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# *Encyclopedia of Animal Behavior, 2<sup>nd</sup> Edition: Article Template*

## **Insect spatial learning, a stroll through Tinbergen's four questions.**

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### **Abstract\***

Insects display a large array of spatial behaviors, from maggots tracking fruit scents on the floor to bees visiting sequences of flowers over kilometers. Here we will explore the proximal and ultimate causes of these behaviors through Tinbergen's four questions, with a special emphasis on learning. First we will focus on the ontogeny of spatial behaviors through the life of an ant forager. Growing from naïve to expert navigator requires multiple steps and great plasticity. However, learning too fast is rarely the best option and we will see, notably with parasitoid wasps, that the dynamics of learning speed and memory are finely tuned to fit a species' ecologically relevant tasks, that is, their ultimate function. We will then dive into the neural mechanisms underlying spatial learning, especially two key areas of the brain: the mushroom bodies and the central complex. This will enable us to compare insect species across the phylogenetic tree and ask how a large diversity of spatial behaviors can result from such similar brains. Part of the solution lays in the design of insect brains, which facilitate the emergence of new adaptive behaviors across evolutionary time as well as within an individual's life.

### **Keywords\***

Ant – bee – beetle - behavior – brain - central complex - compass – evolution – fly - head direction – insect – mushroom bodies – navigation – olfaction – ontogeny – path integration – plasticity – snapshot - spatial learning – Tinbergen – vision.

### **Glossary**

#### **Nomenclature**

PI: path integration

CX: central complex

MB: mushroom bodies

### **Body Text\***

#### **1. Ontogeny**

'Learning' implies a change: the organism that learns becomes different. Since the organism is now different, this will change how it responds to the environment, and consequently this altered

response may expose the organism to novel perceptions of its environment. These novel perceptions may in turn trigger further learning, causing the organism to change again and respond differently, etc... This constructive interaction with the environment reflects the nature of all living systems, from cell reproduction to an organism's development and is particularly apparent when considering the ontogeny of spatial behaviors. Let's exemplify this interaction with solitary foraging ants, as the ontogeny of their navigational behaviors shows many steps of construction, which we may call spatial learning.

When leaving the nest, a naïve ant forager experiences the bright sun for the first time. This experience of light, particularly UV light, triggers strong neuronal changes in the brain regions required for learning and extracting compass information from the sky (Grob et al., 2017; Schmitt et al., 2016). These neuronal changes may arguably be called 'maturation' rather than 'learning', in the sense that they seem to happen only during a specific period of time and are probably irreversible. However, these changes are probably also specific to the structure of the visual environment experienced around the nest, resulting in individual differences.

During its first trips outside, the ant is safely connected to the nest through its path integration (PI) system. With PI, compass information and walking distance are continuously combined such that, at all times during a journey, the forager knows the approximate direction and distance required to take a direct path home (Ronacher, 2008; Wehner and Srinivasan, 2003). This PI system enables the forager to guide a series of "learning walks": a carefully orchestrated series of scans, loops and turns around the nest (Fleischmann et al., 2016). During their first learning walks, the ant's PI system uses the earth's magnetic field as a compass cue to control its bearings (at least in *Cataglyphis* species (Fleischmann et al., 2018). Such a magnetic compass might already be effective inside the nest and probably serves as a scaffold to calibrate their celestial compass during learning walks. Thus, after some trips, the ant relies instead on celestial cues such as the sun's position and the pattern of polarized light for compass orientation (Wehner and Müller, 2006).

But learning how to use celestial cues is not the only purpose of learning walks. During learning walks, the ant – by using its PI system - often turns back towards the nest direction, exposing its visual system to just the right terrestrial cues for learning. After a few trips, the insect has learnt the appearance of the visual scenery and is able to rely on terrestrial cues to find its nest (Wystrach et al., 2012).

Here we have seen how an arguably innate strategy, PI based on magnetic cues, can guide an ant's learning walks and prompt the organism to experience just the right information within its environment, enabling it to learn the relevant celestial and terrestrial cues.

Interestingly, learning walks seem to be prompted not because the ant is naïve, but because of the unfamiliarity of the surrounding terrestrial cues. This is why learning walks can be triggered in an already experienced forager by modifying the visual environment around the nest (Müller and Wehner, 2010). In other words, what triggers learning is the need to learn. As a corollary, once the local scene has been learnt, it appears familiar and the forager's path therefore becomes straighter and it finally leaves the vicinity of the nest to forage.

Here again, the organism's route through the unknown is not completely arbitrary. It is shaped by spontaneous responses to ecological cues (e.g. attraction to vertical trees in wood ants (Graham et al., 2003); avoidance of bushes where predators may be lurking (Heusser and Wehner, 2002; Wystrach et al., 2011); attraction to linoleic acid released by appetizing dead insects (Buehlmann et al., 2014) or social (i.e. pheromone trails) stimuli. If the ant finds food, it will remember the PI coordinates of this successful location, and thus will now be able to use its PI system – that is, celestial

and idiothetic cues – to chart both homebound and foodbound routes (Collett et al., 1999; Wehner et al., 1983).

Here again, these strategies act together as a scaffold to enable just the right and consistent visual experience across trips to guide visual learning. After a few trips back and forth the ant no longer needs its PI system to recapitulate its route; it instead uses a combination of visuo-motor routines based on the now familiar terrestrial cues (Kohler and Wehner, 2005; Mangan and Webb, 2012). At this stage, foragers are usually most efficient; they run along their well-known routes between nest and food sources at their fastest and without hesitation.

It is worth noting that the previously used strategies are not completely overlooked and if the scenery changes, an experienced ant will display scans and turns (Wystrach et al., 2014a), spontaneous responses to altered environmental cues and rely on its path integrator again (Andel and Wehner, 2004).

To conclude, multiple ontogenetic steps are employed in enabling a naïve individual to reach the stage of a mature and highly efficient ant forager. At each step, both the knowledge and the information used by the insect changes. Each new step modifies the way the organism behaves, which enables it to ascend to the next step. The system is ‘open’ because of its ability to change by means of learning, but this process is guided (quite literally in this context) by the organism’s own changing behavior.

## **2. Function**

The adaptive function of spatial behaviors in insects is often straightforward. Whether finding a mate, finding food or returning to a shelter, these behaviors are obviously linked to the insect’s fitness. Yet, spatial learning seems remarkably optimized to suit subtler cost-benefit trade-offs. Indeed, learning is obviously beneficial, but it also incurs several types of costs.

First, learning has concrete metabolic costs (Laughlin, 2001). For example, artificial selection for good learners in *Drosophila* reveals that high learning strains have shorter life spans (Burger et al., 2008). Over evolutionary time, there must be a selective pressure for parsimonious uses of learning.

Second, there is a subtle ecological trade-off between naivety and expertise. Learning fast is not always a good strategy. In a highly variable environment, learning associations that may be incorrect the next day would be maladaptive. In that case, learning more slowly would warrant the long-term reliability of the information. Conversely, in a stable environment, why endure the cost of exploring and learning when the behavior could simply be expressed innately? Fast, long-term learning becomes valuable only in-between these extremes, that is, when information is typically stable within a generation but not across generations.

Learning dynamics in ants and bees appear to reflect such a trade-off. For instance, information about the nest or hive surroundings, which enables the insect to home successfully, is typically stable for a lifetime but not across generations (as new nests/hives are at new locations), which makes it appropriate for fast learning. As expected, ants and bees learn this information quickly. A few learning walks or flights is enough to return home after displacement (Capaldi and Dyer, 1999; Wystrach et al., 2012) and the memories of the nest surroundings can be stored for a lifetime (Ziegler and Wehner, 1997). Regarding food locations, however, the time for which the information is valid is variable, and ants typically take multiple trials before reaching asymptotic performance in their ability to relocate the food (Graham and Collett, 2006). This prevents the formation of maladaptive

strong memories for short-lived food sources. Remarkably, insects can also modulate the learning effort based on estimation of the food source quality and quantity. For instance, bees display longer learning flights when departing from a new feeding site that contains a higher sucrose concentration (Wei et al., 2002). Similarly, ants seem to learn more accurately a feeder location that contains more cookie crumbs (Bolek et al., 2012), even though each ant forager could only carry one cookie crumb back to the nest. This suggests that ants and bees use intrinsic knowledge to estimate the reliability of the food source and adjust their learning efforts accordingly.

Perhaps the most beautiful examples of how learning dynamics reflect ecological constraints are found in parasitoid wasps (Hoedjes et al., 2011). Female parasitoids have to find a host – typically an egg, larva or pupae of another insect – on which to lay their eggs. Hosts are obviously under strong selective pressure to remain inconspicuous, therefore parasitoid wasps use indirect information about the favorite food source of the host in order to find them. Different parasitoid wasp species are bound to different host species, and the learning and memory dynamics of the wasps seem to reflect the ecology of their specific host. Typically, as observed in *Leptopilina* species, if the host is a specialist of a given plant species, the wasps will display a stronger innate attraction to that plant, and rely less on learning than a generalist-host wasp species (Simons et al., 1992). Also, for egg parasitoids such as *Cotesia* species, the way the host disperses its eggs influences the wasp learning dynamics. If the host tends to lay its eggs in dense clusters on a given plant, the associated wasp species typically forms long-term memories of the oviposition substrate's odour, even after a single encounter (Smid et al., 2007). Indeed, one discovered egg likely means many eggs are present. Conversely, if the host typically scatters its eggs over different plant species, the associated wasp species is more cautious, and requires a minimum of three successful trials spaced out over time before forming a long-term memory (Smid et al., 2007). Here again, such slow learning prevents maladaptive memories of egg-free plants.

Overall, this shows how spatial learning dynamics are finely tuned to the environment. Shall an insect learn fast, slow or not at all? Tuning of the organism's learning and memory appears to be mediated not by the type of spatial task per se (whether finding home, a mate, food or hosts) but rather the reliability of the information used to find the goal. Estimation of this reliability seems partly hard-wired, such as in parasitoid wasps where learning dynamics reflect the host's ecology, but there is also some flexibility, such as in the case of foraging ants assessing the number of remaining food items to modulate learning of the site. These examples show that even though the function of spatial behaviors may be obvious and similar across insects' species, the underlying spatial learning dynamics vary greatly, and understanding the ultimate reasons for this variation requires detailed knowledge of the insects' ecology.

### **3. Mechanisms**

There are multiple mechanisms underlying any given spatial behavior. First of all, moving requires a body, and surprisingly, a great deal of the solution for a given spatial task is directly implemented in body mechanics (Tytell et al., 2011). But for the purpose of this chapter, we will focus on the neural mechanisms underpinning spatial learning. In the last decade, insect research has made huge progress in understanding brain circuits. Two particular brain areas have attracted much attention: The Mushroom bodies (MB) and the Central complex (CX). Even though these areas perform very different types of computation, both integrate information from multiple modalities and both are involved in spatial learning. We will consider them in turn.

The mushroom bodies consist of a pair of bulging neuropils sitting at the top of the brain. They were first described by Félix Dujardin in 1850 who believed these were the seat of insect intelligence (Dujardin, 1850). It was not a bad guess; as we now know the MB have much to do with learning and are key to some spatial behaviors. Among the first evidence, lesions of the MB in cockroaches were shown to prevent the insect from learning to return to a location using the surrounding cues (Mizunami et al., 1998). Also, in social insect species, we observe an increase in MB volume at the onset of foraging tasks, that is, when an insect needs to solve complex spatial tasks (Kuhn-Buhlmann and Wehner, 2006; O'Donnell et al., 2004; Withers et al., 2008).

But what types of computation do the MB perform? The neural architecture of the MB is very specific. It contains thousands of parallel neurons called Kenyon Cells (KC). Roughly, these KCs receive input from olfactory and visual (among other) sensory areas via a few hundred (at most) projection neurons in a region called 'the MB calyx', and project up to a hundred 'output neurons' in a region called 'the MB lobes'. These 'output neurons' transmit the signal further to different brain regions. This strong divergence/convergence pattern of connectivity (from a hundred inputs to a thousand KCs and then back to a hundred output neurons) - so-called sparse coding - separates input signals into unique patterns of activity in the KCs and enables the categorisation of these signals into a small number of classes (the different 'output neurons') given the co-activation of reinforcer neurons mediating different types of rewards and punishments (Heisenberg, 2003). In other words, the MB are ideally suited for Pavlovian associations of arbitrary sensory inputs to a few meaningful values.

Given olfactory input to the KCs, this type of computation can support odour-tastant or odour-shock associative learning. In natural conditions, such olfactory learning may be useful to guide the insect towards a rewarding location by tracking odours, as in the case of *Drosophila* larvae (Gerber and Stocker, 2007) or parasitoid wasps (Hoedjes et al., 2011). Interestingly, with visual input, the MB circuitry can categorise experienced panoramic views as attractive or repulsive, and could thus be the seat of the visual memories that enable ants and bees to learn long routes in complex outdoor environments (Webb and Wystrach, 2016). Neural models have shown that a biologically plausible MB circuit can enable the recapitulation of an 8 metre ant route in a very cluttered naturalistic environment (Ardin et al., 2016). One can see how the MB circuitry can be used for spatial tasks, yet how such olfactory and visual memories, formed in the MB, are then used to control behavior involves other brain areas, such as the CX.

The Central Complex (CX) is a region at the centre of the arthropod brain. It is composed of multiple interconnected modules, which all show a complex but well-ordered lattice of connectivity ordered in vertical slices and horizontal layers (Pfeiffer and Homberg, 2014). Many studies have pointed to a role for the CX in dealing with space, and some show it is clearly involved in spatial learning. For instance, similar to cockroaches with ablated MB, silencing the ellipsoid body (one of the CX modules) of *Drosophila* flies prevents them from using the surrounding cues to return to a learnt location (Ofstad et al., 2011).

What type of computation does the CX achieve? Recently, researchers have recorded the neural activity of a population of CX neurons of a fly while it was walking on a trackball. They targeted neurons whose dendrites connect in the ellipsoid body by forming an actual donut shape in the brain, hence the name of this structure. Remarkably, the neuron population showed a single 'bump' of activity that was moving around the donut in a way that closely reflected the fly's body rotations (Seelig and Jayaraman, 2015). These neurons function as a 'ring attractor' and are actually tracking the fly's current orientation using both visual and self-motion cues (as it also works in the dark). In addition, neural recordings in locusts and dung-beetles have shown that the CX tracks body

orientation relative to celestial cues, providing the basis for a proper internal compass (Heinze and Homberg, 2007; el Jundi et al., 2015). Finally, the CX may well be the seat of path integration. Indeed, some neurons in the noduli (another CX module) respond to optic flow, and could provide odometric information necessary for PI (Stone et al., 2017). Neural models have shown that the way this odometric information is integrated with the internal compass in the CX is perfectly suited for path integration (Stone et al., 2017) as well as the memorisation of long-term vectors for food locations (LeMoël et al., in prep).

Additionally, the CX receives multiple pre-processed sensory signals from many different modalities, enabling the insect to keep track of the direction of these specific cues relative to its own orientation (Seelig and Jayaraman, 2015). Contrary to the MB, the CX outputs can directly modulate locomotion (Martin et al., 2015). Together, this enables the insects to display suitable oriented responses to ecologically relevant stimuli, such as escape response to looming cues (Rosner and Homberg, 2013), or attraction to trees' vertical edges (Wystrach et al., 2014b). The neurons that convey these sensory signals to the CX are subject to plasticity (Liu et al., 2006), and thus insects can learn to approach rewarded cues and avoid punished ones, even if these cues are innately attractive (Ernst and Heisenberg, 1999). Such memories can be rapidly formed. For instance, ants subjected to a sudden wind gusts manage to memorise the compass direction from which the wind is coming, and if subsequently blown away, backtrack this memorised direction to increase the chance of returning to familiar terrain (Wystrach and Schwarz, 2013).

To conclude, we have seen poignant examples of how computations in the MB and CX can underlie insects' learnt spatial behaviors. But it should be understood that there are no such things as neural modules dedicated to spatial learning. All brain areas, more or less directly, eventually contribute to the insects' movements, and most if not all regions, even sensory areas (Arenas et al., 2012; Hourcade et al., 2009), undergo experience-dependant synaptic changes and can thus mediate a behavioral change that we call learning. A given spatial behavior does not result from one brain region, but emerges from the interaction between multiple brain regions, involving several types of memories simultaneously. For instance, route following behavior results from the simultaneous integration of direction based on visual memories (via the MB), and celestial vector memories (via the CX) (Legge et al., 2014; Wehner et al., 2016). Recent evidence in navigating ants has shown that the direction obtained from visual memories of terrestrial cues can be stored and maintained using celestial cues, thus presumably involving a transfer of information from the MB to the CX (Schwarz et al., 2017). How exactly the different brain areas are orchestrated to produce meaningful behaviors is poorly understood but promises to make for an exciting research agenda.

#### **4. Phylogeny**

Spatial behaviors vary widely across insect species: from maggots crawling over only a few centimeters towards a tasty fruit to bees visiting sequences of flowers across multiple kilometers. Even when it comes to similar behaviors within species of the same genus, the underlying dynamics of learning and memory can vary greatly.

As we have seen, a parasitoid wasp can memorize the odor associated with a successful oviposition site after a single pairing, while its sister species won't learn this association and will stick to its innate preferences (Hoedjes et al., 2011). We also see great variation in the way solitary navigating ants rely to innate (such as PI) or learned (visual route following) strategies (Cheng et al., 2014), as well as in the rate at which they learn visual cues when forced to (Schwarz and Cheng, 2010). Therefore, it seems clear that spatial behaviors and their learning dynamics can be molded to fit

precisely the ecological constraints of a given species. Are there no limit or constraints to the way the brain can be modified over evolutionary time?

Perhaps counterintuitively, all insects' brains share a very similar general design. We find the same brain areas in the same brain regions, and their general structure is typically conserved across species. However, there are differences in their size and connectivity.

For instance, while most insects' MB receive olfactory inputs, in some species they also receive visual input. Visual input to the MB is typically more pronounced in insects that use vision for navigation, such as wasps, bees and some ants (Gronenberg, 2001). In ants, species using vision for navigation have large visual projection tracts into their MB, while we observe mainly olfactory input in species that rely on chemical trails (Gronenberg and Holldobler, 1999). In whirligig beetles, there is no olfactory input (probably the ancestral pathway) to the MB left, but visual input may explain the ability of these insects to maintain a stable location within their territory using visual memories (Lin and Strausfeld, 2012). The number of Kenyon cells in the insect MB are also highly variable across species, from 2500 in *Drosophila* flies to 200,000 in some cockroaches (Webb and Wystrach, 2016). It appears that the evolution of large MB correlates with tasks that typically require navigational skills, such as parasitoidism or generalist scavenging (Farris and Schulmeister, 2011). Indeed, there are physical constraints to memory capacity, and learning the specificity of the landscape to enable flexible navigation over a large territories probably requires a large number of KC's (Ardin et al., 2016).

Perhaps even more strongly conserved, the CX structures have been present in arthropods for at least 500 million years. Though their shape and size can vary between species, the general architecture of its connectivity is remarkably similar. The need to keep one's bearings is probably ancient. But here again, what an organism learns depends on its sensory inputs, and the nature of these inputs varies across species. For instance, dung beetles memorize the configuration of the current celestial cues to maintain a direction and keep rolling their precious dung-ball away in a straight line (el Jundi et al., 2016). Yet, different dung beetle species tend to memorize different compass cues. A night active species favors the sky's polarization pattern, while a diurnal species prefers celestial bodies, such as the sun, or if forced to run at night, the moon (el Jundi et al., 2015). Remarkably, compass neurons in the CX respond to the different types of cues in the two species, reflecting the dung beetle's preference. Interestingly, the homologous neural population, but this time in *Drosophila*, responds instead to the relative position of a vertical bar (Seelig and Jayaraman, 2015). Terrestrial cues such as vertical trees may be relevant to a fly craving fruit, but are completely disregarded by dung beetles, who just want to leave the dung pile in the straightest possible line.

We have seen how homologous brain areas can be exapted for subtle differences in the cue that is used. But how can highly divergent spatial behaviors emerge from homologous brain areas? Part of the explanation has to do with the way in which insects move. Many insects display left/right oscillations when moving. A moth tracking a pheromone trail (Namiki and Kanzaki, 2016), an ant running along its route (Lent et al., 2013), a wasp approaching its nest (Stürzl et al., 2016) or a fly larva going up an odor gradient (Wystrach et al., 2016), all display little zig-zag movements when moving forward. This is likely due to reciprocal inhibitions between left and right motor neurons (Bregy et al., 2008; Namiki and Kanzaki, 2016). Modelling studies have shown that, if one assumes that MB output neurons project to such an oscillation generator, sending olfactory input (encoding changes in perceived odor concentration) into the MB results in chemotaxis towards a learnt odor (Wystrach et al., 2016), while sending visual input to the MB (encoding the perceived panoramic



scene) enables route following behavior (Kodzhabashev and Mangan, 2015). No change within the brain areas themselves is needed for these drastically different learnt spatial behaviors to emerge.

## 5. Conclusion

It seems that the insect brain is built in such a way that changing types or strengths of the connections between areas does not disrupt behavior, but allows for new meaningful behaviors to emerge. Over long evolutionary timescales, what is selected for is not only a design that is efficient for a given ecological task, but one that can be effectively and easily modified to fit other tasks. This may explain both the large diversity of spatial behaviors we observe across insect species as well as why they can be so precisely tuned to each species ecological constraints. At a proximal scale, such a plastic design also facilitates the potential to modify the brain through learning, and thus explain the diversity of behaviors we observe across individuals, as well as along their ontogeny.

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### **Change History\***

I wrote this chapter from scratch and am not aware of a previous version of this chapter.