

Spend an hour or two watching a colony of ants and you will see hundreds, even thousands, of ants working diligently and cooperatively, perhaps to kill and carry a large prey item, build a large nest structure or develop and use road-like networks for foraging. It is evident that collectively, colonies of social insects can do amazing things (Figure 1) and scientists invest lots of time trying to work out how ant colonies organise themselves so neatly and effectively. In this article, Paul Graham and Andrew Philippides set out to answer the question: just how smart is a single ant?

Many ants = 1 super-organism

To explain collective behaviours, ant-colonies are thought of as super-organisms, where each ant is like a single neuron in a large collective brain. In this analogy, an individual ant is seen as a simple automaton. But each ant has a brain and here, we are interested in how intelligent an ant is when she is separated from her nest-mates. To assess the intelligence of a single ant, we investigate how theytheir performance in a task which is fundamental to their survival and the survival of the colony:, how they navigate back to their nest after finding food.

To find new sources of food, animals must safely explore novel places while remembering something of their outward journey so that they can return efficiently to their nest having found food. The mechanism used by ants is called *path integration*.

Key words
insect behaviour
memory
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experiment

Box 1 How do we know the mechanisms of ant path integration?

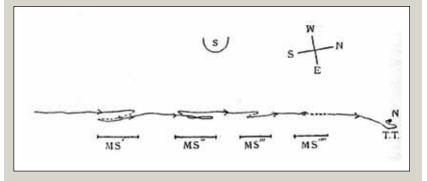
To perform path integration, an insect must know continuously the direction she is traveling in and also how far she travels during each segment of the route, i.e. she needs a compass and a measuring tape. For distances, ants keep track of the number of strides they have taken. We know this because scientists have manipulated the lengths of ants' legs as they try to find their nest. In path integration experiments, scientists move ants from the food to a new test ground and then see how far they walk before they stop and begin to search for their nest entrance.

If you take ants to an unfamiliar place as they try to get home with food, they will walk the distance that would normally take them back to their nest before then starting to search. However, if you lengthen their legs with pig bristle, they will take the same number of strides but cover a longer distance before they think they are near home and start searching. From this simple demonstration we can conclude that ants measure distances by counting their steps.



An ant of the species Cataglyphis fortis with pig bristles glued to its legs

For a compass, ants use the sun. Felix Santschi discovered this in the early twentieth century. He observed the paths of homing ants as he blocked their view of the sun with a board, whilst simultaneously reflecting a view of the sun with a mirror. In this way, the sun appeared to come from a different direction. The figure shows an ant path recorded by Santschi. Each labeled (MS) section is part of the path recorded as Santschi changed the apparent direction of the sun. In each case, the ant immediately reverses its path direction, showing clearly that it relies on the sun's position for a sense of direction.



When path integrating, ants keep track of the direction and length of every section of their journey (see Box 1). To make use of this information, ants must mentally add together these route segments so that they always have an estimate of the direct route back to their nest, effectively doing vector geometry (Figure 2).

Always knowing the fastest path home is particularly useful when the ant finds food or when she is trying to escape a predator. The fact that ants can perform path integration tells us about the processing power of their tiny brains. Not only can they do something similar to counting, their brains are wired up to perform calculations which approximate to trigonometry.







Figure 1 The amazing cooperative behaviours of ants.
a) Fire ants cluster together on the surface of water.
b) A foraging highway of Leafcutter ants.
c) The beautiful architecture of a Harvester ant nest.

Meandering outward path Direct homeward path

Figure 2 The long and winding path of a desert ant as she searches for food in the desert. When she finds food (O), after a path of over 100 m, she takes a direct path back to her nest.

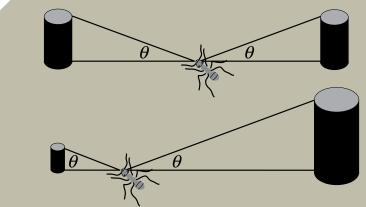
Learning landmarks

Path integration allows ants to explore new places whilst being connected to their nest, but it is not perfect. As an ant travels longer and longer distances, small errors from each path section can add up and result in her missing the nest when she returns, meaning she will have to spend time and energy searching for her nest entrance. Fortunately, when an ant has become familiar with her environment she can avoid this problem, because, just like humans, ants are capable of learning an important location by remembering the visual landmarks close to it.

When an ant is at a place that she wants to return to (perhaps the nest or a food source), she memorises the appearance of the world from that place. We liken this to 'taking a mental snapshot'. When she wants to get back to the important place all she has to do is recall this mental picture and try and make the world look like the remembered snapshot (Box 2). This is an elegant strategy for navigation. At no point does an ant need to calculate where she is. She simply moves in whatever direction makes the world look more similar to her memory. However, it still requires brain-power because ants have to have a photographic memory.

Box 2 How do we know how ants use visual landmarks?

The basic method for investigating how ants use snapshots is, as with path integration experiments, based on the fact that when an ant thinks she is very close to her goal, she will start a special search behaviour. To understand what ants have learnt about visual landmarks, we observe how changes to the landmarks influence where ants search. The diagram represents a simple experiment. Ants are trained to find food between two identical landmarks. If you change the landmarks so that one is small and one large, ants will search for food closer to the small cylinder, where both landmarks appear to be the same size. Unlike humans, ants don't see in 3D and, to an ant at the location close to the small cylinder, the world looks identical to a snapshot which was stored from the feeder during training.



The ant learns that food is half way between two identical cylinders (above). When the cylinders are changed (below), she searches at the point where they appear to be the same size.

Smarter than the average insect

All animals, including humans, have to move through the world. Despite the fact that colonies of ants can work together to provide specialist highways to travel along, individual ants also use individual strategies to explore new territory. Studying these behaviours allows us to understand the impressive feats animals can achieve with tiny brains. Using path integration and memorised snapshots requires ants to be able to do calculations similar to trigonometry and also to have a photographic memory. So, how smart is an ant? At least when it comes to finding her way home, pretty smart.

Paul Graham and Andrew Philippides study the navigational abilities of insects at the University of Sussex. They are interested in how small brained animals can produce clever behaviour and whether we can replicate that behaviour in robots.