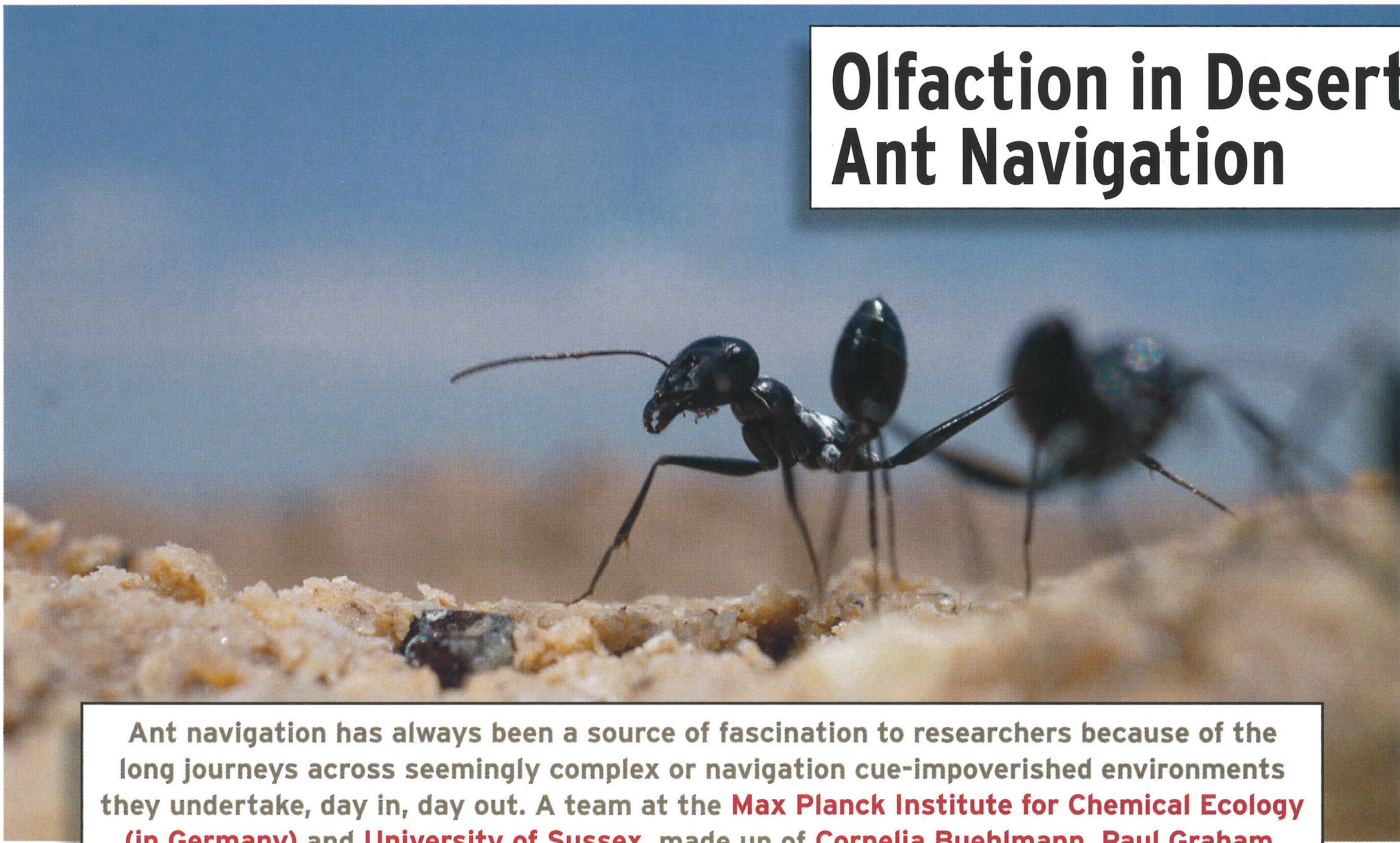
Olfaction in Desert Ant Navigation



The desert ant Cataglyphis fortis. Credit: Markus Knaden

Ant navigation has always been a source of fascination to researchers because of the long journeys across seemingly complex or navigation cue-impoverished environments they undertake, day in, day out. A team at the Max Planck Institute for Chemical Ecology (in Germany) and University of Sussex, made up of Cornelia Buehlmann, Paul Graham, Bill Hansson & Markus Knaden, has been looking into olfaction and its role in desert ant navigation. Ahead of their presentation at the RIN16 Orientation and Navigation Birds, Humans and Other Animals conference, Cornelia walks us through their findings.

It is early in the morning in Tunisia but the sun rising on the horizon is already strong enough to have warmed the morning air. It would be a perfect day to spend at the beach but we are driving from the bustling coastal town of Mahares to a desiccated salt lake about 60 km inland. As we do every morning, we are heading to the natural habitat of a navigational expert – the desert ant *Cataglyphis fortis*. When we arrive at the edge of the salt pan close to the village of Menzel Chaker, the ground has already heated up, and black shiny desert ants are flitting around on the salty desert ground, foraging for food. Together with other researchers from German and English universities, we spend the summer months in this scorching desert heat watching ants, all to get a better understanding of animal navigation. In the late 1960s, the neuroethologist Ruediger Wehner popularised the study of the North African *Cataglyphis* desert ant and we are still learning from them today. Ants provide a useful model for unravelling the mechanisms of navigation and people have studied ant navigation for a long time, not least because it is easy to do. Data can be recorded by simply scratching their paths in the sand with a stick, and with such methods 100 years ago, Santschi was able to investigate the sun compass of ants. The methods haven't changed a lot since the early years, and even though we occasionally use more high-tech equipment we still learn new things by simply looking at the paths of ants as drawn on paper.

Large test fields painted on the ground allow us to record the ants' homing paths on paper.
Credit: Kathrin Steck

Exploring Unfamiliar Terrain While Keeping Track of the Journey

The main task for an ant forager is to collect food and bring it back to its colony, which demands sophisticated spatial skills from an animal that possesses only a tiny brain. The hostile habitat does not provide stable or plentiful food sources and ants are looking for arthropods that have perished in the heat. It is this heat, coupled with the unpredictable food distribution, which means they have to be solitary foragers instead of using shared odour trails as observed in other ant species. We have recorded the journeys of individually foraging ants with GPS and observed ants travelling up to 1500 metres when screening the desert for food. When travelling such extreme distances, ants are in unfamiliar terrain and must keep track of their position to be able to return to the nest. With a good directional sense, driven by celestial mechanisms and a step counter to measure the distances covered, ants can implement an innate navigational mechanism called path integration, which is widespread among animals and similar to an old maritime navigational trick. A continuous update of direction and distance informs ants throughout their foraging journey, where they are relative to their nest so that they can take the quickest route home when they have a food item, or it becomes too hot.

Learning Features From the Environment

Path integration is great for exploring unfamiliar terrain while being safely connected to your nest, but ants complement this strategy with the learning of visual features from the world. The salt lake is surrounded by large olive tree plantations that provide to some extent a useful visual panorama, and also a few little salt-tolerant plants survive the aridity and occasionally the nest entrance is marked by a small sandy nest hill. However, compared to the environments of other ant species, this environment seems to be largely featureless. Recent findings reveal that the ants' excellent sense of smell is also part of their navigational toolkit. It has long been known that ants, equipped with their two big antennae, have a great sense of smell. Of course, scientists know lots about ants travelling on pheromone trails, which have been studied intensively. However people haven't really studied navigation based on environmental odours not laid down by other ants.

Following an Attractive Odour Plume

Imagine the situation of an ant forager leaving its safe nest and searching for a dead insect that could be as small as a tiny fruit fly, somewhere on the desert floor hundreds of metres away. Ants are able to detect dead insects through olfaction, as desert ants are highly sensitive to specific odours emitted by a dead insect. Having detected these airborne odour molecules, they walk against the wind along the odour plume to the food item. Ants have developed a clever strategy to maximise the efficiency of locating these sparsely distributed odour plumes.

Different food odours were tested for their behavioural responses. The small tubes with the odours were put at the end of the stick and presented to ants that were searching for food. Credit: Markus Knaden

When leaving the nest, they initially head back to the approximate area where they have previously found food. When we tracked ants' foraging paths in such areas, we found that the ants exhibit extensive path segments that are crosswind. Therefore, ants have developed an elegant way of maximizing the chances of encountering an odour plume from a food item, by combining long path segments perpendicular to the wind with a high sensitivity to food odours. Having grabbed a food item, an ant might be over 300 metres away from her nest. Path integration guides her back close to the nest but the final nest approach is supplemented by the use of environmental features, and olfaction comes into play again. Carbon dioxide (CO_2) is a product of respiration and the degradation of organic matter, and it is present in an increased concentration just at the ant's nest entrance. Thus, the ants can use it as an olfactory cue to accurately pinpoint the nest entrance, which may be an inconspicuous small hole in the desert ground. After installing a camera at the nest entrance, we could look closer at the ants' homing paths, and we could see that ants pinpoint the entrance by walking upwind following this CO_2 odour plume emanating from the nest. Moreover, we could test that, when artificially supplied, CO_2 alone is sufficient to induce plume following in these homing ants. The downside of using CO_2 as a nest signal is that it is not a nest-specific cue because its concentration is increased at all neighbouring nests that ants may walk by. However, ants are smart enough to deal with that problem. By performing a further experiment we could set path integration and olfactory nest cues in conflict and we found that the ants only respond to an attractive nest odour when the path integrator has guided them close to their nest. Hence, this clever interaction between mechanisms ensures that a homing ant does not end up in the wrong nest, which would be at best inconvenient and at worst deadly.

Olfactory Scenes Used for Navigation

Above we have shown two examples – olfactory-guided food and nest approach – which show how smell can be used to orientate towards a specific target. Following an attractive odour plume is a well-known orientation strategy in lots of insects when locating a feeding site, mating partner or a host, ie a discrete 'smelly' target. In their more general navigation, animals have to maintain a sense of where they are, or what direction to go in, as they move between important locations, such as home and food. Is it possible that ants use olfactory information in this more complex navigation? For instance, this type of complex olfactory navigation is shown by homing pigeons, where birds use information carried by the wind, ie the chemical profile, to orient to their home loft even from unfamiliar areas. Another fascinating example of olfactory navigation is the wandering albatross that travels hundreds of kilometres over the relatively featureless ocean locating food by using odours produced by rich food areas before navigating back to its home island. We have recently demonstrated for the first time that *Cataglyphis* desert ants can also perform this more sophisticated olfactory navigation, which is beyond simply following an attractive odour plume. When it comes to olfactory navigation it is valuable to have some knowledge of the sensory world through which the animals are moving. However, little is known about the occurrence of environmental odours over larger scales in natural environments. To remedy this, we collected and analysed odour samples over an area of 100 m x 100 m. To our surprise, we found that the seemingly homogenous salt pan provides place-specific environmental odours which might be useful for the ants. This is a realistic possibility as we have demonstrated that ants trained to forage on a route alongside a sequence of artificial odours were able to use olfactory cues for navigation. It is difficult for us to imagine how airborne odours provide spatial information but it seems to be highly beneficial as a complementary navigation mechanism. In general it seems that ants use whatever cue is available to navigate efficiently, and usually they will be using cues simultaneously rather than in a hierarchical way. Studying ant behaviour in their natural environment allows us to closely investigate the ants' natural sensory ecology. It is important to keep this in mind as we hope to gain a better knowledge of the mechanisms behind olfactory navigation and how this interacts with other guidance mechanisms.

We follow individual marked foraging ants with a handheld GPS device to track their entire foraging journeys.

References & further readings:

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