Spatial Memory in Insect Navigation   Review

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A wide variety of insects use spatial memories in behaviours like holding a position in air or flowing water, in returning to a place of safety, and in foraging. The Hymenoptera, in particular, have evolved life-histories requiring reliable spatial memories to support the task of provisioning their young. Behavioural experiments, primarily on social bees and ants, reveal the mechanisms by which these memories are employed for guidance to spatial goals and suggest how the memories, and the processing streams that use them, may be organized. We discuss three types of memory-based guidance which, together, can explain a large part of observed insect spatial behaviour. Two of these, alignment image-matching and positional image-matching, are based on an insect's remembered views of its surroundings: The first uses views to keep to a familiar heading and the second to head towards a familiar place. The third type of guidance is based on a process of path integration by which an insect monitors its distance and direction from its nest through odometric and compass information. To a large degree, these guidance mechanisms appear to involve modular computational systems. We discuss the lack of evidence for cognitive maps in insects, and in particular the evidence against a map based on path integration, in which view-based and path integration memories might be combined. We suggest instead that insects have a collective of separate guidance systems, which cooperate and train each other, and together provide reliable guidance over a range of conditions.

Introduction

The spatial abilities of insects have engaged naturalists' curiosity since at least the 19th century. It was found early on that insects could home from long distances even after displacement. Fabre, for instance, marked individuals of several species of bees and solitary wasps caught near their nests, and displaced them to locations up to several kilometres away. Many of these insects returned home and they did so when carried along extensive detours, or shaken or rotated in dark containers, or deprived of their antennae [1]. As early as 1885, Romanes argued from his own displacement experiments on honeybees that homing requires the bees to have 'special [i.e. acquired] knowledge of the district' [2]. Since then, often with the aid of increasingly sophisticated tracking technology [3,4], we have started to understand the mechanisms underlying those abilities.

A wide range of insects use memories to return to important locations. Water striders, for instance, keep station in fast flowing water where passing prey is relatively abundant, regaining their position after small displacements [5]. Whirligig beetles group in particular locations on ponds or streams [6], with males defending individual territories [7]. Male hoverflies adopt sunny hovering positions, often returning to the same spot [8] after an abortive dash after a potential mate. Cockroaches learn the locations of resting shelters [9]. Crickets [10] and fruitflies [11] can learn the location of a comfortably cool spot in an otherwise hot experimental arena.

Spatial memories are particularly critical in animals that engage in central place foraging. The subsocial stink bug *Parastrachia japonensis*, for example, digs a burrow and provisions its young with drupes collected, day and night, from under nearby trees [12]. These various locations are often inconspicuous (Figure 1A), and the insects learn them only in terms of the visual surroundings. In other cases, at nests or regular feeding sites, they may supplement the naturally occurring cues with scent marks [13,14] or even architectural constructions. The stingless bee *Partamona batesi*, for example, collects white river sand and glues it together with resin into a sculptured portico (Figure 1B) that helps guide the bees on their return [15].

The Hymenoptera (ants, bees and wasps) exhibit the most striking insect examples of spatial abilities, as can be seen in the behaviour of some parasitoid wasps. *Ammophila pubescens* (formerly *campestris*) digs nests in heathland, where dozens of burrows made by different individuals may occur within the space of a few square metres. Individuals dig multiple nests sequentially, and tend up to three at once. Each nest contains one egg or larva, which is provisioned with caterpillars over several days. The wasp remembers much more than the locations of those nests: it knows when a nest was started, whether it has laid an egg in it, when it last provisioned the nest, and whether it has completed provisioning and sealed the nest for the last time [16]. Such feats of memory are matched by the wasp *Argochrysis armilla*, which parasitises the nests of *Ammophila* [17]. Ammophila nests are easy to find while they are being dug, but at that stage are useless to the parasite. They are ripe for attack once completed, during *Ammophila*'s brief provisioning visits; but they are then quite hard to find (Figure 1A). The strategy *Argochrysis* has for coping with this problem is to watch out for digging hosts and to learn the locations of several nests that are under construction and very visible. It then patrols perhaps as many as four known nest sites and can lay its eggs, sometimes days later, if its visit to a site coincides with the host returning with prey.

In part for experimental convenience, a large proportion of behavioural studies have focused on social bees and ants. These insects rear young in communal nests from which foragers often take learnt visual routes between productive foraging areas and their nest [18–20] (Figure 1C). For bees, a single foraging trip frequently involves harvesting nectar from numerous flowers in many locations. Orchid bees [21] or bumblebees [22,23], which exploit multiple small but regularly replenishing patches of flowers distributed over a large territory can, over time, learn to link these patches into a sequence (or 'trapline') that results in an efficient route (Figure 1D).

In the following sections we consider the memories that are responsible for these navigational abilities. After

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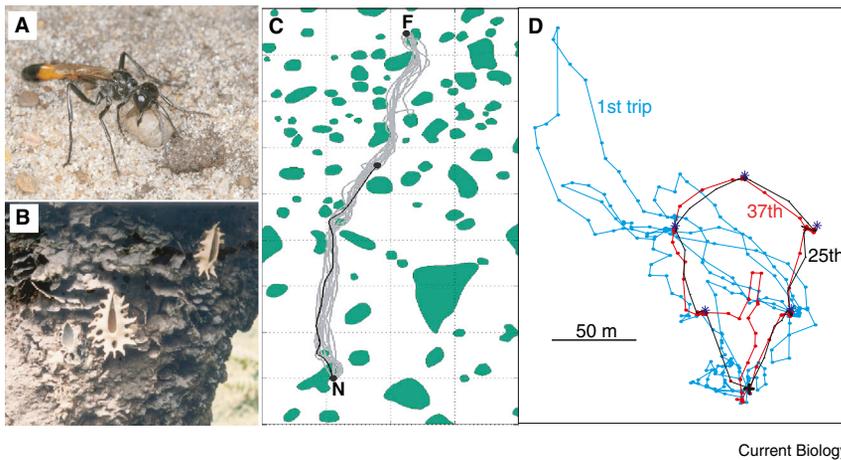
Figure 1. Navigational aids: Nest entrances and habitual routes.

(A) Cryptic nest entrance. Digger wasps of the species *Ammophila pubescens* seal their nesting burrows with pebbles and sand, to protect them from predators and parasites [16]. Locating these hidden nests among the multiple neighbouring nests built by conspecifics places considerable demands on the wasps' spatial memory. (Image by Jeremy Early, with permission.) (B) Conspicuous nest entrance. The Amazonian stingless bee, *Partamona batesi* builds nests in arboreal termite mounds (the bark-like structure seen here) [131]. Often multiple *Partamona* colonies occur close together in a single termite nest. Each colony has its own nest entrance made of white sand glued with resin, ca. 10 cm in height [15]. Carauari, Rio Juruá, Amazonas, Brazil. (Photo by Dr Silvia R.M. Pedro, University of São Paulo, with permission.) (C) Visually guided foraging routes in *Cataglyphis velox*. Individual ants typically follow their own routes between their nest and foraging site amongst dense tussocks of grass (irregular green blobs) taking different food-ward and home-ward paths. Coloured lines show 13 homeward paths of one ant. The black line depicts the same ant's path after it was allowed to home freely, was then picked up close to the nest and released at a location (upper black dot) on its normal homeward route. The ant immediately continues with its usual route with no hesitation or search showing that its path depends on its immediate visual surroundings irrespective of its current path integration state. What it did or saw just before its release does not disrupt its accurate visual guidance. F, food site; N, nest; grid lines are 1 m apart (redrawn by M. Mangan from [20], with permission). (D) The development of a trapline in bumblebees. Individual *Bombus terrestris* foragers swiftly arrive at an efficient multi-destination route between five flowers and their nest. The figure shows individual flight paths tracked with harmonic radar. A naïve forager's path (blue) is highly convoluted with multiple loops back to previously visited, and therefore empty, flowers. After about 25 bouts, foragers typically link the five locations into a consistent and efficient route, combined with occasional exploration perhaps for new flowers and a better route, as seen here in bout 37 (Adapted from [66].)

describing the main types of memory-based navigation, we discuss how these memories are acquired. In the final sections, we discuss how the memories are organized, and in particular, how different types of sensory information are brought together.

Guidance Memories and How They Are Used

Experiments in simplified environments have revealed some of the mechanisms involved in what appear to be three distinct types of memory-based guidance. Two of these are types of image-matching and employ encodings of views, sometimes called 'snapshot memories' [24], of the surrounding panorama. These encodings probably extract elementary features (such as oriented edges) from the retinal image and preserve their spatial relationships. The third mechanism, path integration, uses cues derived from an insect's own movement. In each case, an insect compares its current sensory input with a memory of the desired sensory input to produce a difference signal. This difference signal is then transformed to generate a desired heading direction (an 'output vector' [25–27]) that encodes the direction to the goal. Together, these guidance mechanisms allow insects such as ants and bees to forage far from their nests, and with experience to learn complicated visually-guided routes.

Alignment Image-matching

One of the simplest ways that insects use visual memories can be described as alignment image-matching. This type of guidance [28–30] appears to be used by visually-guided ants when traveling along a habitual route [31]. An ant can orient along its route by aligning itself so that the retinal image of its current panoramic view best matches a previously experienced view stored as some form of retinotopic memory. As long as the appropriate memory is used and the ant is in the appropriate place, then this mechanism will

ensure that familiar features are placed in their familiar places on the retina and thus that the ant will travel in its habitual direction. For wood ants, *Formica rufa*, in the lab, the process of comparison underlying alignment image-matching occurs about every three seconds [32]. After gradually veering away from the specified direction by up to 70°, an ant produces a rapid and accurate saccade-like turn to regain the heading. The size of a turn is governed by the angular difference between the experienced and the desired positions of visual features on the retina [32,33]. Alignment image-matching allows an individual to recapitulate a path that it has previously taken.

Positional Image-matching

A second, and perhaps more general, way of using visual memories can be described as positional image-matching. Computer models (reviewed in [34]) show that, by comparing a snapshot memory acquired at the desired goal with the current visual panorama, it is often possible to compute a heading direction towards the goal. Positional, unlike alignment, image-matching can provide guidance from novel locations and in novel directions. It will be effective so long as the panoramas at the novel and goal locations share sufficient elements in common. The set of such locations is often called a snapshot's catchment area [35]. Generally, the more open the habitat, the larger the catchment area will be [36].

Positional image-matching has been observed in a far wider range of insects and contexts than route-following Hymenoptera. It can, for instance, account for station keeping in water-striders [5] or hoverflies. In the latter case, a fly can approach a favoured spot in mid-air and decelerate and stop in the correct location [8]. In social Hymenoptera, positional image-matching appears to be used to approach the nest or the food site [24,31,37–39] (Figure 2A), and to approach a route when an ant is near but not on it [31,40]

Figure 2. Examples of positional image-matching and other forms of guidance.

(A) Bulldog ants (*Myrmecia croslandi*) home successfully from unvisited release sites. Foragers were caught at the base of their favourite tree (yellow star). Individual ants were transferred in the dark and released at one of eight randomly selected release stations (circles) at 10 m distance from the nest. Individual ants were tracked from these release sites (red trajectories) until they arrived close to the nest (yellow circle), when they were captured and re-released at a release point opposite to the first one (blue trajectories). (Redrawn with permission from [132]). (B) Directional behaviour of ants (*Melophorus bagoti*) restricted to a small area close to their nest or to a narrow corridor to a food site. After two days experience of foraging either within a small circle around their nest (N) or along a route, ants were caught just before entering the nest and displaced to one of three release sites (black circles). Ants experienced with the nest headed roughly in the nest direction, those familiar with the route were biased in the route direction. Different symbols of the circular histograms show data from two nests. Open arrowhead is direction of nest, black arc shows the angle subtended by the route at each release site (redrawn by A Wystrach from [40], with permission).
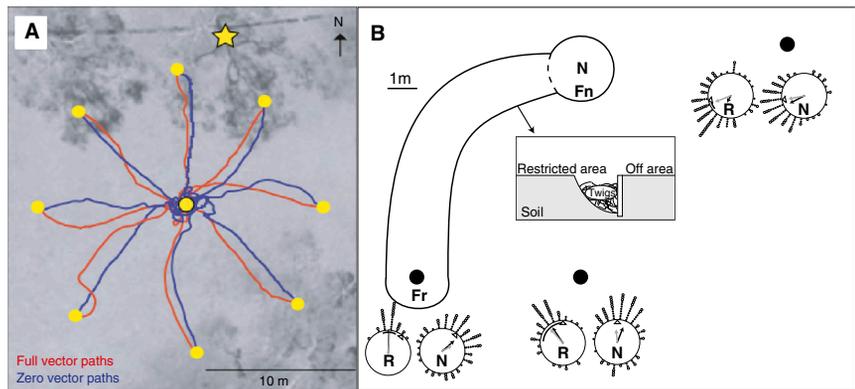
(Figure 2B). It can be shown in ants, for instance by artificially constraining new foragers to a small area around their nest. If they are then released at locations outside this area that they have never visited, they will nevertheless head towards the nest. If instead they are allowed to forage along a narrow corridor, then on release they may also head towards locations along that corridor (Figure 2B). The visual memories acquired at the nest and other locations during foraging allow ants to return to familiar locations from more distant points, even when the ants have not previously explored the intervening terrain.

Path Integration
A third type of memory-based guidance relies upon a form of dead-reckoning, often referred to as path integration (for reviews see [41–43]). When searching for food, foragers keep a running tally of the resultant distance and direction that they have travelled from the nest. They obtain directional information principally from cues deriving from the sun [44] and distance information from monitoring the optic flow [45,46] or the proprioceptive input generated by their movements [47]. When foragers find food, they can use this information to travel in a direct line back to the nest. In subsequent trips, they can also use it to return again in the opposite direction back to the food.

Path integration does not require any familiarity with the visual environment, and thus it enables animals to travel through featureless environments and to return safely after exploring novel terrain. This characteristic gives rise to one of the hallmarks of path integration. If an experimenter displaces a homebound individual to an unfamiliar area, then that individual will travel (guided by the celestial compass) in the direction and for the distance that it would have taken had it not been displaced [18]. A second property of path integration is that it allows an individual to redirect its path after an unexpected detour on its way to its nest [48] or to a familiar food site [49]. To generate a new direction, the ant compares its current path integration state with its memory of the path integration state at the feeder [49]. This comparison effectively transforms nest-based (allocentric) coordinates into a heading direction and the distance for which the heading direction should be followed.

As memories are acquired, and as an individual moves through the landscape towards its goal, the relative precision and reliability of the three guidance systems will change. Both path integration and positional image-matching can guide travel across novel terrain, and can be used the first time an insect returns to its nest or to a newly discovered food site. The relative reliability of these two systems, however, will depend on the weather, the landscape structure, and the distance to the goal. While positional image-matching is most reliable in the vicinity of the goal [24], path integration can be used over large distances, but it becomes increasingly unreliable as the goal is approached. Differences between the current path integration state and the goal memory become smaller so that the errors in either have increasingly large effects on the computed output heading [25].

Path integration requires the availability of celestial compass cues and is vulnerable to errors produced by passive displacements (whether by wind or a curious scientist), but in such cases visual guidance often provides a reliable back-up [50,51]. In contrast to the two goal-directed forms of guidance, the memories used for alignment image-matching take longer to acquire, but can provide high levels of accuracy along an entire route. Together, these three guidance mechanisms can provide insects with considerable flexibility and can account for a wide range of observed behaviours (Figure 3). The following three sections examine how individuals acquire the memories needed for these various types of navigational guidance.

Learning Goals
For most spatial tasks, the most important memories are those that encode the location of a goal, whether a temporary hovering station for a male hoverfly, a profitable food site, or most importantly a nest. These memories generally encode the sensory input or internal state that an insect experiences when it is at, or near, what will be its future goal. For learning a path integration memory of a food site, an ant or bee stores its current path integration state before leaving the food to return home [49]. The visual image that a hoverfly uses to maintain its current hovering station, stored as a short-term memory, can also be used to return after a
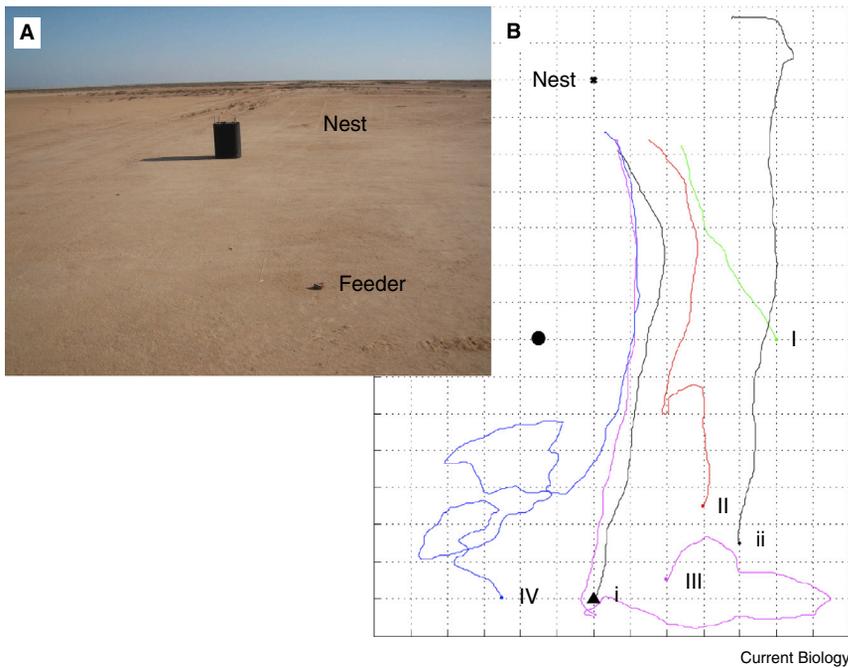
Figure 3. The richness of navigation in the desert ant *Cataglyphis fortis*.

Displacement experiments can reveal guidance mechanisms and when they are used (see supporting analysis in [31]). (A) Ants were trained along a route from a feeder back to the nest past a single large landmark across an otherwise largely featureless area. The low bushes 5–15 m beyond the nest might also provide cues for positional image-matching (from [31]). (B) Trajectories of individual homeward-bound ants released at different locations around a habitual route. Each grid-square is 1 m^2. (i) Trajectory of an ant returning along its route from the feeder (triangle), past the landmark (black circle) to the nest (cross). (ii) Trajectory of a homeward ant displaced from the feeder to a location away from the route. This trajectory is primarily guided by path integration. The ant travels the distance and direction it would have traveled had it not been displaced. (I–IV) Homing ants were captured just before entering the nest and then displaced to various locations. They were then guided only by visual cues. (I) Away from the route, but in the catchment area of the nest, the ant travels straight towards the nest probably using positional image-matching. (II) Away from both the route and the nest, the ant starts out in a non-specific homewards direction, before switching to approach the route (possibly using visual memories of the route for positional image-matching). Once near its route, the ant travels parallel to its normal homeward trajectory (shown in i) showing that, for travel along a narrow 'route corridor', its visual memories are used for alignment image-matching (positional image-matching would instead lead the ant to converge further onto its habitual route). (III) When released to the right of the feeder, the ant searches briefly before traveling towards the feeder. It then returns along its habitual route back to the nest. The homeward-motivated ant appears attracted to the feeder as the start of its homeward route. (IV) When released at a location from which the landmark was seen in an unfamiliar direction, an ant searches as if lost. Upon reaching a location where the landmark is viewed in familiar direction, the ant uses its route memories to travel home. (Trajectories selected and redrawn by M. Collett from data in [31]).

short excursion [8]. The encoding of the appropriate view-based memories for distant goals, however, is more complex because no single view will generally encapsulate all the necessary information. Hymenoptera in particular have developed specialised learning manoeuvres devoted to extracting the information from a set of views that will allow guidance over multiple spatial scales.

When a wasp, bee or ant leaves its nest or a profitable food site for the first few times, it does not leave in a straight line but instead performs a series of arcs or loops covering increasing areas as it moves away [52–56]. At certain points, the insect turns back and looks so that it is facing in the direction of the nest, or towards prominent nearby landmarks [57]. These moments when it turns back appear to occur increasingly sporadically as an individual gets further away [54]. During these turns, an individual could potentially be acquiring snapshots to be used for positional image-matching.

At the end of these learning manoeuvres, bees circle high above the hive, possibly increasing the catchment area of their snapshots around the hive. From an encoding principally of the more distant panorama, snapshots can act as attractors from relatively distant locations. If a hive is transported to an unfamiliar location, a single flight at the new location is sufficient for a honeybee to acquire the visual memories needed to return to the hive from locations 100–200 metres away, where the panorama at the release sites would have been sufficiently similar to the panorama encoded as snapshots near the hive [58].

The early parts of the learning manoeuvres appear adapted to acquiring information required for the final pinpointing of the goal. Their efficacy was first demonstrated by Tinbergen, who showed that the digger wasp *Philanthus triangulum* can learn during a single departure the location of its nest within a ring of pine-cones [59]. Subsequent studies using video analysis have revealed intriguing regularities in these manoeuvres, suggesting that the insects use optic flow patterns to extract information about landmark distances [52,60]. The orientations that a wasp or bee adopts during the arcs appear to stabilize the view of the landmarks close to the goal, while possibly blurring out the more distant panorama [52]. The parallax experienced during these arcs will be related to the distance of the objects. At the end of the arcs, the insects briefly face and fly towards the nest [53,56,61], often resulting in loops (particularly obvious in bumblebees [56]) as the insect starts the next more distant arc (Figure 4A).

The importance of these manoeuvres is evident when the insect next returns [56,60]. It approaches the goal, in bumblebees often in a type of zigzag flight (Figure 4B), so that the optic flow during the turns of the zigzags matches that experienced during its loops at the ends of the departure arcs (Figure 4C). This putative 'parallax-matching' means that the wasps or bees will search for the goal at the correct metric distance from a landmark that is close to the goal [60]. They fly at this distance even when the size of the object differs from that encountered during the learning flights [60,62].

The effort that an individual puts into the learning manoeuvres depends on a variety of factors, including the individual's level of uncertainty, the complexity of the surroundings, and the quality of the reward at the site [57,63]. On each of the subsequent trips to the goal, as the

approaches become faster and more direct, the learning ma-
noeuvres become progressively shorter, until the individual
leaves without turning back at all [57,60]. Should the insect
have to search for its nest on an approach, the manoeuvres
briefly recur when the insect next emerges, sometimes
many hours later. The experience of having had insufficient
information to find the nest can thus influence the behaviour
long after.

Learning Routes

During their first returns to a food-site or nest, bees and
wasps pay attention to 3-D information in the surrounding
landscape, using features that were extracted during the
learning manoeuvres. After several returns they start to
ignore depth information, reacting simply to the retinal image
of the panorama [60,62], though still paying more attention to
features near the goal that were highlighted during the
learning manoeuvres [64,65]. These stored quasi-two-
dimensional views are likely to be acquired or amended
during the insect's approaches to the goal [57,62]. A
bumblebee, for instance, tends to approach the goal along
a relatively constant direction [56,66], so that whilst being
guided to the goal by positional image-matching, it might
learn the views that it will subsequently use for alignment
image-matching. Approach flights tend to get simpler in con-
cert with learning manoeuvres on departure [53] and the
acquisition of views for alignment image-matching may
accompany this simplification.

The likely interplay between positional and alignment
image-matching illustrates a form of bootstrapping in which
information that is already acquired can help with the acqui-
sition of other information. A guidance system that already
has sufficient information to guide travel towards its goal
can provide a scaffold or framework for teaching another
guidance system; it ensures that an individual is both in the
appropriate location, and oriented in the appropriate direc-
tion for encoding useful retinotopic views. Both path integra-
tion and pheromone trails can act in a similar manner to train
route memories [67,68]. By having route-learning turned on
only when being guided by an experienced guidance system
such as a path integration system or an active pheromone
trail, an individual can avoid storing the uninformative views
experienced during the convoluted paths taken during
search. In this way, the experienced guidance systems could
regulate learning so that it occurs not just when leaving
goals, but anytime when an individual is traveling towards
its goal.

The way in which visual route memories are learnt may
thus be different from the learning of goals. The learning
manoeuvres on leaving a goal can be thought of as an 'active
learning' process, where uncertainty causes an individual to
move to locations purely in order to acquire information.
Route memories are acquired through a more 'incidental
learning' process, while the individual is traveling directly
to its goal.

Learning from Others

In addition to learning during their own exploration, individ-
uals can also profit from information that has been acquired
by others. At its simplest, an individual's search for profitable
resources is speeded up by attraction to the presence of
other individuals [69]. Such 'local enhancement' is found in
a variety of flower visitors [70,71]. In social insects, attraction
may also be promoted actively through the release of
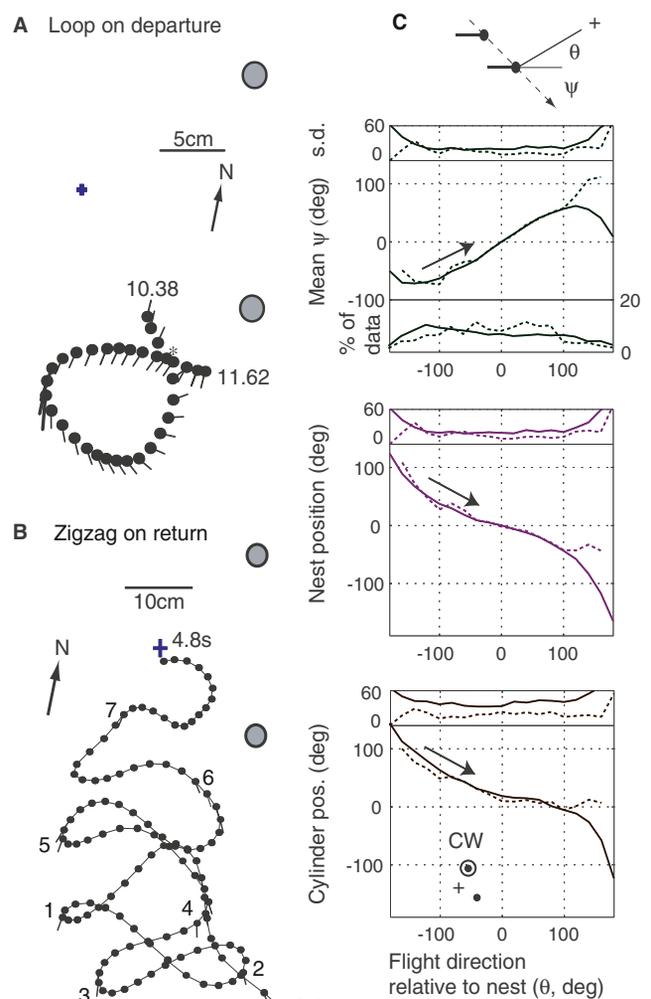
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Figure 4. Similarities between the learning manoeuvres and returns of
the bumblebee, *Bombus terrestris*.

(A) Loop from a departure flight. Camera is placed above the nest (+)
and two black cylinders (circles) nearby. Ball and stick indicate position
and orientation of bee every 20 ms. Stick is extended when bee faces
nest (±10°). (B) Ziz-gag sequence from a return flight. Stick indicates
orientation when bee faces the nest at turns. (C) Similarities between
loops and zigzags. Each panel shows one parameter plotted against
the bee's flight direction relative to the nest during clockwise loops
(———) and the clockwise turns of zigzags (- - - -). Data show means
and standard deviations of 112 loops from 9 bees and 27 zigzags
from 8 bees. Arrows indicate direction of time. Left: angular difference
between bee's flight direction and body orientation. The two are
aligned when the bee faces the nest and diverge as flight direction
moves away from the nest. Centre: position of nest on retina. Diver-
gence between body orientation and flight direction tends to keep
bee facing towards the nest. Right: position of northerly cylinder on
bee's retina illustrating consistency in the bees' compass direction of
flight across multiple loops, zigzags and bees. (Reproduced with
permission from [56].)

pheromones [72] or vibratory calls [73]. It can also occur
through visual observation. Bumblebees, for instance, will
copy the foraging choice of experienced bees after observing
them through a transparent screen. The observing bees later
fly to flowers of the same colour on which they had observed
the demonstrators to be perched [74,75]. Such strategies

can lead to copying the choices of both conspecifics [76] and others [71,77].

Individuals can potentially learn the locations of distant resources by following others. Parasitic flies, for example, follow laden digger wasps back to their nests. But, more generally, following another is likely to be successful only if the individual being followed is knowledgeable, interested in the same resource and allows itself to be accompanied. In social insect colonies, which rear brood communally and share their resources, foragers have common interests and these requirements are often met. These insects have evolved a range of mechanisms with the essential property that successful foragers provide others with locational information after finding somewhere worth recruiting to [72]. In addition, the successful foragers will often encourage potential recruits with a sample of what they have found [78]. Once at the new location, the recruited follower can acquire visual and path integration memories for guiding itself to the goal on later occasions.

One way in which individuals of many species of ants transmit spatial information is through laying down long-lasting pheromone trails between valuable food sites and their nest. These trails, radiating and branching out from the nest, can provide a long-term, universally accessible, external memory of a colony's activities. Individuals from the nest will be attracted to the particular trails both by recruitment activity [79] and more volatile recruitment pheromones [80]. The mass recruitment permitted by pheromone trails is particularly efficient for exploiting large patches of food. Where resources are too scattered, for instance in a desert ant's habitat, pheromone trails would not be profitable [18].

Pheromone trails are generally built gradually, as an exploratory tip becomes increasingly established through the actions of multiple ants. A long trail newly-laid by a single ant would generally be insufficient to provide reliable guidance. One possible solution is for individual foragers to lead a single recruit or a group of recruits following closely behind the leader. In such so-called tandem running [81,82], a knowledgeable individual attracts a follower with a volatile pheromone, and then the two ants set off together. The recruit stays in antennal contact with the lead ant and, if contact is broken, the leader will pause and wait for the follower to catch up. In the ant *Temnothorax albipennis*, locomotion speed is four times slower during tandem running than if travelling unaccompanied [83]. But with a potentially exponential increase in the number of knowledgeable individuals, it provides a reliable way for a single individual to recruit along large distances or through the concentrations of pheromone signals already present around the nest.

The art of conveying location information is arguably most sophisticated in honeybees, where successful foragers can transmit the path integration coordinates of a valuable food source within the hive itself [72,84]. Bees that have discovered a rich food source return to the nest and release a pheromone to attract recruits which will follow a waggle dance, in which the direction and distance of a food source are encoded [85]. The waggle dance consists of a repeated figure of eight circuit built around a central 'waggle run'. The duration (1–11 sec) of the waggle run encodes distance, so that longer waggle runs indicate larger distances of the food source. If performed on a horizontal surface open to the sky, the straight segment is oriented in the direction of the food source. On an inclined surface, the dance orientation uses a combination of sky compass and gravitational inputs. When bees dance in a dark nest or hive, the sun compass is entirely replaced by gravity and the angle of the central waggle run relative to the direction of 'up' on the vertical comb indicates the direction relative to the sun's azimuth outside the hive [72]. The equivalence between the sun compass and gravity suggests that these two orientation cues may well have a common neural encoding.

The waggle dance is frequently described as a symbolic language [72]. But it might also be acting similarly to a compressed tandem run. To perform the waggle run, the dancer could be following a speeded-up version of its path integration output vector. When a recruit is following, in close antennal contact, the dancer produces a precisely directed jet of air [86] and a precisely timed period of vibrations at 280 Hz [87]. These signals ensure that the information is received accurately. Might these intense mechanical stimulations be acting by super-charging the follower's path integrator? In this way, as in the tandem runs, the dancer may be guiding the movement of the follower so that the follower acquires the appropriate path integration information from its own directional and movement sensors.
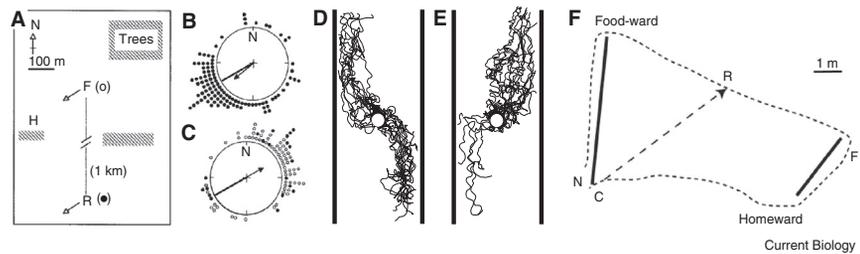
Selecting Memories

Parasitoid wasps can remember and track the development of multiple host locations [17,88]. Foraging bees do something conceptually similar, often visiting several locations, each at a particular time of day when the flowers there produce the most nectar [89]. In such cases, the insects must be sure to use the appropriate set of memories to reach a particular goal. A variety of behavioural results suggest that these insects may in some way group related memories together by associating them with a specific goal. When a dancing honeybee, for instance, communicates where to forage, odours on the dancer's body and in the nectar she distributes tell naive bees which floral odours to search for [72,90]. When perceived by knowledgeable bees, the dances and odours may activate a whole set of memories that include both spatial memories and flower colour [91]. When a goal is chosen, the entire group of memories could be primed for use.

One significant factor in choosing a goal, and so determining which set of memories should be used, is an insect's motivational state. Several studies show that how a forager uses its navigational memories depends on whether or not it has food. If honeybees are captured at a feeder, displaced to an unfamiliar test site and released immediately with a full crop of nectar, then they will fly off in the direction of the nest as indicated by their path integration guidance system. If instead they are kept for four hours so that their crops become empty before being released, then they fly in the opposite direction — in the accustomed nest to feeder direction [92]. Having a full or empty crop can thus determine whether a forager uses its path integration memories for guidance to the nest or to a feeding site (Figure 5A–C).

The use of visual route memories is similarly state-dependent, ensuring that foragers travel in the appropriate direction along a habitual route. In one experiment, wood ants were trained along a simple foraging route parallel to a low wall so that on the way to the feeder the wall was on their left, while on the way home it was on their right. In tests, the ants were released halfway along with either a full or empty crop (Figure 5D,E). With full crops, the ants used the visual cues to travel in the homeward direction. With an

Figure 5. Goal-dependent use of memories.
(A–C) Feeding influences how path integration memories are used. (A) Diagram of experimental area. Honeybees were trained from their hive (H) to a feeder (F). In tests, they were taken after feeding. Bees were captured after feeding at *F*, as they were about to head home. They were then kept for 3 hours released either at *F* or 1 km to the south at R. (B) Vanishing bearings (compass directions in which bees were seen disappearing from view) of bees released at R, which were fed just prior to release. The radial line is the compass direction from F to H. Vanishing bearings of the fed bees (the mean orientation is indicated by the arrow) follow this direction. (C) Vanishing bearings of bees released, without further feeding, at F (open circles), where bees would also be able to use homeward route memories, and R (closed circles). These directions are in the opposite direction, following instead the direction given by path integration from the hive to the feeder (A–C from [92]). (D,E) Feeding influences which visual memories are used. Wood ants (*Formica rufa*) were trained along a foraging route next to a wall so that the wall was to their left on the way to the food and to their right on the return. In tests, unfed or fed ants were placed between two barriers. Most ants approached and then followed the wall so that it was (D) on their left when unfed and (E) on their right when fed (reproduced with permission from [93]). (F) Diagram of an experiment with the Australian honeypot ant, *Melophorus bagoti*, in which barriers were placed so that ants learnt a one-way circuit from their nest (N) to a feeder (F) and back. In tests, returning ants were caught just before entering the nest and displaced to a release site (R) on the food-ward route. The terrain was full of low scrub so that the release point was not in the catchment areas of the feeder, the nest, or the homeward route. Upon release, the ants searched as if lost. They did not use their food-ward route memories to travel to the feeder. Nor did they take short-cuts to the nest. (Adapted by T.S. Collett from [94].)

empty crop, they used the same visual cues to travel instead in the opposite direction [93].

A similar experiment, but using a one-way circuit that separated the food-ward and homeward routes, showed even more clearly how the use of memories depends on an individual's motivational state (Figure 5F). If ants (*Melophorus bagoti*) that had food were displaced from the feeder to somewhere on the food-ward route, they searched as though lost, ignoring their memories that could guide them along the food-ward route [94]. When an ant is in a homeward motivation, only its homeward memories appear to be active.

The motivation-dependence in the use of the various types of memory raises the question of how the associations are learnt. One possibility that can probably be dismissed is that insects are simply forming an associative link between their motivational state and the memories they acquire when in that state. That explanation would not account for the memories acquired during the active learning on leaving a goal: The food-ward memories, for example, are then acquired when a forager has food and is on its way to the nest. An alternative account is that insects form associative links between memories and the goal to which those memories lead. This hypothesis also has the advantage of accommodating the ability of foragers to select between routes leading to different food sites. It can also provide an explanation for the ability of honeybees to use the same visual cues in different ways at different food sites [95,96].

Do Insects Have Cognitive Maps?
Tolman [97] coined the term 'cognitive map' to express his disagreement with a viewpoint prevailing in the 1930s that learnt, complex behaviour can be explained through stimulus–response associations. Spatial behaviour was an excellent arena in which to argue this general point. The more limited issue here is whether insects have an encoding of a familiar environment that allows them to take routes between places as though, to put it metaphorically, they could consult a mental map in which visually defined goals are associated with allocentric coordinates. The issue of whether insects have cognitive maps touches on at least two fundamental questions about how the guidance systems work: one addresses how different types of sensory cues are

brought together for guidance; the second is whether memories can be used not just for the goal states, but also as a substitute for the current sensory inputs.

With the ability to remember visual scenes and to remember path integration information, insects have two components that could potentially be brought together into what can be described as a path integration-based cognitive map [35]. An insect might remember its path integration states at familiar locations and associate those states with the views that they experience there. The insect would then have a neural representation that encoded visual memories within a nest-based coordinate system. Such a representation could be used with the same path integration guidance system described above, with the only difference that a path integration memory would be used in place of an individual's path integration state produced by its current dead-reckoning.

Whether the view at a familiar location might reset an insect's current path integration state to the value that is normally experienced at the location — in other words, whether a path integration state memory can be substituted for the ideothetic sensory input — has been addressed explicitly in a series of studies in the Mediterranean desert ant *C. fortis* [25,51,98–101]. The rationale behind these experiments exploits the finding that an ant's current path integration state can be read out by releasing it with food in an unfamiliar test area. On release, the ant performs a 'home vector': travelling in the direction and distance to where the path integration system indicates the nest should be [102]. To test for resetting, ants were first trained along routes so that specific locations were repeatedly experienced with a consistent path integration state. In tests, manipulations produced a mismatch so that the ants reached those locations with a different path integration state. If the familiar location then caused that state to be reset to its accustomed value at the location, then that resetting could later be observed from the home-vector on an unfamiliar test field. The consistent finding is that the path integration state reflects the distance that the ant has really travelled, rather than a memory triggered by the familiarity of the locations that it experiences [25,51,98–101]. Memories of previous path integration states are not substituted for the current
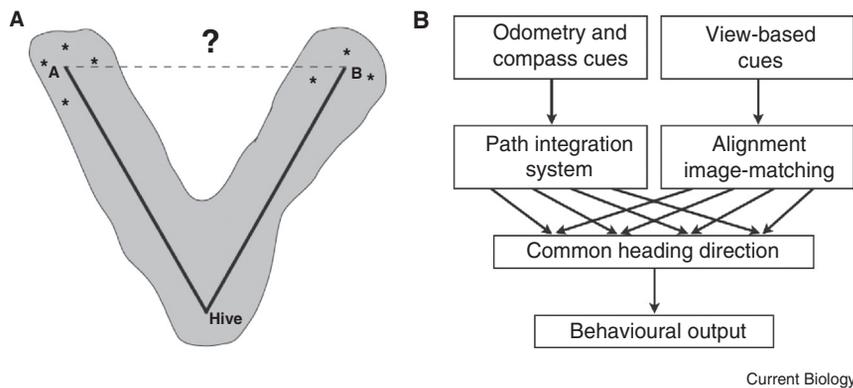
Figure 6. Cognitive maps, or decision-making by a collective of guidance systems?

(A) A hypothetical short-cut experiment to test for the existence of cognitive maps in bees (or other animals). Honeybees are trained to feeders at two sites (A and B) so that each individual is familiar with both sites and the routes to those sites, but not the area in between. The experiment tests whether, if a honeybee intending to fly to B is displaced to A, it can then travel a novel shortcut from A to B. This ability would be predicted if honeybees had a cognitive map. But depending on the landscape, such shortcuts could also be produced by view-based guidance. The reach of view-based guidance is probably frequently under-estimated. A commonly made anthropomorphic (and possibly often misleading [30]) argument is that if a honeybee can see and recognize landmarks near A when it is at B, then it can use them for visual guidance. But an argument based instead on positional image-matching (which doesn't need to recognize individual landmarks [24]) suggests something different. If a large part of the panorama seen near B can also be seen near A, then a honeybee will be able to take a novel shortcut directly to B. Similarly, if the bee enters the catchment areas of other locations along the route to B, then it can also reach B, potentially along a novel path. In such cases there would be no need to invoke a cognitive map (from [133], with permission). (B) Schematic showing proposed organization of the guidance systems (only two systems shown). Each guidance system calculates its preferred heading direction. The preferences from all the guidance systems converge onto a single population encoding where they are pooled. The highest level of activity in the common encoding determines the insect's heading direction. (Adapted from [26].)

sensory input. These experiments argue strongly that ants (and quite possibly insects more generally) do not have path integration-based cognitive maps.

The experiments on path integration leave open a question as to whether insects might have a cognitive map based on some other, currently undescribed, mechanisms. Most behavioural studies that have been interpreted as providing evidence for cognitive maps in insects [103–105] are based on their observed abilities to produce novel shortcuts between familiar locations (Figure 6A). One challenge in designing and interpreting such experiments is to rule out that any observed shortcuts are produced by the guidance mechanisms we currently know. The most difficult challenge is to exclude the use of the two view-based image-matching mechanisms (Figure 3).

Recent studies reporting novel shortcuts made by honeybees have used harmonic radar to follow the entire trajectories of the bees after release [104,105]. In some cases, bees first searched and then flew in a direct path to the hive. It is very hard to exclude that this direct path was not guided through mechanisms that we have already discussed. The panorama in the broad vicinity of the hive included features on the ground, for instance, a group of 3.5 m high tents and a boundary between differently mown areas of grassland. Further away the skyline profile was low, but it is still possible that across the wide panorama detectable guidance information is available. Where a panorama shares sufficient commonalities with the panorama viewed from near the goal (or indeed other familiar locations *en route* to that goal), then positional image-matching can potentially produce a novel shortcut to reach the goal. Controlling for this possibility is particularly difficult in flying insects such as honeybees that may fly many metres above the ground.

Two studies that demonstrated conditions in which insects were not able to produce shortcuts between familiar locations are particularly worth noting. In one study, honeybees were trained to feeders at two sites, one of which was on open ground (A) and the second in a quarry (B), so that the surrounds of A were not visible from B unless the bee were to ascend to 20 m above the site. Bees released at A flew a novel shortcut towards B, which they could do using the panorama around the quarry for positional image-matching. However, bees released at B, from where it would have been difficult to see the surrounds of A, did not perform a short-cut and instead flew back to the hive [106] (see also [107] for a similar failure to demonstrate cognitive maps in bees). In ants, which do not have the ability to fly up to see more distant features, trajectories can show clearly that novel shortcuts between familiar locations are not generally found if visual cues for positional image-matching are not available [94] (Figure 5F). In summary, it seems that the findings of all the insect studies that we have reviewed are explicable in terms of known guidance systems without the need to invoke a 'cognitive map'.

In the next two sections, we address the second implicit question behind the cognitive map debate: How are different types of information integrated?

Decision-making by a Collective of Guidance Systems
The collection of path integration and view-based guidance systems is often described metaphorically as a 'Swiss-army knife' or 'toolbox' to capture the idea that an insect's guidance is controlled by a set of independent 'tools' or guidance systems. Each guidance system is specialised to deal with a particular type of sensory information; processing the information in a particular way and computing its own preferred heading direction.

How does an insect coordinate the guidance systems so that the appropriate ones are used at the appropriate times? The tool metaphors suggest two additional characteristics. One is that at any particular moment, only one guidance systems might be used, while the others are put away until needed. The second is that there may be something (an 'arthropodunculus') deciding which is the most appropriate tool for the moment. It now appears that the guidance systems may act more like a collective, performing their computations in parallel and providing simultaneous contributions to guidance [26].

Evidence for the parallel activity of the guidance systems comes from experiments in which the various guidance

cues are made to conflict. If only a single system were to provide guidance at any one time, then an individual's behaviour would reflect only one of the cues. In fact, insects often take a compromise bearing when given conflicting directional cues [105,108–110]. Such a compromise is particularly obvious in conflicts between route memories and guidance from path integration in desert ants [26,111]. These observed compromises between the guidance systems suggest a possible architecture for the way in which the different types of information are integrated for guidance. Each system uses its sensory information and memories to compute a preferred heading direction. These various preferred heading directions converge in a single heading direction that determines the individual's behaviour (Figure 6B).

If the heading directions are implemented using population encodings [112], then when a guidance system has a stronger directional preference, it will tend to have more influence on the final outcome. A strong preference will contribute a pronounced peak to the common encoding, whereas when a guidance system has no strong directional preference it will contribute weakly across many possible heading directions. An output determined by a summation of the inputs will thus predominantly reflect the pronounced peaks. In this way, much Bayesian-type decision-making, whereby more precise or reliable cues have more influence, emerges automatically. This mechanism can explain why travel along routes reflects route memories more than guidance from path integration [68,99], and why guidance from path integration becomes weaker as the goal is approached. It is not yet known whether any lateral inhibition between the guidance systems or within the common encoding might amplify differences between inputs and so provide additional help in resolving the outcomes between competing responses.

One uncertainty is how heading directions computed in terms of a celestial compass are integrated into the same encoding as heading directions in terms of visual features. A simple solution might be for them to converge where the signals have been converted to an egocentric reference frame, such as a heading direction with respect to an insect's midline. But an alternative possibility is also suggested by findings that bees can use information that they acquire from waggle dances when the sky is completely overcast [113,114]. Is there then perhaps a neural encoding of the desired heading direction that combines view-based panoramas with the celestial compass cues?

Separate Visual Memories for Recognition and Guidance?

When a homeward-bound ant is placed at an arbitrary location on its homeward route, it picks up the route and follows it as if it had followed it right from the start [19,20]. In the right motivational state, the ant recognizes its location and the path that it takes is a direct response to its immediate surroundings (Figure 1C). How does the ant ensure that the guidance memory for the appropriate location is used?

One line of reasoning suggests that visual route following may involve two classes of visual memories [31,115]: In addition to the guidance memories, which could be thought of as a set of parameters for the visual control systems, there could be a separate class of memories for recognizing a scene. Their function is in part to set up the guidance memories and set their parameters — for example, which retinal region should look at which bit of a panoramic scene — and in part to provide a persistent context in which rapid guidance memories can act. The guidance memories

themselves might well encode not just the momentary desired heading direction [28], but a set of headings for a segment of route that is governed by a consistent panorama or feature [31].

One of the functional advantages of a separation between recognition and guidance is that the two processes can collect different types of information and use different types of computations. The benefits of such separation are particularly well illustrated by an example in a different sensory domain. Male crickets identify and locate conspecific females through their song. Species recognition involves an assessment of the pattern of a sequence of sound pulses and takes a relatively long time [116]. Steering occurs through short latency (55 ms) turning responses to individual pulses of sound [117]. Turning tendencies are weak when elicited by sound pulses that occur at an unnatural rate. But when conspecific song is added to such a pulse train, the turning response to the individual pulses becomes stronger. The enhanced response associated with species recognition persists for several seconds after the song has ceased [116]. Recognition can be a relatively slow process, relying on elaborate sensory information that takes a period of time to gather. Conversely, guidance can be rapid, using brief and simple cues. A second aspect of the temporal separation is that once recognition occurs, it may continue to influence how guidance memories are used for some time.

One implication of a separation between recognition and guidance processes would be that the visual processes studied in discrimination experiments (for example [118–120]) will not necessarily have identical properties to the visual processes studied in guidance experiments. A further possibility is that visual recognition and visual guidance memories might be encoded in different areas of the brain. For example, recognition memories may reside in the mushroom bodies, which in ants and bees can receive visual as well as olfactory input [121]. Guidance memories, in contrast, might be more connected to the central complex — which is known to be involved in heading directions [122] and turning [123], and is also implicated in some guidance related visual memories [124].

A recognition process is not necessarily limited to a single sensory modality. The desert ant, *Cataglyphis fortis*, learns to recognise its nest location more rapidly and the triggered search is initially more accurate when the nest is marked by both visual and olfactory cues than when just one of these cues is available [125]. Of particular interest is what happens over time when an ant is trained with both cues present. Ants learn enough about the two cues in a single training trial for a precise search for the nest entrance to be triggered whether the ant is given either cue separately or both cues together. A dramatic change happens after 15 training trials: a precise search is only found in tests with both cues — a single cue is no longer enough. Ants appear to have linked the two cues together.

One challenge to the idea of separate recognition and guidance processes has been raised by a recent computational model of route guidance [126]. It works without the need to retrieve discrete visual memories. Instead, a two layer neural network receives input from a retina and outputs how familiar the current panorama is. During a learning phase, all views that are encountered by the network are used to adapt the synaptic weightings of a single holistic encoding. The trained 'ant' follows the route by periodically interrogating the network by performing a rotational scan.

The facing direction that is registered as the most similar then determines the ant's heading. The current simplicity of this model is appealing, but it may require further modifications before it can fully describe an ant's route behaviour.

To explain the results described in the 'Selecting memories' section, each route to a different goal would need a separate set of synaptic weights. There is also some strong behavioural evidence pointing towards subdivisions in the encoding of a route [115,127] — such results are more difficult to reconcile with the model. Finally, a complete model would need to include the computations of the saccades observed when ants are following their routes [32]. It remains to be seen whether after the necessary modifications the model continues to be at odds with the idea of separate recognition and guidance processes.

Conclusions

The majority of experiments on insect navigation have been performed on a very few species of social Hymenoptera, chosen because of the relative ease of handling, training and obtaining good-quality data sets. Are the conclusions reached from social Hymenoptera applicable to other insects, and to what extent will we be able to integrate the lessons learnt from the behavioural experiments on these species, with the neurophysiology that has been performed primarily on larger and more robust insects such as flies, cockroaches and locusts, and with the discoveries beginning to arrive from uses of the powerful techniques of neurogenetics in the fruit fly *Drosophila melanogaster*?

Both path integration and positional image-matching are found in diverse groups of insects. But it remains to be seen to what degree the alignment image-matching used along habitual routes, and the learning manoeuvres used on leaving a goal may be Hymenopteran inventions. Many Hymenoptera are unusual amongst insects in being central place foragers. They travel out from a nest and must be able to return successfully in order to provision their young. In the evolutionary history of the Hymenoptera, the transition from a vagabond lifestyle to central place foraging occurred in the early Jurassic [128].

One brain structure that may have adapted to this life style is the mushroom bodies, which are impressively large and elaborate in the social Hymenoptera. These prominent areas are involved in learning and memory in a wide range of insects [121]. Interestingly, the elaboration of the mushroom bodies in the Hymenoptera preceded the development of sociality and is associated more with the adoption of parasitoidism, which in turn is linked to larval provisioning and central place foraging [128]. A feature of the complex spatial memory of both parasitoids and social Hymenoptera is their capacity to learn several locations and select which one to visit. Other insects, like flies, have less rich spatial behaviour, but may well share much of the same underlying computational structure.

One significant lesson that has emerged from our understanding of the mechanisms of insect navigation is just how much can be done without cognitive maps [26,27,66]. Looking beyond the insects, it will be interesting to see to what extent visual guidance in reptiles, birds, and even mammals [129,130] may share similarities with the alignment and positional image-matching of insects.

The example of insects suggests that effective and robust navigation from the very first trip in a new area can be achieved with a collection of specialized and limited guidance systems that support and train each other. Such a cooperating, and at times discordant, collective can deal with a surprising variety of situations and environments.

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