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Review

The neuroethology of ant navigation

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SUMMARY

Unlike any other group of animals, all ant species are social: individual ants share the food they gather with their nestmates and as a consequence they must repeatedly leave their nest to find food and then return home with it. These back-and-forth foraging trips have been studied for about a century and much of our growing understanding of the strategies underlying animal navigation has come from these studies. One important strategy that ants use to keep track of where they are on a foraging trip is 'path integration', in which they continuously update a 'home vector' that gives their estimated distance and direction from the nest. As path integration accumulates errors, it cannot be relied on to bring ants precisely home: such precision is accomplished by using views of the nest acquired before they start foraging. Further learning is scaffolded by home vectors or remembered food vectors, which guide a route and help in learning useful views experienced on the way. Many species rely on olfaction as well as vision for route guidance and the full details of their foraging paths have revealed how ants use a mix of innate and learnt multisensory cues. Wood ants, a species on which we focus in this review, take an oscillating path along a pheromone trail to sample odours, but acquire visual information only at the peaks and troughs of the oscillations. To provide a working model of the neural basis of the multimodal navigational strategies of ants, we outline the anatomy and functioning of major central brain areas and neural circuits — the central complex, mushroom bodies and lateral accessory lobes — that are involved in the coordination of navigational behaviour and the learning of visual and olfactory patterns. Because ant brains have not yet been well-studied, we rely on the work that has been done with other species — notably, *Drosophila*, silkworm moths and bees — to derive plausible neural circuitry that can deliver the ants' navigational strategies.

Introduction

Ants probably evolved from social wasps and all ant species are social, facing the same task of leaving their nest to find food for the nest's inhabitants and then returning safely home. Much of what is known about the detailed strategies of ant navigation has come from studying these journeys, providing insights into ways in which ants see and smell their world, move around within it, and remember some of its properties. This knowledge is sufficient to tempt us to explore how the ant brain might implement such intricate behaviour. The modern era of the experimental study of insect navigation began early in the 20th century with Felix Santschi's work in Tunisia[1]. His best-known discovery is that ants rely on the sun for directional information: he found that an upright board, placed along a section of an ant's route to hide the sun, disoriented the ant so that it moved back and forth; if he placed a mirror along the route to reverse the apparent direction of the sun, the ant reversed direction. Santschi was hard-headed about what his findings revealed about the intelligence of ants: "It is as superfluous for a navigating ant to possess profound astronomical knowledge as it is for a grazing cow to possess any kind of botanical knowledge"[2]. Only later was it appreciated that ants and bees are somewhat smarter and learn the trajectory of the sun through the sky relative to their local surroundings, enabling them to use the sun as a compass[3,4].

Desert ants have been particularly valuable for exploring the navigational strategies that enable ants to learn and perform foraging journeys. One experimental advantage of this species is that the surface of the desert is too hot for pheromones to persist and be useful for social trails, and consequently each ant relies on its individual skills to navigate, employing a variety of navigational tools that we discuss below. While many major insights were made using desert ants as a model, illuminating the full repertoire of ant navigation behaviour has involved meticulous research on a range of species, such as wood ants, fire ants and bull ants.

In the following sections we first summarise current knowledge of the ants' different navigational strategies, we then examine the details of the paths of individual ants, before considering what we know about the neural basis of these behaviours.

Path integration

Path integration is an essential navigational mechanism for both homing and for learning routes: it allows an ant on leaving home to continually monitor and update its estimate of the direction and distance from the nest. On finding food or sensing danger, the ant can employ path integration to return directly home by the shortest route, using what is known as its home vector. A simple way to picture path integration is to imagine taking a walk in a large expanse of desert. Fearful of being lost, we tie a

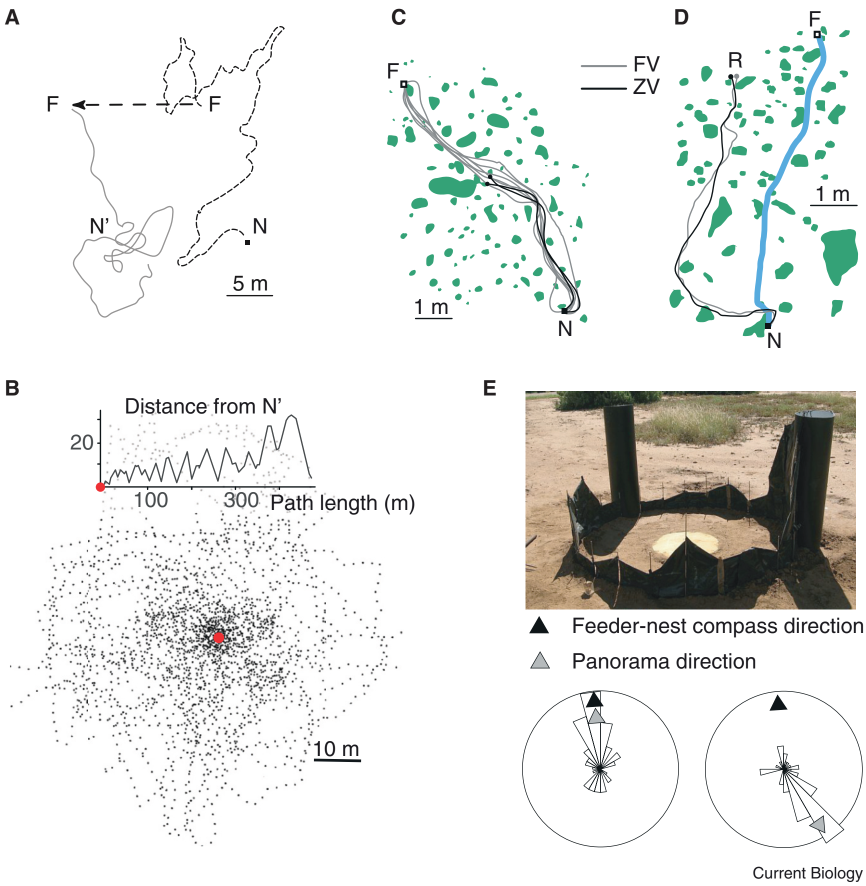

Figure 1. The navigational repertoire of ants.
(A) The dashed line represents the foraging path of a foraging *Cataglyphis fortis*. An ant is taken from the food site and released on a test ground where it performs a home vector and searches for its nest. Adapted from[144]. (B) Top: an ant's search path as it moves away from and towards the release site. The duration of the illustrated path is 72 min: Bottom: search distributions around release point (red dot) of eight ants, each followed for one hour; grey dots show the ants' positions every 2 m along their path. Adapted from[5] with permission from Springer Nature. (C) Visually guided habitual routes through cluttered terrain. Grey paths: nest-ward full vector journeys from one individual. Dark paths: zero vector ants released part way along their normal homeward route. Adapted from[18]. (D) An ant is taken from food, F, and released with full vector at a novel location (grey path). As a zero vector ant, she produces the same route (dark line). Blue shows the corridor of previous homeward routes. Adapted from[22] by permission of Oxford University Press on behalf of the International Society for Behavioral Ecology. (E) Top: an arena used to simulate a panoramic skyline. Below: the distribution of heading directions of ants caught on their return and released in the centre of the simulated skyline. Ants move in the return direction indicated by the simulated skyline (grey triangle) rather than in the familiar feeder-nest compass direction (black triangle). Adapted from[37].

piece of string to a post at the starting point and keep it taut: when tired of exploring, we can always follow the string along the shortest route back.

This analogy is imperfect in one major respect: it is errorless, whereas path integration accumulates errors as a journey continues. To compensate for errors, desert ants have an elaborate search strategy to locate their nest. It is best examined when an ant is taken to an unfamiliar test ground when it has found food; on release, the ant performs its home vector (Figure 1A). Finding no nest at the end of the home vector, the ant searches close by, where the nest is most likely to be. With no success, it searches increasingly far from that position in a kind of spiral that takes it away and then back to the end point of the home vector (Figure 1B). This vain search on a test ground can continue for several hours with the endpoint of the home vector actively maintained[5,6].

Path integration needs reliable measures of compass direction and of distance travelled. As Santschi showed, the compass direction usually comes from the sun. Further research has revealed that many celestial cues, such as polarised skylight, spectral and luminance gradients, but also non-visual cues like the wind direction or the inclination of the Earth's magnetic field lines, are used by ants to monitor their heading within a global reference frame.

To estimate the distance that they travel, desert ants have been shown to 'count' their footsteps. The slightly gory experiment involved a surgical operation to change the lengths of their legs by either attaching stilts made of pigs' bristles or shortening by partial amputation. The ants' home vector was then recorded: ants with shortened legs ran a shorter distance than expected and ants with lengthened legs ran further[7]. The number of steps taken in both experimental conditions was similar to the number taken by ants walking normally. While the stride integrator appears to be the major source of distance information, translational optic flow is also used by *Cataglyphis bicolor* when carried by nest mates[8]. This ability is likely a residue of the ants' wasp ancestry, but more work is needed to see whether optic flow based odometry might be more widespread in species that live in visually richer environments than that of desert ants[9].

A key finding is that ants perform path integration as though they always move over a two-dimensional surface. That was discovered by increasing the length of an ant's outward journey by making it travel up and down a series of humps. Given a return journey on flat ground, ants stopped and searched as though the outward journey had also been on flat ground. Cancelling out the distance travelled vertically has the benefit of preventing errors when, as often happens, the three-dimensional profiles of the terrain encountered on outward and inward journeys differ[10].

The accumulated direction and distance components of a home vector are stored while the vector builds up during a single outward journey. This memory is labile and erased when a new home vector is accumulated. Tests of memory retention show that a home vector has a short life compared to environmental memories: home vectors in ants start to decay after just one day and are very imprecise after two days[11].

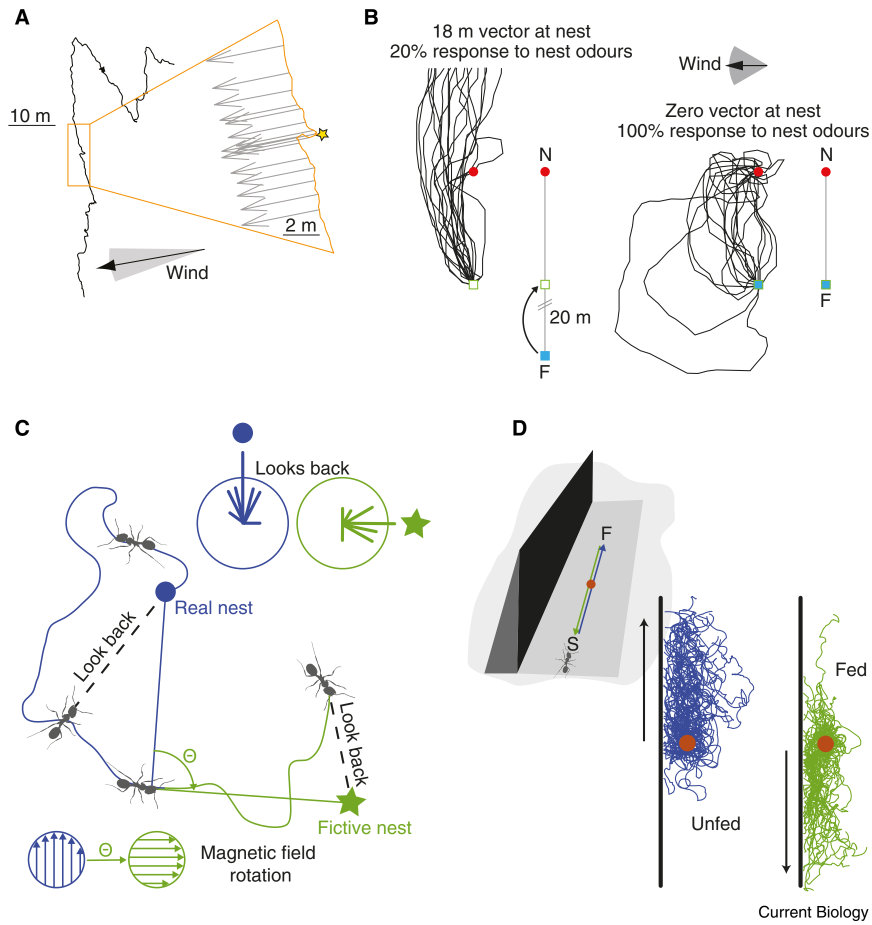

Figure 2. Multi-modal features of ant navigation.
(A) An ant's crosswind trail to find prey. On detecting prey odour, the ant moves downwind. Arrows show direction of wind. Star shows momentary downwind movement of the ant[42]. (B) Ants ignore an odour until they are close to the nest. Left panel: nest odour 20 m from nest. Right panel: odour close to the nest. Adapted from[44] (CC BY 3.0). (C) Ants can use magnetic cues to face their nest. Blue is the direction of Earth's geomagnetic field. When the field is rotated, ants face the fictive nest in the rotated direction (green). Adapted from[14]. (D) Motivational state sets the ants' expected view, F. Ants are trained from a start position (red dot) to find food by moving parallel to a wall, keeping the wall on their left side (blue paths in middle section). If ants are fed before being placed at the start position, they move so as to keep the wall to their right as in their accustomed homeward direction (green paths in right section)[21].

Some desert ants have discovered that environmental features can reduce the need for costly search behaviours. They have nests in flat open deserts where prey is scarce. They may have to travel several 100 m for food so that the ants return with large errors in their home vector. In such areas, a tall nest mound provides a visual cue to help guide ants home. Should an unkind experimenter reduce the size of the nest mound, the mound is rebuilt. But should a kindlier experimenter erect an artificial landmark close by, the landmark acts as a substitute and the ants feel no need to rebuild the dismantled mound[12].

The example above shows that when an ant is close to the nest, learnt views of home are of paramount importance, and path integration is likely to play an essential part by enabling ants to know in which direction they need to turn to face the nest. View learning happens when a new forager, on first emerging from its nest hole, walks around the nest, often looking back at the nest to memorise its surroundings[13]. The supposition that facing the nest relies on path integration and not on any visual cues has been tested by applying an artificial magnetic field to an area around the nest while new foragers performed these so-called learning walks. When magnetic north was rotated relative to geographical north, the ants faced a fictive nest in the direction signalled by the artificial magnetic field[14]. Nonetheless, long fixations of the nest are by no means essential. *Myrmecia croslandi* conducts successful learning walks with no nest fixations at all[15]. Once the learning walks are completed the ants can reach the nest from any direction[16].

Visual route learning

Path integration, by enabling an ant to face its nest, allows it to store views of its nest immediately on departure, so that the ant can pinpoint the nest entrance on its return from a foraging trip. Furthermore, path integration allows the ant to face in the direction of its nest anywhere along its foraging route, meaning it can learn views along the whole homeward path from a regular foraging site. After an ant has reached its nest, it may rest for a while before making another foraging trip that is guided by inverting the direction of its home vector. This 'food vector'[17] can then enable the ant to learn views along its outward path.

After the visual cues along a route have been memorised (Figure 2), routes can be followed irrespective of the state of home or food vectors. Kohler and Wehner[18] caught an experienced ant at the end of a foraging trip close to the nest when its home vector was essentially zero (known as a zero vector state) and returned it to the food site. The ant re-ran its route relying entirely on what it had learnt on previous trips with no help from path integration (see also[16,19]). Despite the importance of path integration in learning a route, we see that once acquired, visual route memories override path integration and the route is followed whatever the state of the path integrator.

An example in which visual route memories are evoked independently of path integration comes from wood ants using visual route memories according to their motivational state. Ants in the lab were taken from their nest and placed at a starting position (red disk) to collect sugar water at a point at F along a wall (Figure 2D). Between each training trial, the apparatus was rotated to face in one of four cardinal directions. Trained ants placed at the start position when they were hungry walked in the direction of food, with the wall on their left. If they were fed before being placed at the start, the ants walked with the wall on their right. An ant's state of hunger thus sets which visual memory guides its choice of route[20,21].

Can we gain insights into the mechanisms underlying view memories from behavioural data? Firstly, we can see that memory acquisition is impressively fast. One *Cataglyphis velox* ant observed near Seville in Spain took just one trial to learn a complex route as it weaved between tussocks of grass (Figure 1D). This individual was taken from the feeder with a full home vector and released some metres away from the food. It then followed a path among the grass tussocks close to its nest where it was captured and returned to the release site. The now zero vector ant then repeated the same path home, essentially demonstrating one trial learning[22], as also confirmed by additional experiments[23,24].

Second, experiments in which an ant was made to re-run a route several times revealed that there are mechanisms for downplaying the use of a memory that has been recently recalled. Ants returning home along a simple route in bare desert with a single vertical post as a landmark were caught before entering the nest and replaced at the feeder. One or more recapitulations of this kind led to confusion, as though the ant ignored its well-embedded memory. A possible explanation is that an ant following a route activates a sequence of visual memories and suppresses the operation of each memory after it has been applied[25]. A similar, but more extreme, experiment was to force ants to run portions of their visually defined homeward path many times and each time thwart them from reaching their nest. Ants would eventually lose trust in their visual memories and, in a pique of despair, run in the opposite direction[26]. Importantly, the 'despair' was not due to a mistrust of all visual memories, it was specific only to the memories associated with the portions of route that the ants were forced to repeat.

The many memories guiding visual routes can persist for the lifetime of an ant[27], suggesting that route memories involve long-term synaptic changes. A large repository of visual memories needs a brain region with a large memory capacity, ensuring that previously learned information need not be erased when new routes are learnt[28,29].

Another navigational tool that enhances the performance of routes involves local vectors[30,31]. One way to picture a local vector is as a memory of the direction and distance between clear-cut route segments, for instance, one local vector between nest and a large rock, and a second between the large rock and food. Local vectors are particularly useful when there is a sharp bend in the ant's path and home vectors are less helpful for guidance. It is uncertain how long memories of local vectors last, but experiments in walking bumblebees have revealed nest-ward pointing vectors, stored in parallel with path-integration-based home vectors, that have a lifetime of at least 24 hours[32].

Compared with the rich literature on form vision in bees, rather little is known about the way in which ants recognise natural scenes. Using ingenious analytical methods, Jochen Zeil[33] showed that a simple snapshot of a scene, relying only on pixel values with no feature detection, gives an excellent reference view for defining a location. This works because images change smoothly as one translates or rotates away from where a reference view was stored. Ants therefore can use vision for navigation without having to identify and label specific landmarks within a scene[34,35].

Nonetheless, *Cataglyphis bicolor* ants do recognise the shapes of artificial landmarks placed within desert surroundings[36] and laboratory studies on wood ants have revealed a complex means of encoding visual scenes. Natural shapes viewed out of doors are usually seen against the sky as shown, dramatically, in *Melophorus bagoti* ants. Ants of this species that had been trained on a foraging route were caught on their return to the nest. They were then placed in the centre of a 1 m diameter cylinder with its wall roughly sculpted to simulate the skyline as seen from the feeding site (Figure 1E). The ants moved in the homeward direction as indicated by the artificial skyline, ignoring compass cues that signalled the real direction of the nest[37]. The sensitivity of insect eyes to UV light makes the skyline particularly prominent because of the contrast between the relatively UV-rich component of sky light compared with UV-poor reflections from the ground and terrestrial objects[38,39].

Laboratory studies in wood ants have uncovered some of the visual details of a scene that ants store in their brains. They can detect and remember the orientation of an edge[40] and compute the centre of mass of a two-dimensional shape[41]. Their vision is tuned towards making navigation efficient. Thus, ants segment scenes into regions and pay most attention to the region that lies along their visually guided path: if a scene is composed of two adjacent triangles, ants focus on the triangle that they face while following their route and neglect the other triangle. When a route is directed to some point lying within a large shape, like a triangle or a rectangle, ants store the visually defined route direction as the proportion of the two-dimensional shape that lies to the left and to the right of their approach path. This somewhat abstract 'fractional position of mass' enables the ants to economise on what needs to be remembered when following a route. The proportions to the left and right of the ant's path will remain constant over a useful segment of the ant's approach[40].

Wind, odours and pheromones in navigation

Although *Cataglyphis fortis* is a highly visual species and does not make or use pheromone trails, these ants complement other navigational strategies with innate responses to specific odours, like food odours or CO_2 from their nest. Their use of odours is facilitated by a sophisticated strategy of responding to the direction of the wind. A desert ant exploring its surroundings for food (Figure 2A) moves crosswind to detect an odour that is blown across its path and, should an odour be detected, moves upwind to locate the odour's source[42]. Furthermore, if desert ants have found a permanent food site, they adjust the direction of their path so that they can approach the feeding site from a position that is downwind of the site. This behaviour was nicely demonstrated in a location where the direction of the prevailing wind changed dramatically over the course of a day[43].

Cataglyphis fortis also rely on odours — CO_2 and pheromones — when returning to their nest. They only respond to such odours when they think they are close to home because their path integration home vector is short. This precaution helps them avoid the unwelcome greeting that would follow an inadvertent entrance to a foreign nest[44]. Ants will also learn that their nest site can be labelled by artificially applied odours. Their use of foreign odours was demonstrated by training ants in a channel that gave direct access to their nest, with an odour placed at the entrance from the tunnel to their nest. After training, the ants were run in a test channel with the odour placed at one position on the floor of the channel. The ants tended to stop and search around the location of the odour with which they had become familiar during training[45].

A similar test has revealed a close interaction between olfaction and vision. Learning the nest position in the training channel is slow if ants must rely on a single visual or olfactory cue. Given the two cues together, learning is fast and precise. After a single training trial, ants trained with both cues at the nest entrance search as precisely with one cue as with two, whether the single cue is visual or olfactory. After 15 training trials, the ant searches precisely given both cues, but it is inaccurate should only one cue be available. Thus, over time the two cues become more strongly bound[46]. It is an interesting puzzle to work out how or where in the brain this connection between olfactory and visual cues is formed.

Many ant species navigate primarily by following pheromone trails. This strategy is well understood in fire ant workers[47] whose trails dissipate rapidly and must be continually refreshed to remain effective. Ants check that a trail leads to food before adding pheromone themselves on their return to the nest: the better the food, the denser the pheromone trail. The rapid disappearance of pheromone, if the food at the end of the trail is sparse, means that the ants readily abandon an old declining food source.

Pharaoh's ants go one step further and label a fruitless trail with a 'no entry' pheromone. One group of ants was trained on a Y shaped maze with a paper floor to find food at one end of the Y and no food in the other branch. A second group was trained on a similar Y maze to find food along both branches. When the paper covering the unrewarded branch of the first maze was placed on the floor of one branch of the second maze, ants were reluctant to choose that branch[48].

Big-headed ants (*Pheidole megacephala*) have two separate pheromones. One is for exploration which ants lay when looking for food. The pheromone laid on these trails is weakly recruiting but long lasting. The trail system marked by this pheromone may provide a network of possible routes. When ants return from finding a rich source of food, they lay a short-lived pheromone that recruits strongly: it invites ants to exploit this find and then mark the trail themselves. When that supply is depleted, the pheromone on the marked trail rapidly vanishes and the ants disperse, perhaps exploring the network of marked trails for a new source of food[49].

Walking patterns of individual ants

Crucial to understanding the neural basis of the control of directed movement during ant navigation is detailed knowledge of ant walking patterns and how a walking ant extracts the olfactory and visual information available along a route. Most probably all ant species move in an oscillating path[23,50,51]. With such a path having a clear function for ants following a pheromone trail (Figure 3A), it also occurs in primarily visual species, presumably even including species like *Cataglyphis bombycina* that lives in the extreme heat of the Sahara and does not use pheromone cues or learn visually defined routes. This ant is only active for about 10 minutes a day when it leaves its nest to search for dead insects. Ants emerge from their nest in a group to exploit the few moments when it is too hot for predatory lizards but just bearable for the ants at $\sim 50^\circ C$[52].

Fire ants following pheromone trails clearly take an oscillating path, turning alternately in the direction of the antenna that detects the higher concentration. Most likely, their antennae monitor the volatile odorants that rise from the trail. Hangartner[53] found that with one antenna removed, the ant follows the edge of the trail that is detected by the remaining antenna. When he fixed the two antennae so that they were crossed, the ant became unable to follow the trail.

A recent study[54] has examined similar details of antennal movements in carpenter ants. While searching for an odour trail, carpenter ants hold their antennae wide apart and move the tips of the antennae over a small range. When following the trail, the ants keep their head and body aligned with the artificially laid path and move their antennae in an oscillating pattern (Figure 3A). The consequence of this active sensing strategy is that the ants' paths naturally oscillate about the overall direction of movement. Such an oscillation is also useful should a trail diminish or disappear because the oscillation maximises the search area for additional olfactory information.

Rules guiding the detailed walking patterns of ants

The wood ant, *Formica rufa*, like many ant species, guides its passage along familiar routes relying on olfactory and visual cues[55–57], having found effective ways of correcting errors relative to each cue. The ant's oscillating path ensures that it casts over a large range of directions to maximise the detection of odours. To avoid disrupting this pattern, visual features are only attended to at the peaks and troughs of each oscillation. If the ant's facing direction is along the familiar learned route at these moments, nothing happens. Any departure from the correct facing direction is eliminated by a rapid saccade-like turn[58]. This temporal partition allows the two sensory modalities to operate independently to keep the ant on track (Figure 3D).

The ant reduces its translational velocity just before and during a saccade-like turn. Immediately after facing the goal, the ant tends to increase its translational speed and so cover more ground while moving in its intended direction (Figure 3C). The precision of this phasing is highlighted by an experiment on ants that were trained to approach a black vertical edge generated on a screen. If the edge is made to jump sideways during an approach, the ant makes a corrective saccade-like turn that is delayed until it has reached a peak or trough in its zigzag path. This rule is still followed even if it results in a saccade-like turn delayed by a second or more (Figure 3D).

Recent technology allows ingenious experiments in natural environments where ants are fixed on a trackball, such that they can rotate the trackball with their legs but are unable to change their facing direction (Figure 3E). With this device, it is possible to analyse an ant's turning response evoked by specific static views. If a *Cataglyphis velox* forager is positioned on a familiar outdoor route so that it faces 90° to the right or left of this route, it attempts to face along the route by turning to the left or right, respectively. The ants can thus recognise a familiar scene even when they do not face along the route and respond by trying to align themselves with the route[59]. This behaviour is reminiscent of heading errors that evoke the saccade-like turns of wood ants[58], suggesting a commonality between the behaviour of the two species.

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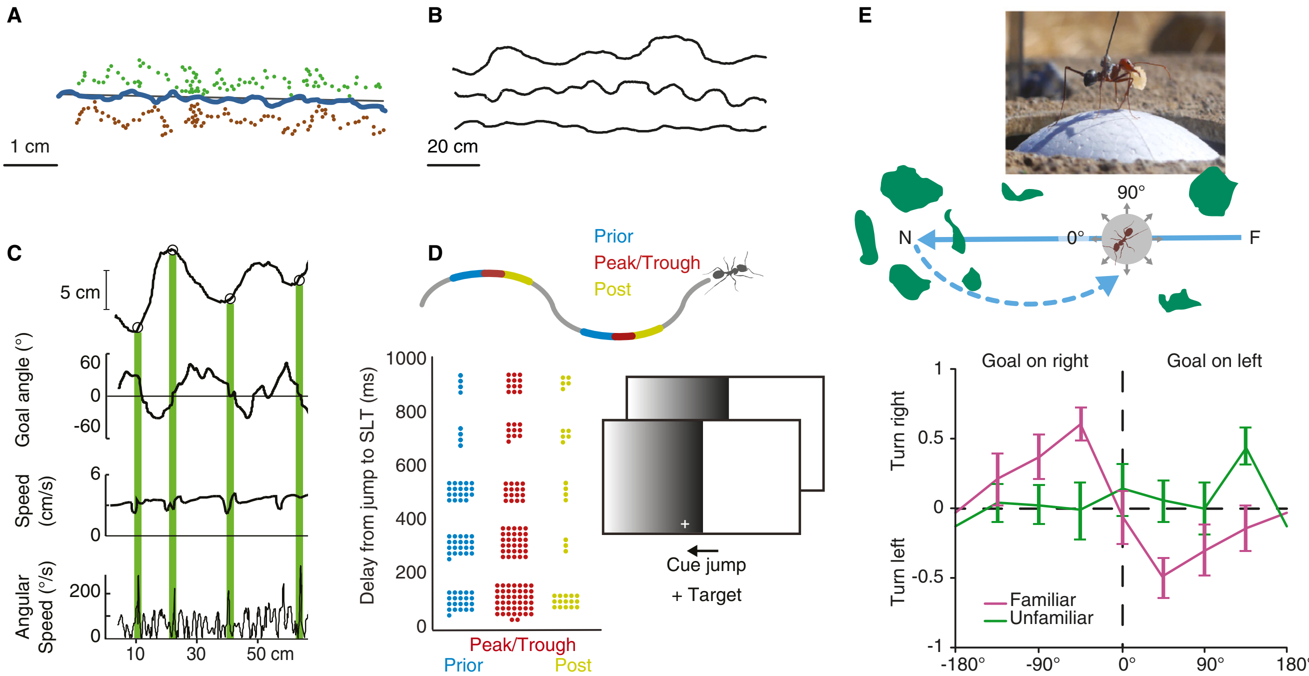

Figure 3. Path oscillations and visual route control.
(A) Trail following by carpenter ants producing a sinuous path along a straight pheromone trail. Grey line: artificial odour trail. Thick blue line: path of ant head. Dots: positions of antennae. Adapted from[54] with permission from the *Journal of Experimental Biology*. (B) Different zigzag walks of wood ants guided by a visual cue (from[58]). (C) Top: segment of path along a route. Vertical scale of the path is expanded by a factor of 3 relative to its major direction. Bottom: Traces show: angle between the ant's longitudinal body axis and the goal (goal angle); translational speed; angular velocity. Solid vertical lines indicate the occurrence of saccade-like turns. Note that translational speed is low and angular velocity is high during peaks and troughs of the zigzag. The duration of this path is about 40 sec. Adapted from[145]. (D) The zigzag path of an ant trained to face a black-white edge. The ant makes a rapid turn (saccade-like turn) to fixate the edge when the edge is made to jump (bottom right). Top: the phase of the path is colour coded. The turns (saccade-like turns) only occur at the peaks of the ant's path towards a feeder (+). Each saccade-like turn is shown as a dot with its proximity to a peak colour coded (bottom left). Even when delayed by several cycles, saccade-like turns still occur close to the peaks (adapted from[58]). (E) Top: photo of ant fixed on trackball and schematic of open-loop test conditions with zero vector ants held at fixed orientations relative to a familiar route. Bottom: turn direction when ant is held at different orientations relative to familiar route or at an unfamiliar location. Adapted from[59] and ant image used with permission from Antoine Wystrach.

We have so far summarised how ants use a wide range of sensory inputs to make navigational decisions that, at each moment, determine whether the ant turns to the left or to the right. These elementary navigational decisions are then chained together in different ways to produce the robust efficient navigation behaviour. How does the ant's brain with only ~250,000 neurons implement such complex behaviour?

Brain regions involved in navigation

The navigational abilities of insects have been studied for many decades in a variety of species. Three major regions of the brain have emerged as housing the core neural circuits responsible for navigational behaviour (Figure 4), which will be described in the next sections.

Central complex

The central complex (CX), the 'brain within the brain'[60] is a set of interconnected neuropils that control an insect's directed movement within its multi-modal sensory environment. The basic layout of the CX is similar across all insects and crustacea, with a core of similar neurons and neuronal arrays[61,62]. In pterygote insects, including ants, there are four major areas: the ellipsoid body (EB), the protocerebral bridge (PB), the fan-shaped body (FB) and the paired noduli (Figure 4B). One striking characteristic is the presence of repeating functional units (columns), which are interconnected with one another via intricate, but highly regular, connections[63–65]. These columnar projection patterns orchestrate the information flow between the four CX neuropils, providing the foundation for spatial processing in the CX (Figure 4B).

Although many functional studies have been carried out with a range of insect species, most of what is known about circuit level functions of the CX comes from recent research on *Drosophila*. Whereas these small flies are not as sophisticated in their navigational abilities as hymenopteran insects, their brains generate at least the rudiments of most navigational tasks observed in ants. Exceptions appear to be the lack of a time-compensated compass in flies[66], no evidence for complex vector navigation, as well as no clear evidence that flies can use magnetic fields for orientation purposes[67,68]. For all other navigational abilities, the fly brain very likely provides a valid starting point for understanding the more complex navigational repertoire generated by the hymenopteran brain. Advances in brain imaging techniques in *Drosophila* have made it possible to visualise neural activity across entire populations of defined neuron types while tethered flies performed naturalistic, visually guided behaviour[69–71]. This methodology has revealed that the columnar structure of the EB, PB and FB subserves a

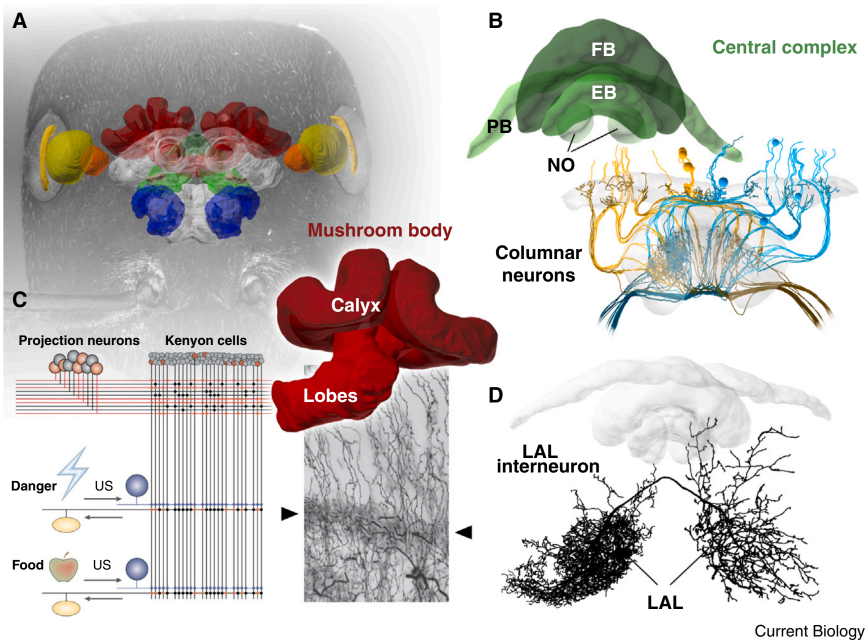

Figure 4. The navigational centres of the insect brain.
(A) The brain of a desert ant (*Cataglyphis nodus*), superimposed on the ant's head. Key brain regions are highlighted in colour: yellow/orange, optic lobes; red, mushroom body; blue, antennal lobes; green, central and lateral complex. Adapted from[54] with permission from the *Journal of Experimental Biology*. (B) Top: the central complex of *C. nodus* with its compartments. FB, fan-shaped body; EB, ellipsoid body; PB, protocerebral bridge; NO, noduli. Bottom: three-dimensional tracings of a population of columnar neurons in the brain of an army ant (*Eciton hamatum*), based on volume electron microscopy (S.H., unpublished data). These cells are suited to encode the ant's heading as the peak of a bump of activity across the width of the CX. (C) Left: schematic of how sensory projection neurons contact the mushroom body calyx. The processes of mushroom body output neurons (MBON) and dopaminergic neurons (DAN) extend across the array of Kenyon cell axons in the mushroom body lobes (details in text) to enable associative learning. Filled circles show synapses. Right: the ant's mushroom body, detailing the arrangement of calyx and lobes (three-dimensional reconstruction in red) and its internal architecture composed of parallel Kenyon cell axons that are orthogonally intersected by output neurons (arrowheads; Golgi staining from[146]). Left diagram adapted from[147] with permission from SNCSC. Right image reused from[146] with permission. (D) Lateral accessory lobes (LAL), visualised via the projections of a single interneuron interconnecting the two LALs in each hemisphere. Data from the tropical sweat bee *Megalopta genalis* (S.H., unpublished data). Ant photograph by April Nobile, AntWeb.org (CC-BY 4.0); desert ant neuroanatomical images generated with the Insect Brain Database (CC BY 4.0)[148], based on data from[103].

topologically organised coding scheme, in which 360° of azimuthal-space is mapped onto eight 45° segments. The EB in conjunction with the PB encodes head direction[70,72–75]; the FB contains circuitry that encodes the direction of movement independently of body orientation[69–76], and also neurons that can signal goal directions[77,78].

Sensory signals reach the CX through tangential input neurons that connect to the entire array of columns[63,79–81]. The three CX neuropils receive different inputs. First, a large set of visual input (ER) neurons transmit signals from the visual system and wind detectors to the EB to aid the computation of head direction[82–84]. Second, tangential neurons of the noduli carry self-motion signals — optic flow and wind based — to the noduli for estimating the insect's angular and forward velocity[69,76,85,86]. Third, a diverse group of tangential neurons of the FB links this region to a variety of neuropils located largely in *terra incognita* — poorly understood regions of the unstructured protocerebrum[63,87]. These cells probably relay contextual cues, like internal states or the valence, positive or negative, of sensory inputs, which can modulate information processing in core CX circuits[88,89]. The main output cells of the CX, linking the **P**B and the **F**B to the lateral accessory lobes (**L**AL) (PFL neurons), monitor the activity of head direction cells in the PB and goal neurons in the FB to generate corrective steering commands[78,90,91]. These commands are then sent to premotor centres. Overall, evidence from many species suggests that the CX contains conserved circuits underlying head direction coding, goal encoding, as well as the generation of steering commands that are required when heading and goal directions are not aligned[92].

Navigational computations within the fan-shaped body of the CX are implemented as vector operations. The direction of a vector is given by which columns are active and the amplitude of the vector by some measure of the excitation level within the columns. A remarkable feature of CX circuitry is that the distribution of activity across the columns is shaped into a sine wave[63,78,86]. This organisation of activity, perfect for vector computations, is accomplished by the sinusoidal distribution of the input synapses of intrinsic neurons in the PB (Δ7 cells)[63].

These details established in *Drosophila* reinforce the accuracy of an anatomically constrained computational model of path integration in the CX of the bee[86,93] and indicate that the CX must be heavily involved in the control of ant navigation.

Mushroom bodies

The mushroom bodies (MBs), so called because of their fungoid shape, evolved as a centre for olfactory learning and memory[60], but have subsequently increased in size and complexity in a variety of insect families, including trap-lining heliconid butterflies, cockroaches, and ants, bees and wasps. All are insects which learn about their visual surroundings[60,94–96].

Anatomically, the MBs form a large association matrix, in which visual and olfactory sensory cells provide input to MB intrinsic neurons known as Kenyon cells (KCs). In *Drosophila*, each KC receives input from a random selection of approximately six olfactory or visual projection neurons, of which most must be active to make a particular KC fire. The long processes of groups of KCs form giant parallel tracts known as lobes, which are orthogonally intersected by MB output neurons (MBONs) and dopaminergic reward neurons (DANs) (Figure 4C). The strength of the connections between the KCs and output neurons is modulated by the reward neurons in response to the positive or negative reinforcement of the insect's sensory experience[97]. Thus, patterns of KC firing that are linked to good or harmful behavioural consequences can be memorised so that the insect moves to approach or avoid that sensory pattern in future.

Behavioural experiments going back to the last century indicate the involvement of the MBs in the learning of odours and visual cues, most notably in the context of navigation. Early evidence was that lesions in the MBs of wood ants disrupted their memories of visual mazes[98]. Some thirty years later, cockroaches were trained to find a visually marked cool refuge on an otherwise uncomfortably warm surface: cockroaches trained to find the cool spot took longer to do so after MB lesions[99]. More recent studies on ants[100,101] have found that visual route learning is disrupted after inactivation of the MB. For instance, anaesthetising the MBs of *Myrmecia midas* foragers with procaine, thus eliminating electrical activity close to the injection site, resulted in ants' paths in familiar surroundings becoming tortuous with ants failing to reach their nest[101]. Such findings emphasise that the MBs play an essential role in mediating the memories needed for visual navigation.

The link between memories stored in the MB and navigation behaviour presumably occurs via the MB output neurons. These MBONs tell other brain areas, including the central complex (CX), whether the current pattern of sensory information is attractive or aversive[97]. The most prominent targets of MBONs in the CX are the dendrites of cells in layers 4 and 5 of the FB[63,97,102], and so can contribute to the generation of steering commands[69,76].

The organisation of the MB in *Drosophila* and ants is very similar[103,104] so we can expect that the functional details found in *Drosophila* also apply to ants. The most notable difference between flies and ants is that there are about 25–70 times more KCs in hymenopteran insects than in *Drosophila*[105]. This enhanced memory capacity is needed by ants, bees and wasps learning visually guided routes through complex surroundings[106,107].

Lateral accessory lobes

The third brain region critical for navigation consists of the lateral accessory lobes (LALs) (Figure 4D). These are large, irregularly shaped regions located on both sides of the CX, where they receive and transmit signals to and from the CX[63,108]. The function of the LALs has become clear through research on the silkworm moth (*Bombyx mori*), which zigzags as it tracks odour plumes. The moth's alternating left–right turns are driven by corresponding oscillations in the left and right LALs, generated by 'flip–flop' neurons[109–112]. The flip–flop neurons also have inputs from visual signals and are thus widely engaged in sensory-driven steering behaviour[112].

In all the species that have been examined, the LALs are the site of convergence of the major class of CX output neurons, the PFL cells, often referred to as steering neurons[63,79,80,113–115]. These cells form an interwoven mesh of axonal branches with LAL neurons. They include descending neurons, which send steering signals to the thoracic motor centres, and inter-LAL neurons that probably coordinate the activity between the LALs of the two hemispheres[108,110]. Additionally, numerous FB tangential neurons receive input from the LALs, providing a potential pathway for signals that inform the CX about the motor state of the animal.

Data from other insects corroborate these findings, including studies in *Drosophila*[116], cockroaches[117] and locusts[118]. From these findings together with immunohistochemical data on a variety of neurotransmitters[119–121], the LAL emerges as a highly conserved pre-motor control hub of the insect brain. It is located both upstream and downstream of the CX and is connected directly to the visual system, to the mushroom body and to a range of other regions in the unstructured protocerebrum. Together, the CX, the MB, and the LAL orchestrate insect locomotor patterns.

Neural basis of navigation strategies

How do the neural circuits of the CX, MB and LAL generate the complex navigational strategies of ants? While the answer to this question is not known, recent data from fruit flies suggest some of the key principles involved in generating vector-based navigation, route guidance, and orientation towards innate and learned goals. In each of the following sections we deal with different forms of navigation, reviewing the relevant circuits and suggesting how they might apply to ants, relying as we must on insights gained from *Drosophila*.

Plume following

One of the simplest navigational tasks is the tracking of an odour plume. An insect encountering an attractive odour turns upwind and flies or walks in an oscillatory pattern to stay centred on the plume. Each time the plume is crossed, a turn should be initiated, leading to another plume crossing.

The key circuit that mediates this oscillatory behaviour is located in the LALs. As described above, it consists of neurons that switch their activity between tonic high and low states, called flip-flip neurons[110,112]. The switching between the states is triggered by encountering a pheromone pulse. Reciprocal inhibition between neurons that interconnect the LALs in both brain hemispheres ensures that activity alternates between the left and right hemispheres. Neurons with dendrites in the LAL send their axons to the motor system driving the neck muscles[111] and initiating the head turns that precede steering movements of the whole body. While the real neural circuitry is more complex, a functioning steering circuit can be simulated with only a basic set of four flip–flop neurons[122,123]. Such a model circuit can be activated by simulated odour plumes, but also by output from CX navigation circuits. The LAL is thus thought to be the site of convergence for neural signals influencing turning decisions for many behaviours, from simple, innate cue tracking to complex navigation using learnt cues. As the ground pattern of this circuit appears to be conserved across insects, it is likely that the circuit acts similarly in navigating ants.

The LAL flip–flop circuit can be viewed as an oscillator that generates alternating turning movements. In line with recent behavioural data in ants and maggots, as well as computational models, modulation of the amplitude and frequency of such oscillations can lead to adaptive behavioural responses[51,124]. Input of pheromone signals as well as optic flow signals from the lobula to the flip-flop circuit have been reported in silkworm moths and flies[123], allowing direct triggering of oscillatory steering movements.

When following an odour plume, these inputs must be combined with knowledge of wind direction to resolve the direction of the plume. Aversive odours should trigger downwind orientation, while attractive odours should trigger upwind orientation. Similarly, along a pheromone trail, ants must decide whether to move food-wards or nest-wards when encountering the trail (Figure 2D). How are such additional cues integrated with the oscillatory LAL circuit?

Orientation towards a goal

A stable wind direction is an example of a sensory cue that provides a simple option of two goal directions. Either the insect flies upwind (exploitation of the source) or downwind (dispersal), depending on the context provided by the olfactory environment. The neural circuit underlying this context-dependent switch has been described in the fruit fly[89]. Directional wind signals reach the CX via a dedicated sensory channel that ends in the noduli and targets a specific population of columnar neurons[63,89,125]. These connect to PFL output neurons either directly or indirectly via a population of FB intrinsic neurons. These intrinsic neurons have a morphology that enables them to invert an activity bump in the FB, so shifting the phase of the directional signal by 180 degrees. The direct pathway causes the fly to turn downwind: to disperse. In contrast, in the presence of an attractive odour, the odour input is relayed to the FB via tangential neurons that receive input from regions encoding the valence of innately relevant or learnt odours[89]. This activity is thought to increase the strength of the synapse between the intrinsic neurons and PFL output neurons, thereby strengthening the weight of the indirect pathway. This indirect pathway contains circuitry implementing a 180 degree phase shift, thereby driving upwind orientation[63,89]. Therefore, the presence of an attractive odour leads to the opposite behavioural response to the same directional wind input by exploiting the unique neuroarchitecture of the CX.

Anatomically, many such pathways can be extracted from the FB connectome of the fly, all terminating on the dendrites of the PFL neurons[63]. A tempting hypothesis is that many goal directions are encoded in various populations of columnar and intrinsic cells of the FB[92]. The contextual inputs from tangential cells could adjust the weight of those connections, allowing the PFL neurons to integrate many goal signals. How this circuit selects between competing goals remains an exciting area of research and the recent discovery of a visual goal signal in the population of columnar neurons[78] might provide a tangible model to study the interaction between upwind odour tracking and visual goal seeking.

Ultimately, the output of the CX has to provide a direct, corrective steering instruction to the LAL, where it presumably overrides any ongoing oscillations and alters the course of the insect[123]. All the anatomical evidence suggests that the involved circuits discovered in flies also exist in other insects, such as ants. However, the details of which goals are encoded, how goals are weighted and how mismatches between heading and goal angles affect steering are likely to differ between species.

Path integration

Path integration gives ants a positional estimate of where they are with respect to a point of origin as a vector holding their current distance and direction. By exploiting the general CX connectivity matrix for encoding directional vectors, a home vector can be encoded as a distributed population code in which direction is given by the phase of a sine wave of neural activity and distance by its amplitude[86].

The sensory signals required to build up such a representation have been investigated in flies and bees during flight, when distance is estimated through optic flow[126,127]. As a path integrating bee follows a meandering flight path, the rotation and translation experienced by its visual system are transmitted from the lobula complex to the noduli of the CX (Figure 4B) and then to the EB and FB[73,75,78]. Rotational self-motion cues contribute to the coding of head direction in the EB. Translational self-motion cues derived from optic flow are integrated with the head direction signal in the FB to encode the insect's allocentric movement direction — the movement of the animal relative to its surroundings, irrespective of its own body orientation[69,76]. These continuously changing allocentric vectors are the basis of path integration. The distances moved in the different allocentric directions are continuously added to the appropriate 45° columns. The summation of these signals, constructed from the intersection of direction and speed inputs, is thought to result in a stored home vector distributed across the eight columns of the FB[86,128]. Such a memory in the FB differs from long-term memories in the MB in that it is acquired by accumulating inputs rather than by associating an input with a reward. It is also more labile, being overwritten as new information is accumulated: even when undisturbed, it degrades in a couple of days[11].

A path integration vector stored in the CX in the proposed format can be directly compared to the current heading, probably by means of the PFL output neurons[63,86]. If so, the PFL dendrites in the FB would be the site of convergence of path integration-based goal vectors and other directional goals. This would allow contextual inputs to adjust the relative weights of these different goals. For example, this model could explain the switch in desert ants from ignoring to responding to nest odours once their home vector signals that they are close to their nest[129] (Figure 2B). As the distance to the nest is encoded in the sinewave amplitude of the population code, one can assume that the weak signal close to the nest can be easily overruled by olfactory signals.

Route following

When navigating using view memories, an ant needs to compare its current view with memorised views, leading to an estimate of the familiarity of the current view. The MB is the most likely site for long-term storage of these view memories, given its established role as an associative learning centre of the insect brain[97]. It is relatively straightforward to hypothesise how extensive view-based information is stored in the brain and computational models have demonstrated that the MB is capable of achieving this task[106].

How the output signals of the MB, coding familiarity of a visual scene, are integrated with the navigation network in the CX and LAL is currently not known. As outlined above, many MB output neurons target the FB, so it is tempting to assume that the mechanisms mediating olfactory-guided wind orientation[89] are also involved in view-based navigation. This idea has been proposed earlier[130] and has been shown to guide route following in computational models[131]. The key point is that if the valence signal resulting from encountering a familiar view is used as contextual input to set the current view as the goal direction, then the direction of this view-based goal signal could be encoded as an activity bump across a population of FB columnar cells. These cells would target the PFL neuron dendrites and compete with other goal-direction signals for impact on the steering signal. This way, all navigational goals, including path integration vectors, familiar views, innate visual goals, and odour plumes, would be

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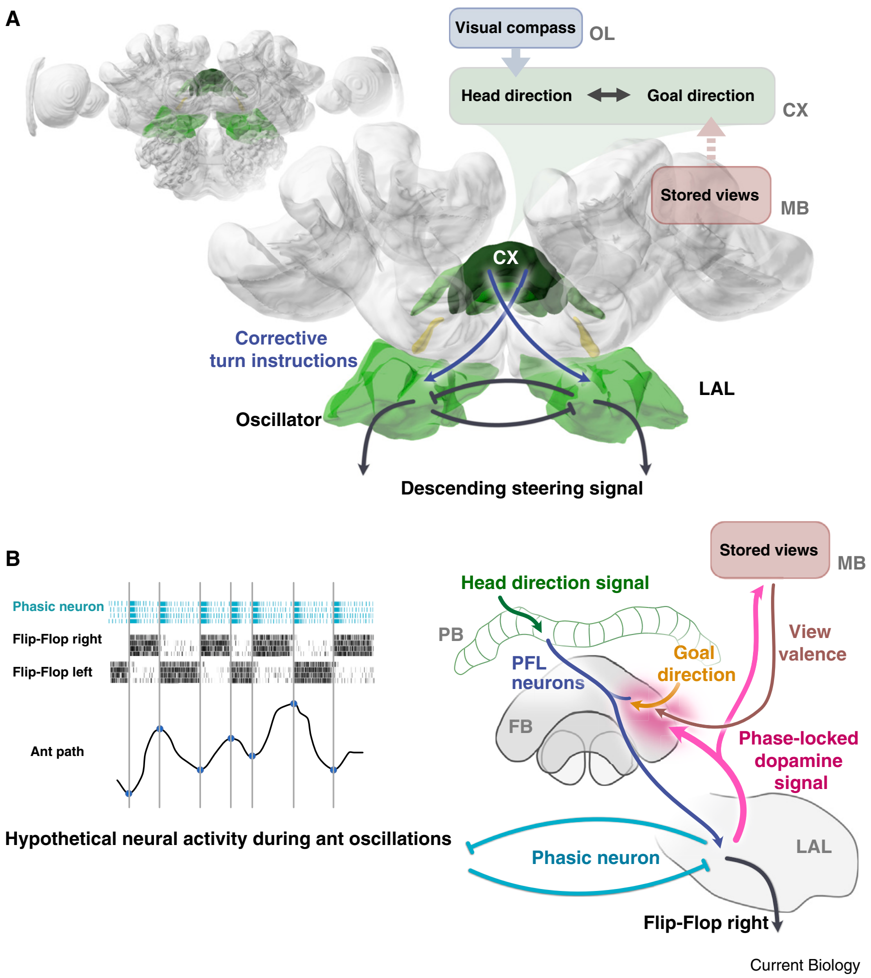

Figure 5. The central control circuits for steering.
(A) The ant central complex (CX) and lateral complex (highlighted in colour) are embedded in the centre of the ant brain (top left) and located in close proximity to the mushroom bodies (MBs). Data from flies and moths, as well as other insects, have crystallised the role of the CX as an integrative centre to compare the head direction and goal direction of the insect and to instruct the motor system to make corrective turns. The head direction representation is based predominantly on visual information from the optic lobes (OL). The lateral accessory lobes (LALs) are known as premotor control centres that receive CX output and contain reciprocally connected neurons that, at least in moths[110], drive oscillatory steering behaviour. The mushroom bodies (MB) are the likely location for storing view memories that contribute to defining the momentary goal of the insect. Images from the Insect Brain Database[148], data from[103]. (B) Conceptual model of how view learning and corrective steering could be phase locked to zigzagging behaviour[110]. Left: hypothetical neural activity of lateral accessory lobe (LAL) neurons during ant zigzagging behaviour. Activity patterns are inspired by data from silkworm (*Bombyx mori*) neurons that control the tracking of pheromone plumes via zigzagging behaviour[114]. In addition to neurons regularly alternating between up and down states (indicating right/left), other cells show phasic excitation when the states switch (blue). Such neurons in an ant would be highly suited to drive the phase locking of corrective turns. Right: suggested role of dopaminergic feedback from the LAL to the fan-shaped body (FB) and MB to phase lock the occurrence of saccade-like turns and view learning to the turning points of behavioural oscillations, as signalled by hypothetical phasic LAL neurons. Neuroanatomical images © Insect Brain Database (CC BY 4.0).

integrated in one spot within the FB neural network and provide a single steering instruction to the turn generator located in the LAL (Figure 5A).

Sensory motor coordination

Possible dynamic control of steering signals during behavioural oscillations

As outlined in the behavioural section of this review, ants perform their characteristic corrective (saccade-like) turns only during specific phases of their oscillatory paths. This timing means that the output of the CX should only impact the LAL steering network at the peaks and troughs of the ant's oscillations. The state of the LAL steering network must thus be coupled to the steering instructions provided by the CX. Interestingly, in the described flip–flop circuit of the silkworm moth, there are neurons that fire very briefly, exactly when there is a switch between the activity of the left and right LALs[110], thus providing a precise signal that encodes the phase of the ongoing oscillation. If such cells occur in ants, they could provide the phasic information that is key to explaining the tight linkage of corrective (saccade-like) turns to the phase of the ant's oscillatory movements.

We outline a theoretical scheme based on this assumption in which feedback from the steering network of the LAL signals when an ant is at the peak or trough of its sinuous path (Figure 5B). By targeting the dendrites of PFL neurons in the FB, these signals could coordinate the corrective turns initiated by these cells and tie them to the appropriate phase of the ant's path. The CX would thus restrict steering commands to the peaks and troughs of the ant's oscillations.

There is a parallel in *Drosophila*, where phasic information originating in the LAL is known to trigger effects in the CX, where rapid learning in the EB is enabled by input from the LAL[132]. This process results in consolidating the current visual scene into a head direction signal by linking weight changes at specific synapses to episodes of high rotational velocity. The dopaminergic inputs that drive this learning are activated by rotational velocity inputs originating in the LAL. That means updates of the scene memory happen briefly and only when there is new visual input, as occurs when a fly changes direction or encounters a new scene[132,133].

Although physiological evidence for equivalent roles of LAL information triggering processes in the FB is missing, there is a possible anatomical substrate. Some of the many tangential neurons of the FB that receive input in the LAL are dopaminergic cells that exist largely unchanged across a wide range of insect species, including the ancient, apterygote zygentoma[121]. These highly conserved FB tangential cells are well-placed to use phasic information from the flip-flop network in the LAL to gate steering output from the FB, a process likely to be of key importance for any walking insect.

Additional evidence of the role of precisely timed motor signals from the LAL is their influence on the responses of wide-field motion detectors in the lobula plate of *Drosophila*. The fly's tripod gait means that the fly rapidly changes between turning left and turning right. Signals routed from the LAL facilitate the activity of motion detectors in the direction of the turn[134]. Conversely, when a fly makes an intended turn, it generates image motion in the opposite direction. The activity of wide-field motion detectors activated by this intended turn is suppressed so that the image motion does not interfere with the turn[135]. The LAL thus seems to have a widespread role in providing timing signals that tie different neural processes to the locomotor state of the animal. Behavioural evidence suggests that similar efference copy signals also occur in ants[136].

Possible dynamic control of view learning during behavioural oscillations

When wood ants navigate along a route, they only correct visual errors in their path at the peaks or troughs of their zigzags (Figure 3D). This indicates that it is only at the peaks and troughs that ants acquire visual information while learning a route. If so, the reward signal triggering learning in the MB must also be limited to that phase, perhaps mediated by dopaminergic output neurons from the LAL, as proposed for locking saccade-like turns to the peaks and troughs (Figure 5B). This suggestion is supported by numerous LAL neurons interacting with neurons in the MB[63] and by the finding that the activity of some DANs correlates tightly with movements in flies[137]. Indeed, the idea of a reward signal from the LAL to the MB coordinating the learning of views in ants through precise timing has been successfully modelled computationally[131].

Another possibility is that view memories are stored in the FB as well as the MB, using a similar mechanism as in the EB. There, at the synapse between visual-input cells (ER neurons) and head-direction cells (EPG neurons), plasticity modifies the connection strength when both pre- and postsynaptic neurons are active at the same time, so that prominent visual features become associated with particular body orientations[133,138].

As in the EB, numerous tangential neurons innervate the FB with densely overlapping branches[63,87]. While less is known about these neurons compared with the tangential ER neurons in the EB, it could be that they have a similar connectivity pattern to provide the same synaptic plasticity that allows visual scene learning in the EB. But rather than serving as input to the head-direction signal, the view information could be preserved in the FB and be explicitly used for steering based on visual scene memory. Besides anatomical evidence, including the presence of conserved dopaminergic input into the FB[121], data from *Drosophila* suggest that elements of visual scenes are indeed stored in tangential neurons of the FB[139]. As the relevant dopaminergic neurons originate in the LAL, learning of visual scenes in the FB might be coupled to the locomotor state in the same way as proposed for the corrective steering signals. The capacity of such a FB-based memory would depend on the number of tangential neurons forming its neural substrate, which varies between species. Interestingly, our own preliminary observations show that, based on volume EM data from bees and ants, hymenopteran insects possess many more FB tangential cells than the fly.

In summary, it appears likely that the CX uses panoramic scene information to set an orientation and may also store features of a visual scene[139], much as happens via the MB. It is not yet clear how this system might interact with the visual learning that occurs in the MB. One possibility is a partition of roles. Insects often learn and maintain several visually guided routes. The MB has the capacity to remember many routes[106,140,141] for a long time. The CX's storage capacity is probably smaller, so visual memories may need to decay faster than those of the MB. The MB may thus be the library that is consulted daily and the CX a newspaper that is in tatters by evening.

Conclusion

After a long review, a reader deserves a short conclusion. Throughout the review it has become clear that ant navigation is well understood at the level of behaviour, but that the investigation of the neural basis of the ants' abilities lags behind. Furthermore, interpretation of ant behaviour relies on neural circuit information from other species, in particular, the fruit fly. Hence, we are left with the question: What is to be done next? Further successful probing of the mechanisms of navigation at the behavioural level is likely to come from new techniques and their descendants, for instance, insects navigating on track balls in virtual reality, or high-resolution recordings of insect paths as they travel over various natural terrains. However, the main task ahead will be to apply at least some of the methods available in *Drosophila* to hymenopteran brains.

While it is difficult to catch up with decades of groundbreaking research in flies, there is now significant progress in applying methods pioneered in *Drosophila* to hymenopteran brains. New methods of creating transgenic animals using the CRISPR method have generated transgenic hymenopterans, using clonal raider ants to express calcium sensors in brain neurons[142]. Thus, for the first time it is possible to perform functional brain imaging in an ant. Developing a whole connectome in the minute fairy wasp is also underway[143], complementing the ability to image patterns of brain activity with synaptic-level connectivity maps in hymenopteran insects. Research on the connectome of larger hymenopterans is so far limited to the CX[64], but it is only a question of time until whole brain connectomes will become available for many species, including the expert navigators described in this review. Real progress in understanding ant brains is perhaps not far away.

All data associated with this work are fully referenced within the article.

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The authors declare no competing interests.

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