Review

Cognition in insects

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A traditional view of cognition is that it involves an internal process that represents, tracks or predicts an external process. This is not a general characteristic of all complex neural processing or feedback control, but rather implies specific forms of processing giving rise to specific behavioural capabilities. In this paper, I will review the evidence for such capabilities in insect navigation and learning. Do insects know where they are, or do they only know what to do? Do they learn what stimuli mean, or do they only learn how to behave?

Keywords: insect; robot; perception; learning; navigation

1. INTRODUCTION

The interaction of organisms with environments, to survive and reproduce, often involves rich and complex internal processes. The term ‘cognition’ is sometimes extended to embrace all such processing; yet at the same time, a more specific set of capabilities are usually implied. The obvious ability of insects to survive and thrive, which clearly depends on non-trivial neural circuitry, is not usually considered sufficient alone to conclude that they are cognitive creatures. Rather, evidence is cited for ‘higher level’ capabilities such as concept learning and cognitive maps [1], although at times it is taken to be sufficient to show they have more basic abilities such as associative learning, integration across sensory modalities, choice behaviour or, in general, the ability to act as more than reflex machines [2]. On the other hand, opposition to attributing cognition to insects can arise because it is taken to imply capabilities for which there is little or no evidence in insects, such as rational planning.

Owing to these widely varying conceptions of what ‘cognition’ implies, it seems unlikely that a clear demarcation of cognitive from non-cognitive is possible. Nevertheless, some capabilities seem more obviously cognitive than others. The label is perhaps not so important as is the identification of particular kinds of neural mechanisms that support particular kinds of capabilities of organisms to act in the world. A key type of mechanism, that aligns well with traditional conceptions of cognition [3], is an internal process that simulates or models some process in the world. This will improve the animal's functional interaction with that process by facilitating prediction and anticipation, or allowing it to align behaviour to some critical state of the world while not in direct sensory contact with it. Moreover, the internal simulation might be used in multiple flexible ways in behaviour. This in turn suggests the animal knows something about the state of the world, not just what to do— one might say that cognition involves declarative as well as procedural knowledge.

My main aim in this study is to discuss the extent to which evidence from insect behaviour and neurophysiology is consistent with the assumption that they are, at least sometimes, using internal simulation. This evaluation is grounded in a modelling approach, where hypothesized neural mechanisms are replicated in the form of embodied behaving robots. Building a real device that replicates an animal's behaviour is a strong demonstration of the sufficiency (although not the necessity) of a particular mechanistic hypothesis [4]. Using a physical robot enforces consideration of the physical dynamics of sensing and action, which can often provide complementary insights, and sometimes rather direct solutions. For example, the apparent choice behaviour by a female cricket for males with songs closer to the species-specific carrier frequency was replicated on a robot without any internal mechanism for evaluating or comparing songs, by copying the pressure difference receiver functionality of its peripheral nervous system [5].

Both the target of insect behaviour and the method of robotic implementation are strong motivations for considering non-cognitive explanations as the default: a small brain and an efficient implementation call for simple sensorimotor shortcuts if these will suffice to produce the behaviour. As a consequence, they can help us to sharpen and enrich our criteria for inferring internal simulation, in ways that might be useful for comparative cognition in general.

However, to avoid misunderstanding, I will first clarify what I mean by internal simulation (§2), in particular to distinguish this idea from the (mistaken [6]) tendency to think of all neural activity that is influenced by processes in the world as representing the world. I will then focus on two examples of insect behaviour where there is current active discussion over cognitive versus non-cognitive interpretations: navigation (§3) and learning (§4).

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One contribution of 14 to a Discussion Meeting Issue 'Animal minds: from computation to evolution'.
2. NOT ALL NEURAL PROCESSING IS COGNITIVE PROCESSING

Nervous systems have a crucial and adaptive property that underpins, but does not (in my view) constitute cognition. This is the ability to transduce a variety of forms of environmental energy into a common form (electrochemical), carry out complex transformations on this pattern of inputs, and ultimately produce outputs that guide in minute detail the mechanical motion of a body. We should not forget, in admiring this arrangement, how important are the contributions of the physical transducers and their configuration, and the body itself, to the final success of this system. Nevertheless, neural activity as a common mediator between diverse inputs and outputs makes possible complexities of operation far beyond that of direct energetics or mechanics. An obvious parallel is the complexities of operation far beyond that of direct feedback systems, but not all feedback systems are cognitive. A neural circuit that uses the difference between internally and externally generated signals to produce behaviour that reduces the difference between them need not be anticipating that its action will achieve a desired goal. The robot cricket mentioned above will reach a singing male cricket but has not predicted that it will do so.

Yet at least some neural processes in some organisms (such as ourselves) do seem to be actively simulating external processes: for example, to predict the likely outcomes of several alternative sequences of actions before actually executing any of them. But does interpreting brain processing as simulation have explanatory power for any simpler behaviours than explicit planning?

There are at least three ways in which even insect brains may need to implement neural mechanisms that track and predict processes in the world. The first arises from the need to distinguish stimuli caused by its own behaviour from stimuli with an external cause, for which one solution is to use efference copy. That is, when a motor command is sent to the muscles, a copy of the command can be sent via an internal neural loop to the perceptual system to prepare it for the environmental feedback the execution of the command should produce. This process requires, in principle, that the internal loop models the external loop through the world that produces the feedback [8]. The need for a brain to use efference copy can arise directly from the need to integrate reflex behaviours that might otherwise conflict: for example, to over-ride visual stabilization reflexes when orienting to sound [9,10]. I have discussed the application of these ideas to insects elsewhere [11] and for brevity will not further discuss them here.

A second case is when a sensorimotor response is modulated with respect to the animal’s current interest in the distal stimulus rather than in the proximal stimulus. For example, female crickets do not always respond to the calling song of males, particularly not after they have already mated, but also, for example, in situations where the predation risk of moving through uncovered territory towards the male would be high. This observed behaviour could have alternative mechanisms: movement towards male calling songs could be a fairly direct reflex that is gated by other factors such as hormones released after mating or in response to threat; or the sound could be interpreted by the female as predicting the presence of a male, and the decision to approach be dependent on the current motivation to mate balanced against conflicting motivations. Importantly, these suggest different neural circuitry (in fact, in so far as there is neurophysiological evidence, the simpler gating mechanism is better supported for crickets [12]). The implication is that a cognitive interpretation of a behaviour (e.g. that the female cricket ‘knows a male is present but decides not to approach’) is not just an arbitrary descriptive convenience, but might strongly affect how we subsequently investigate the underlying mechanism. This will be discussed further below in the domain of associative learning (§4).

A third example is when control of the action may involve a complex and subtle combination of...
3. MOVING TOWARDS THE COGNITIVE IN INSECT NAVIGATION

Consider a desert ant *Cataglyphis* homing to its nest. From a short distance away, the nest emits a distinctive odour, carried by the wind. The ant can orient upward and find the odour source, i.e. its nest [13]. This involves perception, recognition of the odour, combining olfactory and wind-mediated tactile inputs, and controlling a complex body. However, throughout its action, the ant is directly connected to the relevant sensory stimuli that indicate the nest location.

Desert ants are famous for being able to do long-range navigation in the absence of chemical trails which evaporate in the desert heat. One well-explored mechanism used by the ant is path integration [14,15]. This is usually described as the maintenance of an internal ‘home vector’ that indicates the direction and distance of the nest; updated constantly as the ant moves around its environment, using a mixture of external, proprioceptive and efferent copy cues as to the speed and direction of motion. The ant appears to be tracking the nest location while not in any direct sensory contact with it.

The state of the ant’s ‘knowledge’ of the home location can be examined by allowing it to find food (so it is motivated to return to the nest) and observing that it will then perform a relatively straight run of an appropriate direction and distance. This use of the home vector can be separated from other possible navigation cues (e.g. moving towards a visible landmark at the nest) by relocating the ant to a new area before it is released, and recording the direction and distance it runs before it begins to search for the nest. In fact, ants (in this case, the Australian desert ant *Melophorus bagoti*) tested this way do not necessarily and automatically run off their entire vector, but can be influenced by the unfamiliarity of the environment [16], and the extent to which different species are so influenced may depend on the visual complexity of their normal habitat [17].

Currently, almost nothing is known about how this capability is neurally implemented. However, several alternative ‘plausible’ neural models have been proposed. A model we have explored [18] is shown in figure 1. The basic principle of operation is as follows. The ant is assumed to have directionally sensitive units (D) that are excited when it runs in a particular compass direction (analogous to rat head direction cells). Ants are known to use the polarization plane of the sky as a compass cue, and an orderly arrangement of cells responding to particular directions of polarization has been found in the brain of several insects, to date [19,20]. In our model, the activity of each unit is summed in memory units (M) as the ant progresses on its path (this could be implemented as resonance in recurrent circuitry in the insect polarized light circuit). When the ant finds food, the simultaneous activity of memory units and the directional units activate the steering units (S) which will collectively drive the ant in the global direction that is the integral of its outwards path, in other words, along a home vector.

Is this a neural process that tracks the home location? This mechanism allows the ant to get directly home after traversing arbitrary outwards paths, and would also allow it to deal with any forced detour on the return. It would not, however, support any more flexible use of the implicit ‘home vector’ contained in the unit strengths. An ant that returns home using this mechanism has lost the information (as the activity in each memory unit is discharged as it moves in the opposite direction). Yet, there are several reasons to think that ants can use their home vector more flexibly in their behaviour. For example, on reaching home and depositing the food, they can run back out directly to the place where food was found [21]. While most reports of such behaviour do not rule out the use of additional cues such as visual surroundings, evidence that outward paths are under vector guidance comes from studies where ants were forced to detour on their outward journey and would then take an appropriate (novel) corrective direction towards the food source location [22]. It is as though the food location relative to the nest (the home vector at the time of locating food, or the path traversed from the food back to the nest) has been stored and can be recovered and inverted at the nest, to guide the ant back to the food location [23].

Ants also use visual memories to home, but so far the evidence suggests that they do not entirely fuse their home vector and visual memories, though these systems may interact. For example, *Melophorus bagoti* will follow a learned visual route from any point along it, whether or not the path integrator indicates that they should already be home [24]; but on the other hand visual learning in *Cataglyphis cursor* is affected by whether they perceive their home vector to be increasing or decreasing [25]. One recently reported interaction between these capacities is that, when the visual environment is changed, *Ocymyrmex* will turn back and look in the direction of their nest entrance [26], presumably to re-learn the visual scene. In this case, the actual entrance is not visible; so they must be using home vector information to orient towards it. That is, the home vector, or at least its directional component, is being used for something other than homing.

Further flexible use of the home vector can be seen in other animals that also use path integration. Perhaps most impressive is that bees are able to express the vector indicating the food direction in a completely different motor form, the dance; and other bees can interpret the information in this form and use it to guide their subsequent flights [27].

Evidence from bees suggests that, during learning flights, they additionally associate home vectors with specific views of the environment, and (if displaced) are able to recover the relevant vector when they re-encounter the view. They may even be able to combine vectors to traverse novel routes [28]. For example,
if a bee emerging from the hive to follow a specific vector to food is displaced to another location, but recognizes where it is and recovers a home vector, then adding these two vectors will point from the new location to the food. Bees appear to be able to make such novel journeys from the new starting point to the food [29], though it is still in debate whether some simpler underlying mechanism than vector addition, or a cognitive map, could account for such journeys [30].

Another arthropod that maintains a home vector is the fiddler crab. Crabs evade predators by retreating to a burrow. The entrance to the burrow is inconspicuous, but foraging crabs use path integration (believed to be based mostly on ideothetic cues) and are able to move quickly and directly in the burrow direction when disturbed [31]. Interestingly, they also appear to be able to anticipate when another crab is moving towards their burrow, and will retreat to defend it [32]. Again, one interpretation of this capability is that the crab can do vector addition, this time to calculate the distance of the intruder from the burrow by combining the home vector and the distance and direction from the crab to the intruder. Yet, it remains possible that a simpler more reactive solution is used; that the home vector modulates sensitivity to other crabs in regions of the omnidirectional visual field that correspond to relative positions in which the attacker would be closer to the burrow than the defender [32]. Nevertheless, this still implies that the home vector is being used for more than just homing.

It is possible to imagine how at least some of these behaviours could be implemented by extensions of the simple neural model described already. The main addition required would be to add a storage mechanism, that is, the state of the home vector can be preserved either at crucial times (e.g. when food is found) or associated with other sensory inputs (e.g. the surrounding visual scene). The state of the home vector might also be allowed to modulate other behaviours, such as the sensitivity to predators. But is the addition of memory alone enough to make a mechanism cognitive? Or the fact that it can be used by more than one behaviour, which may have been a simple co-opting of one neural circuit by another in evolution? These animals do seem to be tracking, internally, the distance and direction to a target in the world, their nest, with which they have no direct perceptual...
contact; and this tracking is more than just an implicit behavioural disposition to return to the nest. In a sense, it is not important what degree of memory or flexibility of use is the cross-over point to cognition; each of these adds to the competence of the animal in an interesting way. High-level cognition may involve the meta-level ability of the animal to realize, in the abstract, that it has a piece of information, perhaps assess the reliability of that information, and work out how to reuse it in really novel ways. So far, this seems beyond the capabilities of insects.

4. IS INSECT LEARNING COGNITIVE?

A *Drosophila* larva essentially lives to eat. If one odour is repeatedly paired with a sugar substrate, and another is not, it will start to preferentially approach the first odour. If the pairing is with a quinine or high salt substrate, it will start to avoid the odour. This seems a straightforward example of associative learning as found across most species of animals: an unconditioned stimulus (US) that innately evokes an unconditioned response (UR) when paired with a conditioned stimulus (CS) comes to evoke a conditioned response (CR). Yet even for the larva, it is not entirely clear exactly what is associated with what, inside the animal, that leads to this external change in behaviour. Some interpretations of conditioning imply internal (cognitive) states that track a process in the world, such as contingency between events (the larva detecting an odour can predict food and thus behave appropriately). Yet it is often argued that if a ‘simpler’ associative explanation can account for an observed behaviour, it is best not to assume a ‘cognitive’ interpretation, implying that basic associative mechanisms are not cognitive.

Considering this problem from the point of view of a robotic model may be useful. The question to be answered is not so much about how ‘storing’ and ‘recovering’ of memory traces occurs, but rather, how a stimulus comes to evoke a different response than it did before it was paired with a reinforcer. In particular, if this can be explained simply as the strengthening or weakening of direct, reflex-like, connections from the stimulus to the response (the larva’s experience of the pairing has modulated its innate tendency to approach or avoid the odour) then I would argue it does not constitute an example of internal tracking of a state of the world while not in contact with it. The behaviour may successfully ‘anticipate’ the currently absent food, but not because the larva internally anticipates it.

Does the evidence support this simple explanation for the larvae? It is worth noting that, unlike instrumental learning, there is no direct explanation for why a particular stimulus–response connection should be strengthened in Pavlovian conditioning. In an instrumental paradigm, one can hypothesize that the occurrence of reward or punishment will increase or decrease the strength of whatever CS–CR pathway was activated immediately prior to its occurrence. But in Pavlovian conditioning, the animal will continue to experience the rewarding or punishing substrate during the pairing irrespective of its behavioural response to the CS. Indeed, it has been noted that ‘In terms of the actor–critic model’ [the most successful computational model of reinforcement learning] ‘there is no justification for the performance of CRs at all’ in the Pavlovian paradigm [33, p. 288].

But what about ‘stimulus substitution’? Does not the CR simply come to drive the same behaviour as the US because a connection from the CS to the internal pathway normally activated by the US has been strengthened? In fact, it has long been recognized [34] that a problem with such an account of Pavlovian conditioning is that the CR often does not clearly resemble the UR. In the case of the larva, it is immediately evident that the CR—chemotaxis towards an odour—is not identical to the UR—attempted ingestion of the food substrate. But the difference can be even more strikingly illustrated by the following case [35]. *Drosophila* larvae find low levels of salt attractive, but higher concentrations become aversive. When salt at a concentration just above the aversive threshold is paired as a US with an odour the difference can be even more strikingly illustrated by the following case [35]. *Drosophila* larvae find low levels of salt attractive, but higher concentrations become aversive. When salt at a concentration just above the aversive threshold is paired as a US with an odour the difference can be even more strikingly illustrated by the following case [35].
This clear difference between CR and UR becomes less surprising when we consider what is currently known about the neural pathways involved in *Drosophila* olfactory learning. Odours are detected by olfactory sensory neurons that innervate the antennal lobe. From there, projection neurons follow two pathways, to the lateral horn which is thought to be a relatively direct route to the motor system, and to the mushroom bodies, where they synapse onto Kenyon cells [37]. The clearest evidence for the site of learning is at the connection of Kenyon cells to mushroom body extrinsic neurons [38]. These output neurons project in turn to the lateral horn and other potential premotor areas [39]. In short: 'The MB model of olfactory short-term memory in *Drosophila* [Heisenberg 2003] proposes that output synapses of the KCs representing the CS+ increase their gain in the course of conditioning to drive an MB output neuron (CR)' [40, p. 15988]. Strengthening occurs when the Kenyon cell activity coincides with the release of aminergic neuromodulators in response to the reinforcer: at the molecular level, this involves a PKA/cAMP cascade [41]. In odour–taste learning, the modulatory signal comes from the subsesophageal ganglion where octopaminergic neurons are activated by gustatory sensory neurons responsive to appetitive tastants, and dopaminergic neurons activated by aversive tastants. It has been shown that direct experimental activation of these neurons paired with odour can establish CRs of attraction and aversion, respectively [42].

It is notable that a similar basic neural circuit for classical conditioning—a US-induced reinforcement signal modulating a CS–CR pathway—is found both in simpler systems, such as tactile conditioning in *Aplysia* [43], and more complex ones, such as the cerebellar circuit involved in eyelid conditioning [44]. Importantly, there is no (need for) activation of the neurons that were originally activated by the US to control the subsequent behaviour. But is this the complete story—has the larva just acquired a new but non-cognitive sensorimotor reflex? If so, one might expect that, after learning, the conditioned behaviour would always be evoked by presentation of the CS. But in fact, it has been shown [45,46] that the expression of attraction or aversion to rewarded or punished odours in larval *Drosophila* depends on the context of the test conditions, specifically, whether or not the larva’s situation would be (predicted to be) improved by the CR. That is, a larva that is already on food does not approach an odour that has been paired with food, and whether a larva avoids an odour that was paired with high salt depends on whether the current concentration of salt is higher or lower than that paired with the odour.

An additional neural mechanism that may underlie this selectivity is that during learning, the CS itself may come to affect the reinforcement signal directly. In insects, it has been shown that the dopaminergic signal may be modulated by the CS (in bees [47], in *Drosophila* adults [48]), although it is not yet clear that this effect also includes a decreased response to the ‘predicted’ US, as would be expected if it really represented the ‘prediction error’ as has been described for dopamine signalling in vertebrates [49]. However, whether this effect has a direct role in behaviour, or instead relates to limiting the strengthening effect of the US, or supporting second-order conditioning, remains unclear. Direct involvement of dopamine neurons in modulating the effects of internal motivation on conditioned behaviour in adult *Drosophila* has been shown [50].

Such a mechanism would suggest that the larva not only learns a response to the CS, but also learns its ‘value’, and can use this more flexibly in controlling behaviour: the CR is not a reflex. The question remains as to whether the larva (or other insects) actually ever learn the contingency, i.e. to predict the specific US that occurs after the CS, rather than just that the CS is ‘good’ or ‘bad’. One way to answer this question would be to use a ‘devaluation’ paradigm ([51], see also Dickinson [52]). In rats, this involves training an association between an odour and a reinforcing flavour, then devaluing the specific tastant by pairing it with poison. In subsequent tests with the odour, the animal no longer exhibits attraction: the revised valuation of the US is immediately (without further training) transferred to the CS. To my knowledge, such a test is yet to be done on insects.

If insect associative conditioning involves (in at least some cases) ‘re-presentation’ within the animal of the US, evoked by the CS, then I would argue that this counts as a minimal example of internal simulation, and hence cognition. The external process (CS precedes US) is now being tracked by the animal to predict the US before it occurs, and this prediction is used in determining action. But note that this is a weaker criterion than that proposed by Dickinson [52] in which the system’s deployment of this prediction should be demonstrably rational, that is, have a specific role within an overall architecture for goal-directed action. There does not seem any obvious reason to suppose the components described in Dickinson’s associative–cybernetic model could not exist even in small insect brains, but nor have they yet been demonstrated to exist.

5. CONCLUSION

My aim in this paper was to argue that cognition should not be an umbrella term for all neural processing but should refer to certain kinds of mechanism supporting certain kinds of behaviour: those that require explicit tracking and prediction of external stimuli not immediately present to the animal.

Note, however, that this concept of cognition is about the mechanism rather than the behaviour *per se* (cf. [53]). As discussed already, an apparently cognitive behaviour such as relocating a nest that is no longer visible may be explained by a mechanism that does not explicitly track the nest location: the ant does not necessarily need to know where it is to know what to do to get home. Contrastingly, apparently simple behaviour such as a Pavlovian conditioned response may involve explicit internal prediction of a previously experienced contingency. Indeed, it is reasonable to expect that in different species, in different individuals,
and even in the same individual at different times, the same behavioural problem may be solved by more or fewer cognitive processes.

In both insect navigation and insect learning, the possibility that non-cognitive specialist solutions may account for the behaviour remains open. Indeed, it may often be better (in terms of both behavioural success and processing efficiency) to use such solutions wherever possible; so we might expect evolution to have exploited them. But it seems increasingly evident that some of the internal processing in insects may be predictive in an interesting sense. That is, control of behaviour is best explained by a neural mechanism that extracts and tracks an environmental regularity and uses this to anticipate the consequences of actions and thereby select between or refine them to be more adaptive. The relatively small insect brain is thus a promising place in which to further unravel the mechanisms of cognition.

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