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Orientation by Central-Place Foragers

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Almost all known social insects, from honeybees to stingless bees, hornet wasps to mud dauber wasps, and from ants to termites, solve the task of navigating to and from locations that are of significance to them. Individuals within each burrow, hive or nest carry out these navigational tasks several times each day. In addition, when animals discover large food resources, they need robust navigational strategies to regularly revisit these locations. The navigation strategies that social insects use, the variety of cues they rely on and the sensory basis required of navigational behavior are impressive for animals with small brains.

Our main attention here is to ants (Fig. 1), primarily because navigation strategies have been extensively mapped, largely because of their pedestrian nature which allows for tracking and record their movements over several meters with great precision. The principles of navigation are similar across animals and hence lessons learnt from ants have relevance to other social insects.

In the absence of a distinct trail, whenever one encounters an ant, the location of her nest tends to be far from evident. However, if the ant is offered a small food item, such as a freshly killed insect or some sugar, she picks it up and walks home by an almost direct route, thus revealing the location of her home. It is this 'home' which makes ants and other social insects rather special since at the end of each foraging trip, be it successful or not, they must return home, since if they do not – they die. These animals are hence called central place foragers. Hence every individual member in a social insect colony places immense importance on the location of its home, be it a nest, burrow, hive or a mound. Before beginning a foraging journey, each individual animal must learn enough information about their home to ensure successful return. Then, individuals embark on long arduous foraging journeys in search of food and upon finding food return home by the most efficient route. Information learnt during their outward journey is then used to chart a course for the return trip to first orient towards home and to head towards it. Once they are close to home, the final challenge is to pinpoint the often cryptic and inconspicuous nest entrance. This feat of orientation in space can be understood in three components: (a) learning walks or learning flights; (b) returning home after finding food; (c) pinpointing the inconspicuous home. In accomplishing these feats, the individual makes use of a variety of cues.

Learning Walks or Learning Flights

When the adult form of a social insect emerges from pupal case, she typically spends a few days

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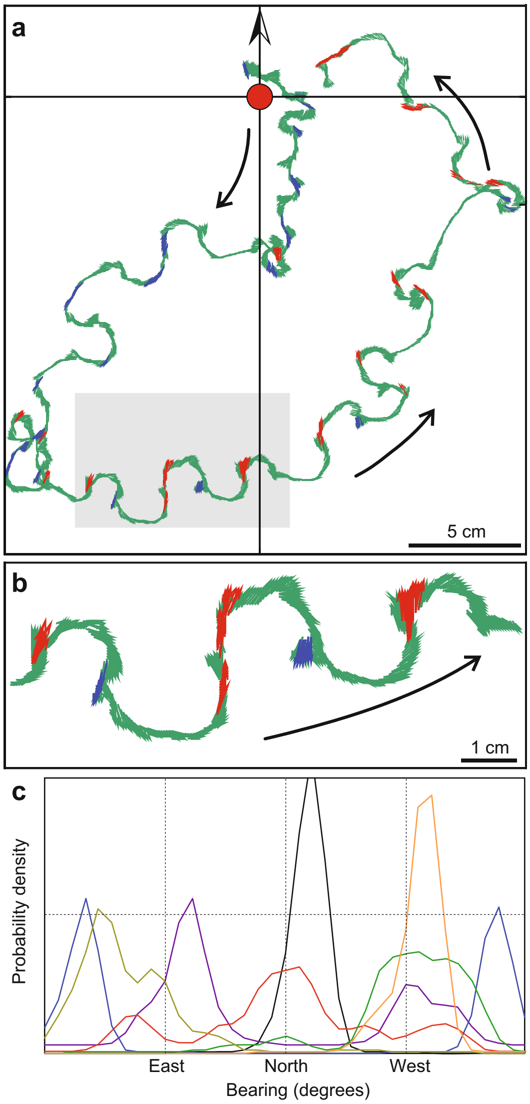
Orientation by Central-Place Foragers, Fig. 1 Australian ants that have been the focus of navigation: (**a**) Nocturnal bull ant ► *Myrmecia pyriformis* detects subtle changes in their dim light visual world; (**b**) intertidal ant ► *Polyrhachis sokolova* navigates using landmark panorama; (**c**) central Australian desert ant or honeypot ants, *Melophorus bagoti* establishes idiosyncratic routes; (**d**) in the trunk-trail forming meat ant ► *Iridomyrmex purpureus*, experienced foragers rely on visual landmarks and naïve animals rely on pheromone trails. Photo Credit: Ajay Narendra

in the dark confines of the nest before starting to forage. Naïve foragers that leave home experience light and other visual information for the first time. This triggers major neural reorganization in brain regions relevant to navigation [17]. On leaving the nest, she must learn the spatial position of the nest in relation to the surroundings. This information must be learned individually and cannot be genetically passed from the parents. For this reason, she typically undertakes idiosyncratic walks or flights of learning, based on mode of locomotion, before departing home.

In ants, naïve foragers emerging from the nest for the first time walk slowly around the nest entrance and then return to the nest; this is termed a learning walk [19]. Ants carry out anywhere between two and seven such learning walks over 1–4 days before their first foraging trip. Learning walks are highly individualistic, with successive walks covering larger areas and different compass bearings relative to the nest entrance (Fig. 2c). A similar pattern is seen in flying social insects, such as ► honey bees and ► bumble bees [5]. Flying insects, after leaving the nest, immediately turn back to face the nest, fly backwards and slowly, gaining height and distance from the nest. Wasps during their learning flights back away from the nest in a series of arcs roughly centered around the nest entrance, enabling them to view the nest from multiple orientations.

During learning walks, ants regularly turn back and look in the nest direction. In the case of *Ocymyrmex robustior*, they fixate at the nest, whereas ► *Myrmecia croslandi*, ► *Cataglyphis nodus*, and *Melophorus bagoti* ants do not fixate at the nest, but their nest-directed gazes are immediately followed by gazes in the direction opposite to the nest [10]. In a latter scenario, high-speed videography has shown that the gaze sweeps through the compass bearings of the nest and anti-nest (Fig. 2a, b). Collecting regular nest views and anti-nest views appears to be characteristic of ants that inhabit complex habitats. Behavioral and modeling data shows that memories of both these views result in high familiarity when the ant is at the nest, thereby providing information about its location. Together these views must allow the ants to find their home especially when they overshoot their nest entrance [9]. Given animals that carry out more learning walks are more efficient in pinpointing the goal, learning walks are an essential part of an insect's navigational repertoire.

Flying insects may be able to see their home during their learning flights that allow them to pivot around the nest entrance with precision.



Orientation by Central-Place Foragers, Fig. 2 Choreography of learning walks in ants. (**a**) Learning walk of a naïve ant, ► *Myrmecia croslandi*. Green arrows show orientation of the ant at every 40 ms. Red arrows show the orientation of the ant toward the nest (±10° of the nest), and blue arrows show the orientation in the opposite direction, referred to as anti-nest view. Nest is shown in red circle. Large black arrow indicates the direction in which the ant moves. (**b**) Shows the magnified view of the shaded area in (**a**). (**c**) Consecutive learning walks by a single ant cover different compass directions. Each learning walk, shown in a different color, ends with animals returning home. Probability density distributions were determined by measuring the compass directions in every frame. (Modified from Ref. [9])

But from the pedestrian ants' perspective the nest entrance is usually not visible, so that they must use an external reference point for this purpose. In *Cataglyphis noda*, ants orient toward the nest even without a sky compass, but are unable to maintain orientation if the magnetic field is disrupted [6]. Moreover, rotating the horizontal component of the geomagnetic field by 90° results in a shift in the gaze, as expected, confirming the use of geomagnetic field for orientation during learning walks.

Learning walks are also carried out by experienced foragers in three cases: (a) when animals have difficulty locating the nest on the previous trip, a behavior that has often been used to study learning flights in wasps, (b) when animals that leave the nest detect changes in their visual world [12], and (c) on leaving a large food source that is to be revisited. In all these three cases, a significant feature is that the animal completes the learning walk and continues foraging or returning home, unlike learning walks by naïve foragers that loop back to the nest.

Returning Home After Finding Food

Once an animal has learnt sufficient information about her nest surrounds, she embarks on a foraging journey. During these foraging trips she continuously updates her position relative to home [4]. On finding a good food source she immediately returns home. One of the most impressive forms of return navigation was discovered in the ► seed-harvesting ant *Messor barbarus*, in which homing ants experimentally displaced to an unfamiliar location continued to travel toward home. This mode of navigation, in which animals update their position relative to the origin by integrating travel speed and direction, is called path integration [7]. Determining compass directions and distance travelled are key components of path integration. Directional information is derived from an external compass cue, typically information provided by the pattern of polarized skylight [20]. Polarized light is detected by specialized ommatidia present in the dorsal rim area of the compound eye of many social insects. In addition, almost all flying social insects have simple eyes (ocelli), which also consists of polarization receptors and that are likely to assist animals in maintaining heading direction. To reliably estimate the distance travelled, insects have an odometer [7]. In walking insects this takes the form of a 'pedometer' where individuals integrate the number of steps taken to measure distances, allowing them to estimate the real horizontal displacement, rather than the distance walked on undulating terrains. Specialized proprioreceptors located on body joints are thought to be involved in providing this distance readout.

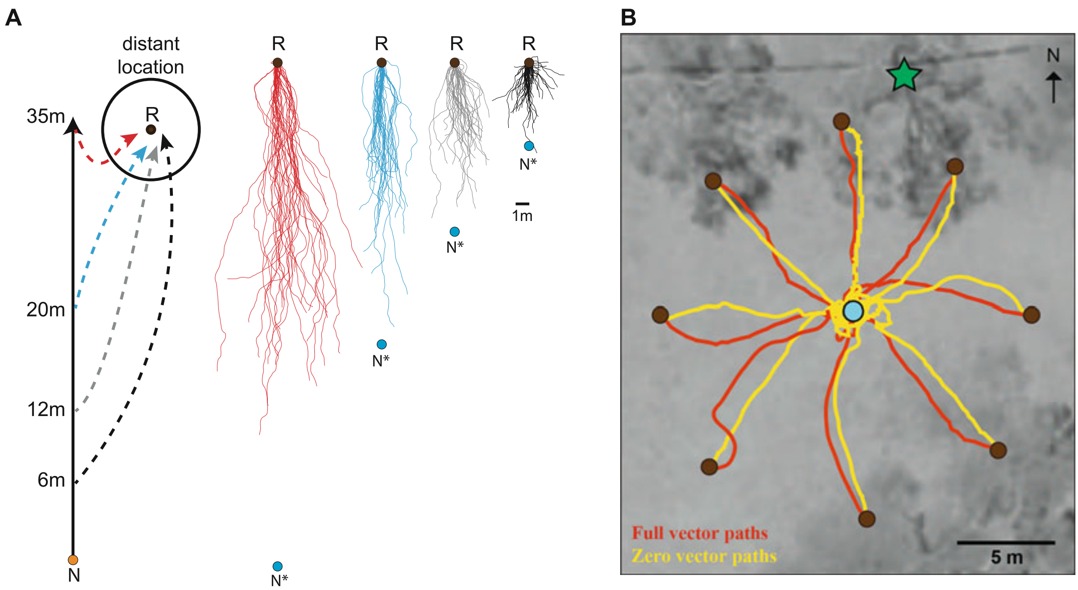
Flying social insects also rely on path integration [7]. Bees estimate their distance travelled by measuring the rate at which visual information moves over the retina (optic flow). This was discovered in the honey bees that dance to communicate the location of profitable food resources by a ▶ waggle dance. In this, a returning forager wags her abdomen while walking in a straight line and then loops to left or right, and on the next straight run loops in the other direction. The waggle duration is proportional to the distance between the hive and the food source, and the angle between the axis of the waggle and the vertical direction provides the direction to the food source with respect to the sun.

The extent to which animals rely on the path integrator is dependent on the navigational information content of their environment [11]. Insects that move in visually structured environments (e.g., urban and rural landscapes, tropical rainforests, semi-arid deserts) rely less on path integration (Fig. 3a). Such insects rely on visual landmarks to steer towards home and to establish routes between nest and food source. Insects use their path integrator as a framework to learn and build visual landmark information. Once animals have learned the visual landmarks, they store this information in the long-term memory. Some insects attach a vector to learned landmarks, which provide information on "where to go next" when they encounter a familiar landmark. Route following is often seen in the Australian desert ant *Melophorus bagoti* and African desert ant *Cataglyphis velox* that walk through a cluttered environment to reach the nest. In such habitats, ants establish individual nestbound routes. Impressively, they can recall these route memories when captured at the food or nest site and released anywhere along the route. Reliance on visual landmarks increases both the precision and navigational efficiency of finding the goal.

For animals that travel under dense canopies, access to polarized skylight may be severely limited. For such animals, the tree canopy, which includes silhouettes of leaves and branches against the sky, may provide a high contrast and serve as a reliable compass cue. The canopy pattern is known to provide orientation information in two ant species, *Paltothyreas tarsatus* and ▶ *Odontomachus hastatus* [8, 16]. This was tested by providing an artificial canopy to which the ants were trained. During tests, the canopy was rotated which led to the ants shifting their orientation in a predictable manner.

There is growing evidence that animals rely on the visually rich landmark panorama to obtain trajectory information and to structure routes. Both experimental and theoretical analyses have shown that homing insects when far from the goal match their current view to nest-oriented views acquired during learning walks [1]. Comparing these views, animals choose to head in the direction that provides the maximum view similarity. In the Australian jack jumper ant, *Myrmecia croslandi*, such decisions are made within a few seconds [14]. If the correct heading direction is chosen, the view similarity will increase as animals continue to walk in that direction. The information content in the panorama is robust enough to allow ants to navigate even from locations they have never previously visited (Fig. 3b), as long as they had acquired nest-oriented views from 1 to 5 m away from different cardinal directions.

In honey bees too, experienced foragers when captured at the nest and released at locations they had not visited up to 13 km away were successful in returning home only from a direction where the skyline panorama provided sufficient navigational information for guidance [15]. The landmark panorama can guide animals toward home but is not sufficient for pinpointing the nest.



Orientation by Central-Place Foragers, Fig. 3 Visual navigation strategies in ants. (**b**) Reliance on path integration in the desert ant *Melophorus bagoti* that inhabits cluttered landscapes. Ants were provided a food source at 6, 12, 20, and 35 m. These ants were captured, transferred in dark, and released at a distant location (R). Ants were tracked from the release point till they began a search. These ants travel about half the distance toward the fictive nest (N*) as indicated by the path integrator and is considered to be an optimal navigation strategy in cluttered landscapes where animals have established a familiar corridor [7, 11]. (**b**) Jack jumpers, ▶ *Myrmecia croslandi*, successfully return home from previously unvisited locations within a 15 m radius of the nest [14]. Foraging ants caught at the base of the foraging tree (green star) were captured and transferred in dark and released at one of the eight locations (brown circles) around the nest (blue circle). Paths in red are homing trajectories of ants that had access to both visual landmarks and path integration information. These ants were captured close to the nest and re-released at the opposite release station. On the second release, ants had access to visual landmarks only (zero-vector ants), and these paths are shown in yellow. Note that ants are exceptional in getting close to the vicinity of the nest but have difficulties pinpointing the nest entrance

Locating an Inconspicuous Home in the Return Stage

Once animals reach the vicinity of the nest, they must pinpoint the exact home location. In some instances, ▶ pheromones or nest odor may assist, but they are often volatile and so less reliable under windy conditions. Visual information is most robust for this purpose, and this is learned during the initial learning walks or flights [5]. The first evidence that social insects use visual information to pinpoint the nest came from solitary wasps [18]. A ring of pine cones was placed around the nest entrance. Departing wasps carried out learning flights and, while the wasp was away the pine cones were moved just a few centimeters away. The returning wasps searched for the nest at the center of the new location of the pine cones, rather than at their own nest. This is evidence that animals learn nest-associated visual information in their learning flights, which is used on their return.

Following this, the information used for visual guidance was identified by training honey bees to a food source whose location was defined only by an array of cylinders and recording the search behavior of returning bees to an array of different sizes and arrays of cylinders [3]. From this it became clear that honey bees learn the apparent size of visual landmarks and search at the location where the visual world was most similar to their experience during training. This has been demonstrated in pedestrian ants trained to locate their nest within a landmark array [13]. Following training, homing ants were captured and displaced to an unfamiliar location and presented with a landmark array that was either identical in size or the size doubled or landmark size doubled and distance between landmark also doubled. Because only in the latter condition, the apparent size of the landmarks matches to the training phase; ants search predictably at the fictive nest location only in this condition. Thus, animals returning to a goal move to compare their current view to a previously memorized view and search at the location where the two views provide the best match. Known as the "snapshot model," this is the predominant strategy used by central place foraging insects to pinpoint locations.

In conclusion, the study of navigation/orientation abilities addresses a key set of adaptive needs in social insects. Vision plays a crucial role for navigation in social insects. Ants were thought to navigate almost entirely by means of pheromone trails. Such trails are, indeed, critical in nestmate recruitment, but scout ants must first locate the food source, and vision plays a significant role in locating the food source. In fact, even trail-following ants disregard pheromone information and instead rely on visual cues [2]. Ongoing research across many groups is now attempting to identify the specific features in the landmark panorama required for navigation, the role of color, and the brain regions involved in sensing and integrating different sources of information.

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