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Navigation: How the Recent Past Shapes Future Routes in Desert Ants

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When falling into a trap, desert ants remember the last views preceding this event and avoid them on future foraging journeys. This association of images with negative experience might be responsible for the establishment of stable routes through complex environments.

Desert ants have long been a model species for the study of animal navigation [1]. Despite their tiny brains, these animals perform navigational tasks that most human beings can only dream of [2]. Forager castes of these ants do not rely on a pheromone trail, but rather continuously compute their relative position to the nest using a polarized light compass [3] and a step integrator [4]. This so-called path integration process is, however, error prone, especially so in more cluttered environments where the ants compensate by using local visual [5] and sometimes olfactory [6] cues.

A study reported in this issue of *Current Biology* by Wystrach *et al.* [7] sheds new light on the processes that help the ants to find their way through a complex world. When travelling back and forth between their nest and a feeder through a cluttered environment, individual ants usually stick to their own stable routes [8]. Wystrach *et al.* [7] show that these stable routes can be formed by negative experiences: ants that suddenly fall into a trap — in nature this could be the trap of an ant lion, in the experiment it was a dug-in channel — remember the visual cues they shortly saw before the fall and will later avoid those cues so that they do not fall into the trap again (Figure 1).

The Tunisian desert ant *Cataglyphis fortis* and the Australian honeypot ant

Melophorus bagoti navigate individually. Back in the late 1960s, scientists became fascinated by the ability of *Cataglyphis fortis* to survive and navigate the almost empty saltpans of Tunisia. In 2005, the honeypot ant *Melophorus bagoti* entered the limelight, when Kohler and Wehner [8] were able to show that these ants exhibit extremely precise spatial knowledge of their cluttered habitat, the arid grasslands of Australia. Individual ants follow idiosyncratic routes through numerous tussocks between the nest and a stable feeder, and immediately recognize each of these tussocks when they are artificially displaced along their route. Since these early observations, many researchers have studied these ants and with every new finding it becomes even more evident how much visual information the ants can store and retrieve. While the capacity of their visual memory alone is astonishing, it has so far remained elusive how these idiosyncratic routes become established in individual ants.

Why does an ant choose a particular route at first, and under which conditions does it decide that this route is a good one and should be followed again and again? In short, how do ants learn to navigate their cluttered environment? We know that bees can learn flower odours and shapes [9] and that they can learn nest and food odours [10,11] as well as visual

cues signifying the nest entrance [12]. But in all these cases the conditioned stimulus — be it an odour or a visual sign — is temporally closely connected to a reward, the nectar or food crumb that comes together with the flower or food odour, or even the positive experience of a homing ant reaching the safety of the nest facing the nest-defining visual cues. As they make idiosyncratic routes, *Melophorus* ants do not necessarily continuously face visual cues that are temporally coupled with a reward, so their learning of routes calls for alternative strategies.

Wystrach *et al.* [7] now have discovered one of these strategies. The authors motivated honey pot ants to establish novel routes on their way back from a stable feeder, by digging in a channel perpendicular to the foraging direction of the ants that had already repeatedly visited this feeder. On their next homing run, all ants inevitably fell into this channel trap and needed a long time to find the inconspicuous exit before they were able to continue their homing run. Interestingly, during their next foraging runs the ants learned to avoid the invisible channel — they took a longer, but safer detour on their way back from the feeder. Although this of course seems to be an appropriate behaviour, it calls for a more detailed look at *what* the ants learned *when*.
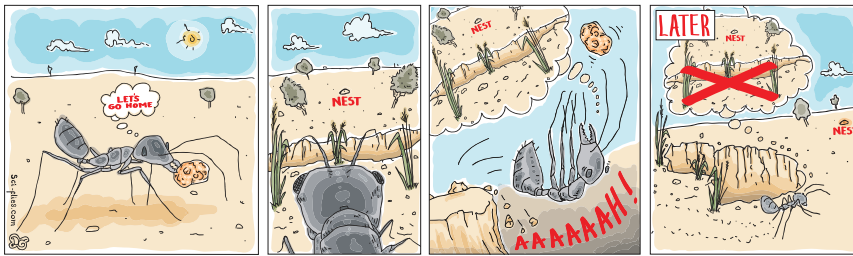
Figure 1. Ants learn to avoid cues they have seen shortly before a disaster happened.
A homing ant that falls into a trap will later remember and avoid the visual cues it has seen shortly before. This avoidance leads to the formation of a safer route back to the nest. (Figure courtesy of Diego Galagovsky; Sci-flies.com.)

As mentioned above, associating a stimulus with a reward usually relies on the two being experienced simultaneously. Wystrach *et al.* [7] show that ants can even learn to associate visual cues with negative experience of being trapped when the negative experience does not temporally overlap with seeing the cues. When the ants suddenly found themselves trapped within the channel, they were unable to see the panorama that preceded this inconvenient event. Nevertheless, the ants later used this panorama to avoid falling into the channel again. When analysing in detail the behaviour of ants approaching the channel in which they just had been trapped before, the authors observed very characteristic turns shortly before the ants reached the channel trap on their next foraging journey. This turning behaviour is known to be strongly coupled with visual learning and especially occurs when ants or bees face challenging navigational tasks [13–16]. Obviously, when reaching the channel again, the ants identified the panorama as the one that preceded the bad experience of being trapped and they then started to look for a better route.

Wystrach *et al.* [7] thus not only describe how ants establish their visual knowledge about their habitat, but recount one of the first examples of 'trace learning' [17] — a special kind of learning, where the animal continuously stores information in a so-called memory trace and only comes back to it when something really special happens. Such a memory trace is reminiscent of a vapour trail behind an aircraft that always can tell you about the last moments of the aircraft's travel but continuously 'forgets' the older parts of the planes journey.

But how far back do the ants remember their journey? Wystrach *et al.* [7] realized that, after a single negative experience in the trap, during their next foraging trip, the ants stumbled and turned a few meters before getting close to the channel trap again. They obviously associated with the negative trapping experience, not only the immediate surrounding of the channel, but also visual cues they had seen several seconds before falling into the channel. Hence, the memory trace seems to cover at least several seconds.

While this finding is very interesting, as it might explain how ants establish such complicated routes through a cluttered environment, it basically can be explained with most of the building blocks for insect learning that we know already. It is well established that associative learning in insects takes place in the mushroom bodies. In ants and bees this neuropil gets a lot of visual and olfactory input and contains numerous so-called Kenyon cells that furthermore synapse to mushroom body output neurons (MBONs), which convey positive or negative valence. An ant viewing for example the landmarks surrounding its nest might associate these landmarks with the positive feeling of being home. From what we know about the neural basis of learning from work on *Drosophila* [18] and ants [19], the positive association between the landmark-view and the rewarding nest might be formed by reinforcing synapses of those specific Kenyon cells that are activated by the view and those MBONs that carry a positive valence. Correspondingly an ant associating a specific landmark pattern with a negative experience, for example the situation of being trapped, might reinforce the connections between the

specifically activated Kenyon cells and MBONs carrying a negative valence. As ants can form such an association even when the view of the landmarks never temporally coincides with the punishment within the trap, one needs to consider some kind of short-term memory already within the Kenyon cells.

Interestingly, this trace learning turned out to be conserved in two desert ant species that are not closely related and have to deal with visually quite diverse habitats: the cluttered grassland desert of *Melophorus bagoti* and the open flat saltpans of *Cataglyphis fortis*. It would be great if similar trace learning were even conserved in insects as far related as the insect model *Drosophila*, as this would facilitate the search for the molecular mechanisms of this kind of memory.

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Symbiosis: Herbivory Alters Mycorrhizal Nutrient Exchange

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A new study shows that a plant gives less carbon to its root-associated mycorrhizal fungus when targeted by herbivores, but the fungus doesn't retaliate.

Mycorrhizae take the central stage in the terrestrial ecosystem. This interaction between plant roots and mycorrhizal fungi is arguably the most common and the most important mutualistic symbiosis in terrestrial ecosystems [1]. The roots of more than 70% of all land plant species are colonized by arbuscular mycorrhizal fungi [2], which enhance the uptake of essential nutrients, such as phosphorus. In return, plants may transfer up to 30% of their carbon fixed through photosynthesis to root-associated arbuscular mycorrhizal fungi [3]. The latter rely exclusively on plant-derived photosynthetic carbon for their survival. This bidirectional 'carbon-for-nutrients' exchange between plants and arbuscular mycorrhizal fungi has been studied in increasing detail [4]. However, the role of other interactions, such as herbivory, on resource exchange between plants and

arbuscular mycorrhizal fungi remains largely unexplored. A study by Michael Charters and coauthors [5], published in this issue of *Current Biology*, shows that a plant transfers less carbon to an associated mycorrhizal fungus under aboveground herbivory stress, while the fungus' phosphorus supply to the plant remains unaffected.

Interactions with other organisms are crucial for the development, ecology, and evolution of plants [6]. Although the importance of these relationships for the biology of plants has been well studied, these studies have primarily been restricted to cases involving only one particular type of interaction. Therefore, we still lack a solid understanding on how the interactions of plants with multiple organisms influence each other. This is particularly relevant for the mutualistic resource exchange between plants and

mycorrhizal fungi. Do plants transfer less carbon to their mycorrhizal fungi when targeted by herbivores, which act as a potential carbon sink? And how does this impact the plants' uptake of phosphorus through these mycorrhizal partners? Charters and colleagues go to the root of these questions by using a tripartite system where wheat plants associated with *Rhizophagus irregularis* — perhaps the most widespread arbuscular mycorrhizal fungus [7] — are under attack by natural enemies, in this case, bird cherry-oat aphids. Rather than assessing changes in biomass and fungal colonization intensity, which has been the standard measures of fitness in species interactions outcomes, the authors quantify how plant–aphid interactions influence the outcome of plant–mycorrhizal nutrient exchange using an isotope-tracing experiment. This is the first time that nutrient