Vision for navigation: What can we learn from ants?

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ABSTRACT

The visual systems of all animals are used to provide information that can guide behaviour. In some cases insects demonstrate particularly impressive visually-guided behaviour and then we might reasonably ask how the low-resolution vision and limited neural resources of insects are tuned to particular behavioural strategies. Such questions are of interest to both biologists and to engineers seeking to emulate insect-level performance with lightweight hardware. One behaviour that insects share with many animals is the use of learnt visual information for navigation. Desert ants, in particular, are expert visual navigators. Across their foraging life, ants can learn long idiosyncratic foraging routes. What's more, these routes are learnt quickly and the visual cues that define them can be implemented for guidance independently of other social or personal information. Here we review the style of visual navigation in solitary foraging ants and consider the physiological mechanisms that underpin it. Our perspective is to consider that robust navigation comes from the optimal interaction between behavioural strategy, visual mechanisms and neural hardware. We consider each of these in turn, highlighting the value of ant-like mechanisms in biomimetic endeavours.

1. Introduction

Navigation is an essential task for most animals (Shettleworth, 2010) and a desired capability for artificial autonomous systems. One of the champions of this behaviour is the ant whose foragers spend much of their working life efficiently bringing food back to their nest (Hölldobler, 1990). Ants possess a number of mechanisms for orientation (Knaden and Graham, 2016) including for some species social cues provided by pheromones. However, for solitary foraging ants the principal source of information for navigation comes from learnt visual scenes (Collett et al., 2006). For a variety of visually guided behaviours, insects have been shown to possess efficient, highly tuned sensori-motor mechanisms which have been inspiring for biomimetic engineers (Webb, 2008). For example, motion detection and collision avoidance (Hassenstein and Reichardt, 1956; Francheschini et al., 1992) and flight stabilisation (Krapp, 2000; Humbert et al., 2010). The visually guided navigation of ants has inspired biorobotic projects (Lambrinos et al., 2000) but we are yet to see a fully integrated neuroethological account of insect navigation (Webb and Wystrach, 2016) and many of the desirable characteristics of ant navigation are not yet captured in autonomous systems.

2. Visual navigation in individually foraging ants — a sketch

On warm sunny days, almost anywhere on the planet, ant foragers will leave their nest, and their task is to retrieve food and return home as efficiently as possible. This may well be the only task that they do for the remainder of their working lives and therefore these ants are foraging and navigation specialists. One particular group of ants, the desert ants, are particularly tuned for navigation because they do not utilise pheromone trails laid by colleagues (Knaden and Graham, 2016). As naïve foragers, these ants are able to use a basic dead reckoning strategy to return home from novel locations (Wehner and Wehner, 1986; Wehner and Srinivasan, 2003). Ants use celestial information as a compass (Wehner and Wehner, 1986) and probably step-counting for odometry (Wittlinger et al., 2006) and continually compute the information needed to take a direct path home at any time. This idiothetic information allows ants to safely explore the world and gradually increase their foraging distance from the nest (Wehner et al., 2004; Müller and Wehner, 2010; Muser et al., 2005). During this phase desert ants learn navigationally useful visual information and the routes of mature desert ants possess the following set of characteristics:

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- Individually foraging ants can use visual information to guide routes between their nest and a stable food site (Kohler and Wehner, 2005; Mangan and Webb, 2012).
- Routes are idiosyncratic, so individual ants will adopt and remain faithful to unique routes. (e.g. Collett et al., 1992; Wehner et al., 1996).
- Routes have polarity; knowledge of a nest-food route does not imply knowledge of a food-nest route (Wehner et al., 2006; Harris et al., 2005).
- Route knowledge defines a corridor as opposed to a sharp ridge, so the overall shapes of routes are stable but ants do not have to recapitulate them with high precision. (e.g. Kohler and Wehner, 2005; Mangan and Webb, 2012).
- The visual knowledge used to define routes can be used independently of the habitual path integration co-ordinates experienced at places along the route and accessed out of the usual sequence (e.g. Kohler and Wehner, 2005; Mangan and Webb, 2012).
- Individual ants can learn multiple routes to the same destination (Sommer et al., 2008).
- Routes will only be re-joined if approached from the familiar direction (Mangan and Webb, 2012).

This set of characteristics shows two important themes. First, it highlights the robustness of visually guided navigation, which is so admired by engineers. Across the experiments referenced above, mischievous experimenters have displaced ants and conflicted visual cues with other sources of information. Despite this, desert ants are consistent in their ability to use visual cues to get back to their nest. Secondly, the style of visual navigation suggests procedural mechanisms, whereby ants use visual cues to trigger appropriate behaviours. We begin by discussing this economical and procedural style of navigation.

3. How do insects use vision for navigation?

Over decades, behavioural experiments with many insect species have given a sense of the way in which insects use vision for navigation. Following Tinbergen's experiments with digger wasps (Tinbergen and Kruyt, 1938), experiments with hoverflies (Collett and Land, 1975), desert ants (Wehner and Räber, 1979), honeybees (Cartwright and Collett, 1983) and even waterstriders (Junger, 1991) have suggested that insects store the visual information required for navigation, as egocentric views of the world as seen from a goal location or from correct route directions. Following Cartwright and Collett (1983), a large volume of research has focussed on the use of egocentric views for navigation in animals and robots. Collectively, these theories and models are referred to as 'view-based matching' strategies. Some models (Cartwright and Collett, 1983; Franz et al., 1998; Lambrinos et al., 2000; Zeil et al., 2003; Vardy and Möller, 2005; Möller and Vardy, 2006) treat a single stored view as an attractor point. An alternative is to use a stored view to set a direction (Zeil et al., 2003; Graham et al., 2010; Baddeley et al., 2012; Wystrach et al., 2013; Ardin et al., 2016). Either class of view-based matching algorithm can be used to guide routes or searches for discrete locations. In fact, behavioural evidence suggests both types of view-based matching strategy might be present in navigating ants (Collett, 2010; Wystrach et al., 2012).

In the context of this paper, the aim is not to discuss the differences in possible view-matching methods. Rather we wish to highlight how view-based matching strategies, in the broadest sense, represent an economical and efficient style of visual navigation. The essence is that an insect derives a movement direction from the comparison of a remembered visual scene and the currently perceived visual scene. This is a computationally inexpensive process because information about the world is stored in an egocentric frame of reference meaning it is an excellent task specific representation of the world. That is, the movements of an agent in space map simply onto changes in the position of parts of the agent's egocentric view of the world, thus there is a direct relationship between the information gained from the comparison of two scenes and the movement needed to go between the locations from where the scenes were perceived. What's more, visual input is by definition egocentric at the point of input and so does not need to be transformed to another frame of reference. In summary, there is a simplicity and elegance to the use of egocentric views for navigation.

Using view-matching strategies has implications for the underlying biological machinery. Firstly, view-based matching provides information about what to do next rather than explicit positional information. Such a procedural strategy of navigation is distinct from approaches that work by locating an agent within a metric map of the world (Cruse and Wehner, 2011; Cheung et al., 2014), which has implications for the necessary neural architecture. Secondly, the directional information that can be derived from the comparison of two egocentric views is not dependent of knowledge of the objects that make up the scene, meaning navigation can proceed with low resolution vision not suited to object identification.

4. The peripheral visual system

In insects the visual pathway begins with the compound eye, which differs fundamentally from simple eyes (i.e. single lens eyes like human eyes) because there are multiple lenses with differing viewing directions but a fixed focal length (Land and Nilsson, 2002 Fig. 1). The multiple facets can act as a flexible optic sheet which can be wrapped around the head of the insect and thus allows for a very large field of view. However, optical limits mean that the resolution of the visual system is limited. The highest visual acuity in insects is found in the large eyes of the dragonfly at about $0.5°$, whereas the acuity of a navigation specialist, such as the wood ant in Fig. 1, might be only $4°$. Artificial compound eyes of a comparable scale to insect eyes would have many applications in space-limited situations and ingenious manufacturing techniques are now allowing for advances in the engineering of such sensors (Jeong et al., 2006; Song et al., 2013; Floreano et al., 2013).

Above we have described how view-based matching for ants works on the appearance of scenes and does not necessarily rely on the identification of specific visual objects. This is not surprising given the generally low resolution of ant eyes. It is curious that view-based navigation specialists do not always possess high visual resolution. For instance in ants, higher acuity can be seen in predatory species (e.g., *Gigantiops destructor*, Beugnon et al., 2001) that visually track prey targets, compared to the species that rely on vision predominantly for navigation (e.g., *Melophorus bagoti*, Schwarz et al., 2011) but use olfaction to pinpoint food items. Evidence from another navigation specialist, *Cataglyphis fortis*, shows that as eyes scale for larger or smaller foragers, resolution is often sacrificed to maintain the large field of view (Zollikofer et al., 1995).

This relationship between visual resolution, field of view and the success of view-based navigation strategies was explored using computational methods by Wystrach et al. (2016). Simulated agents were given stored views representing the views that would be experienced along routes through a series of "random" simulated worlds. These virtual reality worlds were designed to mimic the habitats experienced by desert ants, such as *Cataglyphis velox* (Mangan and Webb, 2012) or *Melophorus bagoti* (Muser et al., 2005). By systematically varying the visual systems of the agents (resolution and field of view) and then measuring their ability to
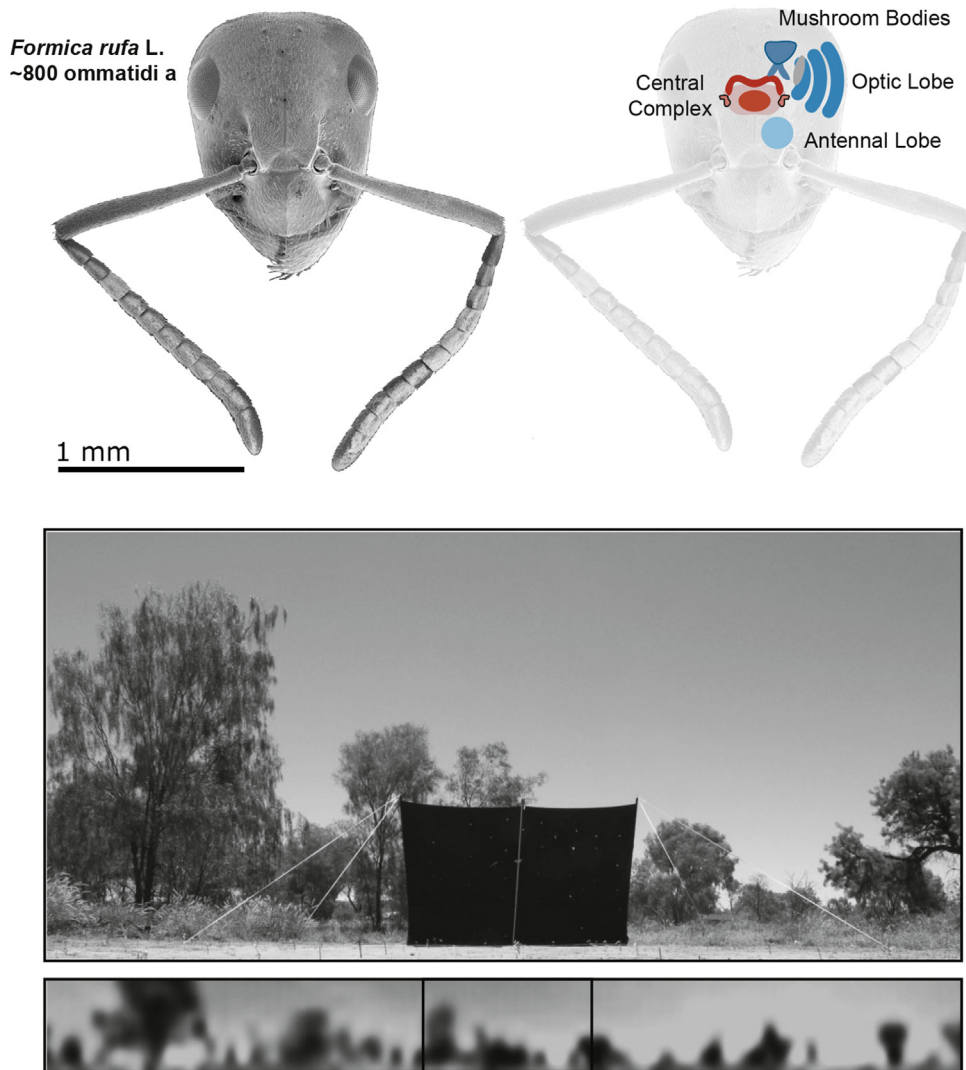
Fig. 1. Left. The head and compound eyes of a wood ant (*Formica rufa* L.). The individual is an average sized worker with somewhere in the region of 800 ommatidia. Photo used with kind permission of Craig Perl. **Right**. A schematic of the major regions in a typical insect brain. The major brain regions that are implicated in visual navigation are either paired, such as primary sensory areas and learning centres (blue). In red, the central complex which is a well conserved brain area seen in all insects. This area is implicated in sensori-motor co-ordination. **Below**. Two images taken from the same location. The upper image represents a human perspective and the lower image highlights some of the differences in an ant's perspective of the world. The ant's perspective is achieved by taking a panoramic image with lowered resolution to match the visual acuity of ants. Note, we have captured the horizontal extent of the ant's eye view, but the vertical extent is limited. Ants would in fact have a full view of the sky. The vertical black lines in the ant's perspective image delimit the field of view of the 'human' picture. The prominent black object from the human perspective view is no longer prominent in the ant's eye view. Images taken with permission from Wystrach and Graham (2012). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

recover route headings from locations on or near the training route, navigation performance can be evaluated as a function of field of view and resolution. The primary finding was that agents with wide field vision and mid-range visual resolution (of the order $1°-10°$) are better suited to navigation. Increasing the visual resolution does not lead to better performance because of the potential for visual aliasing when near, but not precisely on, a familiar route.

That there is information in low-resolution scenes has been demonstrated by studies in autonomous navigation. Milford (2013) asked a car navigation system to localise itself within a previously learnt route. When using very low-resolution versions of panoramic scenes, the algorithm could localise accurately if temporal information was used to mitigate against ambiguities. In a more biologically relevant robot task, Stürzl and Mallot (2006) showed that starting with low-frequency components of a visual image and iteratively matching higher frequencies, allows the robot to home

from a larger region than if visual matching is performed with complete views.

In addition to the resolution of the compound eye, the photoreceptors behind each ommatidial lens have specific spectral tunings that determine to some extent the visual information available for navigation. Most ants have two photoreceptor types that have peak sensitivities to Ultraviolet and Green light. In natural habitats these spectral tunings, when used as part of an opponent mechanism (Möller, 2002; Kollmeier et al., 2007) are particularly well-suited to extracting the contrast boundaries that exist between terrestrial objects and the sky. The importance of these boundaries, that define the skyline, has been shown in behavioural experiments. Disruption of the skyline is detrimental for navigation (Fukushi, 2001) even at dusk, when the sky still has a large UV component (Reid et al., 2011). Similarly, an artificial skyline created to mimic a natural skyline will 'trick' ants into producing their

habitual visually guided direction (Graham and Cheng, 2009). Further evidence for the utility of skylines for navigation is given by the intuitive sense that skylines are robust to variations in lighting conditions. Furthermore, quantitative analyses of natural images (Philippides et al., 2011) shows that navigationally useful information is not degraded when images are simplified to just the skyline, rather than the whole view. The use of skyline information for navigation has now been applied in an engineering context with Stone et al. (2014) showing how UV contrast provides a robust signal for localisation using panoramic views.

5. Neural circuits for visual navigation

Social insects are one of the most studied groups of animals with regard to navigational behaviour, yet despite invertebrate neuroscience playing a key role in understanding fundamental processes, the two areas of research have not significantly overlapped. Thus we know remarkably little about the neuroscience of insect navigation (Webb and Wystrach, 2016). However, comparative and circumstantial evidence points to two brain regions that show interesting navigation relevant properties. The Mushroom Bodies (MB) of insects have long been known to be involved in learning and memory (see Menzel and Giurfa, 2001), specifically associative learning, such as the pairing of food taste and reward. Might the MB be involved in visual navigation? Well, the MB of ants do receive direct input both from the optical and the antennal lobes (Gronenberg and Hölldobler, 1999). Furthermore in ants the MB collar regions, that are sensitive to visual information, are selectively developed at the point when workers begin their foraging life (Stieb et al., 2010). Therefore it is plausible that the MB are used for visual navigation, an idea which is further supported by circumstantial evidence from Farris (2013) who found that the capacity of spatial learning is correlated with the evolution of enlarged and complex MBs across insects.

The architecture of the MB has key properties that mean it is well-suited to learning. The input cells to the MB expand onto a large number of Kenyon Cells (KC), that is, there are more KC than inputs. This creates a sparse code within the high dimensional space of the KC encoding. KC then contract onto a smaller numbers of output cells and learning happens at the synapses between the KC and the output neurons (Wessnitzer et al., 2012). Ardin et al. (2016) used a computational model of a general purpose MB for an agent travelling through a virtual world. Visual scenes were fed to the MB model during training and subsequent navigation was implemented by asking the network to identify familiar views, i.e. views that are likely to represent scenes experienced during training. This builds on Baddeley et al. (2012), who had proposed visual navigation via visual familiarity as a way to utilise a large volume of visual memories with an architecture that does not need memories to be organised in a strict sequence, or for learning to be organised around the selection of key waypoints (Wystrach et al., 2013). The MB model performed well and reinforces the point that the architecture of the MB is well suited to learning visually guided routes as a general associative problem.

However, other brain areas have also been identified as potentially important for visual navigation. The neurogenetic tools available for *Drosophila* have enabled tight relationships to be identified between specific brain regions and particular behaviours. For instance, the ellipsoid body region of the central complex has distinct classes of visually responsive neurons that are essential for a range of visual tasks such as orientation memory for salient objects and simple pattern discriminations (Pfeiffer and Homberg, 2014). The visual receptive fields of the cells are very large and have non-linear responses with excitatory regions surrounded by inhibitory regions (Seelig and Jayaraman, 2013). This classic receptive field organisation, as seen in vertebrate cortical cells, responds optimally to high contrast bars or edges (such as the skyline) and the sub-population of cells are very small in number and thus provide a coarse, low-resolution code which may be suited to navigation. It is known that a subset of these cells (R1 ring neurons) are essential for visual place learning in flies (Ofstad et al., 2011); however, their visual receptive fields have yet to be described. Dewar et al. (2015) used virtual reality simulations of fly experiments to examine the information provided by hypothetical populations of neurons similar to those described by Seelig and Jayaraman (2013). It was shown that these small populations of coarse visual cells are indeed sufficient for visual navigation. Whether or not R1 cells have similar properties to those cells already investigated remains to be seen, and whether cells like those described in flies might contribute to the more sophisticated navigation of social insects, perhaps in concert with the MB, is a live question.

The traditional view of the central complex is that it is a crucial sensorimotor brain area in the control of action (Pfeiffer and Homberg, 2014). The particular organisation of central complex regions suggests that sensory input is represented in an ordered way with respect to the animal's body axis. Further navigational utility is suggested by the discovery of a ring attractor circuit in the ellipsoid body (Seelig and Jayaraman, 2015; Green et al., 2017). This ring attractor maintains a single peak of activity which can be rotated by the movement of environmental stimuli or by the self-motion of the fly. By analogy to the head direction cells of rodents (Taube et al., 1990) it is suggested that this circuit may be involved in the representation of an animal's orientation relative to the environment. However, an alternative idea, that fits with the idea of egocentric procedural navigation, is that the ring attractor holds a behaviourally relevant instruction (e.g. turn left) that could be updated by learnt visual information, routed via ring neurons or the mushroom body.

It is clear is that both mushroom bodies and central complex are interesting studies sites for those interested in the neuroscience underpinning visual navigation (Webb and Wystrach, 2016). With first *Drosophila*, and hopefully social insects soon thereafter, it promises to be a revelatory next decade for the understanding of the neural circuits underpinning navigation.

6. Summary

Insects are an existence proof that low resolution vision and a small brain are not a barrier to the production of exquisite visually guided behaviour. Our aim here was to show that robust navigation comes from the interaction of behavioural strategy, visual systems and neural hardware. Specifically, solitary foraging ants use vision for navigation in a procedural way, the comparison between remembered and current visual scenes provides information about what the animal should do, rather than where it is. This simple strategy can be implemented with low resolution vision and ants do not need to identify objects or landmarks in order to navigate. In addition to low-resolution, ants' visual systems are tuned to extract high contrast boundaries between terrestrial objects and the sky. Various brain regions in insects show properties which are needed as part of visual navigation, but as yet we do not know how navigational behaviours are distributed across these different brain areas. Through further study and modelling, ants may yet deliver specific design blueprints (Webb et al., 2004) to enable engineers to emulate their navigation performance in artificial systems.

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