Invertebrate Memory: Wide-Eyed Ants Retrieve Visual Snapshots

Ants retrieve visual memories to guide them en route to their goal. A new study shows that wood ants use object width to retrieve the correct visual memory at the appropriate position along their route. A computational model that accurately reproduces the ants' behaviour raises questions about the underlying mechanisms.

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Ants, like bees and some other insects, learn the location of a food source and return to it repeatedly. Individual ants may have highly stereotyped routes between their nest and their feeding site [1]. Indeed, the stereotypy of these routes is often remarkable, individuals of some species showing little or no deviation from a specific route over days or weeks [2]. The formation and maintenance of these routes in many species is dependent upon the visual recognition of familiar landmarks using two dimensional retinotopic views [3]. Even species such as *Paraponera clavata*, which uses odour trails for navigation, and *Cataglyphis fortis*, which relies on path integration, may use visual landmark recognition when moving along familiar routes [4,5].

For an ant to use visual memories to guide it along a route, it must have mechanisms for forming, storing and retrieving these memories at the appropriate position along the route. Formation of visual memories in wood ants (*Formica rufa*) is thought to occur primarily during learning walks that occur as the ant leaves a food source and heads homeward [6]. The homeward routes of these ants are often extremely convoluted, individuals turning numerous times to fixate landmarks near the food source allowing them to learn the relative positions of these landmarks [6,7]. These visual memories can be used to guide the ants on subsequent trips to the same food source, provided that the ants can store suitable information about the landmarks observed on their learning walks and retrieve these memories at the correct position along their route.

A recent paper in *Current Biology* [8] addresses how wood ants cue the retrieval of the appropriate visual memory to locate sucrose at a specific point at the base of a landmark. The ants were trained in a circular white arena that contained either a solid black rectangular landmark or a gradient fading from black at one vertical edge to white at the other [8]. The ants learnt to collect food either from the left edge of the solid or the gradient landmark. They also learnt to collect food from a point inset 10 cm from the left edge of the solid or the gradient landmark. The average routes the ants took towards the food were approximately straight, irrespective of whether the food source was at the edge of, or inset from, both the solid or gradient landmarks. Whilst walking towards the food the ants fixated a position close to their goal (the food source).

How do the ants guide their routes towards the food source? As Harris *et al.* [8] point out, the ants heading towards a food source placed at a landmark edge could fixate that edge and keep it within their frontal visual field. But this single-memory strategy would not be sufficient for the ants heading towards the inset food source, because the edge of the landmark will move peripherally as they near the food source, causing their route to become curved. Another single-memory strategy that the ants could use would be to learn an initial heading relative to the landmark edge and continue along this trajectory without additional feedback, a so-called ballistic strategy. Ants using this strategy should veer to the left of their training route when they are released much closer to the landmark. Under these conditions, however, the ants maintain a straight route to their food.

It seems likely, therefore, that a single memory is not sufficient to guide the wood ants. Previous studies (for example [2,7]) have also suggested that ants access multiple visual memories of a landmark en route to a goal. How are the multiple visual memories retrieved by the wood ants? Harris *et al.* [8] point out that one possible strategy the ants could use — continuously recording the distance they have walked — can be excluded by their experiments in which the ants were released closer to the landmark than in training. Under these conditions, if the ants use a distance-measuring strategy, they should veer to the left; however, they walked straight towards the location of the food.

The apparent height or width of the landmark increases as the ants approach it, providing a cue that could be used to retrieve the appropriate memory. If the ants rely on object height then, when they are tested with a landmark half the height of the training landmark, they should veer to the left — again this is not the case. If the ants use the angular width of the landmark to cue the retrieval of visual memories, then manipulating the gradient should alter the routes taken by the ants — the ants should veer to the left with narrower gradients and to the right with wider gradients. Harris *et al.* [8] found that the ants' routes match these predictions very closely, suggesting that they do indeed use object width to cue visual memory retrieval.
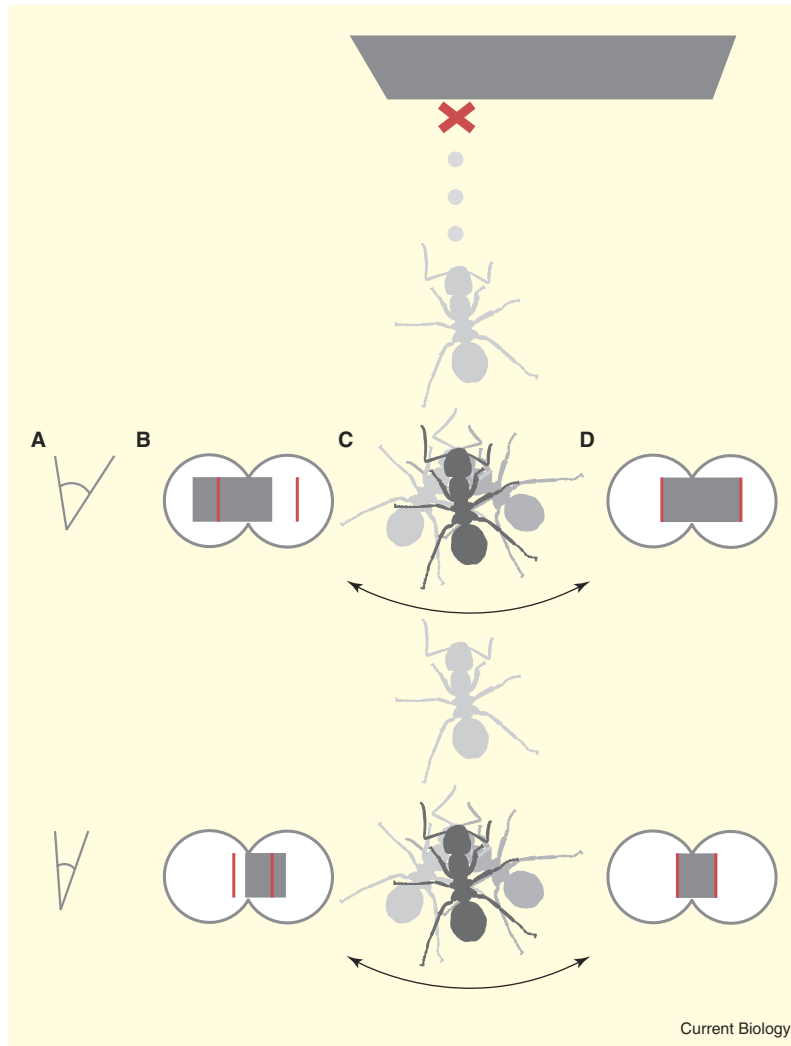
Figure 1. A model of visual memory retrieval in navigating wood ants.

An individual ant approaches a food source at the base of the rectangular landmark, inset from the left vertical edge (red X). (A) The ant assesses the landmark's angular width and (B) retrieves a memory of the retinal location of the landmark's vertical edges (red lines on frontal visual field) from a 'look-up' table. (C) The ant rotates until (D) the image of the landmark in the frontal eye field matches the memory and then walks forward and the process is repeated.

How might the ants use apparent landmark width as a cue for memory retrieval? Harris *et al.* [8] propose that the ants may use a framework similar to that of a 'look-up' table. The ants would use the apparent landmark width to cue the retrieval of a specific visual memory that contains information about the position of the landmark in the frontal visual field (Figure 1). The ants then rotate until the current position of the landmark matches that of the visual memory they have retrieved. Once the retinal image and the memory match, the ant walks forward and reassesses the width. A quantitative model incorporating 100 visual memories linked to specific landmark widths based on this framework is remarkably accurate at predicting the mean routes of individual ants in a variety of experimental situations [8] (Figure 2A). Even more remarkable is that the model continues to simulate accurately the routes of individual ants when the number of visual memories is reduced from 100 to six or even just three memories.

The model itself does not prove that the ants use such a 'look-up' table, but it does suggest that landmark width is sufficient to account for the ants' behaviour.

Although the ants do not have to use discrete visual memories, there is evidence to support this assumption. Ants approaching a cone — or edges that resemble the base of the cone — adopt trajectories that can be subdivided into sections during which the edge of the cone is maintained in a small number of retinal locations [7]. This suggests that the ants use a series of snapshots that are acquired as they fixate landmarks during their learning walks [3,6,7]. The model suggests that relatively few of these snapshots may be necessary to guide the ants accurately. The number of snapshots could be important because this may affect both how accurate the ants must be in measuring landmark width and their tolerance to mismatches between their retinal image and their snapshot. This could be particularly important if the ants are moving forward whilst trying to match their retinal image to the snapshot.

Harris *et al.* [8] highlight one failure of the current model — if landmark width does not increase monotonically throughout the route, then there may be two different retinal positions for a given width, causing ambiguity. One obvious solution for the ants would be to associate procedural information with each snapshot to determine the order in which the memories can be cued. This could be tested by altering the width of 'virtual' landmarks whilst the ant is walking towards them. Some desert ants (*Melophorus bagoti*), however, appear to retrieve visual memories irrespective of whether they have encountered the preceding ones [2]. Another possibility is that under natural conditions ambiguities from one landmark can be ignored in favour of the 'weight of evidence' from other local or global landmarks.

Unlike the mean routes of individual ants, single routes often show distinctive sinusoidal 'wiggles' [9] (Figure 2B). A substantially more sophisticated model will be required to simulate these single routes. Intriguingly, however, Harris *et al.*'s [8] model may explain the possible role of the 'wiggles' during single trials.
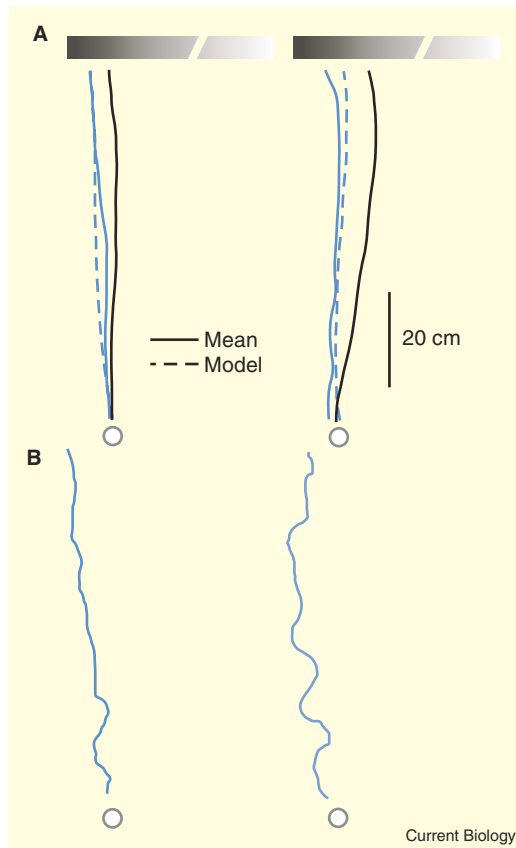
Figure 2. This model predicts the average routes of individual ants.

(A) The average routes of an ant whose behaviour is similar to that of most other ants (left) and an idiosyncratic ant (right). Black routes are to the training gradient landmark and blue routes to a steeper gradient landmark. Model predictions for these routes are shown with dashed lines of the same colour. (B) Single approaches of an average ant (left) and an idiosyncratic ant (right) to an object often contain significant deviations from the mean route and characteristic 'wiggles'.

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Ants that have learnt to walk in parallel with a wall of a set height at a specific distance alter their 'wiggles' to move further from the wall if the height of the wall is increased [9]. This behaviour maintains the elevation of the wall on their frontal retinal field. Likewise, ants walking straight towards a landmark may use the 'wiggles' to adjust the position of the landmark's edges within their frontal visual field, allowing them to match the edges to their visual memory.

The robustness of the model proposed by Harris et al. [8] under the conditions tested so far suggest it may also account for wood ant behaviour in more complex situations. Although the model contains many assumptions, such as whether the visual memories are discrete, subsequent experiments should be able to test these key assumptions of the conceptual framework of the model.

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Fungal Pathogenesis: Gene Clusters Unveiled as Secrets within the *Ustilago maydis* Code

The genome sequence of a second plant pathogenic fungus is now available, revealing unique gene clusters encoding secretory proteins that are induced during infection and regulate pathogenesis. Gene clusters play important roles in pathogenic fungi, yet their evolution and maintenance remain a mystery.

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How microbial pathogens as diverse as viruses, bacteria and fungi infect myriad hosts is essential for understanding, preventing and treating the infectious diseases that are scourges of agriculture and challenges for medicine. Genomics is revealing much about both the pathogen and the host, and providing new tools to understand these interactions. The recently published [1] complete genome sequence of maize pathogen *Ustilago maydis*, and the identification of clusters of genes involved in this host–pathogen interaction, is an important advance in understanding microbial pathogenesis. We consider this research in the context of the evolution and roles that gene clusters play in pathogenic fungi.

Plant pathogenic fungi have diverse host-specificities and lifestyles. The basidiomycete