

point display (Fig. 1b) and the corresponding amount of time spent in each view was recorded. The ants were then released and the experiment was repeated. The experiment was repeated 10 times for each ant.

The visual navigation of ants is a beautiful demonstration of how small brains can produce impressive and robust behaviours in

Observations of ants suggest that the views used to guide a search



study. The major difference is that, in the original study, a neural network was trained with the visual input experienced along an entire route whereas here we trained the network using only the visual input experienced during the portions of learning walks where ants turn and fixate the goal (Fig. 1B, Fig. 2B). These points are clearly identified in the original papers of Judd and Collett (Judd and Collett, 1998) and Müller and Wehner (Müller and Wehner, 2010). During training, the views are presented one by one and the network gathers information by adjusting weights between the visual input and 800 hidden units so as to maximise the extraction of information across the whole set of training views. After training, the overall activity of the network providegato0 Tc 0s58 ET09Dwall activity of

nestward routes (Fig. 2A, dark segments). We replicated these portions of the routes and used the views experienced along these segments to train the network (Fig. 2B). After training, a single simulated ant was released 30 cm from the feeder, corresponding to the commencement of tracking in the original study. The path was terminated when the simulated ant reached 0.25 cm from the goal. The path followed by the simulated ant and the retinal position of the cone's edges were recorded.

The aim of our modelling was to query the pervasive view that ants store and retrieve discrete views of the world independently. We first asked whether a model based on a single holistic memory could reproduce the observations of homing ants searching for their nest in triangular arrays of landmarks (Fig. 1C–E). The network that instantiates the holistic memory was trained with a set of views selected to mimic the nest-focused views generated by the learning walks of desert ants (Fig. 1B). The model accurately reproduces the search distributions across all three conditions (Fig. 1F–H). That is, simulated ants search at the fictive nest position when the visual panorama viewed from the fictive nest matches that of the training situation, and the search pattern loses its accuracy when the landmarks are moved to twice the distance without changing their size. Crucially, this is achieved without the agent storing a view from the nest position itself. That is, the stored views are not acting as point attractors to discrete locations in space.

Having shown that a single memory network can take information from multiple views experienced in training and produce goal searches that match those observed with ants, we then attempted to replicate the results that provide the strongest support for the independent retrieval and matching of multiple discrete views. Judd and Collett (Judd and Collett, 1998) observed that an ant approaching a single black cone (Fig. 2C) will hold the edges of the cone at several discrete positions on its retina, as if matching discrete retrieved views in turn (Fig. 2E). We show here that this pattern of behaviour can arise from the use of a single memory network (Fig. 2F) supplied with training paths taken directly from the original Judd and Collett paper (Fig. 2A).

The explanation of how a holistic memory can reproduce patterns of behaviour suggestive of the retrieval and use of discrete views is quite clear. The use of a single network to learn views and drive subsequent navigation makes an explicit connection between the paths taken during learning and subsequent behaviour. Thus the distinct preferred retinal positions of edges during approaches to the cone is a consequence of the discrete nature of the views used for training and not a result of the system forming, storing and retrieving discrete memories. In other words, we show that the discrete nature of the output behaviour reflects the discrete nature of the input (or training) data. The philosophy of 'embodied cognition' explains how an intelligent interaction between the physical agent and its environment can simplify the neural processing required. Here, some of the processing has been outsourced to the active sensing behaviour of the learning walks, allowing navigation without the cognitive machinery required to store, retrieve and use discrete views.

In summary, our data demonstrate that retrieval-type memory of the views from discrete places in the world is not a prerequisite for visual navigation to those places. Instead, a single holistic memory structure can store sufficient visual information to allow navigation

from a range of locations by simply following the most familiar direction. By avoiding the problem of retrieving appropriate memories, the familiarity-based approach is a parsimonious method that enables both the pinpointing of a specific location and the following of long routes through complex environments. Furthermore, the model provides accurate replications of behavioural data reported in key research papers.

The use of familiarity as a criterion for choosing a direction is an attractive and viable scheme for navigating ants because of the constraints of the task (i.e. moving between physical goals) and their motor systems (i.e. coupled viewing and walking direction). However in its current form, this model cannot explain all view-based behaviours in insects. For instance, hoverflies (Collett and Land, 1975) and waterstriders (Junger, 1991) use views to maintain a fixed position in a fluid space, so there may be a requirement for a view-based mechanism that acts as an attractor. Conceivably this could be implemented using an absolute familiarity threshold as a stop signal, or by the use of a snapshot in the traditional sense (Cartwright and Collett, 1983). Similarly, our current model does not capture all that we know about the sensorimotor implementation of visual navigation in ants. For instance, Lent et al. (Lent et al., 2009) show how ants can perform some form of mental image rotation to generate corrective saccades during visual orientation whereas our model relies on an exhaustive rotational search. The inclusion of a saccadic mechanism like this would improve the efficiency of the model but would not alter the pattern of results presented.

Another issue not currently addressed in our modelling concerns how ants modulate learning. During learning walks, the views used to guide a return to a nest are learnt at the beginning of the outward journey, and reciprocally, views used to pinpoint the food source are learnt at the beginning of the return journey. However, we know that ants form distinct memories for foodward and nestward navigation, and that those memories are insulated from each other (Wehner et al., 2006). It may be possible that ants learn continuously but switch between foodward and nestward motivational contexts to decide to which memory the current visual information is allocated. Switching motivational context would also lead the ant to turn and face the appropriate goal, by means of path integration.

This work has been driven by the philosophy of trying to produce parsimonious hypotheses for observed behaviours. In this spirit, we proposed a simple solution that can explain key observations of visual navigation in ants from both experimental and natural conditions. Our belief is that ant experiments and insect-inspired modelling can be used to generate valuable hypothetical mechanisms for understanding animal navigation in general (Wystrach and Graham, 2012). Given that the idiosyncratic routes that are characteristic of ant navigation are also seen in many vertebrate navigators as they move through familiar terrain, one should ask whether the ideas presented here may apply to vertebrates. Certain lines of evidence suggest that this is not an entirely fanciful notion. Route following in humans does not have to engage the map-like memory formed in the hippocampus (Hartley et al., 2003), and familiarity-type memories are also independent of the hippocampus (Fortin et al., 2004). This makes the familiarity-based solution proposed here an interesting candidate to explain route following in vertebrates. The next step is to design experiments that conclusively test whether animals use such a familiarity-based memory for navigation.

