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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