suggesting that it might participate in the regulation of mitophagy — the selective removal of defective mitochondria by autophagy. Atg32 is a mitochondrial outer membrane protein (interestingly, itself identified by application of yeast library screening) that is exposed on the cytosolic face of the organelle. Mitophagy is initiated through the recruitment of the autophagy proteins Atg11 and Atg8 to the mitochondrial surface for subsequent autophagosome formation mediated through the phosphorylation of Atg32 by casein kinase 2 (CK2), which acts downstream of signalling pathways involving the mitogen-activated protein kinases Slt2 and Hog1 [9]. Any links between Rph1 and other forms of organelle-selective autophagy remain to be determined.

While acknowledging that these findings concern yeast, autophagy — similar to many cellular processes — is highly conserved from yeast to humans. Thus, information gained in yeast is likely to have application to our understanding of autophagy in mammals. Indeed, as highlighted by the authors themselves, the function of Rph1 is conserved with four isoforms of KDM4, the homologue of Rph1 in mammals. While KDM4A is shown to be a negative regulator of autophagy [2], the involvement of the other isoforms remains to be investigated. Importantly in this context, Bernard *et al.* [2] noted that knocking down KDM4A can increase autophagy activity, suggesting that modulation of the KDM4A pathway could have therapeutic potential in the treatment of pathological conditions where autophagy is perturbed.

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Insect Navigation: Do Honeybees Learn to Follow Highways?

Radar studies of a honeybee’s flights when it first leaves its nest suggest the features of the surrounding landscape that it learns guide future foraging trips.

Thomas S. Collett* and Paul Graham

Orientation or learning flights are performed on the first few departures of a wasp or bee from its nest, when it learns the position of the nest relative to its near and far surroundings. The flights are intriguing because they contain elaborate manoeuvres that are likely to be adapted to acquiring navigational information. They begin with a portion within about 0.5 m of the nest often lasting about 20–30 seconds, which can be recorded with video. These manoeuvres and their possible function in gathering information are to some degree understood. The likely role of larger-scale flight patterns is more uncertain. Three recent radar studies of bee learning and return flights [1–3] are valuable in showing the pattern of flight paths in relation to large landscape features. They suggest that one function of learning flights is for bees to learn properties of elongated features of the landscape, like hedgerows and boundaries between fields, and to follow these features. These ground-based features can then help guide future foraging routes. In two of the new studies, led respectively by Juliet Osborne and Randolf Menzel, the paths of individual bumblebees [1] and honeybees [2] have been tracked as these novice bees first learn and explore the terrain around their nest. The third study, led by Stephan Wolf [3], describes the homeward routes of experienced foragers after they were displaced from their hive. All three studies show flight tracks parallel to landscape features; the first two also reveal functional differences between the learning flights of honeybees and bumblebees and we begin by comparing these flights.

The large-scale portion of learning flights extends over 100 m or more [4]. To monitor this part of the flight, a tiny radar transponder is fixed to an insect’s thorax [5]. The transponder, when illuminated by a pulse from a stationary radar transmitter, emits a signal of half the wavelength of the activating pulse. This signal emerges uniquely among the many reflections from other objects to give the bee’s position and allow its path to be tracked. The sampling frequency is limited by the rotational frequency of the radar beam and is only about 0.3 Hz. Nonetheless, the technique gives invaluable information that so far cannot be obtained in other ways.

There are marked differences in the social organisation of foraging in honeybees and bumblebees which are reflected in their learning flights. Foraging honeybees are told by other foragers where to find food through the waggle dance, whereas bumblebees, with no waggle dances, explore for food individually. Honeybees leave the hive to start foraging quite late in life. On their first flights, these novices gather information that will later help them to return safely back to their hive after foraging. They are reported not to follow waggle dances at this stage [6] and they perform an average of approximiately six learning flights before starting to forage [2]. Honeybees thus seem to separate the tasks of learning their surroundings and of finding foraging areas. Bumblebees differ and intermingle learning about their surroundings with exploring for food. Perhaps because they are part of a much smaller foraging force, bumblebees tend to start foraging a few days after eclosion [7]; quite often they return with pollen on their very first flight [1,8].

Corresponding differences are seen in the bees' flight paths. Honeybees tend to restrict the large-scale portion of each learning flight to a single quadrant around the nest and often fly in narrow, hairpin loops taking almost the same ~100 m track away from and back to the hive [4], with successive flights tending to occupy different quadrants [2]. The sequence of learning flights in Figure 1A gives an example. Individual bumblebees explore more widely on each flight. Their initial flights consist of three or so wide loops in different directions [1]. Over their first three flights, bumblebees tend to increase the distance that they travel from the nest from about 50 m to 300 m. In contrast, the maximum range of honeybees stays relatively constant across the three flights [2,4] with a median distance of just under 100 m.

Because honeybees learn to navigate in the neighbourhood of the hive before they start exploring for food, the details of their initial flights are likely to reveal in a straightforward way the features of the landscape that they find significant for travelling to and from the hive. Evidence that honeybees do learn visual properties of the surroundings of the hive on a single flight came from transporting a hive to a new location and allowing foragers, which were presumably experienced with the former surroundings of the hive, to perform one learning flight in the new terrain. These bees were caught on their return to the hive and released at different sites ~100 m away. The directions of the bees' flights from the release sites were oriented towards the hive, provided that visual features around the hive were visible from the release site [9]. The new honeybee study [2] contributes an interesting rider to this one trial learning of older bees: novice bees with learning flights that took them more than 30 m from the hive spent less and less time within 30 m of the hive on each successive flight, suggesting that once they are acquainted with the landscape near the hive they stop lingering there and venture further to learn more widely.

A remarkable characteristic of a novice honeybees' tracks [2] is the strong impact of elongated ground features on its flight direction (Figure 1A,B). The experiments were conducted in flat farmland in northern Germany with clear visual boundaries between adjacent fields. One field boundary about 20 m from the hive ran along an ESE–WNW axis that was echoed in the direction of tracks left by farm machinery. Portions of flight paths of many bees were biased in this direction (Figure 1B). Although it is not obvious in this distribution of flight segments, the paths of some bees appear to follow other field boundaries near the hive. In one example, a bee performed several learning flights and subsequently two much longer foraging flights (Figure 1A): both learning and foraging flights tracked the same ground features. There are signs that bumblebees also follow linear paths [1], but this characteristic has not yet been analysed.

The importance of elongated landmarks is also seen in the homing of experienced foragers reported in the third study [3]. This research was chiefly concerned with the question of whether a gut parasite, *Nosema ceranae*, might influence the navigational abilities of infected honeybees. About a third of infected bees failed to return home compared with about 7% of control bees, but, irrespective of treatment, most of those that returned followed the same indirect homeward route. Foragers returning to the nest were caught and displaced 120 m SW from the hive. The majority of bees first flew roughly N and parallel to a prominent path between fields; after about 60 m the bees turned approximately E flying close to a hedgerow before finally curving towards the hive (Figure 1C).

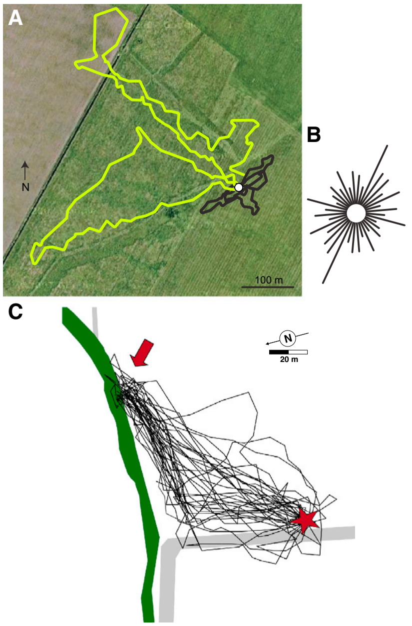

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Figure 1. Radar tracks of honeybee flights.

(A) Smoothed radar tracks of a sequence of learning flights (black lines) followed by two foraging flights (yellow lines) superimposed on a map of the landscape with the hive marked by a white dot. (B) Circular distribution showing that, taken over all bees, the bees' predominant fight direction during learning flights is parallel to the field boundary near the hive. (Adapted from [2].) (C) Homeward routes along linear features in a landscape. Radar tracks of 37 bees after displacement to a release site (star). Many bees took the same indirect two leg route to the hive (arrow). The first leg was along a field-track running N and the second on the southern side of a hedgerow running E. For clarity tracks longer than 200 m (120% of the length of the indirect route) are excluded. The path is coloured grey and the hedgerow (3-4 m high) dark green. (Figure kindly provided by Stephan Wolf based on data from [3].)

Such detailed correlations between landscape features and flight tracks seen during learning and foraging flights indicate the features that guide bees, but do not tell us about the contents of their landscape memories. Do bees, for instance, remember the compass direction of a field boundary and follow that direction when their memory is triggered by a particular view, or do they learn to fly parallel to particular elongated features below them?

Questions of this kind may be answered through an experimental protocol developed by Uwe Greggers and Konstantin Lehman. In their initial studies summarised in [10], a colony of bees first became familiar with a particular terrain. Bees performed learning flights and foraged there for more than a week. To obtain some of these bees in a known motivational state, they were then trained to a feeder 10 m from the hive. Bees that had fed at the feeder and so wanted to return to the hive were fitted with radar transponders and released to search for their hive in an unfamiliar test terrain about 4 km away. The test terrain was in a similar agricultural landscape to the training terrain with some landscape features providing a partial match to features in the training terrain. The test terrain thus evoked navigational responses that would help a bee reach home in the training terrain.

To approach the question raised above: suppose that bees matched a NE–NW boundary in the test terrain to a N–S field boundary close to the hive in the training terrain. Do the bees in tests fly straight up and down this field boundary, suggesting that they had learnt to follow the boundary in the training terrain, or do they fly in a saw-tooth pattern with one side of the saw-tooth running N–S, suggesting that the familiar boundary triggers flight in a particular direction?

Use of this methodology is likely to uncover much detail about the array of strategies that enable honeybees to navigate within a familiar landscape. The data so far suggest a convergence between birds and bees. A decade ago it was found that homing pigeons follow conveniently placed man-made roads on their way back to their lofts [11,12]. It now appears that honeybees may also exploit linear features of a landscape as offering economical and reliable navigational guides.

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