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Current Opinion in Behavioral Sciences

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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Current Opinion in Behavioral Sciences 2017, **16**:1–8

This review comes from a themed issue on **Comparative cognition**

Edited by **Ben Hayden** and **Jessica F Cantlon**

http://dx.doi.org/10.1016/j.cobeha.2017.05.011

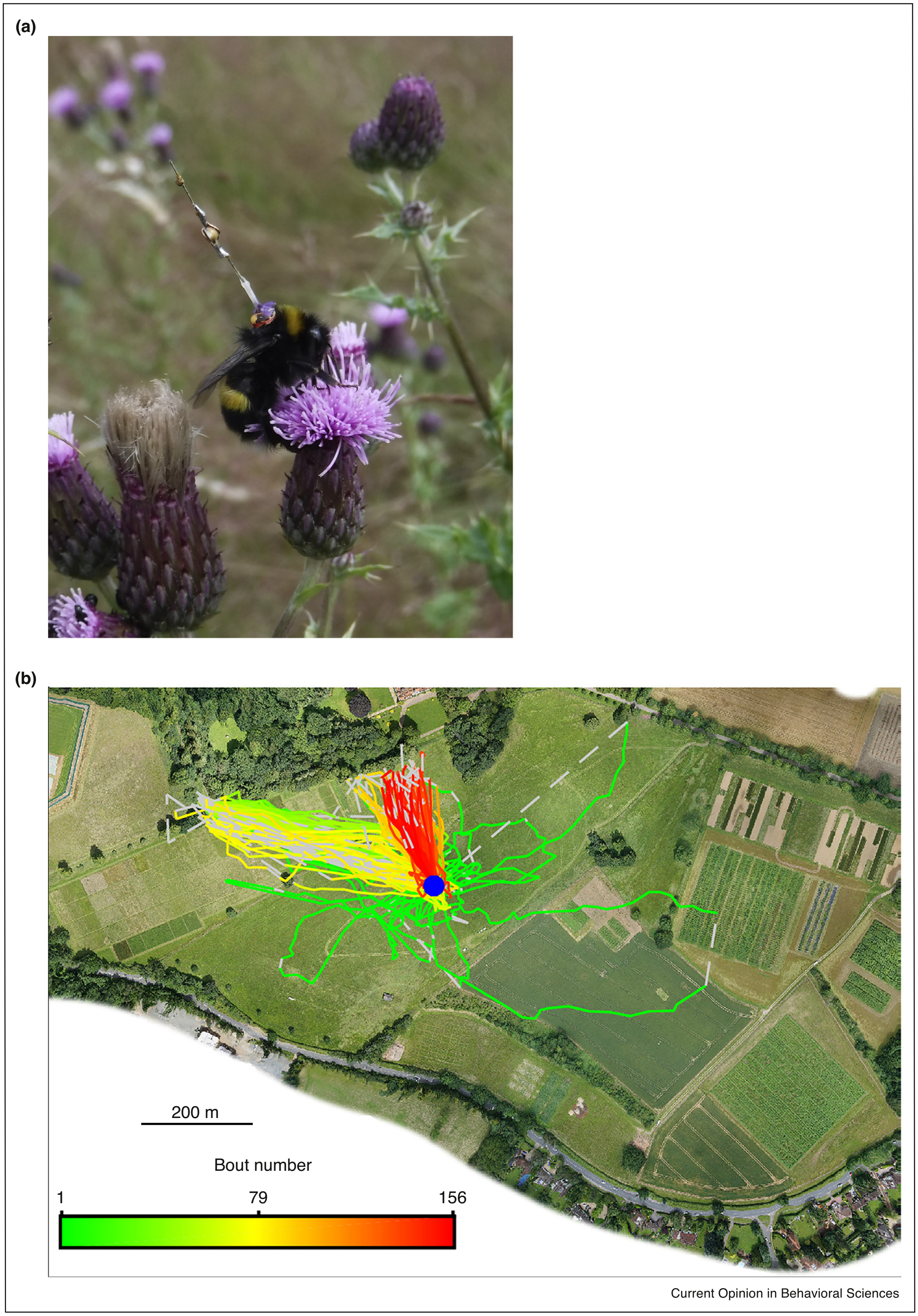
Introduction

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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