Dispatch

Insect navigation: some memories like it hot

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Summary

Using path integration insects update direction and distance information whilst moving, but they can also retain it. Two studies now demonstrate how both pieces of information are represented in a vector memory that is susceptible to cold-induced anaesthesia.

Insects are mostly active when ambient temperatures are warmer and neuromuscular functions are not affected by variations in their body temperature. Some tolerate cold conditions better than others[1], but any insect, when cooled down for several minutes at temperatures below a species-specific critical lower threshold, falls into an immobile state that is reversible within certain time limits. Anaesthetic effects of such prolonged cooling include the disruption of neural activity in the insect's brain which can affect memory[2]. Whether a memory is cold-resistant, or whether it will be degraded and lost depends both on the duration and timing of cooling, because memory processes are dynamic. For example, honeybees will quickly learn and remember which sensory stimulus, such as a colour or an odour, is associated with an appetitive sucrose reward. However, this memory is lost if the bee is cooled immediately after learning[3,4]. Cooling key areas of the honeybee brain has similar effects which demonstrates the causal link between cold-induced anaesthesia and memory loss[5]. If cooling is delayed by just a few minutes, the memory survives. Timing the delivery of cold shocks to various intervals after training reveals when and how memories are formed and consolidated[6-8]. The method has been mainly used in the study of associative memories in insects, but two new reports by Yilmaz[9] and Pisokas[10] with colleagues explore the effect of cooling on navigational memories in experiments with dung beetles and ants. Combined with neural network modelling, this work offers interesting insights into how distance and direction information is encoded and stored as vector memory in the insect brain.

Like other insects, the African dung beetle, *Scarabaeus galenus*, uses path integration to compute and store information about the distance and direction of a habitual route. It shuttles back and forth in a straight line between the burrow and a pile of dung (Figure 1). Remarkably, it does not take notice of landmarks in the surrounding landscape, such as bushes and trees[11], which makes it a very suitable study species for investigating vector memories. Yilmaz and colleagues[9] applied cold-induced anaesthesia to manipulate the beetle's vector memory and find out whether it impairs their homing behaviour. To attract willing participants for their experiments, they just had to put out fresh dung each morning. Upon arrival, most of the beetles started to build their burrow some distance from the dung. The dung was replaced by feeders to ensure that each beetle travelled over the same distance and acquired the same level of experience with this new location. Before testing they were cooled on ice for ten minutes which was sufficient to reduce their body temperature and induce immobility. After recovery, the beetles were able to walk in the correct compass direction, but they did not cover the same distance as control animals. After one hour of cooling, the beetles were completely disoriented and walked off in different directions, showing that both types of information are affected by cooling, albeit to varying degrees.

Similarly, Pisokas and colleagues[10] found that cooling impairs activated vector memories. They tested Australian Jack jumper ants, *Myrmecia croslandi* that unlike the solitary dung beetles, forage over longer distances and live with their colony in a permanent nest in the ground. The ants travel along individually-learned routes to collect honeydew in *Eucalyptus* trees, returning many times to the same tree throughout their lifetime. Experienced foragers were caught at the base of their preferred tree and cooled for 30 minutes. Since these ants are strongly guided by the rich visual panorama with many salient landmarks around their nest[12], they were released in an unfamiliar area further away. Like beetles that were cooled for ten minutes, they initiated their home run correctly with the ants heading off in the direction that would normally take them back to their nest. The distances were shorter, however, than in controls. It is yet to be found if longer cooling results in a complete loss of vector memory or just partial impairments. The state of the path integrator is also an important factor influencing how the activated vector memory is affected, as the authors illustrate in examples from ants that were cooled after arriving at the nest. The return to the nest at the end of a foraging trip resets the path integrator, although motivational factors, such as hunger, potentially may also trigger it[13].

Going forward, it would be interesting to know how vector memories recover from cold-induced anaesthesia or change. Some observations by Yilmaz and colleagues hint to the possibility that beetles easily acquire new vector memories after cooling[9]. Beetles might not need to form long-lasting vector memories, since they exploit a location for a relatively short period of time, whilst the dung is fresh, moist and easily available[11]. It could well be that vector memories are more robust in ants, since they forage at the same location for long times. Testing them at different stages of a foraging trip could be useful to elucidate under which conditions vector memories are susceptible to manipulations.

Both studies show that vector memories depend in a time-critical manner on mechanisms that are sensitive to cooling. It is yet unknown how vector memories compare to other forms of memory in insects[10]. They could well differ in their dynamics and susceptibility to anaesthesia compared to associative memories. The fact that distance information was affected more strongly, raises the question of how information is encoded in the path integrator. When ants are simply prevented from returning home, their vector memories decay over the time course of hours and days, in contrast to landmark-based visual memories that are reliably recalled throughout an insect's lifetime[14,15]. The decay appears to be slower for directional information, as the ants remain accurately oriented for longer. The systematic difference between the distance and direction components of vector memory might suggest that they are encoded independently. However, this seems implausible since both define the shape of the homing trajectory. Here, Pisokas and colleagues emphasise that both distance and direction of the home vector can be stored together if it is encoded not in a polar but Cartesian representation[10]. This idea is implemented in a neuronal model of the path integration circuit that has been anatomically and functionally described in the central complex of the insect brain[16,17]. The home vector for the current position on the route is encoded in the distributed sinusoidal activity pattern of eight putative neuronal units, each memorising the insect's coordinate along one of eight cardinal axes. When simulating the impairment of vector memory after anaesthesia and corresponding home runs, a proportional reduction of memory values across all memory units gave the closest match to the recorded paths. Although the current findings do not allow to conclusively pinpoint the kind of changes that take place at neuronal level, the model simulates homing paths well and generates testable predictions. For now, it is evident that the prolonged interruption of neural activity during cold-anaesthesia does not cause a quick loss of vector memory. This points towards a lesser dependence on continuous reverberating activity in recurrent networks than previously assumed[10].

Further tests in which cooling is applied at various time points after training would be the next step to understand vector memory. Both species are accessible and experimentally-tractable, and thus well suited to elucidate generalisable principles and mechanisms of spatial cognition in insects. Whilst it is not possible to fully control their navigational experience, the training and test conditions could be sufficiently to uncover how vector memories are formed, activated and updated. The authors rightly suggest that species-specific differences could be found[9,10], as for instance the reliance on vector memory differs in fundamental ways between ants and dung beetles which live either in a permanent or temporary home. It is also reflects how diverse the navigational strategies of insects are, when they explore and exploit their environment in different habitats. For example, larger-sized bees can travel further away and cover a larger foraging area, which provides them with more choices of flowers and foraging locations to which to return[18]. Some questions might be difficult to examine in insects like dung beetles and *M. croslandi* ants when they preferably visit a single location. Other ants, bees and wasps can travel along different routes with multiple destinations, deal with detours or adjust segments and headings making navigational choices at both smaller and larger scales which has a number of implications for memory selection and interactions between visual and vector memories in insects [19,20]. How the central complex handles multiple vector memories in such scenarios is another fascinating area for future research.

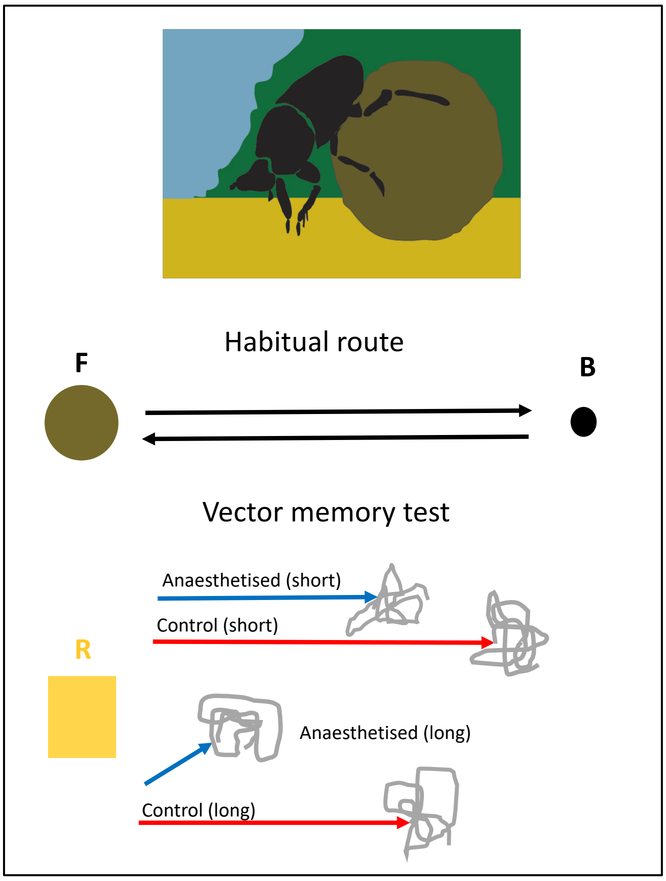

Figure 1. Exploring the effect of cold-induced anaesthesia on vector memory.

The African dung beetle, *Scarabaeus galenus*, is one of few species that collect dung. It forms a ball and pushes it with the middle and hind legs. The beetle undertakes frequent trips to collect as much dung as possible before it dries out or is contested by other competitors. To follow its habitual straight route (black arrows) between the burrow (B) and the feeding location (F), it relies on path integration as it cannot see much of the landmarks in the surrounding landscape, whilst walking backwards. Yilmaz and colleagues[9] captured experienced beetles that arrived at the feeding location and cooled them for a short and long period of time before releasing them in a test area (R). The beetles initiate a home run in the direction and over the distance indicated by their full home vector. When they fail to find the nest at the end of the home run, they start to search for it (grey lines). After cooling paths were shorter, and after long anaesthesia also disoriented (blue arrows), compared to control animals that were kept in the warm (red arrows). Note, that the longer delay to initiate the home run in the control animals caused impairment in the distance component of the home run, as also seen in ants[14] but at a faster rate, possibly indicating a weaker vector memory. Pisokas and colleagues[10] used a similar design when testing Australian Jack jumpers *Myrmecia croslandi*.

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