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# The frontiers of insect cognition

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Insects have often been thought to display only the simplest forms of learning, but recent experimental studies, especially in social insects, have suggested various forms of sophisticated cognition. Insects display a variety of phenomena involving simple forms of tool use, attention, social learning of non-natural foraging routines, emotional states and metacognition, all phenomena that were once thought to be the exclusive domain of much larger-brained animals. This will require re-evaluation of what precise computational advantages might be gained by larger brains. It is not yet clear whether insects solve nominally similar tasks by fundamentally simpler mechanisms compared to vertebrates, though there might be differences in terms of the amount of parallel information processing that can be performed by various organisms.

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## Introduction

Insects' associative learning capacities are well documented, and electrophysiological and neurogenetic research on insects have elucidated the cellular basis of such capacities [1–3]. But what about more advanced cognition, involving the ability to use internal representations of information acquired in separate events, and to combine these to generate novel information and apply it in an adaptive manner, or indeed generating novel problem-solving behaviour spontaneously [4,5]? Working on small nervous systems, insect researchers often have healthy reservations about ascribing sophisticated cognition to their study organisms. Indeed, one of the most valuable contributions of invertebrate research to comparative cognition has been to frame the debate over whether animal minds are best interpreted as cognitive-affective agents or as cause-effect mechanisms; albeit dynamic, integrative and responsive, but lacking any internal representations or goal-directed behaviour [6–9]. But new experimental research, mostly on Hymenopteran insects, provides evidence for some forms of cognition in insects that have previously been thought to be restricted to a few clades of vertebrates only. Below we discuss these, and how they are changing perspectives on the capacities of the insect brain.

## Spatial navigation

Some of the cognitive demands confronted naturally by insects become clear when one considers the challenges faced by their spatial orientation. Some parasitoid wasps, for example, tend multiple, carefully hidden nests simultaneously, and store memories about the quality and recency of the provisions that have been stored in each nest [10,11]—that is, they know the *what*, the *where* and the *when* of the storing events, which is qualitatively equivalent to 'episodic-like' memories in food storing birds [5] (though perhaps not quantitatively in terms of the numbers of locations memorized). Pollinating insects sometimes have to remember multiple foraging locations and link them in a sequence that minimizes travel distance and time [12]. Recently, harmonic radar tracking has been used to record the natural foraging behaviour of bumblebee workers over their entire foraging career [13•]. Every flight ever made outside the nest by some foragers was recorded [13•]. The data reveal, at an unprecedented level of detail, how their behaviour changed with experience. Bees' careers invariably began with exploration flights—looping flights covering a large territory around their nests (Figure 1), interspersed with the probing of floral food sources [13•]. (In recent laboratory work, it was found that such loops take place in three dimensions, when bees know that targets can vary in height rather than just along a horizontal plane [14].) Exploitation of learned resources took place using straight flight paths [13•]. Even after bees had familiarised themselves with some floral patches, further exploration flights were made throughout the bees' foraging careers [13•]. Bees showed striking levels of variation in how they explored their environment, their fidelity to particular patches, ratio of exploration to exploitation, and duration and frequency of their foraging bouts. One bee visited a single patch exclusively for six days before abandoning it entirely for another location; this second location had not been visited since her first exploratory flight nine days prior, suggesting exceptionally accurate long term memory [13•]. Other bees showed more frequent switches between exploration and exploitation, and such

**Figure 1**

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exploratory activity helps optimize existing foraging routes as well as to incorporate novel foraging destinations into their routes [15]. These observations lend further support to the notion that variation in behaviour (even in highly experienced individuals) is not noise or the result of errors, but constitutes an active probing of the environment, with interindividual variation for such activity being a direct predictor of problem-solving abilities [16,17].

Recent modelling has shown that even a strongly simplified interpretation of the insect mushroom body circuit can store a very large number of visual panoramas, and navigate between them in a highly efficient manner [18]. New experimental work shows how insects use landmarks and segregate visual scenes around them into recognizable components to enable reliable navigation [19•,20] and how it might be mediated on a neural level [21,22•].

## Selective attention

Selective attention refers to the capacity of a nervous system to selectively up-weight processing of stimuli that are of greatest relevance. There is a long history of work on the mechanisms of selective attention to visual stimuli in vertebrates. However, evidence from behavioural, optogenetic, and electrophysiological studies of bees and flies has now built a convincing case for attentional processes directing behavioural choices in insects [23–25]. The small brains of insects might constrain attentional resources to the point that they can only search for targets by scanning the scene sequentially rather than taking in the entire visual surroundings simultaneously [23,26••]. Taking together the evidence from bees and flies, neural correlates of attentional processes have been found in almost all of the regions of the insect brain involved in visual processing and learning: mushroom bodies, central complex, anterior optic tubercle, lobula and medulla [22••,27,28,29•,30], leading to the proposal that in a brain as compact as that of an insect selective attention seems to be a brain-wide phenomenon achieved by coordination of region-specific processing into larger and unified functional assemblages [25,31]. In honey bees, electrophysiological correlates of attention to a visual stimulus recorded from the medulla slightly preceded the bee turning to fixate the visual stimulus, suggesting that attentional processes could be causal, as well as consequential of behavioural choice [32•]. It appears that the small brains of insects might limit representational and attentional capacity, meaning rather than taking in entire visual scenes simultaneously and at a glance (Figure 2), there are tighter links between action and perception, forcing insects to scan scenes for salient features sequentially [26••,33].

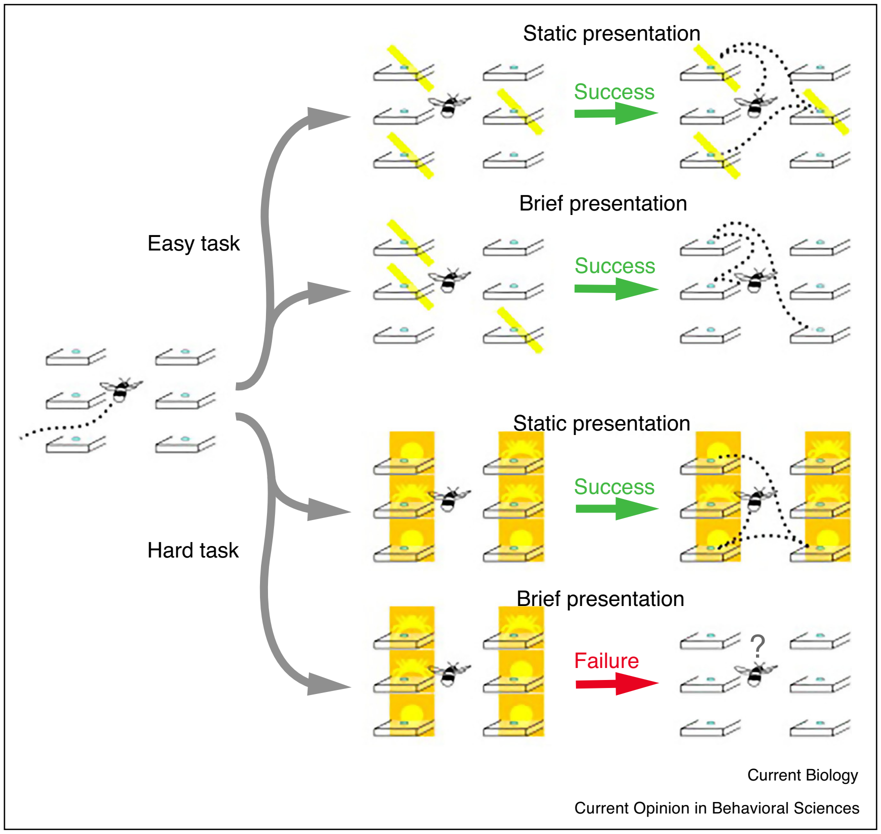
## Social learning and cultural transmission

The organization of interactions in social insect colonies was long thought to be orchestrated by a rich repertoire of instinctual routines, but little importance of learnt behaviour. In this view, social insect societies were viewed as fundamentally different from, for example, those of primates, where individual recognition is viewed as part of the glue that holds societies together. This perceived dichotomy has eroded somewhat since it was discovered that in some social wasps with small colonies, individuals learn the distinct facial features of all colony members, and associate them with the position of an individual in the colony's hierarchy, which in turn is determined by each individual's fighting skills [34]. While it is likely that the depth and detail of information that many primates store about group members exceeds that in wasps, the actual qualitative and quantitative differences remain to be determined.

In some cases, fascinating interactions exist between innate behavioural routines and learning. In the 'dance language' by which honeybees can learn from one another about locations of profitable food sources; while the symbolic code is innate, the information is learnt by 'dance followers' and subsequently applied in spatial and temporal removal from the act of picking it up [35]. This 'language' is also used when a swarm of honeybees searches for a suitable new cavity in which to reside [36]. In what has been discussed as equivalent to democratic decision making, there is initially a lot of disagreement between scouts advertising potential locations. But in a process equivalent to the 'hill-climbing' properties seen in cumulative cultural processes, the swarm as a whole progresses gradually from poor or mixed-quality information (and dissent across the swarm) to the ideal location – and finally complete agreement across the swarm for the best possible location [36] – a unique consensus building process that is however largely driven by innate behaviours, where learning is restricted

**(Figure 1 Legend)** Life-long radar tracking of bumblebee spatial foraging behaviour. **(a)** A bumblebee worker with a lightweight (15 mg) harmonic radar transponder attached to its back (photo by L. Chittka). **(b)** The figure shows all 156 flights that a single individual ever undertook during its foraging life of 12 days, before it disappeared on a regular foraging flight, presumably as a result of predation. Colour of the flight path marks the sequential position of the bout since the bee left the nest. Flights start in green, progress through yellows and oranges and the end of the foraging career is shown in red. Dashed grey lines join radar observations more than 30 s apart where the location of the bee is uncertain. Exploration flights (on the first day of the foraging career, marked green) involve loops covering a large area around the nest, and repeatedly looping back through the nest location (blue dot). During these explorations on day 1, the bee discovered two patches, North and Northwest of the hive. It subsequently visited the Northwestern location exclusively for several days, before switching to the Northern location and exploiting that site exclusively for the final days of its life. Reproduced from Ref. [13], with permission.

**Figure 2**

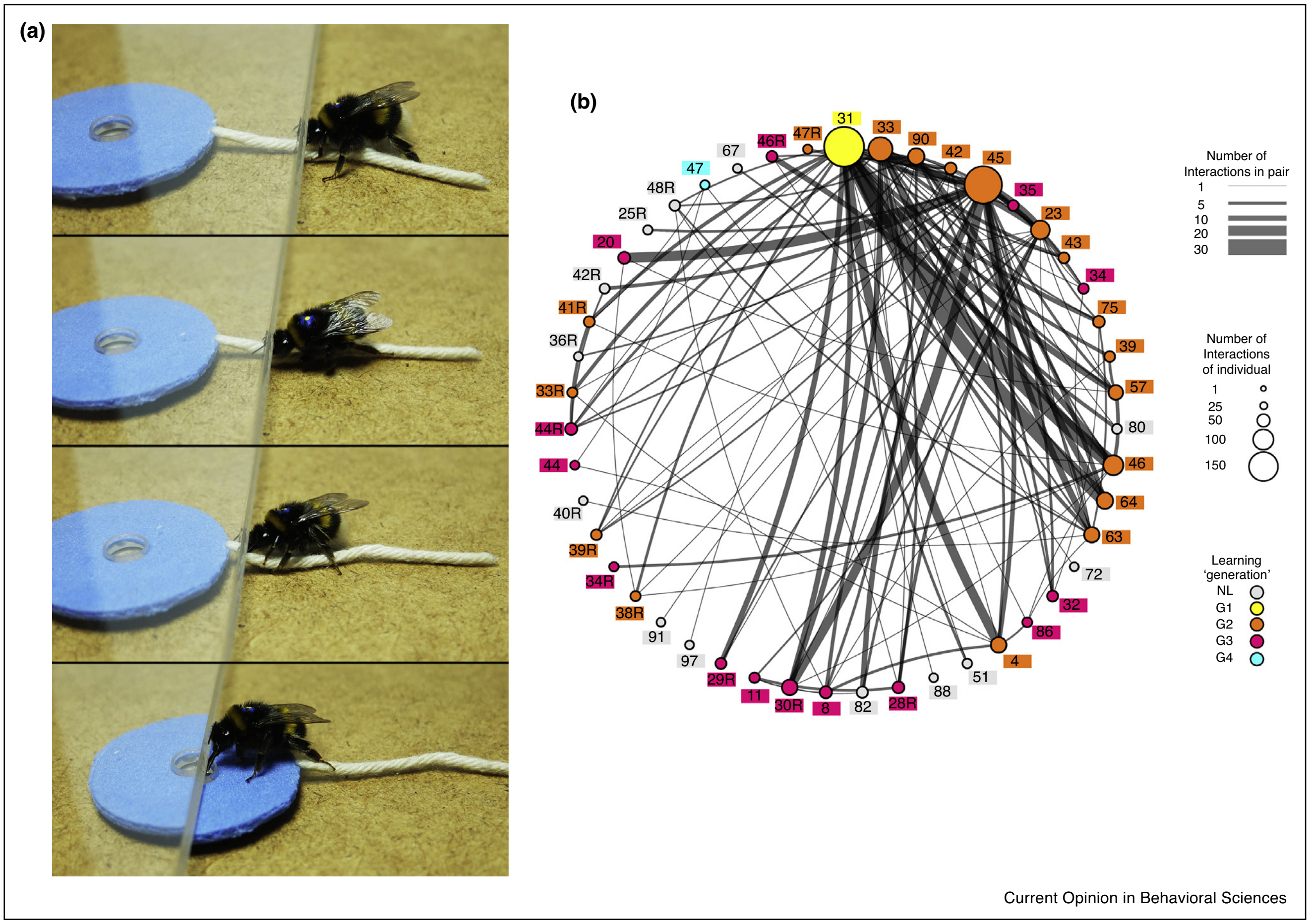


Can bees see at a glance? A fundamental difference between bee vision and primate vision is revealed when stimuli are flashed at increasingly short durations. While primates can spot salient details in a visual scene at a glance by parallel processing, bumble bees require a longer view to solve a more complex visual pattern task than a simple task. Bees were trained to six perches, three of which offered sucrose reward and three of which offered quinine punishment. Bees could successfully solve a simple task (such as locating a yellow diagonal bar marking the sucrose perches) when given either long or brief (25 ms) presentations of the diagonal bars (upper right). For a harder discrimination (such as discriminating a circle-marked sugar feeder and a spider shape-marked quinine feeder) bees could only solve the task when given a static presentation of the visual stimuli (lower right), indicating that active scanning was required for the resolution of shape. Reproduced from Ref. [24], with permission.

to predictable information content about locations and cannot be used for other contexts.

Bees can also learn from other pollinators which flowers to visit, and the techniques by which nectar can be extracted, even when naïve individuals observe knowledgeable demonstrators from a distance [37,38••]. Such social learning generates an opportunity to explore how group-specific behaviors spread from 'innovators' to others in the group. In a recent study, it was first explored whether bumblebees can learn a non-natural object manipulation task by using string pulling to access a reward in an artificial flower under a Plexiglas table [38••]. Only two of some hundred individuals 'innovated' and pulled the flower from under the table spontaneously. Most naïve bees, however, learnt the task by observing a trained demonstrator. Such learning relied on associative mechanisms, whereby observers were drawn to the site where they had observed a demonstrator, and subsequently figured out the technique by individual trial-and-error learning. In cultural diffusion experiments, the skill spread rapidly from a single trained bee to the majority of a colony's foragers [38••]. It was found that there were several sequential sets ('generations') of learners, so that previously naïve observers could first acquire the technique by interacting with skilled individuals and, subsequently, themselves become demonstrators for the next 'generation' of learners, so that the longevity of the skill in the population could outlast the lives of informed foragers (Figure 3). This suggests that a basic toolkit of associative and motor learning processes suffices for the cultural spread of foraging techniques. Recently, it has also been discovered that ants [39] and bumblebees [40] move unattached objects ('tools') from one location to another to gain reward (or indeed to transport it). In bumblebees, the social spread of the 'tool use' technique cannot easily be explained in simple associate terms: rather than simply copying an observed technique,

**Figure 3**



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String-pulling in bumblebees, and its cultural spread. **(a)** The image series shows the sequential steps of an experienced bumblebee forager pulling a string in order to gain access to a blue artificial flower placed under a transparent Plexiglas table (photos by Sylvain Alem). **(b)** The spread of string pulling in a bumblebee colony. Numbers (and number letter combinations) are bee identifiers. Nodes represent individual bees with node size indicating how many interactions each individual had with other individuals. Lines link interactions between individuals with line thickness indicating number of interactions in a dyad. Node colour and number background colour indicate learning 'generation'. The first individual trained to string-pull is marked in yellow and at 12 o'clock (G1). Bees that began to string-pull after first interacting with the 'yellow bee' are marked orange (G2). Bees that began to string pull after first interacting with orange bees are marked pink (G3), and bees that began to string-pull after first interacting with pink bees are marked blue (G4). In short, after a bee learned to string-pull, its designated generation was one higher than the highest generation it had interacted with prior to learning. Bees that never learned the task are marked grey (NL: non-learner). Reproduced from Ref. [34].

observers spontaneously improved on the strategy displayed by a demonstrator [40].

## Emotion-like states

Conscious emotions are directly accessible only in humans, but emotion-like states can be inferred in other animals as subjective states, underpinned by physiological, behavioral and cognitive phenomena that affect animals' behaviour in a variety of contexts, and which are triggered by appraisal of environmental situations [41–44]. For example, Bateson *et al.* [45] showed that bees that were previously trained to associate one odor with reward and another with punishment, and subsequently shaken vigorously were more likely to classify ambiguous stimuli as predicting punishment. In humans, this negative cognitive bias reliably correlates with negative emotions. Fruit flies, when exposed to stressful events that are beyond their control, will display a state similar to 'learned helplessness' in humans with decreased locomotion and more frequent episodes of resting [46].

Perry and co-workers [41] broadened this scope to positive emotions in bumblebees. Bees were trained on a go/no-go task where they learned to approach a rewarding stimulus and avoid a punishing stimulus. Bees that received an unexpected small droplet of high concentration sucrose solution prior to a test perceived an ambiguous stimulus as predicting reward. This behavioral response generalized to an entirely different situation where bees that received the unexpected droplet of sucrose solution took less time to recover from a simulated predator attack [41]. The neurochemicals involved in the observed behaviors were the same as those known to be involved in similar emotional states in humans [41]. Accumulating evidence suggests that a variety of invertebrates display some of the behavioral and physiological responses and cognitive biases very similar to those observed in mammals, though there is no question the richness and differentiation of humans' emotional lives has no parallel in the insect world. However, given the likely adaptive value of the interaction of both negative and positive emotional states with decision-making processes, it may be unsurprising that insects possess some basic emotion-like systems.

## Metacognition

Both honey bees and bumble bees can be readily trained in a range of free-flight tasks using sugar water as a reward and quinine solution as a punishment. Honey bees will selectively opt-out of trials if they lack the information to solve them and can opt out of a trial at no cost [47•]. Bees were trained in a visual discrimination task in which they received reward for a correct choice, quinine for an incorrect choice, or could simply depart the trial without making a choice. The difficulty of the discrimination was varied, and bees opted-out more when the task was difficult than when it was easy. Bees performed poorly in the difficult discrimination trials, but if given the option to selectively opt-out of these trials their performance in the difficult discriminations improved overall [47•]. This indicates that bees did not opt out of difficult trials at random. Rather their use of the opt-out was biased toward trials they were most likely to fail at. In vertebrate studies this has been interpreted as behavioural evidence of animals adjusting their choice behaviour according to their certainty of success [48,49], which meets some operational definitions of metacognitive behaviour [50,51]. The question of whether the type of behavior demonstrated by bees (and other animals) in this assay is the result of metacognitive processing or simpler associative mechanisms remains open.

## Complex cognition in insects: what are the limits?

The experimental studies highlighted above suggest that some insects are capable of cognitive capacities that until recently have been considered the preserve of the much larger brained vertebrates. An oft-touted argument for the limitations on insect cognition are that their miniature brains simply do not have enough neurons to support cognitive capacities that parallel those of vertebrates [52]. But in parallel to the behavioural demonstrations of insect's cognitive capacities described above, neural network models of various kinds have emphasized how even outwardly complex cognitive tasks can sometimes be resolved by relatively simple and compact circuits [18,53••,54]. Even consciousness-like phenomena, such as foreseeing the outcome of one's own actions, could be mediated with neuron numbers so low that they could easily be accommodated in insect brains [55]. Indeed it is now clear that insects have the behavioural capacity to make such inferences at least over short time scales, with the neuronal mechanisms being explored for such fascinating behaviour routines as dragonflies intercepting their rapidly moving prey [56], or flies suppressing the perception of motion during self-generated (intentional) movements [57].

Taken together, these findings do not just call into question the notion that large brains are required for *any* cognitive capacity: in neural-computational terms, the task that requires a large brain remains to be discovered. Before we have well-founded hypotheses about the minimal circuits required for a particular type of cognitive operation there is little mileage in quantifying such correlations [58,59]. This is all the more so since there are multiple ways of measuring brains to choose from, and measures of cognitive capacity are equally ill-defined—in such an environment, it is almost impossible *not* to find correlations.

It is clear that there are some abilities in, for example, apes or corvids that do not have an equivalent in insects. It is quite possible, for example, that bees lack a theory of mind. But without information about the required circuitry for such mental perspective taking, it is impossible to conclude whether the reason for its absence in bees is that their brains are prohibitively small, or simply that there has been no selection pressure for it.

While it is tempting to explore ever more human-like types of cognitive operations in insects and other animals, the field of comparative cognition needs to move on to discover the neural underpinnings of cognition. The same cognitive capacity might be mediated by entirely different neural circuitries in different species, with a many-to-one mapping between behavioural routines, computations and their neural implementations. In fact, before we can understand a cognitive operation as a circuit function we should be wary of rating them as 'higher' or 'lower' forms of cognition.

Insect brains are not simple. Numbers of neuron types and connectivity can give better estimates of computational complexity than neuropil sizes or neuron numbers. For example, a *Drosophila* brain, small in comparison to a bee's [60], may have only 100 000 neurons, but it has an estimated 10 000 000 synaptic connections between neurons [61]; not a simple network by any measure. There are >150 identified types of neurons in just its visual periphery (the ganglia lamina, medulla and lobula) [62] and there might ultimately be well above 250 (Michael Reiser , personal communication); the human retina, with its billion neurons, may have only 80 distinct types [62]. The insect lobula contains so-called hypercomplex cells, comparable in complexity to advanced orientation-sensitive neurons in the mammalian visual cortex [63].

Nonetheless, insects' nervous systems of course have orders of magnitude fewer neurons (and connections between them) than many vertebrates, and the establishment of connectomes (brain-wide wiring diagrams) [64] and a tight link between identified neurons, circuits, and functions, might therefore be an easier task in an insect, than for example a rodent, or indeed a human. The mechanisms supporting cognition in insect brains will give a very valuable comparator for the larger brained vertebrates.

## Conflict of interest statement

Nothing declared.

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