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COMMENTARY

Insect navigation: do ants live in the now?

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ABSTRACT

Visual navigation is a critical behaviour for many animals, and it has been particularly well studied in ants. Decades of ant navigation research have uncovered many ways in which efficient navigation can be implemented in small brains. For example, ants show us how visual information can drive navigation via procedural rather than map-like instructions. Two recent behavioural observations highlight interesting adaptive ways in which ants implement visual guidance. Firstly, it has been shown that the systematic nest searches of ants can be biased by recent experience of familiar scenes. Secondly, ants have been observed to show temporary periods of confusion when asked to repeat a route segment, even if that route segment is very familiar. Taken together, these results indicate that the navigational decisions of ants take into account their recent experiences as well as the currently perceived environment.

KEY WORDS: Ant, Navigation, Route guidance, Visual guidance

Introduction

As animals move through the world, they gain experience of the paths leading to locations of importance, such as plentiful food sites or the safety of home. Individuals learn and replay the guidance instructions that produce these paths and thus many animals display habitual and idiosyncratic route-following behaviour (rats: Calhoun, 1962; humans: Dee, 2005; monkeys: Di Fiore and Suarez, 2007; pigeons: Biro et al., 2004; ants: Kohler and Wehner, 2005; Mangan and Webb, 2012). The resultant routes may not be the most efficient in terms of path length but through route repetition, individuals presumably gain reliability, safety and computational efficiency.

By studying this habitual route behaviour in ants, it is hoped that we might discover the basic mechanisms that give rise to this common form of visual navigation. Ants have both small brains and low resolution visual systems and thus may, in some way, embody the minimal computational requirements for visually guided route navigation. Furthermore, we have a chance to uncover these mechanisms because of the practicalities of studying ant foraging behaviour in natural environments (e.g. Narendra et al., 2013; Wystrach et al., 2014). A corollary of searching for efficient mechanisms is that as a discipline we take a bottom-up approach. This entails looking for the simplest mechanisms that can account for observed behaviour (e.g. Mangan and Webb, 2009) and waiting for new behavioural evidence before changing one's current model (Wystrach and Graham, 2012).

A simple model of ant visual route navigation

We can learn much about the style of ant route navigation from simple behavioural demonstrations. If desert ants are allowed to become familiar with a permanent feeder location, then individual foragers will develop habitual idiosyncratic foraging paths between nest and feeder in both directions (see Fig. 1). The fact that these

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paths are idiosyncratic suggests that ants are guided by individually learnt cues rather than social cues such as pheromones. In fact, we know route guidance is based mainly on visual cues (Collett, 1992; Harrison et al., 1989; Reid et al., 2011; Wehner et al., 1996) but can also include information about magnetic anomalies (Buehlmann et al., 2012), odour (Steck et al., 2009) and wind direction (Wolf and Wehner, 2000). If experienced ants are displaced from one location on their route to another (e.g. from the nest back to the middle of the route), they will recapitulate the remainder of their habitual route seemlessly (Fig. 1) (Kohler and Wehner, 2005; Mangan and Webb, 2012). Thus, the learnt guidance memories that are needed to control a route can be implemented independently of path integration (PI), the innate mechanism by which animals can keep track of their approximate position relative to the start point of a journey (Muller and Wehner, 1988).

Although we know vision is important for guiding habitual routes, there are many different ways of using vision for navigation. A simple strategy is to aim for an identifiable beacon as flies innately aim towards vertical black bars (e.g. in Buridan's ass paradigm; Bülthoff et al., 1982). At the opposite end of the complexity spectrum, one might use visual information to build a detailed metric map of the world that can subsequently provide navigational information (Bailey and Durrant-Whyte, 2006; Durrant-Whyte and Bailey, 2006). Such a use of visual information allows an agent to answer the 'Where am I?' question.

Somewhere in between innate attraction and complex map building, one could also use visual cues for navigation with simpler, more procedural strategies. That is, instead of calculating where you are within a map, you could instead seek to answer the 'What do I do?' question (e.g. Cartwright and Collett, 1983). Imagine, for instance, standing at a junction between woodland tracks. If one takes a photograph when facing the desired direction, that photo is specific to the location and orientation at which the photo was taken. Therefore, it can be used to select the same track when encountering the same junction in the future. One has to simply rotate until the currently perceived scene matches the photo. Using the photo in this way tells you 'what to do' (i.e. which direction to move in) without telling you exactly where you are. Similarly, ants could use a set of views, remembered whilst travelling along a route, to set appropriate directions when trying to recapitulate that route (Baddeley et al., 2012; Philippides et al., 2011). That is, if a route-following ant was to compare a range of views from different orientations at their current position (cf. Wystrach et al., 2014) with their visual memories from a previous successful route, then the best match would be found when the ant aligned similarly to the previous completion of the route (Fig. 1B,C). This scheme of rotational image matching ties actions (moving in a particular direction) to visual scenes, giving an agent a set of scene-action behaviours that can guide a familiar route.

What's more, when using such a scheme, an agent (be it ant, human or robot) can live in the now, responding only to the currently perceived scene and comparing only that scene to its visual memory. Even if the agent's memories are not stored in a

Glossary

Path integration
Path integration (PI) is a strategy by which animals continuously combine odometric and compass information into a vector that can be used to guide a direct path home, even from previously unvisited terrain.

Full vector ants
During foraging, ants will accumulate a home vector through PI, which gives the bearing and distance back to their nest. Such ants are termed full vector (FV) ants.

Zero vector ants
In contrast to FV ants, ants that have travelled back to the nest will have 'run off' their home vector and are hence termed zero vector (ZV) ants.

View-based guidance
This is the general term used for navigation strategies where a remembered visual scene is used to set a direction or drive a search for a location, through comparison with the currently perceived scene.

Rotational image matching
This is a particular style of view-based guidance where a remembered view is used only to recover a direction.

strict sequence, they will still be used in the correct order because in a visually rich world the best match between the current view and the visual memory will generally correspond with the memory that is most appropriate for that location. That is, the visual sequence is a property of the route through the world and does not have to also be a property of the visual memory. Thus, we have outlined an attractively simple visual navigation scheme whereby ants might use a set of scene-action responses in order to guide a familiar route. However, two recent observations of ant behaviour during route guidance cause us to reconsider this simple model of visual route guidance.

Hysteresis in ant navigation: Wystrach et al. (2013)

When a returning forager is captured close to her nest and placed in a visually unfamiliar situation, she is deprived of the two primary sources of information that usually drive navigation.

Because she was near to the nest (after walking from the feeder) she is a zero vector (ZV) ant, so called because she no longer has any directional information provided by her PI system. She is also in an unfamiliar visual situation and so her stored visual memories will not produce coherent directional information from view-based guidance. In this situation, we would expect ants to engage a symmetrical systematic search for familiar terrain (Wehner and Srinivasan, 1981), which has long been thought of as the last chance strategy for ants.

Wystrach and colleagues investigated the role of visual experience in the systematic search of the Australian ant *Melophorus bagoti* by firstly establishing a straight route between an active nest and a permanent feeder. Returning foragers were then captured near their nest and released on unfamiliar ground (Fig. 2). Counter to expectation, these ZV ants did not always produce the randomly distributed headings predicted by a systematic search strategy. Rather, the departure bearings of ants showed a clear bias in the nest–feeder compass direction (i.e. they backtracked opposite to the just-travelled bearing). Intriguingly, the key determining factor as to whether ants would show this bias was whether they had recently experienced the visual surroundings close to their nest (compare Fig. 2A and C with 2B).

Why is it sensible for ants to backtrack in this way? Well, the behaviour seems adaptive if one considers the degree to which ants are familiar with different parts of their world. For ants that have experienced the route multiple times, the ground surrounding the nest and route will have become familiar to different degrees. The areas close to the nest on its feeder side will be the most familiar, with lateral areas less familiar, and areas behind the nest the least familiar (Fig. 2, left). Therefore, with no information from PI and finding itself in a visually unfamiliar part of the world, but crucially remembering being near the nest a moment previously, a sensible ant might reasonably expect that it has found itself on the far side of the nest, which is possible as passive displacements, by gusts of wind, are commonplace for these ants (Wystrach and Schwarz, 2013). Thus, in this situation, its best option is to backtrack to recover familiar territory. The behaviour certainly seems functional, but what does it suggest about the underlying mechanisms? We return to this question later.
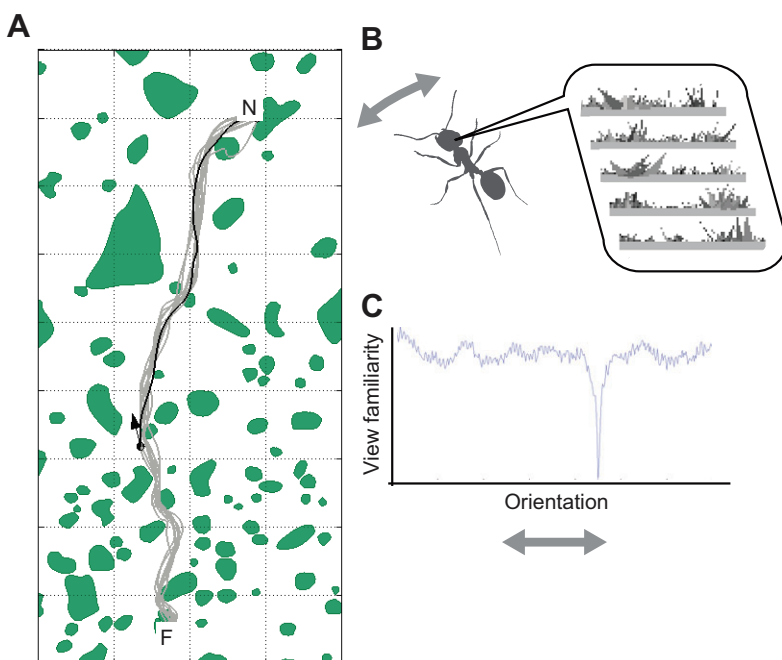
Fig. 1. How simple visual guidance can lead to route following. (A) The paths (grey lines) of an individual ant across multiple trips from a feeder (F) to her nest (N). The ant shows an idiosyncratic route through shrubs and tussocks (green shaded areas). If the ant is returned to a location along the familiar route (black arrow), she immediately recovers the habitual homeward route. (B,C) This visually guided route performance could be explained by a simple algorithm. An ant that is experienced with this route has a memory of panoramic scenes corresponding to the appropriate directions for different parts of the route. To negotiate the route, ants could rotate on the spot trying to match their current view to previously stored views (B). When assessing the familiarity of the views experienced at different headings, a minima would be found at the heading parallel to the route (C). Repeating this procedure would then lead the animal home without it ever having to resolve its absolute position. Data redrawn from Mangan and Webb (2012) and P. Ardin, F. Peng, M. Mangan, K. Lagogiannis and B. Webb (submitted).
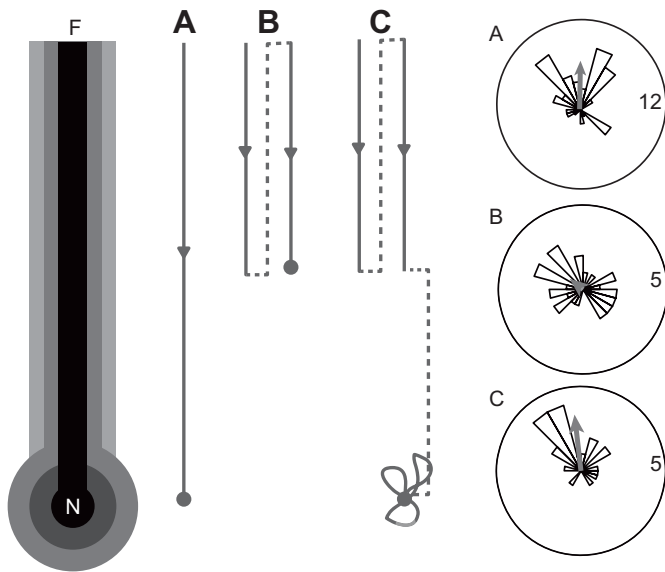
Fig. 2. Ants show a biased search after a glimpse of their nest environs. Ants are allowed to become familiar with an enclosed route between a feeder and their nest. Following training, ants will be familiar, to differing extents, with the nest–feeder (N–F) surroundings. In the schematic diagram of the experimental design (left), familiarity is represented by greyscale with black showing the most familiar areas. Individuals are transported to distant unfamiliar terrains and their departure bearings measured on a goniometer. (A) Ants are captured close to their nest (zero vector, ZV, with recent near-nest experience). (B) Ants complete the first half of the route twice (ZV with no recent near-nest experience). (C) Ants complete the first half of the route twice and are then allowed to experience the area close to the nest for a short time (ZV with no recent near-nest experience). The circular histograms on the right indicate the heading in 15 deg sectors; the grey arrow shows the mean vector. Numbers indicate the scale, so that the centre is 0 and the radius extends to this number of ants per sector. Only ants in conditions A and C show a bias in their headings, with ants much more likely to head in the nest–feeder direction. Data redrawn from Wystrach et al. (2013).

Hysteresis in ant navigation: Collett (2014)

As outlined above, one of the canonical demonstrations of ant navigation behaviour is that foragers with habitual visually guided routes can recapitulate those routes independently of their PI system. This has been demonstrated many times (e.g. Kohler and Wehner,

2005; Mangan and Webb, 2012; Wehner et al., 1996; Wystrach et al., 2011). Collett (2014) returned to this question and analysed in detail the paths of ZV ants when asked to recapitulate a visually guided route. Individual *Cataglyphis fortis* were allowed to develop routes through a sparse environment dominated by a single conspicuous black cylinder. These ants reliably take a curved route to detour around such an object and individuals stabilise on habitual curved routes with the visual guidance instructions for these routes learnt quickly (Collett, 2010). Yet, when ZV ants were returned to the start of their route, not all ants immediately recognised and followed it, as in previous work. Instead, Collett reports a new behaviour within a significant subset of ants (Collett, 2014). During the initial part of the route, often after seeming to begin a normal homeward path, these ants appeared confused for a prolonged period. Eventually, the ants recommenced their habitual route home (Fig. 3A) but were, on average, no further along the route when they resumed a fast direct path. We can conclude that the confusion is not just a search for a more familiar location within a visually difficult route. Another possibility is that the confusion is due to a unique conflict between visual guidance cues and PI state in this particular experimental configuration. However, by manipulating the state of the ant's PI system, by starting ants further behind the feeder, one can create a group who experience the same visual scene with the same PI state but are not experiencing the familiar route for the second time (Fig. 3B). In this situation, unlike the ants in Fig. 3A, there is no extensive confusion. So, once more we see that recent visual experience modulates navigational behaviour, in this case leading to confusion despite ants being on familiar terrain.

It is puzzling that ants show temporary confusion when asked to repeat a portion of a familiar route: what is the functional value of temporarily disabling some of your visual route memories? And, why has nobody identified this behaviour previously? Effectively disabling a portion of one's visual route memory (just after using it) may be beneficial by focusing attention onto the visual memories that are necessary for subsequent portions of the route. This would result in a reduced search space perhaps increasing efficiency and reducing the chance of aliasing. The failure to observe this behaviour in previous experiments may be due to variations in the visual complexity of experimental environments. Here, Collett (2014) trained ants in a visually sparse environment such that there was a relatively small degree of visual change across the route,
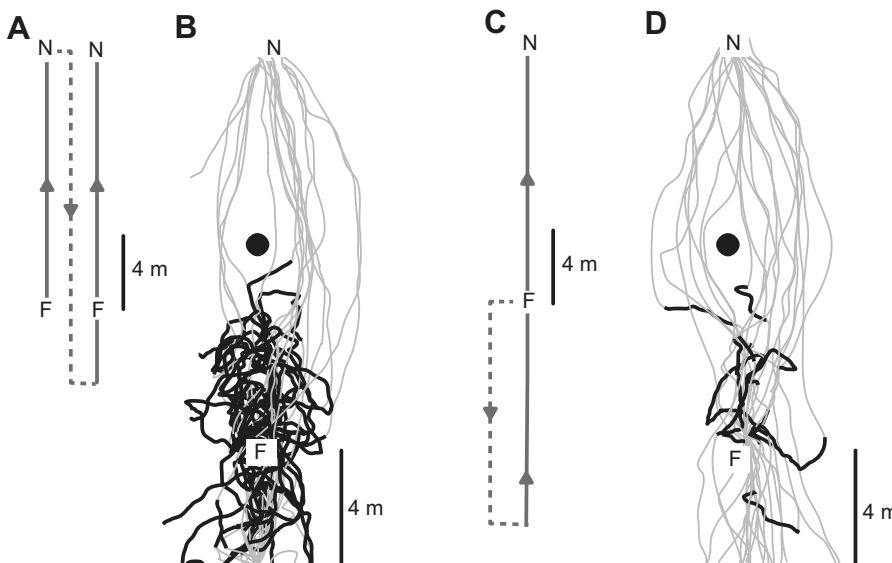
Fig. 3. Route recapitulation creates confusion in navigating ants. Individual ant foragers are allowed to develop habitual routes that detour to the side of a large black cylinder (black dot). In two experimental conditions, ants are transported to positions behind the feeder (F) and released. N, nest. Schematic diagrams of the experimental conditions are given in A and C and the paths of the experimental ants are given in B and D. (A,B) Zero vector ants are released from a position behind the feeder. A significant number of ants show confusion (black path segments) in the area between the feeder and the cylinder, before resuming their normal routes (grey path segments). (C,D) Ants are taken from the feeder and released 18 m behind the feeder position such that at the start of the familiar route they have the same path integration state as in A. These ants, which have not recently completed the return route, show significantly less confusion. Data redrawn from Collett (2014).

meaning those memories that were supressed would act across a larger area and thus the confusion would be across a larger area. In contrast, ZV ants from the study in Fig. 1 were released in a visually dense environment where the spatial extent of any suppressed memories would be much smaller, and as such any confusion would be less conspicuous (Collett, 2014).

Discussion

Both of the recent studies discussed here suggest that ants do not undertake visual navigation by simply acting upon the currently perceived scene. We have two examples of how recent visual experience influences navigational performance. Thus, we have to reconsider the simple model of visual route following that we outlined above.

Cutting-edge algorithms from the mobile robotics domain provide informative examples of how temporal information (recent visual experience) can increase the robustness of visual navigation. For example, with low resolution vision, recognition of a location from the current view alone is hard because of aliasing with other locations along a learned route. However, if one includes recently experienced views, along with the current view, and compares these with the stored route sequence, then robust place recognition can be achieved (Milford and Wyeth, 2012). Stone et al. (2014) have gone further to show that this method, in combination with ant-inspired sky segmented images, is sufficient for route following in complex urban environments across seasons and varying lighting conditions. It appears that engineers have realised the encoding of temporal information is particularly useful for place recognition when visual resources are limited. We may be seeing a convergence of ideas between behavioural studies in insects and engineered autonomous systems.

In the Introduction, we explained our hope that studies of ant navigation might elucidate the minimal computational requirements for visually guided route navigation. We can now reject one minimal model of visual route navigation based on findings in two recent behavioural studies. It may therefore be informative to consider the types of mechanism that might underpin the behaviours presented here. In both examples, the behaviour of interest shows some consideration for the uncertainty inherent in the ant's sense of position. For the *Cataglyphis* desert ant (Collett, 2014), their uncertainty is high even though they are on familiar ground because they have been asked to repeat a route portion. For the *Melophorus* ants (Wystrach et al., 2013), their uncertainty is high as they have been transported to unfamiliar test ground. When navigation behaviours can be described in terms of uncertainty, it is tempting to suggest that insects are manipulating mental representations of spatial information along with estimates of the uncertainty of that information. This might suggest a cognitive implementation of navigation where behaviour is decided upon following the mental manipulation of representations of locations, directions and the confidence in these estimates.

Alternatively, these behaviours might be an emergent property of the underlying sensorimotor circuitry rather than higher level spatial representations. By way of example, the data presented in Collett (2014) could be explained in terms of simple habituation of the visual stimulus. That is, as the visual scene remains largely constant across the initial portion of the route, sensory habituation would lead to desensitisation of that particular view such that in the absence of PI guidance, ants would be left with only its systematic search strategy for guidance until the view dishabituates. Yet, habituation alone cannot explain the reversal of heading direction outlined in Wystrach et al. (2013). One possibility might be that this behaviour emerges from adaptation to the sudden removal of a dominant directional signal. For example, ZV ants that have recently viewed the nest (Fig. 2A,C) will have a strong directional preference driven by the familiarity of the nest surroundings. When displaced to unfamiliar surroundings, this cue would be completely removed, which might in turn cause a rebound effect similar to the 'waterfall illusion' (Purkinje, 1820), causing the ant to temporally head in the opposite direction. If route memories are considered less strong than visual memories from the nest surroundings, any rebound effect would be far smaller for the ants in Fig. 2B, explaining their classic systematic search behaviour. The two mechanisms described above are at opposite ends of a spectrum of mechanistic explanations for these new results. Further experimentation will allow us to fine-tune our hypothesis and learn more about the computational style of insect navigation.

Behavioural studies of ant navigation continue to highlight robust navigational strategies. That these strategies are discovered in a bottom-up way, with hypotheses driven by natural behaviour, gives us confidence that we have not over-reached in attributing complex mechanisms to these small-brained champion navigators.

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