How to navigate without maps: The power of *taxon*-like navigation in ants

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Rodents are said to have two different navigational systems, a map-like *locale* system and a route-based *taxon* system consisting of sensorimotor routines such as beaconing and turns at appropriate stimulus conditions (motor routines). Ants on the other hand are not known for map-like navigation, and seem to get by with a repertoire of taxon-like strategies. I review how this repertoire serves ants in making up for the lack of a *locale* system. Path integration — keeping track of the straight-line distance and direction from the starting point — operates continuously in the background, and can be called upon as necessary, or relied on in habitats in which no useful visual cues are available. Crucial to the power of a taxon-like repertoire is using the full panoramic visual context, both to guide the operation of strategies (context-modulated servomechanisms) and to guide navigation directly. The entire repertoire is backed up by systematic search strategies. I end with some reflections on the power of taxon-like strategies.

Key words: ant, navigation, views, vectors, *taxon*

Introduction

Echoing philosopher Immanuel Kant, O'Keefe and Nadel wrote at the end of the first chapter of their influential (1978) book:

> there must be a pre-existent spatial framework in order for organisms to experience the world coherently. Objects could not be identified, nor localised, nor even seen as extended in the absence of this framework. (p. 59).

They go on to argue for map-like representations in rats, called the *locale* system. This quote can be taken to state the functional advantages of having a *locale* system coding unitary, absolute space. Objects and their locations may be placed in such a unitary overarching framework. The spatial extent of objects may also be coded. Objects may be identified by spatio-temporal continuity. The overarching framework reduces the problem of the re-identification of objects, or perceptual aliasing (Cheng, 2008, Nehmzov, 2008). Too many objects in the world, from doors to trees, look similar, so that they need to be distinguished in part by the location on a map at which they are found.

Yet among insects whose navigation has been much studied, the existence of a map-like representation is debated in the case of honeybees (*Apis mellifera*; Cheng, in press; Cruse & Wehner, 2011; Menzel et al., 2005), or doubted in the case of ants (T. S. Collett & M. Collett, 2002; Wehner, Boyer, Loertscher, Sommer, & Menzi, 2006). Navigational problems have many common elements. The geometric laws governing space over a local region (as opposed to a global scale of travel) are the same for all animals. For instance, in local space, three objects define a triangle whose angles add up to 180°. Trigonometric relations are useful for making spatial inferences based on map-like representations. How could navigating ants get by without any map-like representations, perhaps without experiencing the world coherently? Answering this question forms the major theme in this paper. Hopefully, the answers will also shed some light on comparisons of different strategies in different animals for solving common spatial problems.

The answer in short is that insects, and especially ants, rely

much more on strategies akin to those found in the second major system of navigation that O'Keefe and Nadel (1978) posited, the *taxon* system. The *taxon* system comprises routines and procedures not based on map-like representations but procedures akin to route instructions, to be detailed shortly. The theme that I explore here is that a taxon-like system can be very powerful in the real world with its rich array of cues including trees, bushes, rocks, and perhaps distant hills. Ants seemed to have carved out a taxon-like niche for navigation.

I will first elaborate briefly on locale and taxon systems in rats, without approaching anything like a review. This sets the stage for exhibiting the multitude of taxon-like strategies in a few species of ants (whose navigation has been well studied), with occasional references to honeybees. I end with some speculative reflections regarding navigational strategies in a comparative context.

Locale and taxon systems in rats

The taxon system takes on philosophically-empiricist notions of space, being built out of sensory data and motor routines. It includes path integration, called dead-reckoning or internal navigation in O'Keefe and Nadel's (1978) book, guidance, and orientation.

Path integration means keeping track of the straight-line distance and direction of travel, so that an agent can compute the vector home at any point during the journey (M.-L. Mittelstaedt & H. Mittelstaedt, 1980). In rats, a known compass for keeping track of the direction is internal, based on the vestibular system (Etienne & Jeffery, 2004), although it is possible that external sources such as visual landmarks may also be used.

Guidance is focused on some aspects of the stimulus situation surrounding the navigator as a basis for navigation. As one example, some object is identified from a distance, and the animal heads toward that; beaconing could be another term for this kind of guidance-based navigational behavior (Shettleworth & Sutton, 2005). Beaconing generally refers to identifying a single visual object (which might consist of one or more physical objects), and heading toward it. But more extended stimuli may also guide animals. Rats might follow well worn tracks (Calhoun, 1963), or honeybees might follow the shore of a lake (von Frisch & Lindauer, 1954).

Orientation, on the other hand, is focused on the motoric aspects of navigation. Turning a particular angle at some point on the journey, and then heading in the turned direction would be one example. Together, behaviors based on guidance and orientation can be used to build routes, which might characterize much of rat navigation in the wild (Cal-

houn, 1963).

Locale navigation, in contrast, can be considered flexible, map-based behavior, to which place cells contribute a hypothesized neurophysiological basis in O'Keefe and Nadel's (1978) treatment, and in modern updates (Sheynikhovich, Chavarriaga, Strösslin, Arleo, & Gerstner, 2009). Place cells in the rat's hippocampus fire when the rat is in a particular place in an experimental arena (Jeffery, 2010; O'Keefe, 1976; O'Keefe & Dostrovsky, 1971). The firing rate is in general independent of the direction that the rat is facing, or how the animal got to the place. The key characteristic of the map-based locale system is that places are located in a framework of metric properties and relations, linked to other places and stimuli (e.g., landmarks) in a map-like fashion. This allows the rat to learn to find an unmarked place, for example, a fixed place in a swimming pool at which a platform just under the surface may be found, and to find the target readily when starting from varying and arbitrary locations in the pool (Morris, 1981; Morris, Garrud, Rawlins, & O'Keefe, 1982).

A quarter of a century after O'Keefe and Nadel's (1978) formulation of the cognitive map as a locale system, a significant "unpacking" was presented (Jacobs & Schenk, 2003). The unpacking finds two integrated map systems. An evolutionarily more ancient bearing map system is based on gradients of various kinds (odor, magnetic cues, wind, etc.) as well as distant landmarks, providing coarse positional information and directional compass. A finer but smaller-scaled system called the sketch map is topographic in nature, encoding the positions of objects serving as landmarks and the navigator's position in the local space. The entire map system is an integrated map formed by combining these two kinds of maps, all systems being instantiated in different subsystems of the hippocampal formation. In the integration, the linking of sketch maps with bearing maps is crucial both for identifying the correct sketch map to use and for linking different distant locations.

Taxon-like ant navigation

Insects have long been known to use landmarks for navigation, and much classic work featured ants and bees. For example, von Frisch and Lindauer (1954) trained honeybees (*Apis mellifera*) to travel along some prominent large-scale feature during an afternoon. The feeder at which the bees were feeding was moved further and further from the hive over the afternoon. The large-scale landmarks might be a shore of a lake or a long line of trees (Figure 1). At the end of the day when the bees had stopped foraging, von Frisch and Lindauer closed the hive and moved it to another location at which similar landmark features were found (another shore of a lake or another line of trees) running in a different com-
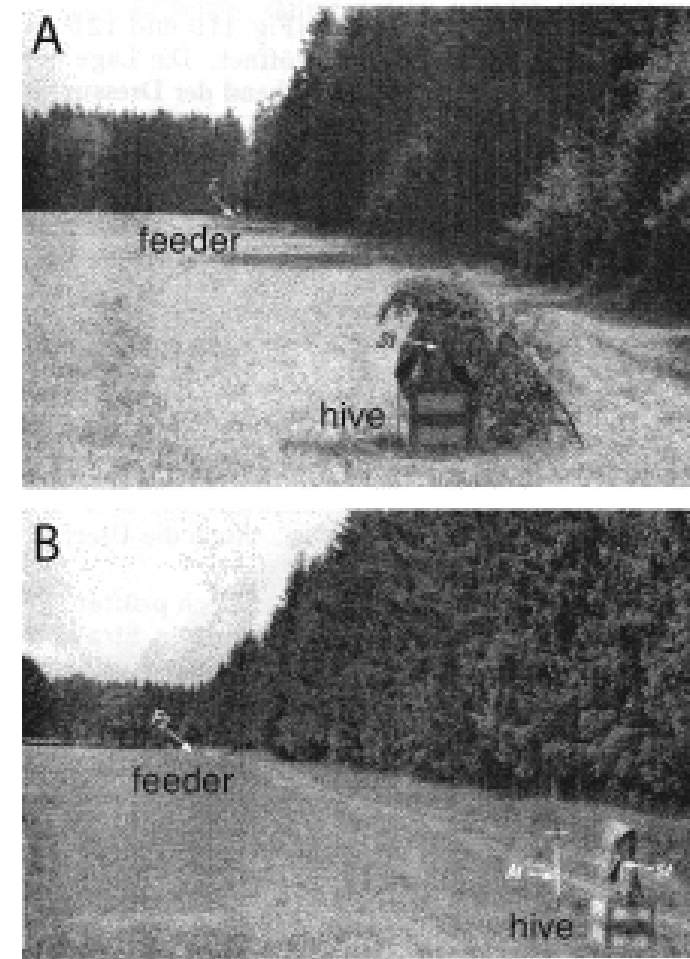
Figure 1. Illustration of an experiment by von Frisch and Lindauer (1954). A. The bees were trained over an afternoon to forage from a feeder beside a line of trees. The feeder was moved further and further along the line of trees over the course of the day until it reached the location shown. B. A test set up the next day at a different location with a line of trees running in a different compass direction from the line of trees encountered in training. One of the feeders (F2) was located along the line of trees. Other feeders (not shown) were placed in other compass directions from the hive. Note the similarity in skyline contour between the test and training situations. Adapted from "Himmel und Erde in Konkurrenz bei der Orientierung der Bienen [Sky and Earth in competition in the orientation of bees]," K. von Frisch and M. Lindauer, 1954, Naturwissenschaften, 41, p. 249. Copyright 1954 by Elsevier. Reprinted with permission.

pass direction. Different feeders were set up before the bees came out foraging the next morning. The bees preferred to follow the landmarks rather than the learned compass direction, thus showing that they were utilizing large-scale landmarks to strike a direction of travel.

Ants move on the ground, and on a small enough scale that experimental landmarks can be provided and manipulated to demonstrate that they use landmarks. Santschi (1913)

reported experiments in the 19th century by John Lubbock showing the use of landmarks in ants (*Lasius niger*). The ants moved back and forth between their nest and a feeder over a circular disk. A candle off to one side was provided as a landmark. Rotation of the circular disk, while leaving the candle in its place, had no notable effects on the ants' behavior. Rotating the disk with the candle on it, however, changed the course that the ants took, showing that they were using the candle to strike a navigational course. This early experiment heralded modern experiments manipulating such moveable landmarks and showing their effects on ant navigation (*Cataglyphis fortis*: T. S. Collett, Dillmann, Giger, & Wehner, 1992; *Formica rufa*: Durier, Graham, & Collett, 2003; *Gigantiops destructor:* Macquart, Garnier, Combe, & Beugnon, 2006; *Melophorus bagoti*: Wystrach, Schwarz, Schultheiss, Beugnon, & Cheng, 2011).

Santschi himself (1911) showed that ants (of the genus *Cataglyphis*) used the sun as a source of direction by reflecting an image of the sun in a mirror. He reported that the ants would reverse their direction of travel upon viewing the sun in the mirror. This has led to a successful program characterizing the nature of the sky compass in hymenopterans and other insects (Rossel & Wehner, 1986; Wehner 1994; Wehner & Müller, 2006).

Among the studied hymenopterans, map-like navigation is not known in ants, and has not been proposed by anyone to my knowledge. A spectacular failure to exhibit map-like behavior was found in the Australian desert ant *M. bagoti* (Wehner et al., 2006). The ants were trained to forage at a feeder, but a direct route either to the feeder or back home was prevented, so that the ants had to detour and complete a loop as they foraged at the feeder. The ants learned such a loop readily. Wehner et al. then asked whether the trained ants could recognize on their way home a place encountered on their usual outbound route, a route that they had traversed many times on the way to the feeder. Ants on their way home with food were displaced just before reaching their nest to some place on their outbound leg to the feeder. Such ants displayed search behavior and failed to head either directly home or in the reverse direction of their outbound route, apparently not recognizing the place.

A number of well-studied ant species exhibit plenty of taxon-like navigation, and can accomplish many feats without resorting to map-like navigation (reviews: Cheng, in press; Cheng, Narendra, Sommer, & Wehner, 2009; T. S. Collett & Collett, 2002; T. S. Collett, Graham, & Harris, 2007; Wehner, 2003, 2008). The most studied genera, *Cataglyphis, Formica*, and *Melophorus*, all come from a segment of the formicine tribe in the ant family (Figure 2). While closely related given the breadth of the hymenopteran order (Hunt, 2007), these genera have nevertheless had 50-75 million years of

evolutionary separation (Moreau, Bell, Vila, Archibald, & Pierce, 2006). The hymenopteran heritage stems from flying wasps (Hunt, 2007), so that ants are derived, somehow evolved from wasps. The derived character and the phylogenetic narrowness should be kept in mind as ant navigational strategies are discussed (see Shettleworth, 2010, ch.
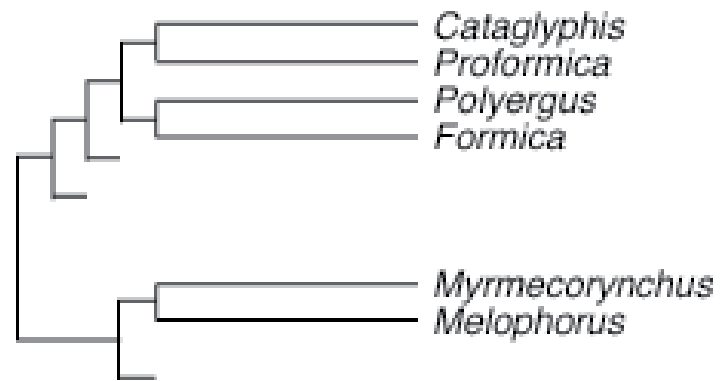
Some formicine ants

Figure 2. A part of the clade of formicine ants, derived from information contained in Moreau et al.'s (2006) phylogeny of ants. A selected number of genera, including those whose navigation has been most studied (Cataglyphis, Formica, and Melophorus), are shown. Formicine ants and myrmecine ants are two large tribes of ants. The branches do not indicate durations of times since the genera have separated, but the times of separation ranged from 50 million years ago to 75 million years ago. Adapted from "Phylogeny of the Ants: Diversification in the Age of Angiosperms," by C. S. Moreau, C. D. Bell, R. Vila, S. B. Archibald, and N. E. Pierce, 2006, Science, 312, p. 102. Copyright 2006 by the American Association for the Advancement of Science. Reprinted with permission.

2, regarding the comparison of species). Nevertheless, these genera provide great illustrations of the power of taxon-like strategies of navigation.

Path integration

The navigational toolkit includes path integration, keeping track of the straight-line distance and direction to the starting point, the nest (Wehner 2003; Wehner & Srinivasan, 2003). This system keeps operating even when the ant is engaging in other navigational strategies (Andel & Wehner, 2004; Knaden & Wehner, 2005), ready to act as a backup when other mechanisms fail. Path integration is compass based to the extent that a celestial compass is required as a component of keeping track of the path (Figure 3). The celestial compass is based on the pattern of polarized light primarily (Wehner, 1994) and the position of the sun secondarily (Wehner & Müller, 2006). The primary mode of distance estimation dif-

fers between ants and bees, probably because one walks and the other flies. In ants, a mechanism based on step counting forms the mainstay of odometry (estimation of distance traveled on a trip; Ronacher, 2008; Wittlinger, Wehner, & Wolf, 2006, 2007), while in honeybees, the measure of optic flow forms the mainstay for odometry (Srinivasan, Zhang, Altwein, & Tautz, 2000; Srinivasan, Zhang, & Bidwell, 1997). What is communicated as an odometric measure in the honeybee's dance (von Frisch, 1967) is actually a measure of the amount of optic flow. Bees flying a short physical distance in a narrow channel nevertheless report a long distance in their waggle dance, and Srinivasan et al. (2000) have calibrated the waggle dance as indicating ~17.7° of optic flow for each millisecond of waggling. Functionally, optical-flow cues in
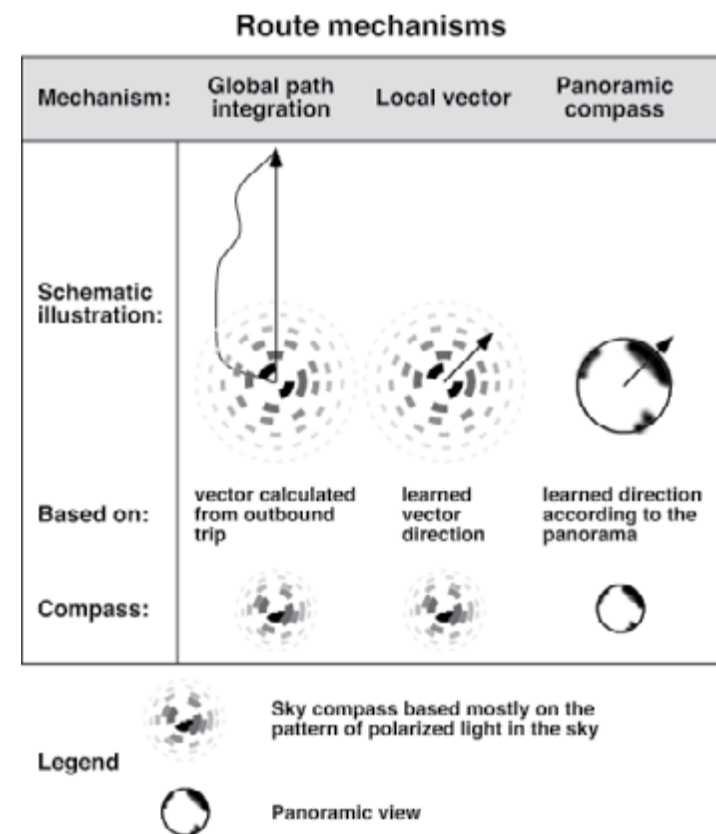

Figure 3. Schematic illustration of route mechanisms in ants. In path integration, the straight-line distance and direction to the starting point (typically home) is kept track of during the entire journey. Navigation based on path integration consists in running off the global vector calculated up to the point of homing. Such a vector contains both distance and directional information. The mechanism uses the sky compass to determine directions. The local vector contains a set of instructions to travel in a direction according to the sky compass. The instructions are triggered under appropriate contextual conditions. The ant runs until conditions for the next servomechanism are met. In a panoramic compass or visual compass, the ant travels in a direction determined according to the panoramic visual cues.

flight are more reliable indicators than internal measures such as energy expenditure or number of wing beats. That is because air is a volatile medium that can blow the flier about and wreak havoc with the internal cues. For animals mostly anchored to the ground (excepting unusual circumstances in which the wind blows the animal off course), a measure based on gait forms a reliable odometric cue.

The ability at path integrating differs across desert ant species, in the direction in accord with intuitive predictions. At least this is true for distance estimation or odometry. Between two species that have been explicitly compared, the one living in the more landmark-free habitat, *Cataglyphis fortis* in North Africa, does better than the one living in a landmark-rich habitat, *Melophorus bagoti* in Central Australia (Cheng, Narendra, & Wehner, 2006; Narendra, Cheng, & Wehner, 2007). The thermophilic *C. fortis* (R. Wehner & S. Wehner, 2011) lives on the salt pans of North Africa, with at most a few low bushes serving as possible landmarks. Most nests are located in the open, a good distance from usable landmarks, making the habitat virtually landmark free. *M. bagoti*, also a highly thermophilic desert ant (Christian & Morton, 1992; R. Wehner & S. Wehner, 2011), is widespread in Central Australia and inhabits a cluttered environment filled with grass tussocks, bushes, even tall trees, and in some areas, distant hills (Cheng et al., 2009; Muser, Sommer, Wolf, & Wehner, 2005; Schultheiss, Schwarz, & Wystrach, 2010). The paucity of visual cues means that path integration is more important for *C. fortis* than it is for *M. bagoti*, as it is typically the only means of navigating home.

The ants' ability to estimate the outbound distance to a feeder was measured. The direction of travel was constrained by keeping the ants running in narrow channels open above to the sky. The measure was unsystematic error, or variance in the odometric estimate of a group tested at an outbound distance. The group variance was bigger in *M. bagoti* than in *C. fortis*, indicating a species difference. This pattern has recently been replicated on the open field (Bühlmann, Cheng, & Wehner, 2011). An unusual *M. bagoti* nest in a open balloon launching field devoid of plants on the field was compared with *C. fortis* in their typical open habitat. Perhaps the most telling comparison took place on the training field itself, without any capture or displacements on the part of experimenters. The ants came to a feeder, and their return paths home from the feeder were recorded after being trained for two days. In this case, the visual conditions encountered on the homebound journey matched the conditions encountered on training runs for both species. Even in this familiar situation, *M. bagoti* performed worse than *C. fortis*. Their distance estimates had larger variance, their paths were more tortuous, and far fewer of them found their way directly to the nest without the need for searching (2 out of 18 vs. 18 out of 20 for *C. fortis*). This species differ-

ence suggests adaptive specialization for path integration in *C. fortis*, but of course, the hypothesis of adaptive specialization needs empirical support from more experiments and a lot more than two species (see Shettleworth, 2010, ch. 2). It would also be informative to compare salt-pan dwelling species (hence, living in an open habitat) with semi-desert dwelling species (hence, living with cluttered scenery) within each genus.

The directional estimate, on the other hand, is comparable between the two species. Ziegler and Wehner (1997) tested the memory decay of the directional component of the home vectors in *C. fortis* ants after 12 or 15 m outbound distance. At zero delay, they obtained a circular distribution of heading directions with vector length $r = 0.97$ (with 1.00 indicating perfect concordance between all ants). Narendra (2007a) tested *M. bagoti* on directional estimation after different outbound distances, with 12 m the nearest to what Ziegler and Wehner used. The vector length for *M. bagoti*'s circular distribution of heading directions measured $r = 0.98$. M. bagoti from the same study, however, only achieved $r = 0.89$ at 6 m outbound distance. *M. bagoti* might have used panoramic landmarks on their outbound trip to help in directional estimation, with increasing travel distance adding such landmark-based compass information. Testing on an open field for both species, Bühlmann et al. (2011) also found similar directional scatter in path integration in the two species under a variety of conditions. *M. bagoti* had a surrounding scene of distant trees, which might have provided them some compass information to keep track of the direction traveled.

A functional explanation for the lack of species differences in determining a direction based on the celestial compass is that the sky compass functions in other mechanisms than path integration. That might make it equally important for the two species. One such mechanism is the local vector, described next.

Local vector

The celestial compass is also used to execute local vectors (often called sensorimotor vectors in bees; Cheng, in press). The local vector can be thought of as a servomechanism that uses the celestial compass, and is triggered under appropriate contextual conditions (Figure 3). Travel instructions for a local vector are based on the sky compass, and not terrestrial objects. Terrestrial cues, along with other cues, might specify when conditions are appropriate for executing the local vector. In other words, a travel direction that is determined according to the sky compass is linked to appropriate triggering conditions, such as coming out of a feeder in an experimental situation, or rounding an obstacle in natural navigation. The ant heads in that compass direction until suitable conditions for engaging the next servomechanism are met.

A human example might be: when you come to the gas station, turn north and go until you come to a traffic light. In the first example in ants in which the term was coined, M. Collett, T. S. Collett, Bisch, and Wehner (1998) trained desert ants *C. fortis* to make a two-legged journey to obtain food at a feeder. They had to head north over open ground to the mouth of a narrow channel, and then turn 90° (to the west) to go to the end of the channel. On the return journey, the ants had to reverse the two legs. On some tests, M. Collett et al. changed the direction of the channel on the return trip, for example making the ants head southeast instead of the usual east. They observed that upon exiting the channel, the ants still headed south for an initial segment. This was the local vector, the normally appropriate compass direction to take upon the contextual situation of exiting from the channel. This direction is in conflict with the direction dictated by path integration (also called the global vector), which should point the ants directly toward their nest. After a short segment traveling south, however, global path integration then took over, and the ants headed in the fictive nest direction.

C. fortis lives in a saltpan habitat largely devoid of surrounding landmarks. It is likely that for ants living in a landmark-rich habitat, a panoramic view can act as a context for executing local vectors. The use of the local vector was demonstrated in a recent study on the Australian desert ant *M. bagoti* (Legge, Spetch, & Cheng, 2010). The ants were trained to enter a cylindrical arena and go to the middle of it for food. The arena had high enough walls that few objects were visible over the top of the walls. And another study showed that objects at high elevations have little influence on navigation anyway (Graham & Cheng, 2009b). Legge et al.'s ants had to exit in a particular direction out of the arena. An obvious set of landmarks (to the experimenters anyway) was set at the exit point to provide what the authors thought was a powerful beacon. For example, one landmark was a prominent yellow diamond against the dark wall of the arena. But tests with the beacon rotated to a different direction showed, surprisingly, that it had no control over the orientation of the ants. The ants relied on heading in a compass direction for the exit, executing a local vector. Importantly, in one experiment, the exit direction differed from the bee-line direction to the nest, meaning that the direction of the local vector conflicted with the global vector as calculated from path integration. Presumably, the context of being surrounded by high walls acted as the contextual trigger for the local vector.

Ants also use landmarks encountered along their route of travel, and something akin to local vectors seems to be at play in these journeys as well. In the course of repeated journeys to and from a feeder, they typically develop stereotypical routes in a cluttered habitat (wood ants, genus *Formica*: Rosengren, 1971; *C. fortis*: Wehner, Michel, & Antonsen,

1996; *M. bagoti*: Kohler & Wehner, 2005; Sommer, von Beeren, & Wehner, 2008). Experimental landmarks are used for steering a route (*C. fortis*: T.S. Collett et al., 1992; *M. bagoti*: Wystrach, Schwarz et al., 2011). How might ants use such landmarks? Some mechanistic details are provided in an elegant study by M. Collett (2010) on *C. fortis* in North Africa. The landmark conditions were the simplest possible: a single cylindrical landmark stood on the route between a feeder and the nest, a little off to the side of the straight line connecting feeder and nest. In such situations, ants end up learning to steer a route, and do not require information from path integration (Kohler & Wehner, 2005; Narendra, 2007b; Sommer et al., 2008; Wystrach, Schwarz et al., 2011). The ants typically took a route between feeder and nest that curved gently on the side opposite the landmark. By capturing ants as they approach the nest, but before they entered the nest, M. Collett could then release the ant for another trip home from a variety of locations, and compare such paired journeys. Results suggest that the ants steered a continuous course based on the direction to the landmark. I would describe the model as a continuous series of local vectors, each triggered by viewing the landmark in a particular compass direction. The view of the landmark in a particular direction, or perhaps on a particular part of the eye (the two being typically confounded) triggers travel in a particular compass direction determined according to the sky compass.

Panoramic context and visually based guidance

On the use of landmarks encountered en route, another species difference between *M. bagoti* and *C. fortis* can be pointed out, this time in favor of *M. bagoti*. The two species were tested in simple discrimination learning in two-choice boxes (Schwarz & Cheng, 2010). The decision box had two potential exits side by side. One side was black while the other was white, and the ants had to choose the black side to exit the box and get home, whether it was on the right or left side. *M. bagoti* learned the task readily, but *C. fortis* on the whole failed to learn the task even with repeated training. The pattern again suggests an adaptive specialization (Shettleworth, 2010, ch. 2) in *M. bagoti*, the ant living in a cluttered habitat, for using landmarks. But again, more experiments need to be done on more species to confirm the hypothesis.

Legge et al. (2010) thought that the panoramic surround provides contextual cues because the visual panorama has been shown to act as a contextual cue in other situations in hymenopterans. For example, panoramic contextual cues can make honeybees tolerate (generalize across) large discrepancies in landmark characteristics. T. S. Collett and Kelber (1988) trained honeybees to forage from two different platforms placed outdoors 40 m apart. With the surrounding buildings and trees, it meant that the panoramic cues were

very different on the two platforms. One platform had two yellow cylinders serving as landmarks, with the food on one side of the two cylinders. The other platform had a blue triangle standing upright as a landmark, base on the ground, with the food on the opposite side. To ensure that the bees had to rely on the landmarks, the entire configuration of landmarks and food was shifted around on the platform from trial to trial. Honeybees learned the tasks readily, as they do in other dual-task situations (Cheng, Collett, & Wehner, 1986). They searched around the target location even when the sugar water and tiny ring indicating the food source were removed on a test. Most interesting were tests in which the wrong set of landmarks were offered, that is, either platform-2 landmarks on platform 1 or else platform-1 landmarks on platform 2. The bees searched most at the side appropriate for the platform, as if treating yellow cylinders as an aberrant blue triangle or vice versa, and tolerating the considerable mismatch in landmark characteristics. The interpretation is that the contextual cues, presumably the panorama, drove the bees to retrieve the appropriate landmark memory for the platform.

Subsequent research has upheld this kind of finding (Colborn, Ahmad-Annuar, Fauria, & Collett, 1999; T. S. Collett, Fauria, Dale, & Baron, 1997; review: T. S. Collett, Fauria, & Dale, 2003). As perhaps the best evidence for the modulatory role played by the panorama, T. S. Collett et al. (1997) trained honeybees to enter a cylindrical arena placed outdoors. The location of the cylinder, and hence the panorama around the cylinder, served to modulate the choices that the bees made inside the arena, now with the view of the panorama cut off. Thus, at the point when the bees were making decisions, the natural panorama was gone; the bees could not be using those panoramic cues directly for guidance.

Similar results can be found in ants. In lab experiments on wood ants (*Formica rufa*), Graham, Durier, and Collett (2004) trained them to search at the middle between two black cylinders for food (sugar water). One cylinder was larger than the other, so that at the goal, the two landmarks subtended different retinal angles. After training, a crucial test was given in which the two landmarks were the same intermediate size. If the ants could interpret which test landmark corresponded to the big one, and which to the small one, then they should search closer to one landmark (the supposed big one) than the other. They failed to do this when white curtains surrounded the platform on which they were foraging. Instead, they searched at the middle between the two cylinders, as if unable to distinguish which of the landmark to treat as the large one. Results were different, however, when the ants were given strong panoramic contextual cues, in the form of black shapes covering one wall. They then behaved as if they interpreted one of the landmarks as the large one, and searched closer to it. The contextual

cues were thought to disambiguate the identity of confusable landmarks. The authors pointed out that when the ants turned to face one landmark, the patterned wall would fall on one eye, whereas when they faced the other landmark, the patterned wall would fall on the other eye.

Results such as these have led to the theoretical view that contextual cues act as powerful triggers for navigational behavior, forging "associative links between long-term memories" (T. S. Collett & Collett, 2002, p. 542) or serving "as occasion setters for the operation of servomechanisms" (Figure 1 in Cheng, in press). It is important to execute these taxon-like mechanisms at the right time and place. Contextual cues, of which panoramic cues are an important subset, provide powerful modulators. The disambiguating role of the panorama featured in T. S. Collett and Kelber (1988), T. S. Collett et al. (1997), and Graham et al. (2004) points to one solution to the problem of re-identification or perceptual aliasing, one that does not rely on a map-like locale system. Other contextual cues can add to the power of running servomechanisms or taxon-like routines. They include time of day (Koltermann, 1971; Prabhu & Cheng, 2008; Wahl, 1932), motivational status (outbound to forage vs. homebound with food; Dyer, Gill, & Sharbowski, 2002), and time-place combinations of circadian-timed episodic-like memory (Pahl, Zhu, Pix, Tautz, & Zhang, 2007).

Using the whole scene for navigation

If the panorama can act as a powerful contextual cue, is it also good for directly guiding navigation? Scene analysis in natural settings suggests that panoramic cues are very useful (Stürzl & Zeil, 2007; Zeil, Hoffmann, & Chahl, 2003). Von Frisch and Lindauer's classic (1954) work suggests guidance by large-scale landmarks. In fact, von Frisch and Lindauer's (1954) study showed that the bees were not inclined to head to clumps of landmarks such as an isolated group of trees, when they were in the wrong compass direction. More recently, Dyer and Gould (1983) and Towne and Moscrip (2008; Towne, 2008) replicated findings on the use of large-scale landmarks in honeybees. Even on cloudy days, ruling out the use of the sky compass, the bees managed to follow the large-scale landmarks that they were trained to use. Towne and Moscrip (2008) put forth a mechanistic hypothesis based on a serendipitous finding from a failed control condition. The interesting finding and ensuing hypothesis more than made up for the failure to control for unsuspecting cues. As a control, trained bees were displaced to a novel location that supposedly did not contain anything resembling the landmarks that the bees had been trained to use. The bees were supposed to be lost and head off in random directions. The control failed in that the bees' headings were directed. Comparing panoramic photos at the training and test sites (Figure 4), Towne and Moscrip suggested that the honeybees

were basing their heading on the skyline contour. What this means is the one-dimensional circular representation of how high the tops of terrestrial objects are. It is the line where ground objects such as trees and bushes meet the sky, stripping away characteristics of the ground objects such as their

Further manipulations on the natural scene surrounding the feeder showed that not all of the panorama is of equal importance (Graham & Cheng, 2009b). When the higher elevations of the natural scene (above ~27°) were blocked out, the ants were still oriented. But ants relying only on the high

Figure 4. An experimental control condition conducted by Towne and Moscrip (2008). A. A panoramic photo of the training setup, with the hive at H. The bees were trained to fly toward D to a feeder. B. The test situation the next day in a completely different environment, with the tested hive at H. The bees were expected to be random in orientation because the features of the scenery mismatch, but were instead oriented toward F. Towne and Moscrip noted an uncanny similarity between the skylines of the two situations. Reprinted from "The connection between landscapes and the solar ephemeris in honeybees," by W. F. Towne and H. Moscrip, 2008, Journal of Experimental Biology, 211, p. 3734. Copyright 2008 by The Company of Biologists. Reprinted with permission.

colors and patterns.

A photo from a serendipitous control condition hardly constitutes solid evidence, and it is hard to control the skyline for honeybees, which can attain quite a height in flying. Testing whether the skyline might be used is far more amenable in ants, which walk on the ground. Skylines can be reproduced in artificial arenas (Graham & Cheng, 2009a). The skyline or the tops of the terrestrial objects as viewed from the feeder was measured directly every 15°, and an artificial skyline was created using black cloth and a couple of tall black landmarks (Figure 5). Linear interpolation was used between the measurements. Such an arena captured a rough approximation of the skyline at the feeder, but nothing else of the visual surround. The colors in the surrounding scene were stripped away and rendered all black, and distances to objects were equalized. Trained ants that had grabbed a piece of food at the feeder were placed in the middle of the arena with the artificial skyline, and their initial directions of travel were noted on a goniometer (a circle divided into sectors). The arena was at some distance from the training site, and nothing but sky was visible above its walls. The ants concentrated their directions of headings in the nest direction according to the artificial skyline, and they did so even when the arena was rotated with respect to the true compass direction to the nest. Given how degraded the artificial skyline was, it seems to be a readily usable cue.

elevations were not oriented.

Much remains to be researched on the use of skyline, from both mechanistic and comparative, evolutionary perspectives. On the mechanistic side, how is the skyline extracted? The sky is brighter than ground objects. But using brightness contrast as a cue requires adjusting the threshold value separating sky from ground. Everything is brighter when the sun is out than when the sun is behind a cloud. Möller (2002) showed that the contrast between ultraviolet (UV) light and green light provides a theoretically attractive dimension. The sky contains more UV wavelengths relative to ground objects, which reflect more wavelengths that look green to us. An opponent-processes channel that measures UV – green in some way could be used to segregate sky from ground. Such an opponent-processes channel would provide constancy in the face of changes in overall illumination. The theory is attractive, but the empirical evidence that any insect uses such a channel is currently lacking. On the comparative side, how widespread is the use of skyline information? Is it common to all hymenopterans, or has it evolved independently in multiple lineages, in those for whom the trait would be useful? Only comparative research can tell.

Work has only just begun to model how well skyline information can guide journeys. Using panoramic photos taken at the habitat where *M. bagoti* live (our field site at

Figure 5. An experiment by Graham and Cheng (2009a) showing the use of the skyline contour by desert ants Melophorus bagoti. A. A panoramic view from the feeder of the surrounding scenery. B. A panoramic view from the middle of the test arena, at which trained ants were released for a test. The arena matched the elevation of the actual scenery at the feeder every 15°. C. An actual photo of the test arena, with a goniometer at the center. Ants were oriented in the nest direction according to the skyline no matter how the test arena was oriented in compass direction. Adapted from "Ants use the panoramic skyline as a visual cue during navigation," by P. Graham and K. Cheng, 2009, Current Biology, 19, p. R936. Copyright 2009 by Elsevier. Reprinted with permission.

Alice Springs), Graham and colleagues have made a first attempt (Philippides, Baddeley, Cheng, & Graham, 2011). The photos were taken along a number of straight transects, unwarped, and then used for modeling in *silico*. The skyline proved useful for view-based matching, often performing not much worse than pixel-by-pixel matching, which of course encompasses much more information. The size of catchment areas (Zeil et al., 2003) is an important measure of how well a strategy works. This represents the distance at which the procedure would actually succeed in bringing the

agent to the goal. Under suitable conditions, using a skyline can produce catchment areas with 4 m to 7 m radius, useful distances for *M. bagoti*'s foraging trips. Thus, Muser et al. (2005), reported that 90% of foraging runs were confined within a maximum distance of 20 m from the nest, with the average maximum ant-nest distance measuring 10.6 m. A small number of panoramic matches then, can in principle guide a homeward journey.

In fact, multiple memories might not even be necessary in some circumstances. In a cluttered lab setting, robots could navigate a curved S-shaped route based on a holistic representation (Baddeley, Graham, Philippides, & Husbands, 2011). Such a representation picks out (learns to use) the most useful features for distinguishing locations on vs. off the familiar route. It is also likely that other parameters than the skyline are used by ants in panoramic matching. Much empirical research and modeling remain to be carried out.

Panoramic matching, no matter what parameters or features are used for matching, works like a panoramic compass based on terrestrial cues (Graham, Philippides, & Baddeley, 2010; Wystrach, Beugnon, & Cheng, 2012; Wystrach, Cheng, Sosa, & Beugnon, 2011; see Figure 3). One reviewer suggested that it is akin to beaconing, except that the entire panoramic scene acts as a beacon. In traditional beaconing, the identified object defines the direction of travel: toward it. Unlike a traditional beacon strategy in which the target object needs to be picked out, in the panoramic terrestrial compass strategy, a remembered direction of travel according to the encoded panorama must be learned. As the entire panorama is used, no single object needs to be segregated and identified. The panoramic terrestrial compass can also be thought of as an oriented panoramic view. It might, for example, be defined in terms of a retinal code, for example, how high the skyline should be on each part of the eye. In finding the correct direction of travel, the ant would rotate on the spot until it finds the best match between the current panorama and the remembered panorama. The direction in which she is facing is then the direction of travel (Wystrach et al., 2012). The traveler might match as many remembered panoramas as are necessary to negotiate all the segments of a route. Such a mechanism strikes me as a form of guidance, *sensu* O'Keefe and Nadel (1978). Evidence from ants suggests that entire scenes, or at least visual information over a large area of the eyes are used for navigation (Graham, Fauria, & Collett, 2003; Wystrach, Beugnon, & Cheng, 2011), and that the panoramic terrestrial compass works especially well for travel along a familiar route (Wystrach et al., 2012).

In lab conditions, or in open saltpan habitats, landmarks stand out readily against the uniform background. In some cases, such as M. Collett's (2010) research on *C. fortis*, only a single landmark is used. The landmark in this case constitutes the only informative part of the panorama, for instance, defining the skyline. It is possible that M. Collett's ants were using a sequence of skylines to guide their behavior.

In wood ants tested in the lab, a single beacon (black cylinder) can stand out against the background of the room and serve to attract foragers (Graham et al., 2003). The ants naturally approached the beacon on their way to a feeder, even though the beacon was off to one side and required a detour. They did this when starting from different locations, so that they did not appear to be executing a motor routine (such as turn so many degrees and walk). But did they learn to approach a beacon object? A most interesting manipulation on the trained ants was to remove the beacon. The ants still approached the location of the absent beacon enroute to the feeder! They apparently did not need the beacon object itself. One interpretation I like to offer is that the ants were not approaching an extracted and identified object, but a salient part of the panorama. In the process, they learned to approach a direction based on the rest of the panorama as well. They could then approach that part of the panorama even when the object was missing, thus showing the robustness of the panoramic terrestrial compass.

But what about ants traveling in natural habitats with complex visual information? The Australian desert ant *M. bagoti* makes an ideal subject in this case, and an attempt was made to train the ants to use a large landmark in cluttered conditions (Wystrach, Beugnon, et al., 2011). The landmark was a black cloth 3 m wide and 2 m high, held up just behind the nest (Figure 6). The training field was cleared of clutter, so that the beacon and the panorama were clearly visible throughout the journeys between feeder and nest. Other objects being a good distance away, the high-contrast edges of the beacon provided dynamic cues on approach: the beacon expanded in azimuthal size (width) from 54° to 118° in the last 2 m of approach to the nest. Surely, it specified the nest's location well. To the primate visual systems of humans doing research there, the beacon looked obvious and stood out. But to the ants, it did not.

The ants were trained to run repeatedly between their nest and a feeder 10 m from their nest. Then a number of different tests were conducted, with each individual ant only participating in a single test. In one test, the beacon was set up at a distant test field with an unfamiliar panoramic view, excepting the beacon. The ants failed to home in on the beacon, in effect showing that they did not treat the beacon as a beacon. They failed to do so even when released just 2 m from the fictive nest position. Apparently, mismatch in the rest of the scenery mattered. Other tests were conducted at the training field with the beacon removed, with only the tested ant homing (and the others trapped temporarily at the feeder). Ants also failed to home on this test, showing that the beacon did
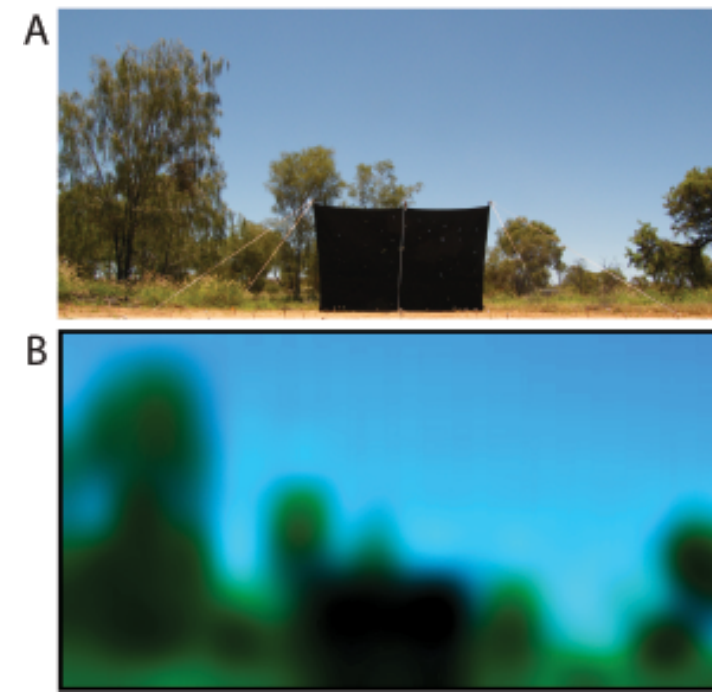
Figure 6. Photos of the beacon setup used by Wystrach, Beugnon, et al. (2011), supplied by Antoine Wystrach. A. A substantial beacon in the form of a black cloth 3 m wide and 2 m high was set up just behind the tested nest of desert ants Melophorus bagoti. *To human (primate) eyes, the beacon stands out as an obvious object to aim for in navigation. B. The view as blurred to 5° resolution, approximating the visual acuity of this species of ants (~4°; Schwarz, Narendra, & Zeil, 2011).*

form an important part of the scenery for the ants. Yet other tests were conducted on the training field with the beacon displaced. When it was displaced 32° to either side, homing again failed, the ants finding neither their nest nor the fictive nest position in front of the beacon. Even having much of the familiar panoramic context did not drive the ants to head to the beacon. When the beacon was displaced 16° to either side, ants again did not home in on their nest, but some managed to find their way to the beacon, in front of which they engaged in systematic searching.

But were the ants beaconing in, in the sense in which the term is usually understood? That is, did they pick out the beacon as an object to head to, and then head straight toward it, using the identified beacon in a guidance strategy *sensu* O'Keefe and Nadel (1978)? Closer examination of their behavior showed otherwise. If the ants had identified the beacon as a beacon, they should have headed straight toward it at some point in the journey. Uncertainties in extracting and identifying the object should be found, if at all, near the beginning of the journey. The last few meters should be a straight run, with the sizeable beacon identified by that stage of the journey. Instead, numerous ants turned around, mean-

dered, and searched before ending up in front of the beacon. Many of these turns first took place 6-8 m into the journey (2-4 m from the goal). Such behavior is inconsistent with a guidance strategy of beaconing in.

It turns out that a panoramic view-matching strategy explains this kind of searching behavior as well as other homing behaviors not discussed here. At the beginning of the journey, much of the scenery matches, with just the beacon out of place. A view-matching strategy would drive the ants straight ahead, toward their real nest, a pattern found empirically. At the real nest, with the beacon missing, the match is very poor, apparently too poor for the ants to search there. In front of the beacon, however, is a partial match, a local minimum in mismatch, so that some ants might end up searching there. Scene analysis also shows that in the middle, especially in the 6-8 m range, is a zone of mismatch. The beacon at this stage looks larger, becoming more prominent for matching, and it is out of place. Thus, a global view-matching strategy, such as the matching of skyline pattern (Graham & Cheng, 2009a, 2009b) explains the searching and meandering behavior of ants in this zone, without the need to invoke object segregation and then beaconing.

Using the panoramic scene not only gets the ants to head in a homeward direction along a regular route, but also when they have been displaced a small amount (review: T. S. Collett et al., 2007). We have observed ants being blown off course, so that small displacements of a few meters are ecologically realistic. Wood ants (*F. rufa*) displaced centimeters from their usual starting point can find their way to an inconspicuous feeder, using landmarks set up in the lab (Durier et al., 2003). Wood ants of another species (*F. japonica*) can also cope with displacements in the field over a larger distance (meters, Fukushi, 2001; Fukushi & Wehner, 2004). The Australian desert ant *M. bagoti* can cope with displacements of up to 10 m sideways from their usual starting point (feeder, Narendra, 2007b), as well as smaller displacements (Graham & Cheng, 2009b; Kohler & Wehner, 2005; Narendra, 2007b). With smaller distances of displacement, *M. bagoti* ants often managed to find their way back to the usual route that they followed home, as opposed to heading directly toward the nest (Kohler & Wehner, 2005; Narendra, 2007b; personal observations). A rare nest of the North African desert ant *C. fortis* located in cluttered terrain also managed to home after displacements (Wehner et al., 1996). Desert ants often search for a while near the release point, before heading off in a direction, something that displaced honeybees have also been observed to do (Menzel et al., 2005). How ants (and bees for that matter) manage to compute a homeward direction from the view at a displaced location poses an interesting research question to be explored. But some initial analysis suggests that navigational mechanisms on and off the route may differ.

In another study on *M. bagoti*, barriers were used to confine ants of two different nests to experimentally defined areas for traveling and foraging (Wystrach et al., 2012). Furthermore, by confining the ants in this way for a number of days before the experiment began, only naïve ants were allowed to take part. The nature of their traveling experience was thus carefully controlled. Some ants were confined to an area of 1.1 m radius around their nest. Others got to forage along a 10 m route that was gently curved. Ants were then tested after different amounts of training at locations on and off the route. A zero-vector ant (captured after she had nearly returned to her nest) was placed successively on a goniometer at each of the three test locations, and her initial heading noted. Ants typically turned on the spot initially, and then headed off unhesitatingly in one direction (for an example of this kind of turning, see the supplementary movie). Importantly, panoramic photos from the experimental sites were taken so that models based on the actual sceneries could be evaluated against the ants' behavior.

The already described panoramic terrestrial compass model accounted for the ants' behavior on the familiar route very well, but it performed poorly for test locations off the route. The trouble arose because to perform well off the route, the most suitable remembered panorama needed to be chosen, and mistakes were often made because remembered panoramas were often similar. Another mechanism, however, had better success in explaining the orientation of the ants off their route. And that was to compare the skyline heights of remembered and current panoramas (Figure 7). These panoramas must already have been oriented according to the sky compass (or in principle, any other compass such as a magnetic compass). In that case, if the skyline in one region of the panorama appears too high (higher than the corresponding part in the remembered panorama), then the ant was probably displaced in that direction, and should turn away from that region. Conversely, if a part of the skyline appears too low, compared to what height it should be according to the remembered view, then the ant has drifted too far from that region, and should be attracted toward that region. Such a model worked reasonably well in accounting for orientation off the route. Ants in general aimed in a direction toward a part of the route. It would be interesting to manipulate skyline heights directly in experimental arenas to test this model.

In sum, the ants seem to use different strategies on and off their familiar route. They might decide whether they are on or off the route by the quality of the match between the current scene and remembered views (Wystrach et al., 2012). The calculations based on the panoramic photos show sizeable differences in the level of matching on and off the route.
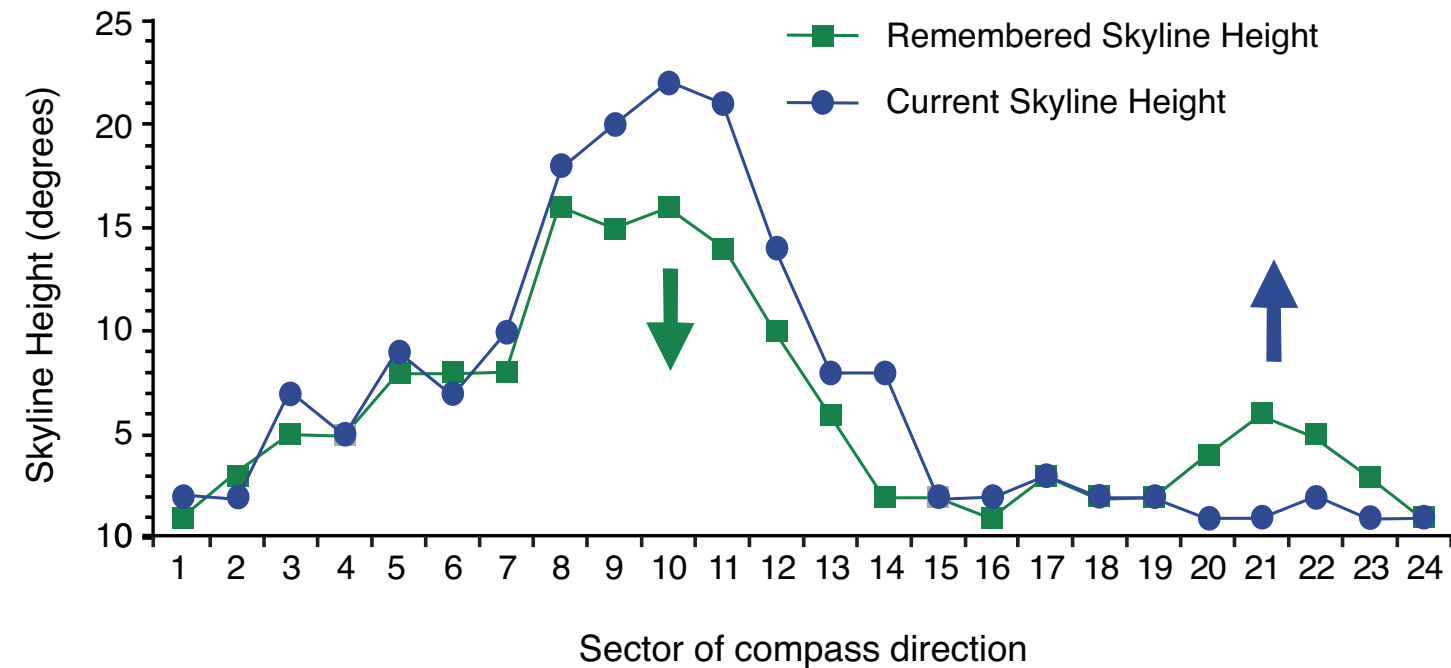

Figure 7. An illustration of the skyline-height-comparison model proposed by Wystrach et al. (2012). A hypothetical remembered skyline is compared with the currently viewed skyline. Both skylines are oriented in compass direction. That is, the x axis codes absolute compass directions, based on the sky compass. The ant would be attracted by parts of the skyline that look too low in comparison with the remembered skyline (blue arrow), and repelled by sections of the skyline that look too high in comparison with the remembered skyline (green arrow). In Wystrach et al.'s (2012) model, only the attraction process was assumed. More research is needed to determine which of these processes (or both) is at work.

Searching as taxon-like behaviour

View-based navigation and especially path integration are not perfect strategies, so that in homing, ants often need to search for their nest on natural foraging trips. I have observed such searching behavior on natural foraging trips in both *C. fortis* and *M. bagoti*. The two cases are different in that *M. bagoti* has a rich panoply of surrounding visual cues — the scenery around her nest — to guide the search, whereas *C. fortis* usually has none. The search of *M. bagoti* in a situation resembling that facing *C. fortis* can be studied by displacing the homing ant to a distant site so that the visual scene provides no useful cues. I now discuss searching with and without visual cues in turn.

In landmark-based search, behavioral records have been obtained on tests in which the target of search was missing. Artificial landmarks defining the goal are provided in many cases. In contrast to searching in the absence of predictive visual cues (to be discussed shortly), the details of search patterns have not been documented. But search distributions that have been obtained indicate tight, concentrated searching around the fictive goal, in honeybees searching for a missing feeder (Cartwright & Collett, 1982, 1983), in desert ants searching for the fictive nest at a test site far from their real nest (*C. bicolor*: Wehner & Räber, 1979; *C. fortis*: Åkesson & Wehner, 2002; *M. bagoti*: Narendra, Si, Sulikowski, & Cheng, 2007b). Most recently, the use of landmarks around the nest has also been found in the Namibian desert ant *Ocymyrmex robustior*, a myrmecine ant (Müller & Wehner, 2010; Wehner & Müller, 2010). In the desert ant studies, plastic cylinders served as landmarks. For *M. bagoti*, the displacement of a set of landmarks meant that the rest of the scenery mismatched, a point whose significance was not fully appreciated by the authors when the research was conducted. It took quite a number of trials of training, at the training site returning to their nest, before the ants learned to use the experimental landmarks at the test site. In contrast, Wystrach et al. (2012) found that even naïve ants arriving at a feeder near their nest were significantly oriented when displaced a few meters away. The panoramic scenery is learned quickly. Some recent advances in this topic include the matching of optic flow patterns created by motion parallax, in honeybees (Dittmar, 2011; Dittmar, Stürzl, Baird, Boedekker, & Egalhaaf, 2010), and turning behavior in wood ants that are finely tuned to anticipated positions of a feeder serving as a goal (Lent, Graham, & Collett, 2010).

This line of research has led to a proliferation of models on this topic, without firm agreement (Cartwright & Collett, 1983; Möller, 2001; Narendra, Si, et al., 2007; Nicholson, Judd, Cartwright, & Collett 1999). These models of image matching differ in specifying what is matched, but what is common to them indicates a taxon-like strategy rather than an insect locale system or a sketch map. Various kinds of parameters are thought to drive the matching in a servo-mechanistic fashion. The insect moves so as to reduce the discrepancy between parameters in the current image, and the remembered parameters. None of the models propose the encoding of distances to multiple landmarks or to distant sites, characteristics of map-like representations.

Detailed search paths of ants have been recorded for searches in the absence of landmarks, sometimes in one-dimensional narrow channels (*C. fortis*: Cheng & Wehner, 2002; *M. bagoti*: Narendra, Cheng, Sulikowski, & Wehner, 2008), other times in the open field (*Cataglyphis*: Merkle, Knaden, & Wehner, 2006; Merkle & Wehner, 2009, 2010; Müller & Wehner, 1994; Wehner & Srinivasan, 1981; *M. bagoti*: Schultheiss & Cheng, 2011). Details of search patterns, along with well-articulated models, have also been obtained in a desert isopod with very limited distal perceptual capabilities, *Hemilepistus reaumuri* (Hoffmann 1983a, b; 1985a, b). An example of a search in *M. bagoti* is shown in Figure 8. The looping area-restricted search patterns found in such ants have been thought to be an evolutionary precursor to cognitive searching (Hills, 2006). The patterns of searching are thought to be close to optimal (Hoffmann, 1983b).

Systematic searching in the absence of predictive visual cues was not featured in O'Keefe and Nadel's (1978) book, but clearly, it is a taxon-like strategy. It is what an animal engages in when nothing familiar instructs the navigator as to a defined direction of travel. Its goal is to find, in the minimum of time, something familiar. This would be the nest or the cues emanating from it in the case of animals searching without landmarks (*C. fortis, H. reaumuri*), or else some familiar scenery from which instructions for directed travel may be derived (*M. bagoti*).

Putting it all together: The power of a taxon-like repertoire

A repertoire that I have called taxon-like has considerable utility for ants in their navigation. It suffices to steer ants traveling on habitual routes. The use of panoramic information also allows ants to cope with some displacements, a job that a locale system is supposed to serve in rats. That is, a map-like representation is supposed to allow the animal to locate itself in terms of distances and directions to key locations. The taxon-like repertoire, on the other hand, retrieves instructions for getting back to a familiar route, based on panoramic information, but does not inform the ant of its location in the world. Harking back to the quote from O'Keefe and Nadel (1978, p. 59) at the beginning of this paper, such a system does not let the animal experience a "coherent"
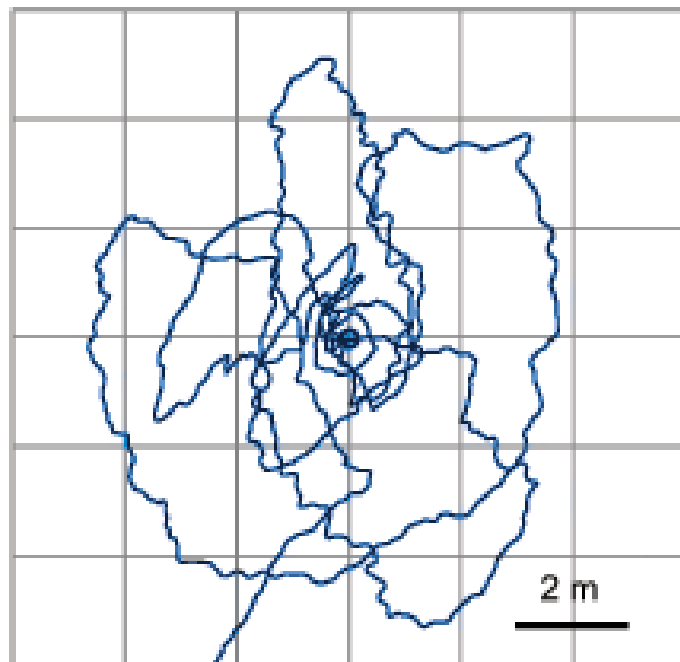
Figure 8. *An example of a search pattern in a desert ant (*Melophorus bagoti*) from Schultheiss and Cheng's (2011) study, supplied by Patrick Schultheiss. The desert ant was trained to run back and forth between a feeder and her nest. On a test, she was captured just before she reached her nest on returning from a foraging trip, and placed at a distant test field marked with a grid. The circle shows the release point of the ant on the test field. Typical search patterns began with tight loops around the release point, expanding to much larger loops as the search went on.*

spatial world. It delivers a set of incoherent but functional instructions based on available visual and idiothetic (based on path integration) cues. Its only sense of place is the vector delivered by path integration connecting, approximately and with cumulating errors, the traveler's current location to its home.

The taxon-like repertoire is much expanded compared with the motor routines and beaconing that form the mainstay in O'Keefe and Nadel's (1978) characterization. Hence, the addition of the suffix "like" expresses some similarity, but also indicates possible differences. The ant can learn to head in a direction defined by a panorama, which is another way of describing a panoramic terrestrial compass mechanism. The taxon-like repertoire includes path integration, instructions linking context to compass-based vectors of travel (local vectors), possibly the comparison of skyline heights, and systematic searching. Aside from path integration, these strategies have not received much attention in vertebrate animals.

I have given some hints that the entire concept of beaconing, taken to be an obvious and easy routine by most of us

humans, may be doubted when it comes to ant navigation. For us, beaconing means identifying an object associated with a goal and heading toward it. Beacons may also be associated with route instructions, such as when we turn left at the corner with the Brand X gas station. It is possible that we are beguiled by our own evolved primate visual system into thinking that that is easy and widespread. We are blessed with high-acuity foveas in the eyes, but more than that, we primates possess an entire stream devoted to object identification, called the ventral stream (Goodale & Milner, 1992; Milner & Goodale, 1995; Mishkin, Ungerleider, & Macko, 1983). Most animals do not have this dedicated machinery for extracting objects. As a consequence, beaconing may be harder for many than it is taken to be. In ants, at least the idea needs serious revisions. Beacons might only attract ants in so far as they form some salient characteristic of the panorama, with the full set of such attractors requiring much research to unravel. The entire panorama might also be considered as a beacon, with some direction in it defined as the target direction. But it is clearer to use instead the term panoramic terrestrial compass to distinguish this mechanism from traditional beaconing in which a single object is identified as the target to head toward.

I suspect that the navigational repertoire in ants, if not in all insects, might have evolved in the absence of any visual object identification. It is possible that landmark-based navigation may not be based on landmarks in this sense. In one recent formulation regarding the honeybee, a landmark is defined as "a coincidence of several different cues in a local region of the eye" (Horridge, 2009, p. 2728). The retino-topically-defined cues are in turn parameters from a limited palette that the bee processes. A thesis to explore is that in hymenopterans, the use of large-scale cues of panoramic terrestrial scenery and celestial patterns of polarized light bypasses any need for navigational object extraction, whose mechanisms would prove too costly to evolve. The extent of visual cognition in hymenopterans is debated (Avarguès-Weber, Deisig, & Giurfa, 2011; Horridge, 2009). But object identification, whatever its form, might only have evolved in insects if some other function than navigation drove its evolution. Thus, honeybees, which need to determine which flowers are the most profitable, may possess some sophisticated skills of visual cognition (Avarguès-Weber et al., 2011; Giurfa, 2007).

Map-like integration?

While the systems or modules of path integration, local vectors, and different matching routines, each operating in isolation, do not amount to a system that we would call cognitive mapping, integrating them by operations computing and combining their outputs would result in a map-like system. Tolman (1948) expressed the idea metaphorically as being "worked over and elaborated in the central control

room" (p. 192). Cruse and Wehner (2011) took this metaphor on board and specified that integrative processes are what makes a system a cognitive map. Thus, linking vectors to panoramic views gives a map-like flavor: from view X, the vector *y* would bring me to location Y. As another example, the comparison of skyline heights gives a gradient in two dimensions with characteristics of a bearing map. Combining this system with representations of vectors between locations, and it looks like calibrating a map. In contrast, a taxon-like system (my term) operates as separate modules, with the only integration being competition over access to a common command system that drives action.

Cruse and Wehner's (2011) modular, taxon-like system accounts for extant navigational performance in ants and bees, including performance that has been taken to show cognitive mapping abilities by some. Menzel et al. (2005) displaced bees from a feeder before their homebound journey. The bees first flew the vector, according to path integration, that would have taken them home. Not finding themselves at their hive, they engaged in some searching behavior. Then, most bees found the way home. The authors interpret the homing behavior as showing reliance on a map-like representation: the bees searched to locate themselves on the map, and then flew home. Yet Cruse and Wehner's (2011) model solves the case by having the agent search until it finds a landmark with which a home vector (a local vector) is linked. And in displacement experiments on *M. bagoti* (not modeled by Cruse and Wehner), the operations in turn of a skyline-height comparison routine off the route (driving the ant to the route) and a panoramic terrestrial compass routine on the route (driving the ant home) solves the case (Wystrach et al., 2012). Map-like integration has so far been unnecessary for explaining hymenopteran navigation.

Panorama and context

Recent research gives some indications of the power of using the entire visual panorama in direct guidance of navigation. Using the entire surround serves one of the functions of a locale system, to reduce perceptual aliasing. Perceptual aliasing arises from the similarities of isolated objects such as individual bushes or trees. The locale system helps to reduce confusions by locating objects approximately on a map. A similar object at a different region on the map is treated as a different object. The taxon-like panoramic strategy reduces perceptual aliasing by taking on the maximum amount of information defining a place, given the constraints imposed by the insect's perceptual systems. Even the limited information provided by skylines does this job well. Wystrach et al. (2012) measured the mismatch levels on and off the familiar route of the ants, and the gap is sizeable: the mismatch was more than 5 times bigger at the experimental off-route test locations than at the on-route test location. It would be inter-

esting to compare this performance formally (quantitatively) with how a locale + taxon dual system would do.

The desert isopod *H. reaumuri* attempts to deal with the re-identification problem even in the absence of external contextual cues (Hoffmann 1985a, b). This arthropod has no vision to speak of, but builds a ring of feces around its nest as landmarks. The ring facilitates the job of finding the nest. But this means that the homing isopod needs to distinguish its ring from the rings of other families of *H. reaumuri*. How much time the isopod searches to determine whether the ring is the correct ring is determined in part by the expected probability (in the statistical rather than the cognitive sense) that the ring is in fact correct. Thus, a ring far from the expected location of home according to the isopod's global vector is deemed unlikely, and the arthropod might linger little if at all at the ring. In short, path integration is used to solve, albeit only partially, the re-identification problem.

Locale and taxon systems revisited

If a taxon-like repertoire suffices for certain kinds of navigation, such as the tasks faced by desert ants, then what kinds of ecological pressures might have driven the evolution of locale systems, and in what animals? The taxon-like system is likely evolutionarily more ancient. The rodent neurobiological literature contains hints of building a locale system using components serving the taxon system. Thus, path integration might be crucial for building up metric maps (Gallistel, 1990; Sheynikhovich et al., 2009). Grid cells in rats (Fyhn, Molden, Witter, Moser, & Moser, 2004; Hafting, Fyhn, Molden, Moser, & Moser, 2005) might be a key component serving both path integration (McNaughton, Battaglia, Jensen, Moser, & Moser, 2006) and as a "metric for the cognitive map" (Jeffery & Burgess, 2006). A recent model of locale and taxon spatial learning in rats starts out with views as the basis for both systems (Sheynikhovich et al., 2009). The views are panoramic, and consist only in an array of the features processed early in the visual system, edge orientations. The taxon system links views directly to behaviors, much in the spirit of the view-based taxon-like procedures of ants. The locale system links path integration and views, via the neurophysiology of place cells (O'Keefe, 1976; O'Keefe & Dostrovsky, 1971). This integrative process linking taxon components makes the system map-like.

As a final speculation, the scale of travel might dictate the need for a locale-like system. I suspect that views of panorama, together with the rest of the armamentarium of the taxon-like repertoire, copes readily with the scale of tens of meters that desert ants deal with. A small number of views together with path integration can probably suffice to cope with navigational needs. On the largest scale of global travel, any landmark-based systems, with or without a locale sys-

tem, fails. Long migrations in the dark, or over or in the sea, are not conducive to the use of landmarks of any kind. Under such circumstances, some Earth-based locale system or bearing map needs to be used. I mean here what others call true navigation (Bingman & Cheng, 2005; Boles & Lohmann, 2003; Griffin, 1952). This is the ability to estimate the approximate longitude and latitude on Earth from some Earth-based cue, of which magnetic cues are the best candidate to date. Thus, sea turtles can estimate latitude (Lohmann, Lohmann, Ehrhart, Bagley, & Swing, 2004) and longitude (Putman, Endres, Lohmann, & Lohmann, 2011) by using magnetic cues. Bingman and I (Bingman & Cheng, 2005) argued that in volatile fluid media (water and especially air), where one may be driven off course, such an ability is necessary for long global-scale voyages.

Rats travel at an intermediate scale. In one recent study (Russell, McMorland, & MacKay, 2010), rats roamed over hundreds of meters, covering up to 8 ha of range over a week of exploring a new island on which they had been released singly. The rat-free island was limited in size, so that with a larger space to colonize, they might move even further. Is it at this scale of travel, rather than the scale found in a lab, that vectors linking different sets of views characterizing a place or region become necessary? Is this when a traveler might want to plan and design routes between locations that are not based on learned routes and path integration, something that a map-like representation can help with? Is it at this scale when integration of bearing and sketch maps (Jacobs & Schenk, 2003) becomes necessary? In hymenopterans, a good test case is the honeybee, which, like rats, also roam over hundreds of meters or more. Although Menzel et al.'s (2005) data can be explained by the taxon-like procedures in Cruse and Wehner's (2011) model, it is worth investigating honeybee performance on a larger scale in more complex environments. Menzel et al. (2005) studied bees on an open field devoid of skyline information — the trees were too far away to define any skyline at all — but with many ground characteristics.

Much remains to be discovered about the evolution of navigational abilities. It is a sphere that promises to reveal much about the origins of intelligence in animals. I hope that I have shown here that a repertoire of taxon-like procedures, without any map-like representation, may go a long way toward solving many navigational problems.

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