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Evidence for the honeybee's place knowledge in the vicinity of the hive

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A B S T R A C T

Upon leaving the nest for the first time, honeybees employ a tripartite orientation/exploration system to gain the requisite knowledge to return to their hive after foraging. Focal exploration comes first- the departing bee turns around to face the return target and oscillates in a lateral flight pattern of increasing amplitude and distance. Thereafter, for the peripheral exploration, the forward flying bee circles the return-goal area with expanding and alternating clockwise and counterclockwise arcs. After this two-part proximal exploration follows distal exploration, the bee flies straight towards her potential distal goal. For the return path, supported by the preceding exploratory learning, the return navigational performance is expected to reflect the three exploratory parts in reverse order. Previously only two performance parts have been experimentally identified: focal navigation and distal navigation.

Here we discovered peripheral navigation as being distinct from focal and distal navigation. Like focal navigation, yet unlike distal navigation, peripheral navigation is invariably triggered by local place recognition. Whereas focal navigation (orientation) is close to unidirectional, peripheral navigation makes use of multiple goal-vector knowledge. We term the area in question the *Peripheral Correction Area* because within it peripheral navigation is triggered, which in turn is capable of correcting errors that accumulated during a preceding distal dead-reckoning based flight.

1. Introduction

Honeybees (*Apis mellifera*) are capable of incredible feats of navigation, being able to fly thousands of meters away from home to forage for supplies and then successfully return. All species of honeybees (Genus *Apis*) are members of the Nesting Hymenoptera (Vespoidea and Apoidea), a monophyletic lineage within the Aculeata or Stinging Hymenoptera, the Euaculeata (Grimaldi and Engel, 2005; Brothers and Carpenter, 1993; Michener, 2007). Being central place foragers, honeybees have highly sophisticated cognitive way-finding skills just to survive. The roundtrip journey of the foraging honeybee is a well-structured sequence of navigation behaviors. Discounting the actions like searching and collecting at the respective terminals, the roundtrip comprises two major travel components: the outward and return path. While these two parts can be independently shaped by exploratory learning (also known for some ants), as a rule they tend to be similar and interdependent (Otto, 1959; Schneirla, 1941; Sommer et al., 2008; Wehner et al., 2006; Weiss, 1954). All roundtrip navigation is based on spatial knowledge acquired during preceding exploration.

The behavioral term *navigation* used above refers to well-oriented movements toward a distal goal that cannot be perceptually localized at the outset. *Orientation* is a more general behavioral term that includes navigation and refers the control of motion in space using any cue (Jander, 1975). Not being guided by stimuli from the goal itself, navigation in bees requires the use of learned *orientation cues*. Three groups of such cues serve this purpose: *compass cues*, *distance cues*, and *terrestrial place cues* (Frisch, 1967). A compass cue is the directionality provided by the solar azimuth and polarized skylight. A distance cue is self-explanatory, as it represents the distance between two goals and is measured by optic flow passing across the honeybee's retina. The settings of particular compass and distance cues may be combined and stored in the honeybee's memory as *navigation vectors*. The third cue is a terrestrial place cue, which is a landmark the bee recognizes and uses in directional navigation or as a beacon to pinpoint a place cue.

Exploration is found in all vertebrate and some invertebrate species, and is defined as active spatial learning behavior in which animals make use of structured home ranges for their daily activities. While roaming more or less systematically through their prospective home ranges the explorers acquire various types of cognitive maps to be used for later way finding (Toates, 1983; Jacobs and Schenk, 2003). In flying insects we speak *of exploration flights* (Jander, 1997; Menzel, 2011), which is synonymous with a variety of idiosyncratic terms like "orientation flight, flight of orientation, learning flight, reconnaissance flight, survey flight, locality study, turn-back-and-look behavior, memorization flight".

Importantly, among insects, only the flying and nesting wasps and bees (Euaculeata) perform unique taxon-specific

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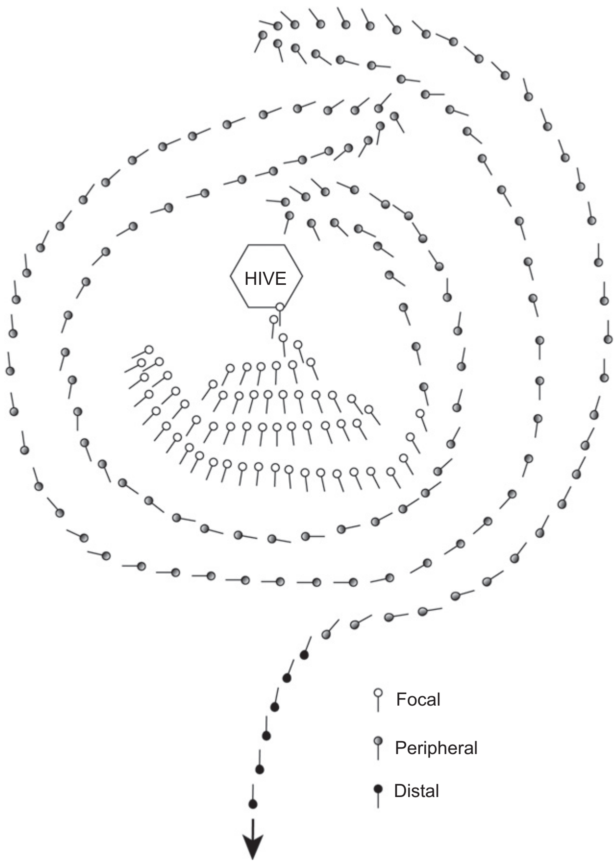

Fig. 1. Schematic of the exploration flight composed of focal, peripheral and distal exploration. For a mapped exploration flight see Zeil et al. (1996) (Cerceris wasp) or Collett (1995) (Vespula wasp and European honeybee).

(synapomorph) three-part patterned exploration flights (Fig. 1). Upon leaving the nest, focal exploration occurs first as the departing bee instantly turns around to face the return target. While still facing the return goal, it oscillates in a lateral flight pattern of increasing amplitude and distance from the goal (open circle, Fig. 1). Thereafter, for the peripheral exploration, the forward flying bee circles the return-goal area with expanding and alternating clockwise and counterclockwise arcs (shaded circle, Fig. 1). Finally, for the distal exploration (filled circle, Fig. 1), the bee flies straight away towards some distal goal area (Capaldi and Dyer, 1999; Capaldi et al., 2000; Jander, 1997; Lehrer, 1991; Lehrer and Bianco, 2000; Vollbehr, 1975; Zeil, 1993; Zeil et al., 1996). Supported by the preceding outward exploratory learning, the return navigational performance is expected to reflect differentially the three exploratory parts in reverse order (Fig. 2).

However, for the navigation back home, previously only distal- and focal navigation had been investigated. The homing bee starts with *distal navigation*, which is dominated by dead reckoning or vector flights, implying distance and direction knowledge (v. Frisch and Lindauer, 1954; Geiger et al., 1994; Menzel et al., 2000; Otto, 1959; Riley et al., 2003; Towne and Moscrip, 2008; Wolf, 1926). The honeybee's dead reckoning proclivity during distal navigation is not restricted to this species. Rather, it seems to be typical for all air-bound and substrate-bound nesting Aculeata. First discovered with displacement experiments in ants (Pieron, 1904), it has subsequently been confirmed for a variety of ant species (Brun, 1914; Wehner and Srinivasan, 1981). There is no research in ants specifically addressing the question of differentiation into peripheral and focal navigation. However, there is a strong use of near-goal landmarks in goal finding by some ant species, similar to proximal

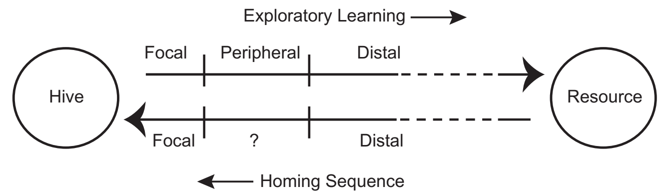

Fig. 2. Sketch of uniquely shared, three-part architecture of outward exploration and subsequent return navigation in the flying and nesting aculeate Hymenoptera.

navigation in honeybees (Collett et al., 2003; Knaden and Wehner, 2005).

Finally, *focal navigation* (terminal navigation in a return flight) requires the unidirectional (sector-limited) approach to the target, the nests entrance, regardless of the distal direction from which the bee homed. Focal navigation is strongly guided by the near-target visual cues at a distance of approximately <1 m (Butler et al., 1970; Cheng et al., 1987; Collett and Rees, 1997; Collett and Zeil, 1997; Dittmar et al., 2010; v. Frisch, 1914/15; Lehrer and Collett, 1994; Wolf, 1926; Zeil and Kelber, 1991).

While there is a good matchup between the previously well-studied distal and focal navigation and their respective exploratory counterparts, to date it has not yet been known whether there is a navigational counterpart to peripheral exploration. To test for this counterpart we performed a set of six experiments to test honeybee navigational performance within the hive periphery under various conditions to better understand external factors relating to their navigational ability.

For the first experiment, we tested the hypothesis that honeybees use vector (distal) navigation when homing from a location 15 m from the hive. Honeybees were passively displaced half the trained distance while collecting a reward (see Fig. 3). If displaced honeybees maintain the initial compass direction then vector navigation was used; alternatively, honeybees compensating for the displacement and departing in the direction of the hive would indicate a previously undescribed navigational tool.

In the second experiment we tested the possible effect of optic flow on bees passively displaced bees within the hive periphery. Honeybees are well known to use optic flow as feedback to keep track of their active displacement in flight (Esch and Burns, 1995; Srinivasan et al., 1997, 2000). For this, bees were displaced as in the first experiment, but either covered or exposed to the pano-

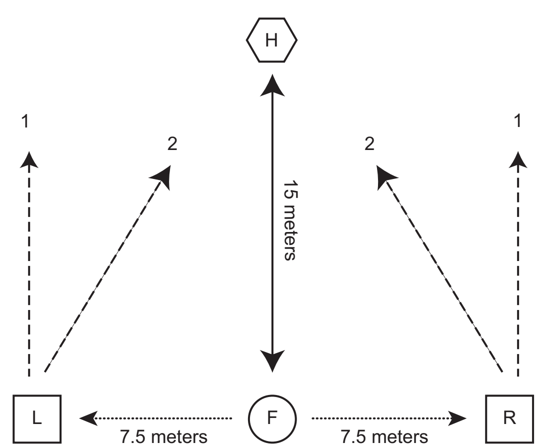

Fig. 3. Hypotheses for homing departures. The dashed arrow represents hypothetical departure bearings indicative of either place-independent dead reckoning, i.e. distal navigation (1) or place-dependent direct goal orientation (2). Solid arrow indicates shuttling of bees between the feeder and hive. The dotted arrow indicates passive displacement.