carrying it, instead using a self-serving strategy analogous to a rat on a sinking ship [3]. It can reduce its rate of separation from beneficial alleles by suppressing recombination in fit individuals, while escaping low-fitness genomes by promoting recombination in those. Little is known about the chemical signaling between *A. nidulans* colonies that leads to hyphal fusion, beyond the involvement of genes resembling those of the MAP kinase signaling pathway that orchestrates mating in budding yeast [5], but instigating fusion with neighbours, especially fitter ones, may be one way for a rat-like allele to switch vessels.

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Animal Cognition: Multi-modal Interactions in Ant Learning

A recent study shows that desert ants use a precise behaviour, based on the internal cues of path integration, to facilitate the learning of visual landmark information. This raises fascinating questions about how insects encode familiar terrain.

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Foraging ants must return to often inconspicuous nest entrances after long journeys using their two primary navigational mechanisms, path integration and visual landmark guidance. Path integration involves the continuous integration of direction and speed information to maintain a record of current position relative to the start of a route [1]. In this way, ants can safely explore unfamiliar terrain whilst 'connected' to their nest. However, as it is based on internal cues, rather than external information, path integration is prone to cumulative error. To compensate for this, most animals also learn visual landmarks to specify important locations. Insects use visual information by storing two-dimensional retinotopic views, known as snapshots, of how the world looked from goal locations [2–4]. They can then return to a goal by comparing their current view of the world with the stored snapshot and using the difference to determine a direction. It is widely held that insects, unlike mammals, do not combine information derived from these two mechanisms into a 'cognitive map' [5]. However, observations of desert ants reported in this issue by Müller and Wehner [6] have reopened this debate by demonstrating a role for precise path integration in the learning of visual landmark information.

Visual landmark information is so useful that insects invest significant time in ensuring it is accurate. For example, upon leaving an important place, wasps and bees perform learning flights, a series of arcs that allow the bee or wasp to view the goal from directions that they will adopt on subsequent return journeys [7–9]. Analogous behaviours have also been observed in ants [10,11], although these 'learning walks' have been less well-studied to date.

Müller and Wehner [6] have begun to provide details of how learning walks are shaped to facilitate the learning of visual landmark information. The desert ant *Ocymyrmex* lives in a featureless desert. Its path-integration-guided home runs often result in a prolonged search for an inconspicuous nest entrance (Supplemental data in [6]). Therefore, any information provided by local landmarks is readily learnt. The authors prompted a bout of learning by introducing a prominent landmark to the nest surroundings of an *Ocymyrmex* nest. Upon noticing the change, ants perform a neatly choreographed learning walk before departing on their foraging run.

The ants loop around the nest entrance, and at a series of points, they stop and rotate to accurately face the nest (Figure 1A). The brief periods where ants fixate the nest are an ideal opportunity to store snapshots.

One particularly interesting characteristic of these learning walks is the accuracy with which ants face the invisible nest entrance. This strongly suggests the structure of these walks is tightly controlled by path integration. In fact, the authors hypothesise that snapshots stored when the ant is facing the nest are labelled with the current path integration co-ordinates to generate a multi-modal spatial representation which could be the precursor to a 'cognitive map'. However, this hypothesis is just one way that path integration and vision could interact and we consider other simpler possibilities. Future experiments addressing these hypotheses are likely to provide insight into the style and level of insect cognition.

The simplest possibility is that ants use path integration during the learning walk only to ensure that a snapshot is learnt when the agent is directly facing the nest. This is sufficient for subsequent homing because snapshots can be used as a visual compass [12]. If panoramic images, from places near a goal, are systematically rotated and each rotation compared to a reference snapshot taken at the goal, then the best match will be when the image has a similar orientation to that of the reference image. Figure 1B,C shows how with four reference snapshots, centered on the nest, one can derive nestwards headings from a large area. Here, path

Figure 1. Landmark learning in ant navigation.

(A) An example of a learning walk of the Namibian desert ant *Ocymyrmex* [6]. The ant leaves her nest (solid black square) after a black cylindrical landmark (solid black circle) has recently been placed nearby. (B) We simulate snapshot homing using panoramic images collected from ground level around an Australian desert ant nest. Four of the images (i–iv) are designated as snapshots, each of which is aligned to face the nest. (C) From the other locations, we derive headings for a hypothetical ant by using each snapshot as a visual compass. To recover a nestwards orientation, we rotate images and find the orientation at which the rotated image best matches a snapshot. This process is performed independently for all four snapshots and the heading for our hypothetical ant is a weighted average (shown in vector plot) showing that ants could return to the nest from any location.

integration is used solely to orient the ant during the learning of snapshots and then discarded.

A next level of complexity would be to associate stored snapshots with a compass direction. With compass information, the current view of the world can be aligned to the stored snapshot. This is a prerequisite for most hypothetical models of snapshot use. In such models, features common to the current and stored snapshots are identified and movement directions are derived from the discrepancy in their positions [13]. Wasps and bees align themselves with stored views by translating whilst holding their orientation fixed. Walking ants need a different solution to align the current view with a stored snapshot. The required image rotation could be performed neurally. Alternatively, ants could store a large set of snapshots at different orientations, something to which the learning walk is well-suited. Then, when returning to the nest, they would use the goal snapshot which is closest in orientation to their current homeward path.

Müller and Wehner's [6] hypothesis represents a third level of complexity in the way that path integration may be combined with view-based homing. Namely, labelling stored snapshots with path integration co-ordinates. By identifying features or landmarks that are common to different snapshots, one could use the co-ordinate information to build a map of the true metric positions of those objects. Although not impossible, this requires large amounts of computational power. A simpler solution would be to build a map in which whole snapshots are labelled with their metric position derived from path integration co-ordinates. Snapshots could then be used to update or correct the current co-ordinates of the path integration system. This behaviour is seen in hamsters where brief viewing of a familiar landmark array can reset the path integrator [14]. Either of these map-like strategies would allow for characteristic behaviours such as the aforementioned path integration resetting and taking novel shortcuts. Behaviours, which it should be reiterated, have not yet been observed in ants [5,15].

Müller and Wehner [6] have shown beautifully how path integration and visual learning interact during specialized learning walks. We have discussed mechanistic consequences that follow from this finding, including that path integration co-ordinates need not be tied to long-term visual memories. Imminent research addressing these and other hypotheses promises to give precious insight into the style and level of insect cognition.

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