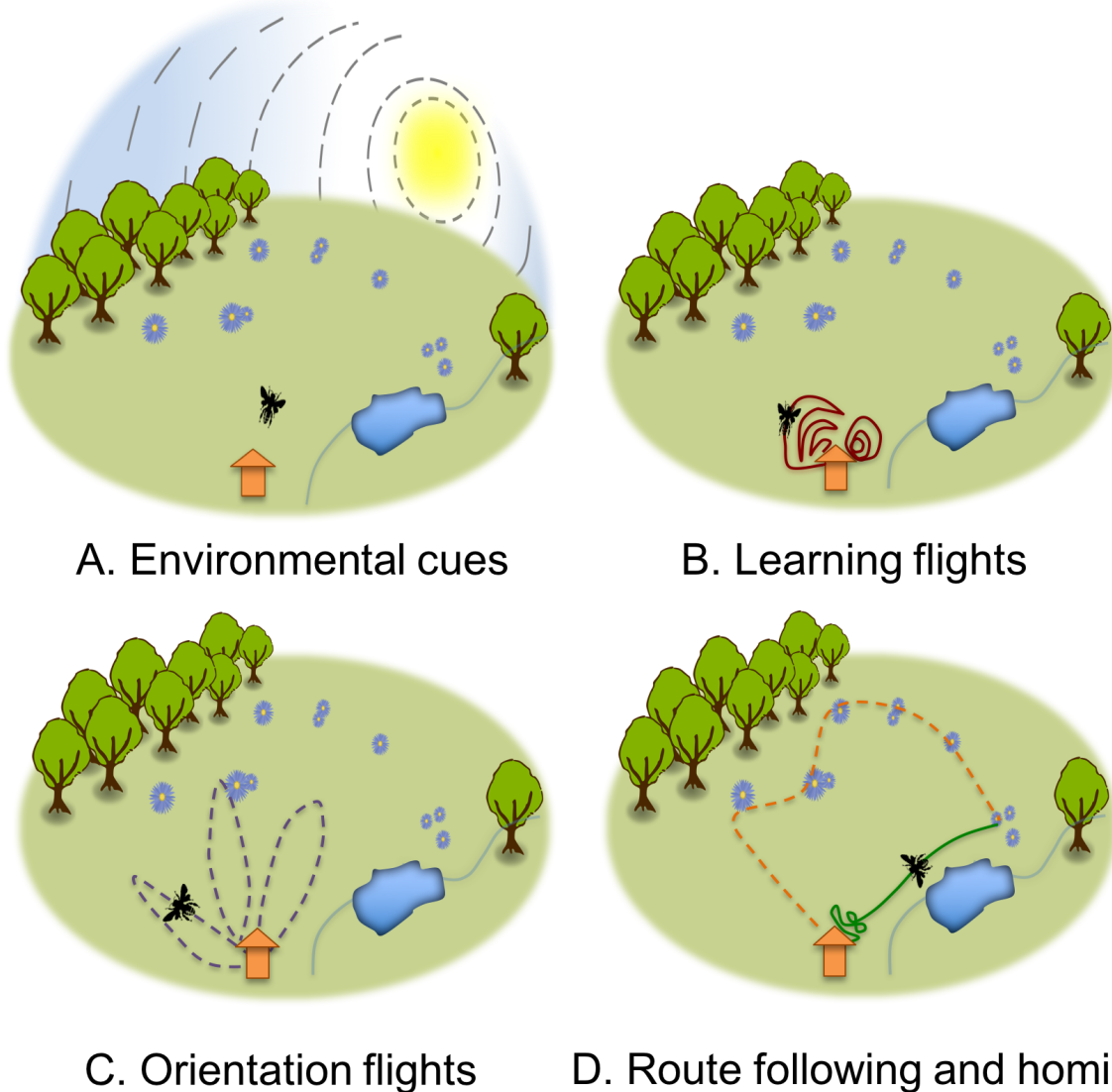
377 Sun compass: Utilisation of the sun’s position in the sky as a directional guide. For
378 honey bees, the position of the sun can be perceived directly (when the sun is visible)
379 or indirectly through the pattern polarized light (when the sun is not visible). To orient
380 when the sun is visible,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

382

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

387

388 Visual landmark: Salient feature in the visual scene. Honey bees can use many types
389 of landmarks spanning from 3D trees or buildings to 2D elongated patterns on the
390 ground (e.g. paths, edges, rivers, roads).
391
392
393



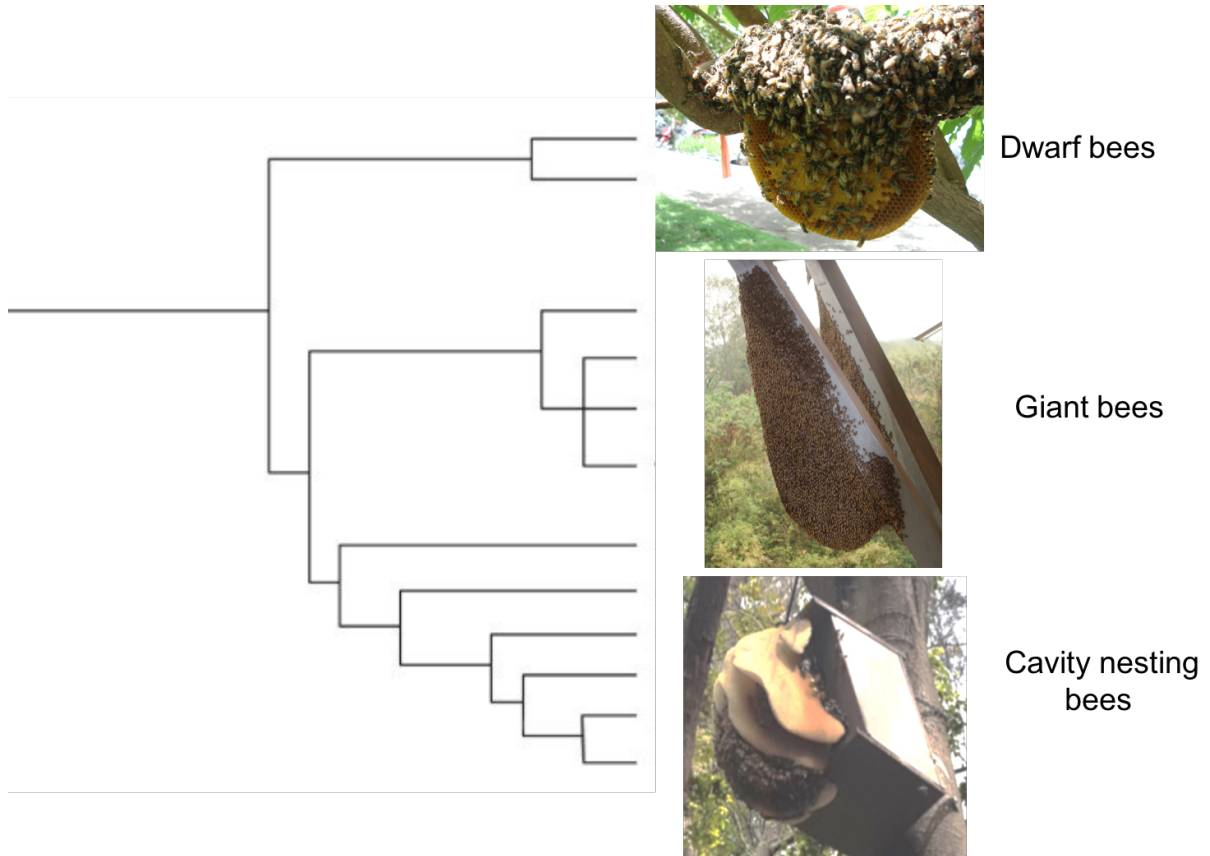
396

397

398 **Figure 1. A.** Environmental cues used by honey bees to navigate. Bees use the
 399 position of the sun in the sky (or polarized light dashed lines under cloudy conditions,
 400 dashed lines) as compass. They learn visual landmarks (e.g. trees, rivers, paths) and
 401 views of broader visual cues like panoramas and skyline (i.e. snapshots). When closer
 402 to the goal, bees use local available information to pinpoint the goal (e.g. shape, colour,
 403 odours). **B-D.** Hypothetical examples of flight sequences performed by a forager as it
 404 gains experience. **B.** Learning flights: during its first excursions outside the hive the
 405 bee learns the visual scene characterising the nest entrance using concentric circles
 406 increasing in size (red plain lines). **C.** Orientation flights : after a few trips, the bee starts
 407 exhibiting sequential exploration of sectors around the nest (orange dashed line) to
 408 find flower patches. **D.** Route following and homing: once experienced, the bee follows
 409 a multi-destination route (trapline) learnt from previous foraging trips (dashed orange
 410 line). The bee returns home following a home vector computed through path integration

411 (inbound in green). At the end of this homing flight the bee corrects eventual path
412 integration errors through small search loops to precisely locate the nest entrance.
413
414

415



416

417

418 **Figure 2.** Honey bees contain 11 species. Dwarf open nesting honey bees like *Apis*
419 *florea* are the most basal group and live mostly in Asia and Middle East. The open
420 nesting giant honey bees like *Apis dorsata* are found only in Asia. The most recently
421 derived group are the cavity nesting honey bees represented by six species: five of
422 which are distributed in Asia. *Apis mellifera* has a natural distribution in Africa, Europe
423 and the Middle East, but has been domesticated and distributed throughout the
424 world. It is now found in the wild on all continents except Antarctica. Photo
425 credits: Dwarf and cavity bees from Naïla Even, giant bees from Benjamin Oldroyd.

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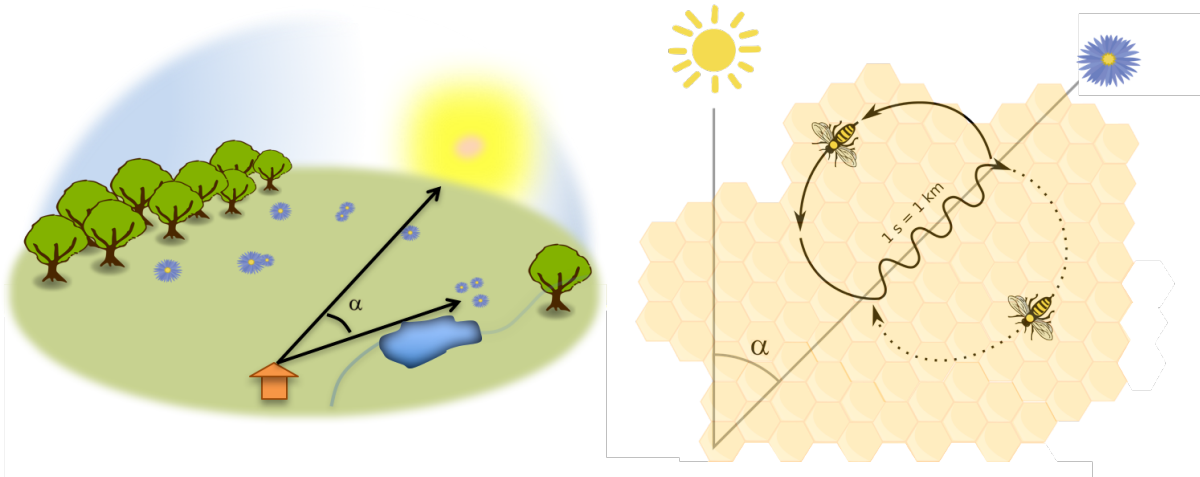
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 440 **Figure 3.** The waggle dance. Upon returning to the colony nest following a successful
 441 foraging trip, a honey bee forager can communicate the location of the discovered food
 442 site to its nestmates by performing a waggle dance. The bee communicates the
 443 direction of the resource by wagging in the direction of the resource relative to its angle
 444 with the sun (α). The duration of the wagging movement is proportional to the distance
 445 of the food. The bee repeats the wagging movement coming back from the left and
 446 then from the right drawing the figure height. The more the dance is repeated the higher
 447 the quality of the resource. Any bee following the dance can thus integrate the
 448 information and leave the hive using the instruction from the dance. The waggle dance
 449 is also performed by scout honey bees to communicate the location of new nest site
 450 before swarming. Modified from Emmanuel Boutet ([CC BY-SA 2.5](https://creativecommons.org/licenses/by-sa/2.5/)).

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453 **Crosslink references** (highlighted in yellow in the main text)

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