Experimental ethology of learning in desert ants: Becoming expert navigators

Cody A. Freas[a,*], Pauline N. Fleischmann[b], Ken Cheng[c]

[a] *Department of Psychology, University of Alberta, Canada*
[b] *Behavioral Physiology and Sociobiology (Zoology II), Biozentrum, University of Würzburg, Am Hubland, Würzburg, 97074, Germany*
[c] *Department of Biological Sciences, Macquarie University, Sydney, Australia*

ABSTRACT

Foraging desert ants are repeatedly presented with the challenge of leaving the nest, searching the scorching desert landscape to find food, and then transporting it back home. To accomplish this task, foragers have a navigational toolbox, which relies on olfactory, idiothetic, visual and magnetic cues. Desert ants have been widely studied with regards to these abilities, including a heavy focus on learned visual cues, the most prominent being the terrestrial panorama. Nest cues are first acquired during pre-foraging learning walks. Once foragers leave the nest area, they also learn a number of cues to aid them when returning both back to the nest and to known food sites, using experience of previous trips to navigate on future trips. In this review, we describe the learning processes involved in accurate navigation in desert ants. We first focus on recent research on nest-site panorama learning during pre-foraging learning walks as well as panorama learning away from the nest during foraging. We also review learning cues beyond the terrestrial panorama, including tactile, magnetic, olfactory and vibrational cues. These studies provide a basis for future work to further explore how these navigators, despite their small brains, acquire, retain and use many cue sets present in their environments. We call for more experimental ethology focussed on learning processes, both by exploring run-by-run and step-by-step acquisition of information for navigation, as well as for other natural tasks in an animal's life.

1. Introduction

Mobile animals require the ability to reliably find goal locations in their environment. These locations can include their home or nest as well as resource patches and conspecifics. An animal's survival is often dependent on how accurately it can navigate to and from these locations, especially when factors such as predation and environmental harshness cause any time spent moving between locations to be hazardous. Navigation to goal locations requires that the navigator detect and use environmental cues indicating the location's distance and direction. Many animals possess a navigational toolbox containing multiple strategies which rely on the acquisition of multiple cue sources to effectively navigate.

Desert ants have long been known to be talented navigators and their navigational toolbox has been extensively studied (e.g. Wehner, 1982; Wehner et al., 1996; Collett et al., 2013; Cheng et al., 2014; Cheng and Freas, 2015; Freas and Schultheiss, 2018; Wehner et al., 2014). The most well studied components of the toolbox are path integration via a celestial compass (Wehner, 1982; Collett and Collett,

2000a; Wehner and Srinivasan, 2003; Ronacher, 2008; Wehner, 2003, 2008; Stone et al., 2017) and the learned terrestrial cues of the panorama (Wehner and Räber, 1979; Wehner, 2003; Collett et al., 2006; Harris et al., 2007; Cheng et al., 2009; Schultheiss et al., 2016; Freas and Cheng, 2017, 2018). Additionally, foragers employ a backup strategy, systematic search, when other systems become unreliable (Wehner and Srinivasan, 1981; Müller and Wehner, 1994; Wehner, 1994; Pfeffer et al., 2015; Schultheiss et al., 2015).

During path integration, foragers keep a continuously updated estimate of their position in relation to the nest entrance by combining dual cue sets (Wehner and Srinivasan, 2003; Wehner and Müller, 2006; Wittlinger et al., 2006; Wehner, 2008). The first is a directional cue mediated by the ant's celestial compass. The ant's celestial compass is dependent on multiple sky-based cues, chiefly the polarised light pattern, which ants detect through an eye region called the dorsal rim (Labhart, 1980; Wehner, 1994; Wehner and Müller, 2006; Wehner, 2008; Zeil et al., 2014; Freas et al., 2017a). The second calculates distance largely through a pedometer or step counter (Wittlinger et al., 2006, 2007). These cues are integrated to create a working-memory-

based homeward vector that points the foragers back to the nest. During the inbound route, foragers run off their current homeward vector and reset this cue to zero once it reaches and enters the nest (Knaden and Wehner, 2006). In addition to this working memory process, foragers can also retain long-term vector information for use during subsequent foraging trips (Ziegler and Wehner, 1997; Collett et al., 1999; Collett and Collett, 2000b; Bolek et al., 2012a; Wolf et al., 2012; Freas and Cheng, 2018b).

Using learned panorama cues involves the acquisition and retention of aspects of the nest's surrounding panorama and the panorama along known foraging routes (Wehner and Räber, 1979; Wehner et al., 1996; Collett et al., 2006; Graham and Cheng, 2009). Before the onset of foraging, individuals first learn the panorama cues at the nest entrance through several pre-foraging learning walks (Wehner et al., 2004; Baddeley et al., 2011; Fleischmann et al., 2016, 2017, 2018a, 2018b; Grob et al., 2017). Foragers retain long-term memories of the visual cues of the nest panorama, and when away from the nest, they can compare these stored views with their current view. When the forager is facing the nest direction, their current view contains the least amount of mismatch with stored views, consequently directing the forager back to the nest site (Wehner and Räber, 1979; Cartwright et al., 1983; Collett et al., 2001, 2006; Zeil, 2012; Wehner et al., 2006; Cheng et al., 2009; Philippides et al., 2011; Wystrach et al., 2011a, 2011b; Baddeley et al., 2012; Kodzhabashev and Mangan, 2015). Panorama learning occurs not only before the onset of foraging at the nest site but also during foraging along the route during both the inbound and outbound routes (Collett, 1993; Kohler and Wehner, 2005; Graham and Cheng, 2009; Zeil, 2012; Schultheiss et al., 2016; Freas et al., 2017b; Freas and Cheng, 2018a; Freas et al., 2018). After performing multiple learning walks, individuals begin foraging and leave the nest area (Wehner et al., 2004; Fleischmann et al., 2016). While leaving for the first time, foragers will occasionally stop and momentarily orient back towards the nest. These turns or lookbacks are likely a learning period at which the forager is acquiring the terrestrial cues along the route (Nicholson et al., 1999; Zeil, 2012; Zeil et al., 2014).

This process of comparing the current view of the panorama with stored views of known locations forms the basis for the most widely accepted models of ant navigation, referred to as view-based navigation models (Cartwright and Collett, 1983; Harris et al., 2007; Collett, 2010; Philippides et al., 2011; Baddeley et al., 2012; Zeil, 2012; Zeil et al., 2014; Ardin et al., 2016). These models posit that foragers collect and retain multiple panorama memories, both from around the nest during learning walks and along routes, acquired during foraging. The memories of these views are subsequently compared to the forager's current view while away from the nest (Zeil et al., 2003; Möller, 2012). The specific cues of the panorama that the ant navigators retain remain unknown. One set of studies has focused on the pattern of the panorama's skyline, where the tops of the terrestrial cues meet the sky (Wehner, 1982; Graham and Cheng, 2009; Schultheiss et al., 2016), which insect UV vision is particularly well suited to detect (Mote and Wehner, 1980; Möller, 2002; Differt and Möller, 2016). One mechanism by which ants may encode the skyline and panorama is the fractional position of mass of the panorama when orienting with multiple landmarks, or when there is only one landmark present, orienting using that object's centre of mass (Lent et al., 2013; Buehlmann et al., 2016; Woodgate et al., 2016).

In desert ants, learned cues that are acquired before and during foraging can be critical for survival given the extreme environments they inhabit. In the last decade, multiple reviews on ant navigation have graced journals and books across biological and psychological disciplines, especially on view-based navigation but including path integration and systematic search (Ronacher, 2008; Wehner, 2008; Cheng, 2012; Collett et al., 2013; Schultheiss et al., 2015; Knaden and Graham, 2016; Graham and Wystrach, 2017; Pritchard and Healy, 2018; Freas and Schultheiss, 2018). This cornucopia focussed on the marvellous achievements of animals with tiny brains (Wehner et al.,

2007). But how ants in particular develop into expert navigators has been neglected as a topic. Enough results have now accumulated on this subject to warrant a first review, one that also calls to action more systematic ethological research on the theme of learning. Reinforcement learning is now touted to play a key role in ant navigation models (Kodzhabashev and Mangan, 2015; Ardin et al., 2016). How the principles of reinforcement learning in natural tasks such as navigation compare with the principles of reinforcement learning in conditioning tasks in restricted laboratory conditions remains to be seen.

In this review, we focus on learning and memory-related research in three areas of current interest in ant navigation. We open by summarising the learning that occurs during pre-foraging learning walks around the nest. Next, we review the learning and retention of panorama cues beyond the nest site during foraging trips. We also describe the plethora of non-visual cues that desert ants learn for navigation. Finally, we call for more experimental ethology—as pioneered by 1973 winners of the Nobel Prize in Physiology or Medicine, Tinbergen, Lorenz, and von Frisch (Tinbergen, 1932; von Frisch, 1953; Lorenz and Tinbergen, 1957)—focussing on learning processes, to examine the assortment of steps in learning and memory acquisition that take place in an animal's natural life in its ecological habitat, including the study of ant navigation. Such an enterprise should combine the expertise and vast fund of findings in the experimental psychology of animal learning with the rich tradition of ethology, the biological study of behaviour, especially of animals doing what they do in their day-to-day lives. Such an experimental ethology of learning can enrich both ethology and experimental psychology.

2. Learning walks and nest defining terrestrial cues

Desert ants undergo age-dependent polyethism (for *Cataglyphis bicolor*: Schmid-Hempel and Schmid-Hempel, 1984), meaning that they perform different tasks at different stages of their lives. After undertaking tasks within the dark nest underground, naïve ants—called *novices*—leave the nest for the first time to become foragers. Experienced foragers search for single food items consisting mainly of dead arthropods which did not survive the heat (Wehner et al., 1983). To become successful foragers the ants have to calibrate their compass systems and acquire the cues of the nest site for future navigation (Fleischmann, 2018), yet it is not yet known how they initially calibrate their celestial compass systems. Recently it has been shown that novices perform well-structured learning walks (Fleischmann et al., 2017) to acquire information about the panorama around the nest (Fleischmann et al., 2016, 2018a). Presumably, novices take snapshots when looking back to the nest entrance during learning walks.

Learning walks of *Cataglyphis* ants follow a distinct ontogeny during which the ants move further away from the nest and stay outside for longer durations with increasing experience (Wehner et al., 2004; Fleischmann et al., 2016, 2017). Novices never bring back any food during their learning walks, which may take up to three days at the beginning of the ants' foraging careers (Wehner et al., 2004; Fleischmann et al., 2016). During their learning walks the ants explore all directions around the nest entrance, but with more experience, i.e. an increasing number of outbound trips, their paths straighten and they increasingly head off in one compass direction, a phenomenon called *sector fidelity* (Wehner, 1987; Wehner et al., 2004; Stieb et al., 2012; Fleischmann et al., 2016).

As part of their well-structured learning walks, *Cataglyphis* ants exhibit conspicuous elements in the form of frequent turns (Wehner et al., 2004; Fleischmann et al., 2016, 2017). High-speed video analysis revealed two different types of turns presumably serving different purposes, called *voltes* and *pirouettes* (Fleischmann et al., 2017). In a volte, the ant walks in a little circle without stopping. In contrast, in a pirouette, the learner executes a full (about 360°) or partial (less than 180°) turn about its body axis. Pirouettes are frequently interrupted by distinct stopping phases—defined phases during which the ant does not
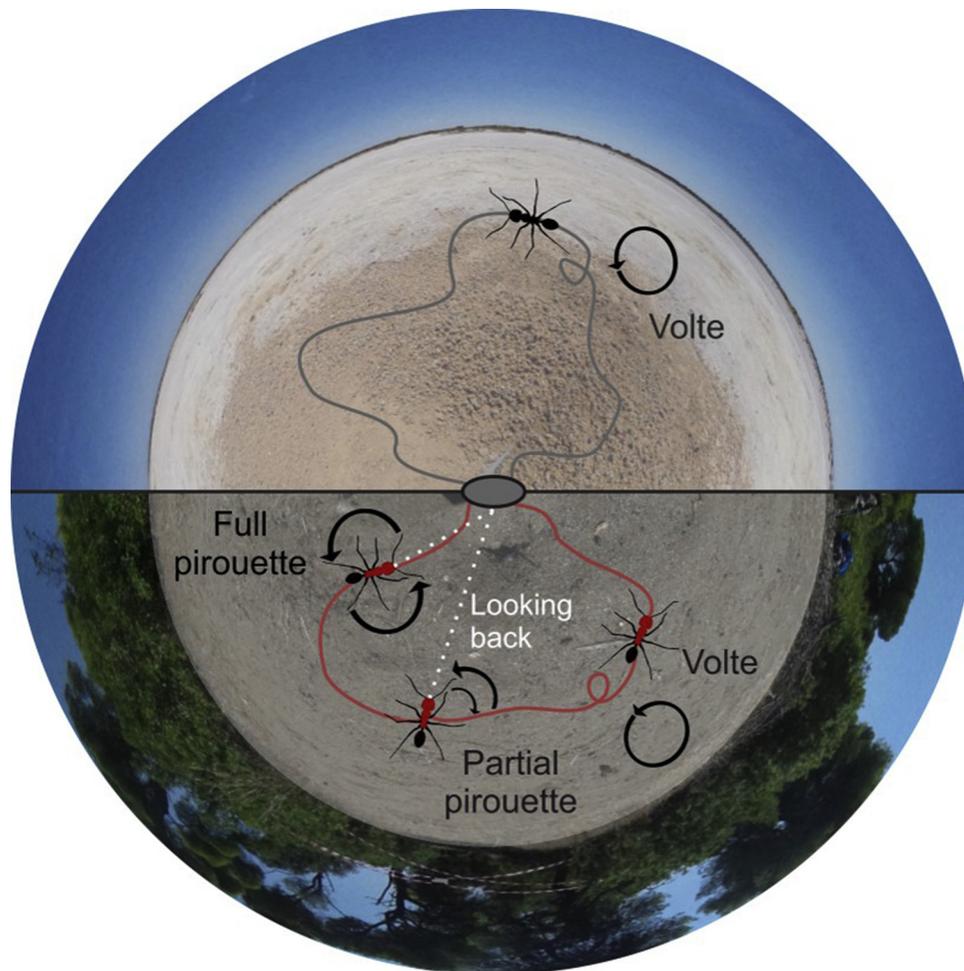
Fig. 1. Learning-walk elements exhibited by different *Cataglyphis* species. **Upper half:** *C. fortis* inhabiting saltpans without any prominent landmarks perform only voltes, in which the ant turns in a small, tight circle by 360° and then continues on her way. **Lower half:** *C. noda* inhabiting pine forests that offer distinctive landmark panoramas perform pirouettes as well as voltes. Both full (turning a full 360°) and partial pirouettes are frequently interrupted by stopping phases. During the longest stopping phase, the ants turn and look towards the nest entrance (dotted line).
Figure reproduced from Fleischmann, 2018 with permission.

move forward and keeps its gaze direction within a 10° range for at least 100 ms (Grob et al., 2017; Fleischmann et al., 2017, 2018b). The function of voltes is currently not well understood. The longest stopping phases of pirouettes, however, are directed towards the nest entrance, presumably to take snapshots from the homing direction (Fleischmann et al., 2017). Other ant species turn and stop in a pirouette-like fashion as well (*Melophorus bagoti*: Wystrach et al., 2014), with some also frequently looking back to the nest (*Ocymyrmex robustior*: Müller and Wehner, 2010; *Cataglyphis bicolor*: Wehner et al., 2004; bull ants *Myrmecia croslandi*: Jayatilaka et al., 2018). Different *Cataglyphis* species perform different species-specific repertoires of turns (Fleischmann et al., 2017). Ants inhabiting a visually cluttered environment, i.e. pine forests in Greece (*Cataglyphis noda* and *Cataglyphis aenescens*), display both voltes and pirouettes during their learning walks. In contrast, ants inhabiting featureless saltpans in Tunisia (*Cataglyphis fortis*) display only voltes (Fig. 1). Even setting up artificial landmarks failed to induce *C. fortis* to perform pirouettes (Fleischmann et al., 2017).

While it is assumed that ants learn the panorama around the nest during their lookbacks to the nest entrance during their learning walks (Wehner et al., 2004; Graham et al., 2010; Fleischmann et al., 2017; Grob et al., 2017; Fleischmann et al., 2018b; Freas and Cheng, 2018a), the crucial question of what information the ants actually acquire during their learning walks remains. Recent studies have shown that *Cataglyphis* novices need both enough time and enough space to perform learning walks before being able to return to the nest by panorama

guidance (see below) as foragers later on (Fleischmann et al., 2016, 2018a).

In contrast to their congenerics, *C. fortis* ants inhabit flat salt pans in Northern Africa devoid of any conspicuous natural landmarks (Dillier and Wehner, 2004). Yet numerous studies have shown that they can use visual landmarks if available (review: Wehner, 2008), especially when foragers are pinpointing the nest after extensive foraging trips (Huber and Knaden, 2015). Learning walks help *C. fortis* learn such experimental landmark arrays. When these ants are confronted with three black cylinders around their nest entrance, they only search for the nest entrance at the correct fictive position on the test field when they have gained enough experience outside the nest before being displaced and tested (Fleischmann et al., 2016). Furthermore, with increasing experience, i.e. with an increasing number of outbound trips, ants search closer to the fictive position of the nest entrance. Thus the acquisition of landmark information around the nest entrance is not instantaneous, but requires gradual (or stepwise) learning (Fleischmann et al., 2016).

Ants' learning walks increase in length, duration, and distance from the nest with increasing experience (Wehner et al., 2004; Stieb et al., 2012; Fleischmann et al., 2016, 2017). To test whether the homing success of *C. noda* foragers is impaired by restricting the space around the nest entrance during learning walks, three differently sized moats filled with water were set up in a Greek pine forest (Fleischmann et al., 2018a). Ants could see the whole natural panorama without any constraints, but could only move within a restricted area (0.3 m × 0.3 m,

1.0 × 1.0 m, or 2.0 m × 2.0 m around the nest entrance). In addition, they could visit a feeder a 5 m distance from the nest entrance. Later these foragers were captured at the feeder and transferred to a release point they had never previously visited. The release point was located at a 5 m distance from the nest entrance in the opposite direction to the feeder. Only ants that had at least 0.5 m of space in each direction to perform learning walks were able to navigate back to the nest. Ants that were trained in the smallest moat setup (0.3 m x 0.3 m space around the nest entrance) never returned to the nest, but followed their path integration vector and pursued a systematic search.

Different possible explanations might account for why ants cannot acquire enough information about the landmarks surrounding the nest entrance under spatially restricted conditions (Fleischmann et al., 2018a). In the moat setups, novices cannot explore all directions around the nest entrance in equal measure, which may lead to an impaired panorama view. Furthermore, their learning walks are interrupted after a certain distance (when they hit the moat), making learning walks shorter in the smaller setup with fewer pirouettes. These altered learning walks may in turn result in fewer snapshots of the nest's surroundings. Moreover, in order to distinguish between different snapshots and to not confuse them as rotations of each other, there may be a vital minimum distance between snapshots, which may not be possible in the smallest setup. Finally, the smaller the space offered by the moat setups, the more often ants actually touch the water during their learning walks. Such a presumably punishing experience might have been aversive to the learners and negatively impacted memory storage. In any case, there is a minimum space around the nest necessary during learning walks for ants to successfully acquire landmark information to navigate as foragers later on (Fleischmann et al., 2018a).

After understanding the functional importance of learning walks and the turns back to the nest entrance at different positions around the nest entrance, a subsequent crucial question remains. By what mechanism do these novices keep track of the nest entrance's position during these learning walks? Taking snapshots in the wrong direction would be fatal. For that reason, novices need a reliable reference system in order to align their lookbacks to the nest entrance during learning-walk pirouettes. Different cues might serve as a possible reference system. The most obvious possibility would be the use of celestial cues, which serve as the directional component of the path integrator during foraging. In *Cataglyphis* ants, polarised light is processed via the ultraviolet (UV) range of the electromagnetic spectrum. Thus, use of the UV polarisation pattern of the sky as a compass cue during learning walks had been suggested earlier (Graham et al., 2010; Müller and Wehner, 2010). Recent evidence, however, has ruled out celestial cues as a reference system for aligning the gaze directions during learning walks (Grob et al., 2017). When different filters are set up above the nest entrance so that novices are confronted with 1) a UV-permeable Plexiglas offering a view of the natural sky, 2) a polarisation filter offering an artificial linear polarisation pattern, or 3) a UV-blocking Plexiglas and a sunshade preventing the ants from seeing either polarised light or the sun, the ants' pirouetting behaviour remains unimpaired. Under all conditions novices perform their learning walks and the included elements. Their lookbacks to the nest are as precise and accurate as under natural conditions (Grob et al., 2017). Neurobiological comparisons of interior workers (control group) with novices that had performed learning walks for three days under different skylight conditions (experimental groups), however, show that only natural skylight conditions induced neuroplasticity in both the mushroom bodies and the central complex (Grob et al., 2017), both of which are higher-order sensory integration centres in the ant brain (Webb and Wystrach, 2016).

Since celestial compass cues have been rejected as a reference system for the lookbacks to the nest, the search for the reference system continued. Other possibilities are the panorama, olfactory cues, internal idiothetic mechanisms, or the earth's magnetic field (Fleischmann, 2018). As already reviewed, the panorama needs to be learned at the

beginning of the ant's foraging career itself for periods up to three days. Therefore, it is very unlikely that it serves as a reference system at the same time to take snapshots from the homing direction. Olfactory cues are only helpful downwind from the odour source (Steck et al., 2009), yet learning walks are performed in all directions around the nest entrance. In turning their gaze directions to the nest entrance, novice ants are very unlikely to be relying on a compass that does not operate in a large range of directions. Another possibility would be internal idiothetic mechanisms, such as relying on proprioceptive and kinaesthetic information to keep track of turns, yet these systems are highly prone to cumulative errors (Müller and Wehner, 1988), making them poor references for a calibrating compass.

The only remaining possibility, the earth's magnetic field, turns out to be the actual reference system for aligning the gaze directions to the nest entrance during learning walks (Fleischmann et al., 2018b). When novices are confronted with a disrupted magnetic field generated by a flat coil under otherwise natural conditions, their gaze directions are distributed randomly and are not directed to the nest entrance (Fleischmann et al., 2018b). Definitive evidence that *Cataglyphis* novices use the earth's magnetic field as a reference system came from imposing a homogeneous artificial magnetic field. Ants were trained to leave their nest via a tunnel reaching an experimental platform in the middle of a Helmholtz coil. High-speed video recordings captured the gaze directions of novices before and after the Helmholtz coil was switched on. When the horizontal component of the earth's magnetic field is eliminated, the gaze directions of the novices are distributed randomly (Fleischmann et al., 2018b). Shifting the horizontal component by 90°, −90° or 180° relative to the natural field direction leads to a predictable corresponding shift of the ants' gaze directions by the same angle (Fig. 2) (Fleischmann et al., 2018b).

While answering one question, that *Cataglyphis* ants use a magnetic compass on initial learning walks, a host of new questions emerge. Do other ant species also use a magnetic compass in initial learning walks? How does the magnetic directional sense scaffold the learning, calibration, and use of the well-studied sky compass, and after how many experiences does this transfer between compasses emerge? Why do experienced ants seem to rely predominantly on celestial compass cues for navigation during foraging? Or rather, do the two compass systems work in parallel? How does the magnetic compass support the learning of terrestrial views? The homing performance of foragers that are disrupted in their learning walk behaviour has to be tested. Last, but not least, the recent findings raise the question of whether the earth's magnetic field is additionally used for other navigational tasks during learning walks or during foraging later on.

3. Visual cue learning while foraging

While learning the nest panorama is critical to foragers' navigational success, desert ants, which are known to forage long distances from the nest site, also need to learn multiple panoramas along the foraging route and at profitable food sites for successful navigation (Graham and Cheng, 2009; Schultheiss et al., 2016; Freas et al., 2017b). This learning is believed to occur during the lookback behaviours the foragers perform occasionally during their first foraging trips away from the nest (Zeil et al., 2014). Lookbacks are also exhibited by foragers when leaving a profitable food site for the first time. Panorama learning appears to be rapid. The number of lookbacks decreases quickly with multiple trips to a food site (wood ants: Nicholson et al., 1999), and on the first trip to a feeder, desert ants (*M. bagoti*) can orient towards the nest using the panorama (Freas and Cheng, 2018a).

The significance of panorama learning that occurs after the learning walks and during foraging trips remains unresolved. View-based models of ant navigation suggest that there should be some catchment area surrounding the nest where views collected during learning walks will direct the forager back to the nest (Zeil et al., 2003; Baddeley et al., 2012; Zeil et al., 2014). The exact size of this catchment area is
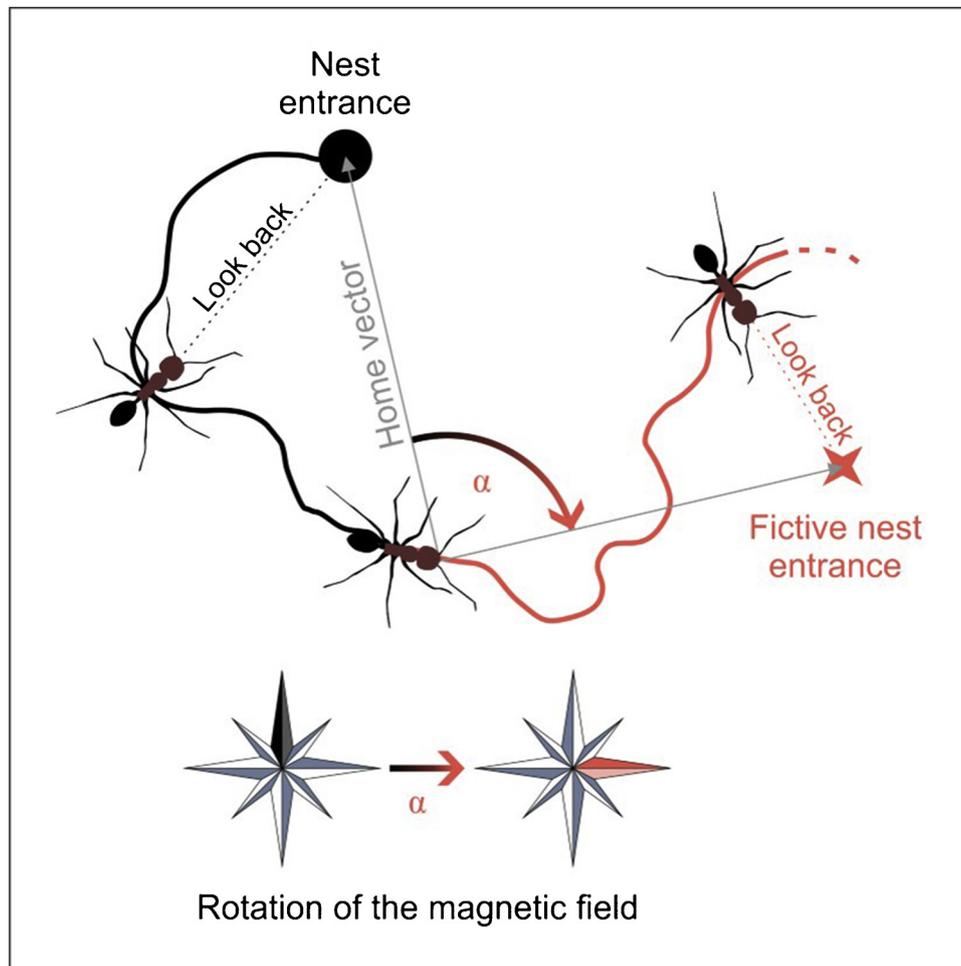
Fig. 2. The gaze direction of *C. noda* novices can be turned systematically by turning the magnetic field. If the magnetic field is artificially rotated (in the illustration, by 90° clockwise) during a learning walk (black line before alteration, red line after alteration), the gaze direction (dotted lines) during the longest stopping phase of a pirouette is no longer directed at the nest entrance (black dot), but also rotated by ∼90° clockwise, and directed at the fictive nest entrance (red star). Figure reproduced from Fleischmann et al., 2018b with permission.

unknown and likely depends on the panorama structure at each nest site, with open environments containing many distant, unobstructed landmarks providing increased similarity when facing the starting location after movement through the environment (Stürzl and Zeil, 2007; Philippides et al., 2011), resulting in larger catchment areas. We have reviewed that *C. noda* requires at least 0.5 m in each direction around their nest to extrapolate what they learn around their nest to other locations (Fleischmann et al., 2018a). This ability to extrapolate from known sites to local unvisited sites has also been studied in the Australian desert ant *Melophorus bagoti*. Studies in *M. bagoti* with naïve foragers artificially restricted to an area 2 m in diameter around the nest entrance have produced conflicting results, with foragers in Wystrach et al. (2012) being able to return home from local displacements. In contrast, in other studies *M. bagoti* could not orient after local displacements, even after large amounts of nest panorama experience, suggesting that under some conditions foragers are unable to extrapolate panorama views from known sites to local unvisited sites (Freas and Cheng, 2017, 2018a). This difference may be the result of experimental set-up differences or the discrepancies in panorama makeup around each nest leading to differences in the navigational information available to displaced foragers to use. The most obvious difference in experimental set-up was that Freas and Cheng (2017, 2018a) surrounded the nest area with a 10-cm high wall whereas Wystrach et al. (2012) did not, blockading the ants with a sunken wall instead. Additionally, an inability to extrapolate from local sites has also been

observed in non-desert ant species that have foragers naturally restricted to the nest area (Freas et al., 2017c). Further study into the abilities of ants to extrapolate and the catchment area of learned views around the nest is warranted.

On a forager's first trip to a non-nest site, foragers exhibit one-trial learning of these cues, acquiring sufficient panorama cues to successfully orient to the nest on future foraging trips (Freas and Cheng, 2017, 2018a). When the foraging route is separated into isolated cue components (outbound views, inbound views), foragers could orient successfully after a single exposure to either foraging segment. These findings are in line with view-based models (Baddeley et al., 2012; Zeil, 2012; Graham and Mangan, 2015; Ardin et al., 2016), which would posit that cue presentation sequence should be unimportant to panorama learning. However, the story of non-nest site panorama learning turned out to be more complex. When Freas and Cheng (2018a) gave foragers only the inbound view sequence along a foraging route they took significantly longer to return to the nest compared to foragers allowed the outbound view sequence alone (Fig. 3). This difference was maintained even when foragers were given multiple exposures to the route (10 in total). Ants with outbound views returned home in a channel that blocked inbound views (Fig. 3a). When displaced back to the feeder site without a vector (after almost reaching home), these ants were efficient at homing from the first trial. Conversely, foragers learning with inbound views only (Fig. 3b) kept repeatedly returning to the start point of the journey, the site of the

A
Outbound View Sequence Only

B
Inbound View Sequence Only

C
First Trip

■ Inbound Views   ■ Outbound Views
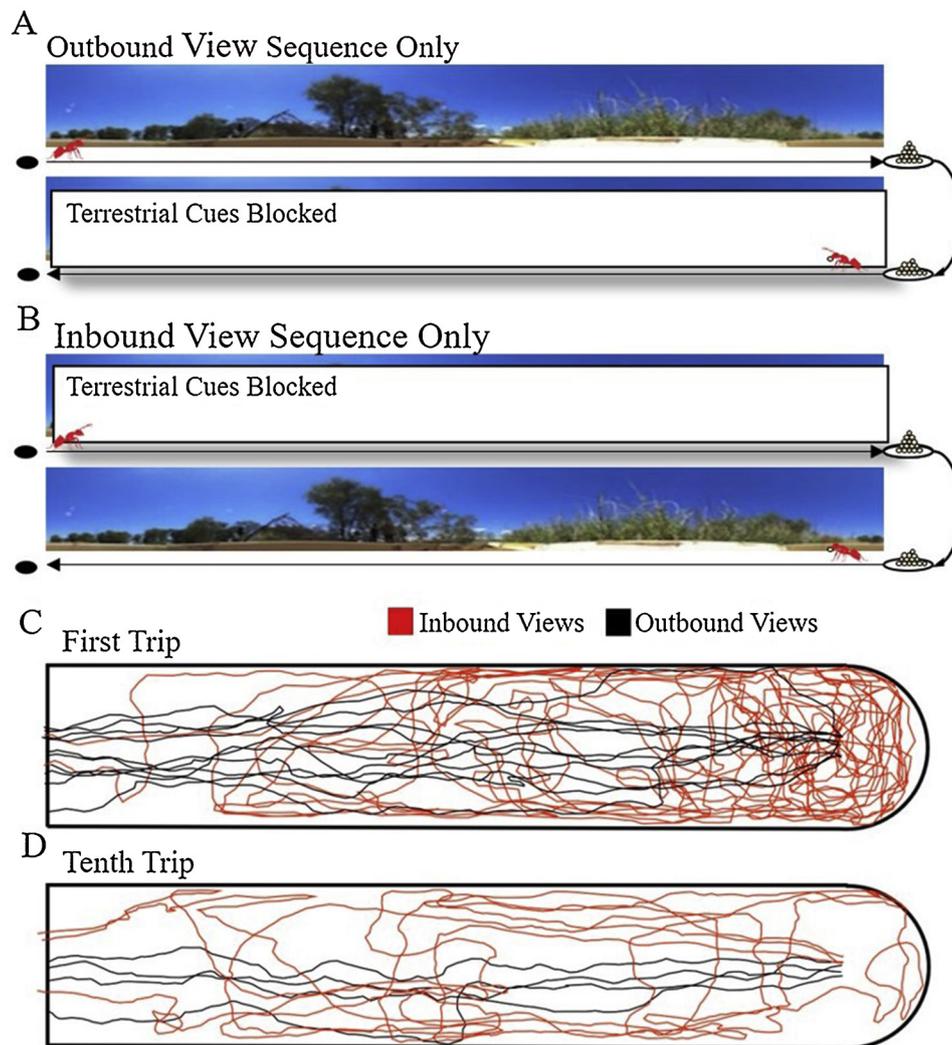
D
Tenth Trip

Fig. 3. Diagram illustrating the learning conditions in Freas and Cheng (2018a). Foragers travelled to a feeder with either (A) the outbound view sequence blocked, or (B) the inbound view sequence blocked. In both conditions foragers were tested by collecting them just as they reached the nest and then returning them to the feeder site with the homeward route unblocked. (C) Sample forager paths during the first inbound route of foragers with access only to the inbound views (red) or the outbound views (black). (D) Sample forager paths during the tenth foraging trips with foragers given the inbound (red) or outbound (black) views.

feeder. When foragers were tested without any vector, the displacement location represents where the nest should be according to the forager's path integrator. These results suggest that the view sequence during cue acquisition affects the cue's memory strength. When foragers are given access to the outbound views they appear to form strong memories of the foraging route compared to foragers with access only to memories during the inbound route. The weak panorama memories of the inbound route would, in turn, lead to higher uncertainty in the navigator and the observed longer return times (Fig. 3c,d).

The differences in memory strength observed in Freas and Cheng (2018a) may be the result of differences in reinforcers, which help establish memories, on the outbound and inbound route. The two potential reinforcers in this context would be finding food at the end of the outbound route and reaching the nest at the end of the inbound route. These results suggest that finding food may be the stronger reinforcer. Additionally, however, the lookback behaviours foragers exhibit during outbound trips, described earlier, may help establish panorama memories while en route. The lookbacks may help ants to learn outbound views by linking them with inbound views and strengthen both view sequences. In Freas and Cheng (2018a), foragers with no outbound views of the route were not able to perform lookbacks and this may result in the observed weaker route memories. The acquisition of these panorama cues and the importance of lookback behaviours during the

outbound route is a ripe topic for future study. Additionally, the small foraging distances involved in these studies mean that learning processes during both foragers' learning walks and route learning may contribute to the ants' route navigation. Studying learning processes over much larger distances from the nest may produce new and interesting findings.

Once a panorama memory is acquired, long-term learned panorama memories have been shown to be robust in desert ants, both for the nest panorama and non-nest panoramas of food sites. *C. fortis* retain lifelong memories of the nest panorama (Ziegler and Wehner, 1997; Wehner et al., 1983) and *M. bagoti* foragers retain permanent panorama memories of multiple locations even after long periods without experiencing the location (Muser et al., 2005; Narendra et al., 2007; Sommer et al., 2007; Freas et al., 2017b).

Additionally, *M. bagoti* foragers show evidence of retroactive interference in their memory retrieval of skyline panoramas after changes to a panorama at a known food site (Freas et al., 2017b). Retroactive interference occurs when the learning of new information interferes with the retrieval of old information (Cheng and Wignall, 2006). In Freas et al., 2017b) study, foragers were first trained to a feeder site surrounded by an artificial skyline for multiple days. After learning the original feeder panorama, this panorama was switched with a different distinct panorama where foragers were trained for multiple days before

testing on both panoramas. This set-up meant the state of the forager's path integrator and the route cues remained identical, thus mimicking large panorama changes at a food site. Over periods up to three days, foragers can navigate successfully in both skylines, but over longer periods of training with the new skyline, foragers show evidence of retroactive interference, suggesting that the two skyline memories compete with one another during memory retrieval (Freas et al., 2017b). Foragers need the ability to choose which panorama-based memories to retrieve, a task they accomplish through context cues (Collett et al., 2003; Collett and Collett, 2002; Cheng, 2005). The observed memory competition at the same spatial location suggests that certain context cues, such as the forager's vector length, may help foragers resolve this navigation decision when memories conflict (Freas et al., 2017b).

4. Other learned cues

The visual cues of the terrestrial panorama can provide foragers with reliable information about goal locations when they are available. Some species, however, live in environments where such cues are absent and need to rely both on path integration and other cues learned while navigating, the Tunisian salt-pan desert ant *Cataglyphis fortis* being a prime example. Recent work in the genus *Cataglyphis* has shown that regardless of panorama availability, ant navigators show learned responses to multiple non-visual cue sets, associating them with goal locations.

4.1. Learned vector cues

The vector cues that foragers accumulate during foraging with their path integrator are typically studied as a form of working memory, which resets after each foraging trip (Knaden and Wehner, 2006). The current vector reading of the path integrator is believed to decay over a 24 h period (*C. fortis*: Cheng et al., 2006; *M. bagoti*: Narendra et al., 2007), yet foragers are also able to retain long-term memories of previously travelled vectors that they can then use during future trips. Previously visited profitable food sites can be revisited by using the mirror (180°) of the inbound route (Collett et al., 1999; Collett and Collett, 2000b; Bolek et al., 2012b; Wolf et al., 2012) and long-term vector memories of trained inbound routes have also been observed (Ziegler and Wehner, 1997; Freas et al., 2017b). Foragers learn and retain distance and direction memories of not only the full route but also of individual segments of their foraging routes, termed local vectors (Collett et al., 1998; Knaden and Wehner, 2006; Collett and Collett, 2009). Local vectors are thought to be linked to contextual cues, which trigger their retrieval. In terms of contextual cues, local vector memory acquisition and maintenance requires support from both the visual memories of the panorama along the route and the global vector (Collett and Collett, 2009).

4.2. Learning as an error correction process: vector calibration

Path integration is an imprecise mechanism, leading to estimation errors that only get the forager close to the nest entrance (Wehner and Wehner, 1986). Foragers can rely on multiple learned navigational cues to successfully complete this final portion of their trip, including local nest-defining olfactory cues (Steck et al., 2009, 2011; Buehlmann et al., 2013, 2015), magnetic and vibrational cues (Buehlmann et al., 2012a), tactile cues (Seidl and Wehner, 2006), the surrounding panorama (Collett et al., 1992; Wehner et al., 1996; Schultheiss et al., 2016; Freas et al., 2017b) and a process known as vector calibration (Collett et al., 1999; Wehner et al., 2002; Freas and Cheng, 2018b). When a foraging trip's inbound and outbound vectors are not the natural 180° mirrors of each other, foragers will alter the direction of their subsequent inbound vectors in the direction of the previous foraging trip's inbound direction (Collett et al., 1999; Collett and Collett, 2000a; Wehner et al., 2002).

This shift occurs rapidly, with desert ant foragers showing significant calibration after only three non-mirrored trips, and with vector calibration reaching its asymptote after 10 trips (Wehner et al., 2002; Freas and Cheng, 2018b).

In barren habitats, there are few terrestrial cues to help guide *C. fortis* foragers in the correct nest direction and vector calibration shifts in this species are incomplete. These foragers travel in a compromise direction between the inbound and outbound directions, (Collett et al., 1999; Wehner et al., 2002), with this compromise possibly being due to the lack of panorama cues, requiring them to rely heavily on systematic search to find the nest. In *M. bagoti*, which inhabits an environment with many terrestrial cues to guide foragers, the vector will recalibrate completely to the inbound route when directional differences are small (45°). These species' differences may be the result of *M. bagoti* using visual cues to help correct this conflict while *C. fortis* must rely on systematic search. Unlike *C. fortis*, *M. bagoti* foragers were also observed to form direct inbound routes back to the nest, suggesting that the observed species differences in vector calibration may be due to panorama cue availability (Wehner et al., 2002; Freas and Cheng, 2018b). Furthermore, in *M. bagoti*, 45° appears to be the directional limit of foragers' vector calibration ability. At directional differences over 45°, calibration decreases both in magnitude and as a percentage, to the point where at 180° foragers show no evidence of vector calibration (Freas and Cheng, 2018b). These limits in calibration may be related to the magnitude of the conflict between the outbound and inbound routes and are remarkably similar to mammalian models when short-term vs long-term memory cues directionally conflict (Etienne et al., 1990, 1996).

4.3. Resource patch learning

As noted earlier, foragers can retain long-term vector memories and use this information on subsequent foraging trips to travel to goal locations such as profitable food sources (Wolf and Wehner, 2000; Wolf et al., 2012). Path-integration-derived memories of resource sites appear to be based on both the outbound and inbound distance of the site, as when these are put into conflict, *C. fortis* foragers will search at an intermediate distance between the two on subsequent foraging trips (Bolek et al., 2012a).

Foragers also retain information about resource patch quality, which will determine a forager's propensity to revisit the site on future foraging trips (Bolek et al., 2012b; Wolf et al., 2012). After a single visit to a new food site, a forager's decision to return to the site, determined through recording their next outbound search path, appears to be based on the perceived quality of the food site, namely the amount of food experienced at the site on the previous trip. After collecting food from the site multiple times, memories of site quality were dominated by learned information regarding the reliability of food's presence at the site and foragers' outbound searches became focussed on the food site regardless of the amount of food present (Bolek et al., 2012b; Wolf et al., 2012).

4.4. Olfactory cues

Despite the salt-pan's barren appearance, the landscape does contain different soil structures and decaying plant materials, which create an array of olfactory landmarks throughout the habitat (Steck et al., 2009; Buehlmann et al., 2014). Desert ants have been shown to use these non-visual navigational cues to find food locations and return to the nest location (Steck et al., 2010; Stieb et al., 2011; Wolf et al., 2012; Buehlmann et al., 2012b, 2014). The nest entrance emits odour cues in the form of a CO_2 plume which foragers orient towards when their path integrator is near zero. This interaction between navigational systems is believed to prevent foragers from entering the nests of conspecifics they pass by on the homeward route (Buehlmann et al., 2012b, 2013). Furthermore, it has been shown that some odour cues are learned

during foraging. When *C. fortis* foragers are trained with odours present around their nest entrance, these foragers learn to associate the nest with these odours and use these cues when navigating home (Steck et al., 2009). This learning appears finely tuned to the distinct olfactory landmark makeup of the nest, as foragers are able to learn the nest entrance's spatial location relative to multiple odour sources (Steck et al., 2010). Beyond the nest site, *C. fortis* foragers actively use olfactory cues to find dead insects through the use of crosswinds (Wolf and Wehner, 2000; Buehlmann et al., 2014) and can learn the odours of a foraging route. Foragers trained along a foraging route with an array of distinct odours, then displaced to a distant identical odour array, biased their search for the nest towards the odours, suggesting that foragers learned the olfactory cues during foraging and used this information while homing (Buehlmann et al., 2015). While current work has shown that foragers are able to learn associations between olfactory cues presented by the experimenters and goal locations, future work could focus on how natural olfactory landmark cues not directly linked with the nest or decaying insects are used and weighted with other navigational strategies.

4.5. Tactile, vibrational, and magnetic cues

C. fortis has also been shown to form associative links between other nest defining cues. Foragers trained with distinct tactile features experimentally placed around the nest will use this learned cue when homing. Foragers appear to learn both the visual and tactile features of these areas associated with the nest, with a portion of the learned ground cues being purely mechanosensory (Seidl and Wehner, 2006). Similar associative learning studies have been conducted on another *Cataglyphis* species, *Cataglyphis noda,* showing that these foragers can learn to associate both magnetic and vibrational landmarks with the nest. When foragers are trained with these cues near the nest entrance and then tested with only the cues, foragers will direct their search for the nest around these cues (Buehlmann et al., 2012a).

While experimental ethological studies have begun to link learning walks and foraging trips to view learning, the learning of the now rich array of non-visual cues has hardly been documented in detail. The studies reviewed here have trained ants really well to use a potpourri of cues but have not described trial-by-trial learning.

5. Discussion

Of the three major tools in the desert ant's navigational toolkit, namely path integration, panorama-based navigation, and systematic search, the use of the visual panorama cues of various modalities requires the most learning. Our review has focussed on view-based navigation, but learning processes in using the other major tools also merit brief discussion.

Performance on path integration is consistently good from the first trial, that is, the first arrival at an experimental feeder (Cheng et al., 2006; Narendra et al., 2007; Merkle and Wehner, 2009); performance does not improve with repeated runs. This makes functional sense because if the ant fails to return home from her first foraging run, the unforgiving desert does not grant a second run. But some calibration of both step length and celestial compass must be done to integrate a path. These processes require more study. Given the discovery of the magnetic compass being used in initial learning walks, the question looms large as to how desert ants either transfer their initially used magnetic compass to the celestial compass, or switch between compass systems, or else use multiple compass systems together on tasks.

Ants also adjust their search patterns based on experience, both in a channel (Cheng and Wehner, 2002; Schwarz et al., 2012) and on open field (Wehner et al., 2002). A normal search is centred on the starting point of the search (Schultheiss et al., 2015), but adjusted nest searches drift in the expected direction of the nest based on past experience—expected from an experimenter's point of view, as it is a different

question whether the ants hold any expectations.

Ants learn a variety of cues while running a route, based largely on visual cues but also on a panoply of stimuli in other modalities. As reviewed here, *C. noda* uses magnetic cues to orient on initial learning walks (Fleischmann et al., 2018a, 2018b). We have already raised many questions to address on this topic. The learning in learning walks also requires more systematic investigation. What learning takes place with each learning walk, and how many are needed before the ant can extrapolate to home from other locations? Studies in parallel on multiple species will help to elucidate such questions and others. Besides the magnetic compass and learning walks, other themes surfaced in our review that also call for further research.

On establishing a route to and from a feeder, learning takes place quickly, unlike the many trials and even sessions required by animals learning an operant task in lab conditions. Freas and Cheng's (2018a) *M. bagoti* ants learned the route well by their first arrival at the feeder. We may have missed the most important learning period of a forager by starting to examine learning only after the forager reached the feeder for the first time. This quick learning is reminiscent of the rapid learning seen in operant labs when tasks are made to resemble an animal's real-world conditions. Pigeons, for example, learn a match-to-sample task two orders of magnitude faster, in a matter of a few trials, when pecking for grain on textured gravel compared with pecking on keys of operant chambers (Wright and Delius, 1994). In experimental ethology examining learning in ants, research needs to focus on their actions in getting to the feeder for the first time. From our personal observations, desert ants do not arrive at a feeder in one trip. Rather, they take multiple trips, venturing farther and farther from their nest on each trip but returning to their nest between trips until they eventually find the feeder. These behaviours durinig this initial foraging period possibly represent a blend between learning walks and route learning. Such pre-arrival behaviour has not been fully systematically documented (but see Wehner, 2003), and is so far regarded as a necessary chore to get ants to a feeder to test after they are trained as opposed to a phenomenon of interest. Scientists need to observe and manipulate these pre-arrival experiences to further unravel the experimental ethology of learning routes.

Also unclear and needing more study is the question of extrapolation or generalisation of learned views. Conflicting results mean that further systematic replication is needed. All the results have come from *M. bagoti*, so that replication with other species, especially those with visually rich panoramic views, would probe the generality of the experimental ethology of learning views.

Studies investigating the learning of cues during learning walks have restricted the focus to the visual panorama. But ants also learn cues from other modalities including magnetic, tactile, and olfactory cues. The corpus on the use of these cues consists at the moment of demonstrations of capability, or proofs of concept. The acquisition of this suite of information during learning walks has not yet been investigated systematically. We here call to action a fuller experimental ethology probing the learning of these multiple forms of navigational cues based on different senses, both as single modalities and in multi-sensory combination. It is likely that learning walks scaffold the learning of all sensory modalities, with novices arming themselves with information from all available cues to launch them on their all-important foraging careers. Only in that way can the multi-modal and multi-system navigational toolkit (Wehner et al., 2016) be stocked and used with "optimal multiguidance integration" (Hoinville and Wehner, 2018, from the title).

Other principles of learning that have been examined in the operant laboratory are also worth exploring in the experimental ethology of navigation, such as extinction and avoidance learning. Extinction of route running can be affected by grabbing an ant just before she enters her nest and displacing her back to the start of her route, a manipulation called *rewinding* (Wystrach et al., submitted). A study on *Cataglyphis bicolor* rewound ants repeatedly along a familiar homeward

route (Andel and Wehner, 2004). The ants reached their nest on each occasion, but were taken back out again, so that the extinction procedure was unusual in that the ants achieved some success on each returning trip. After multiple displacements back to the feeder, foragers began to follow their accumulated path integrator in the opposite direction. Collett (2010) foisted the rewinding experience on salt-pan dwelling *C. fortis* ants just once, with their route on the otherwise barren salt pan adorned by a single conspicuous black cylinder. Some of Collett's rewound ants seemed confused for an extended period before resuming their route again. How would ants behave if repeatedly rewound without reaching home? Avoidance learning can be examined by placing obstacles or traps along the route to generate aversive experiences. A wide trap with only a narrow escape path, for example, would cause ants that fall into it much lost time to escape the trap. Would ants learn to avoid such traps with experience?

In insect neuroethology, reinforcement learning has been modelled multiple times (Bazhenov et al., 2013; Perry et al., 2013; Aso et al., 2014; Galizia, 2014; Ardin et al., 2016; Webb and Wystrach, 2016; Peng and Chittka, 2017; Hoinville and Wehner, 2018), with Ardin et al., Webb and Wystrach, and Hoinville and Wehner specifically concerned with navigation. An underlying question is what constitutes reinforcement, the process said to drive learning. Foraging ants sometimes find food, and as in the operant lab, finding food is presumably a reinforcing event. What about finding home? The function of foraging is not only to sustain the forager, but also to provide nutrients for her nest. Is getting home a reinforcer? In the experimental ethology of learning, we think that, much like what has been revealed from the experimental psychology of learning, different forms of learning are inextricably intertwined in learning to navigate, forms that parallel operant conditioning, classical conditioning, as well as perceptual learning. In lab-based operant conditioning, classical conditioning is inevitably linked. Stimuli associated with primary reinforcers become reinforcers themselves, secondary reinforcers, as well as classically conditioned stimuli (Breland and Breland, 1961). Classically conditioned stimuli would draw forth a suite of behaviours associated with the behaviour system surrounding the unconditioned reinforcer (Breland and Breland, 1961). We would expect parallel processes in learning to navigate in the outdoor world. For example, inbound views along a route home might become secondary reinforcers because they are associated with getting home. Reinforcement processes furnish a rich vein for research in the experimental ethology of learning.

6. Conclusions

Desert ants have been a key group for the study of a number of navigational mechanisms, including their ability to acquire and use a number of learned cue sets both around the nest and at profitable food sites. Here we have summarised three areas of current interest in experimental ethology of learning in this species group: nest site learning that occurs during learning walks, panorama learning that occurs during foraging trips, and the myriad of other cue sets these foragers learn.

Author contributions

KC conceived the original idea for the review. All authors contributed to planning the structure of the review, writing, and revising it.

Competing interest statement

All authors declare that the current review was written in the absence of any financial or commercial relationship that could be seen as a competing interest.

References

Andel, D., Wehner, R., 2004. Path integration in desert ants, *Cataglyphis*: how to make a homing ant run away from home. Proc. R. Soc. B 271, 1485–1489. https://doi.org/10.1098/rspb.2004.2749.

Ardin, P., Peng, F., Mangan, M., Lagogiannis, K., Webb, B., 2016. Using an insect mushroom body circuit to encode route memory in complex natural environments. PLoS Comput. Biol. 12, e1004683.

Aso, Y., Sitaraman, D., Ichinose, T., Kaun, K.R., Vogt, K., Belliart-Guérin, G., Plaçais, P.-Y., Robie, A.A., Yamagata, N., Schnaitmann, C., Rowell, W.J., Johnston, R.M., Ngo, T.-T.B., Chen, N., Korff, W., Nitabach, M.N., Heberlein, U., Preat, T., Branson, K.M., Tanimoto, H., Rubin, G.M., 2014. Mushroom body output neurons encode valence and guide memory-based action selection in *Drosophila*. eLife 3, e04580.

Baddeley, B., Graham, P., Philippides, A., Husbands, P., 2011. Models of visually guided routes in ants: embodiment simplifies route acquisition. In: Jeschke, S., Liu, H., Schilberg, D. (Eds.), Proceedings of the International Conference on Intelligent Robotics and Applications (ICIRA) Part II, Lecture Notes in Artificial Intelligence. Springer-Verlag, Heidelberg, Germany, pp. 75–84.

Baddeley, B., Graham, P., Husbands, P., Philippides, A., 2012. A model of ant route navigation driven by scene familiarity. PLoS Comput. Biol. 8, e1002336. https://doi.org/10.1371/journal.pcbi.1002336.

Bazhenov, M., Huerta, R., Smith, B.H., 2013. A computational framework for understanding decision making through integration of basic learning rules. J. Neurosci. 33, 5686–5697.

Bolek, S., Wittlinger, M., Wolf, H., 2012a. Establishing food site vectors in desert ants. J. Exp. Biol. 215, 653–656. https://doi.org/10.1242/jeb.062406.

Bolek, S., Wittlinger, M., Wolf, H., 2012b. Re-visiting of plentiful food sources and food search strategies in desert ants. Front. Neurosci. 6, 102. https://doi.org/10.3389/fnins.2012.00102.

Breland, K., Breland, M., 1961. The misbehavior of organisms. Am. Psychol. 16, 681–684.

Buehlmann, C., Hansson, B.S., Knaden, M., 2012a. Desert ants learn vibration and magnetic landmarks. PLoS One 7, e33117. https://doi.org/10.1371/journal.pone.0033117.

Buehlmann, C., Hansson, B.S., Knaden, M., 2012b. Path integration controls nest-plume following in desert ants. Curr. Biol. 22, 645–649. https://doi.org/10.1016/j.cub.2012.02.029.

Buehlmann, C., Hansson, B.S., Knaden, M., 2013. Flexible weighing of olfactory and vector information in the desert ant *Cataglyphis fortis*. Biol. Lett. 9, 20130070. https://doi.org/10.1098/rsbl.2013.0070.

Buehlmann, C., Graham, P., Hansson, B.S., Knaden, M., 2014. Desert ants locate food by combining high sensitivity to food odors with extensive crosswind runs. Curr. Biol. 24, 960–964. https://doi.org/10.1016/j.cub.2014.02.056.

Buehlmann, C., Graham, P., Hansson, B.S., Knaden, M., 2015. Desert ants use olfactory scenes for navigation. Anim. Behav. 106, 99–105. https://doi.org/10.1016/j.anbehav.2015.04.029.

Buehlmann, C., Woodgate, J.L., Collett, T.S., 2016. On the encoding of panoramic visual scenes in navigating wood ants. Curr. Biol. 26, 2022–2027. https://doi.org/10.1016/j.cub.2016.06.005.

Cartwright, B.A., Collett, T.S., 1983. Landmark learning in bees. J. Comp. Physiol. A 151, 521–543.

Cheng, K., 2005. Reflections on geometry and navigation. Connect Sci. 17, 5–21.

Cheng, K., 2012. Arthropod Navigation Ants, Bees, Crabs, Spiders Finding Their Way. Oxford University Press https://doi.org/10.1093/oxfordhb/9780195392661.013.0019.

Cheng, K., Freas, C.A., 2015. Path integration, views, search, and matched filters: the contributions of Rüdiger Wehner to the study of orientation and navigation. J. Comp. Physiol. A 201, 517–532. https://doi.org/10.1007/s00359-015-0984-9.

Cheng, K., Wehner, R., 2002. Navigating desert ants (Cataglyphis fortis) learn to alter their search patterns on their homebound journey. Physiol. Entom. 27 (4), 285–290.

Cheng, K., Narendra, A., Wehner, R., 2006. Behavioral ecology of odometric memories in desert ants: acquisition, retention and integration. Behav. Ecol. 17, 227–235.

Cheng, K., Narendra, A., Sommer, S., Wehner, R., 2009. Traveling in clutter: navigation in the Central Australian desert ant *Melophorus bagoti*. Behav. Process 80, 261–268. https://doi.org/10.1016/j.beproc.2008.10.015.

Cheng, K., Schultheiss, P., Schwarz, S., Wystrach, A., Wehner, R., 2014. Beginnings of a

synthetic approach to desert ant navigation. Behav. Process 102, 51–61. https://doi.org/10.1016/j.beproc.2013.10.001.

Collett, T.S., 1993. Route following and the retrieval of memories in insects. Comp. Biochem. Physiol. A Physiol. 104, 709–716.

Collett, M., 2010. How desert ants use a visual landmark for guidance along a habitual route. PNAS 107, 11638–11643. https://doi.org/10.1073/pnas.1001401107.

Collett, M., Collett, T.S., 2000a. How do insects use path integration for their navigation? Biol. Cybern. 83, 245–259. https://doi.org/10.1007/s004220000168.

Collett, T.S., Collett, M., 2000b. Path integration in insects. Curr. Opin. Neurobiol. 10, 757–762. https://doi.org/10.1016/S0959-4388(00)00150-1.

Collett, T.S., Collett, M., 2002. Memory use in insect visual navigation. Nat. Rev. Neurosci. 3, 542–552. https://doi.org/10.1038/nrn872.

Collett, M., Collett, T.S., 2009. The learning and maintenance of local vectors in desert ant navigation. J. Exp. Biol. 212, 895–900.

Collett, T.S., Dillmann, E., Giger, A., Wehner, R., 1992. Visual landmarks and route following in desert ants. J. Comp. Physiol. A 170, 435–442.

Collett, M., Collett, T.S., Bisch, S., Wehner, R., 1998. Local and global vectors in desert ant navigation. Nature 394, 269–272.

Collett, M., Collett, T.S., Wehner, R., 1999. Calibration of vector navigation in desert ants. Curr. Biol. 9, 1031–1034. https://doi.org/10.1016/S0960-9822(99)80451-5.

Collett, T.S., Collett, M., Wehner, R., 2001. The guidance of desert ants by extended landmarks. J. Exp. Biol. 204, 1635–1639.

Collett, M., Collett, T.S., Chameron, S., Wehner, R., 2003. Do familiar landmarks reset the global path integration system of desert ants? J. Exp. Biol. 206, 877–882. https://doi.org/10.1242/jeb.00176.

Collett, T.S., Graham, P., Harris, R.A., Hempel-de-Ibarra, N., 2006. Navigational memories in ants and bees: memory retrieval when selecting and following routes. Adv. Study Behav. 36, 123–172. https://doi.org/10.1016/s0065-3454(06)36003-2.

Collett, M., Chittka, L., Collett, T.S., 2013. Spatial memory in insect navigation. Curr. Biol. 23, R789–R800. https://doi.org/10.1016/j.cub.2013.07.020.

Differt, D., Möller, R., 2016. Spectral skyline separation: extended landmark databases and panoramic imaging. Sensors 16 (10), 1614. https://doi.org/10.3390/s16101614.

Dillier, F.X., Wehner, R., 2004. Spatio-temporal patterns of colony distribution in monodomous and polydomous species of North African desert ants, genus *Cataglyphis*. Insect Soc. 51, 186–196.

Etienne, A.S., Teroni, V., Hurni, C., Portenier, V., 1990. The effect of a single light cue on homing behaviour of the golden hamster. Anim. Behav. 39, 17–41.

Etienne, A.S., Maurer, R., Seguinot, V., 1996. Path Intergration in Mammals and its Interaction with visual landmarks. J. Exp. Biol. 199, 201–209.

Fleischmann, P.N., 2018. Starting Foraging Life: Early Calibration and Daily Use of the Navigational System in *Cataglyphis* ants. PhD Thesis. .

Fleischmann, P.N., Christian, M., Müller, V.L., Rössler, W., Wehner, R., 2016. Ontogeny of learning walks and the acquisition of landmark information in desert ants, *Cataglyphis fortis*. J. Exp. Biol. 219, 3137–3145.

Fleischmann, P.N., Grob, R., Wehner, R., Rössler, W., 2017. Species-specific differences in the fine structure of learning walk elements in *Cataglyphis ants*. J. Exp. Biol. 220, 2426–2435.

Fleischmann, P.N., Rössler, W., Wehner, R., 2018a. Early foraging life: spatial and temporal aspects of landmark learning in the ant *Cataglyphis noda*. J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol. 204, 579–592.

Fleischmann, P.N., Grob, R., Müller, V.L., Wehner, R., Rössler, W., 2018b. The geomagnetic field is a compass cue in *Cataglyphis* ant navigation. Curr. Biol. 28, 1440–1444 e2.

Freas, C.A., Cheng, K., 2017. Learning and time-dependent cue choice in the desert ant, *Melophorus bagoti*. Ethology 123, 503–515. https://doi.org/10.1111/eth.12626.

Freas, C.A., Cheng, K., 2018a. Landmark learning, cue conflict and outbound view sequence in navigating desert ants. J. Exp. Psychol. Anim. Learn. Cogn. 44 (4), 409–421. https://doi.org/10.1037/xan000017.

Freas, C.A., Cheng, K., 2018b. Limits of vector calibration in the Australian desert ant, *Melophorus bagoti*. Insect Soc. 65, 141–152. https://doi.org/10.1007/s00040-017-0595-2.

Freas, C.A., Schultheiss, P., 2018. How to navigate in different environments and situations: lessons from ants. Front. Psychol. 9, 841–848. https://doi.org/10.3389/fpsyg.2018.00841.

Freas, C.A., Narendra, A., Lemesle, C., Cheng, K., 2017a. Polarized light use in the nocturnal bull ant, *Myrmecia midas*. RSOS 4, 170598. https://doi.org/10.1098/rsos.170598.

Freas, C.A., Whyte, C., Cheng, K., 2017b. Skyline retention and retroactive interference in the navigating Australian desert ant, *Melophorus bagoti*. J. Comp. Physiol. A 203, 353–367. https://doi.org/10.1007/s00359-017-1174-8.

Freas, C.A., Narendra, A., Cheng, K., 2017c. Compass cues used by a nocturnal bull ant, *Myrmecia midas*. J. Exp. Biol. 220, 1578–1585. https://doi.org/10.1242/jeb.152967.

Freas, C.A., Wystrach, A., Narendra, A., Cheng, K., 2018. The view from the trees: nocturnal bull ants, *Myrmecia midas*, use the surrounding panorama while descending from trees. Front. Psychol. 9, 16. https://doi.org/10.3389/fpsyg.2018.00016.

Galizia, C.G., 2014. Olfactory coding in the insect brain: data and conjectures. Europ. J. Neurosci. 39, 1784–1795.

Graham, P., Cheng, K., 2009. Which portion of the natural panorama is used for view-based navigation in the Australian desert ant? J. Comp. Physiol. A 195, 681–689. https://doi.org/10.1007/s00359-009-0443.

Graham, P., Mangan, M., 2015. Insect navigation: do ants live in the now? J. Exp. Biol. 218, 819–823.

Graham, P., Wystrach, A., 2017. In: Olmstead, M.C. (Ed.), Animal Cognition: Principles, Evolution, and Development. Nova Science Chapter 4.

Graham, P., Philippides, A., Baddeley, B., 2010. Animal cognition: multi-modal interactions in ant learning. Curr. Biol. 20, R639–R640.

Grob, R., Fleischmann, P.N., Grübel, K., Wehner, R., Rössler, W., 2017. The role of celestial compass information in *Cataglyphis* ants during learning walks and for neuroplasticity in the central complex and mushroom bodies. Front. Behav. Neurosci. 11, 226.

Harris, R.A., Graham, P., Collett, T.S., 2007. Visual cues for the retrieval of landmark memories by navigating wood ants. Curr. Biol. 17, 93–102. https://doi.org/10.1016/j.cub.2006.10.068.

Hoinville, T., Wehner, R., 2018. Optimal multi-guidance integration in insect navigation. PNAS 115, 2824–2829.

Huber, R., Knaden, M., 2015. Egocentric and geocentric navigation during extremely long foraging paths of desert ants. J. Comp. Physiol. A 201, 609–616.

Jayatilaka, P., Murray, T., Narendra, A., Zeil, J., 2018. The choreography of learning walks in the Australian jack jumper ant *Myrmecia croslandi*. J. Exp. Biol. 221 jeb185306.

Knaden, M., Graham, P., 2016. The sensory ecology of ant navigation: from natural environments to neural mechanisms. Annu. Rev. Entomol. 61, 63–76. https://doi.org/10.1146/annurev-ento-010715-023703.

Knaden, M., Wehner, R., 2006. Ant navigation: resetting the path integrator. J. Exp. Biol. 209, 26–31. https://doi.org/10.1242/jeb.01976.

Kodzhabashev, A., Mangan, M., 2015. Route following without scanning. In: Wilson, S.P., Verschure, P.F.M.J., Mura, A., Prescott, T.J. (Eds.), Biomimetic and Biohybrid Systems. Springer, Barcelona, pp. 199–210.

Kohler, M., Wehner, R., 2005. Idiosyncratic route-based memories in desert ants, Melophorus bagoti: How do they interact with path-integration vectors? Neurobiol. Learn. Mem. 83, 1–12. https://doi.org/10.1016/j.nlm.2004.05.011.

Lent, D.D., Graham, P., Collett, T.S., 2013. Visual scene perception in navigating wood ants. Curr. Biol. 23, 684–690. https://doi.org/10.1016/j.cub.2013.03.01.

Labhart, T., 1980. Specialized photoreceptors at the dorsal rim of the honeybee's compound eye: Polarizational and angular sensitivity. J. Comp. Physiol. A 141, 19–30.

Lorenz, K., Tinbergen, N., 1957. Taxis and instinct. C.H. Schiller Instinctive Behavior. International Universities Press, New York.

Merkle, T., Wehner, R., 2009. How flexible is the systematic search behaviour of desert ants? Anim. Behav. 77 (5), 1051–1056. https://doi.org/10.1016/j.anbehav.2009.01.006.

Möller, R., 2002. Insects could exploit UV–Green contrast for landmark navigation. J. Theor. Biol. 214, 619–631. https://doi.org/10.1006/jtbi.2001.2484.

Möller, R., 2012. A model of ant navigation based on visual prediction. J. Theor. Biol. 305, 118–130.

Mote, M.I., Wehner, R., 1980. Functional characteristics of photoreceptors in the compound eye and ocellus of the desert ant, *Cataglyphis bicolor*. J. Comp. Physiol. A 137, 63–71.

Müller, M., Wehner, R., 1988. Path integration in desert ants, *Cataglyphis fortis*. PNAS 85 (14), 5287–5290. https://doi.org/10.1073/pnas.85.14.5287.

Müller, M., Wehner, R., 1994. The hidden spiral: systematic search and path integration in desert ants, *Cataglyphis fortis*. J. Comp. Physiol. A 175. https://doi.org/10.1007/bf00199474.

Müller, M., Wehner, R., 2010. Path integration provides a scaffold for landmark learning in desert ants. Curr. Biol. 20, 1368–1371. https://doi.org/10.1016/j.cub.2010.06.035.

Muser, B., Sommer, S., Wolf, H., Wehner, R., 2005. Foraging ecology of the Australian desert ant *Melophorus bagoti*. Aust. J. Zool. 53, 301–311.

Narendra, A., Si, A., Sulikowski, D., Cheng, K., 2007. Learning, retention and coding of nest-associated visual cues by the Australian desert ant, *Melophorus bagoti*. Behav. Ecol. Sociobiol. 61, 1543–1553.

Nicholson, D.J., Judd, S.P.D., Cartwright, B.A., Collett, T.S., 1999. Learning walks and landmark guidance in wood ants (*Formica rufa*). J. Exp. Biol. 202, 1831–1838.

Peng, F., Chittka, L., 2017. A simple computational model of the bee mushroom body can explain seemingly complex forms of olfactory learning and memory. Curr. Biol. 27, 224–230.

Perry, C.J., Barron, A.B., Cheng, K., 2013. Invertebrate Learning and Cognition: Relating Phenomena to Neural Substrate. Wiley Interdisciplinary Reviews: Cognitive Sciencehttps://doi.org/10.1002/wcs.1248.

Pfeffer, S.E., Bolek, S., Wolf, H., Wittlinger, M., 2015. Nest and food search behaviour in desert ants, *Cataglyphis*: a critical comparison. Anim. Cogn. 18, 885–894. https://doi.org/10.1007/s10071-015-0858-0.

Philippides, A., Baddeley, B., Cheng, K., Graham, P., 2011. How might ants use panoramic views for route navigation? J. Exp. Biol. 214, 445–451. https://doi.org/10.1242/jeb.046755.

Pritchard, D.J., Healy, S.D., 2018. Taking an insect-inspired approach to bird navigation. Learn. Behav. 46, 7–22. https://doi.org/10.3758/s13420-018-0314-5.

Ronacher, B., 2008. Path integration as the basic navigation mechanism of the desert ant *Cataglyphis fortis*. Myrmecol. News 11 (53), -62.

Schmid-Hempel, P., Schmid-Hempel, R., 1984. Life duration and turnover of foragers in the ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). Insect Soc 31, 345–360.

Schultheiss, P., Cheng, K., Reynolds, A.M., 2015. Searching behavior in social Hymenoptera. Learn. Motiv. 50, 59–67. https://doi.org/10.1016/j.lmot.2014.11.002.

Schultheiss, P., Wystrach, A., Scwarz, S., Tack, A., Delor, J., Nooten, S.S., Bibost, A.L., Freas, C.A., Cheng, K., 2016. Crucial role of ultraviolet light for desert ants in determining direction from the terrestrial panorama. Anim. Behav. 115, 19–28.

Schwarz, S., Schultheiss, P., Cheng, K., 2012. Visual cue learning and odometry in guiding the search behavior of desert ants, Melophorus bagoti, in artificial channels. Behav. Processes 91, 298–303.

Seidl, T., Wehner, R., 2006. Visual and tactile learning of ground structures in desert ants. J. Exp. Biol. 209, 3336–3344. https://doi.org/10.1242/jeb.02364.

Sommer, S., von Beeren, C., Wehner, R., 2007. Multiroute memories in desert ants. PNAS

105, 317–322. https://doi.org/10.1073/pnas.0710157104.

Steck, K., Hansson, B.S., Knaden, M., 2009. Smells like home: desert ants, *Cataglyphis fortis*, use olfactory landmarks to pinpoint the nest. Front. Zool. 6, 5. https://doi.org/10.1186/1742-9994-6-5.

Steck, K., Knaden, M., Hansson, B.S., 2010. Do desert ants smell the scenery in stereo? Anim. Behav. 79, 939–945. https://doi.org/10.1016/j.anbehav.2010.01.011.

Steck, K., Hansson, B.S., Knaden, M., 2011. Desert ants benefit from combining visual and olfactory landmarks. J. Exp. Biol. 214, 1307–1312. https://doi.org/10.1242/jeb.053579.

Stieb, S.M., Kelber, C., Wehner, R., Rössler, W., 2011. Antennal-lobe organization in desert ants of the genus *Cataglyphis*. Brain Behav. Evol. 77, 136–146. https://doi.org/10.1159/000326211.

Stieb, S.M., Hellwig, A., Wehner, R., Rössler, W., 2012. Visual experience affects both behavioral and neuronal aspects in the individual life history of the desert ant *Cataglyphis fortis*. Dev. Neurobiol. 72, 729–742.

Stone, T., Webb, B., Adden, A., Weddig, N.B., Honkanen, A., Templin, R., et al., 2017. An anatomically constrained model for path integration in the bee brain. Curr. Biol. 27, 3069–3085. https://doi.org/10.1016/j.cub.2017.08.052.

Tinbergen, N., 1932. Über die Orientierung des Bienenwolfes (Philanthus triangulum, Fabr.). Z. Vergleichende Physiol. 16, 305–334.

von Frisch, K., 1953. The Dancing Bees. Harcourt, Brace & World, New York.

Webb, B., Wystrach, A., 2016. Neural mechanisms of insect navigation. Curr. Opin. Insect Sci. 15, 27–39.

Wehner, R., 1982. Himmelsnavigation bei Insekten. Neurophysiologie und Verhalten. Neujahrsbl Naturforsch Ges Zürich 184, 1–132.

Wehner, R., 1987. Spatial organization of foraging behaviour in individually searching desert ants, *Cataglyphis* (Sahara Desert) and *Ocymyrmex* (Namib Desert). Experientia Suppl. 54, 15–42.

Wehner, R., 1994. The polarization-vision project: championing organismic biology. Fortschr. Zool. 39, 103–143.

Wehner, R., 2003. Desert ant navigation: how miniature brains solve complex tasks. J. Comp. Physiol. A 189, 579–588. https://doi.org/10.1007/s00359-003-0431-1.

Wehner, R., 2008. The architecture of the desert ant's navigational toolkit (Hymenoptera, Formicidae). Myrmecol. News 12, 85–96. https://doi.org/10.1098/rspb.2013.1677.

Wehner, R., Müller, M., 2006. The significance of direct sunlight and polarized skylight in the ant's celestial system of navigation. PNAS 103, 12575–12579.

Wehner, R., Räber, F., 1979. Visual spatial memory in desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). Experientia 35, 1569–1571.

Wehner, R., Srinivasan, M.V., 1981. Searching Behaviour of Desert Ants, Genus *Cataglyphis* (Formicidae, Hymenoptera). J. Comp. Physiol. 142, 315–338.

Wehner, R., Srinivasan, M.V., 2003. Path integration in insects. In: Jeffery, K.J. (Ed.), The Neurobiology of Spatial Behaviour. Oxford University Press, Oxford, pp. 9–30.

Wehner, R., Wehner, S., 1986. Path integration in desert ants. Approaching a long-standing puzzle in insect navigation. Monit. Zool. Ital. 20, 309–331.

Wehner, R., Harkness, R.D., Schmid-Hempel, P., 1983. Foraging strategies in individually searching ants, *Cataglyphis bicolor* (Hymenoptera, Formicidae). In: Lindauer, M. (Ed.), Information Processing in Animals. Fischer, Stuttgart, pp. 1–79.

Wehner, R., Michel, B., Antonsen, P., 1996. Visual navigation in insects: coupling of egocentric and geocentric information. J. Exp. Biol. 199, 129–140.

Wehner, R., Gallizzi, K., Frei, C., Vesely, M., 2002. Calibration processes in desert ant

navigation: vector courses and systematic search. J. Comp. Physiol. A 188, 683–693.

Wehner, R., Meier, C., Zollikofer, C., 2004. The ontogeny of foraging behaviour in desert ants, *Cataglyphis bicolor*. Ecol. Entomol. 29, 240–250.

Wehner, R., Boyer, M., Loertscher, F., Sommer, S., Menzi, U., 2006. Ant navigation: one-way routes rather than maps. Curr. Biol. 16, 75–79. https://doi.org/10.1016/j.cub.2005.11.035.

Wehner, R., Fukushi, T., Isler, K., 2007. On being small: brain allometry in ants. Brain Behav. Evol. 69 (3), 220–228.

Wehner, R., Cheng, K., Cruse, H., 2014. In: Werner, J.S., Chalupa, L.M. (Eds.), Visual Navigation Strategies in Insects: Lessons from Desert Ants. MIT Press, Cambridge, MA, pp. 1153–1163.

Wehner, R., Hoinville, T., Cruse, H., Cheng, K., 2016. Steering intermediate courses: desert ants combine information from various navigational routines. J. Comp. Physiol. A 202, 459–472.

Wittlinger, M., Wehner, R., Wolf, H., 2006. The ant odometer: stepping on stilts and stumps. Science 312, 1965–1967. https://doi.org/10.1126/science.1126912.

Wittlinger, M., Wehner, R., Wolf, H., 2007. The desert ant odometer: a stride integrator that accounts for stride length and walking speed. J. Exp. Biol. 210, 198–207.

Wolf, H., Wehner, R., 2000. Pinpointing food sources: olfactory and anemotactic orientation in desert ants, *Cataglyphis fortis*. J. Exp. Biol. 868, 857–868.

Wolf, H., Wittlinger, M., Bolek, S., 2012. Re-visiting of plentiful food sources and food search strategies in desert ants. Front. Neurosci. 6, 102.

Woodgate, J.L., Buehlmann, C., Collett, T.S., 2016. When navigating wood ants use the centre of mass of a shape to extract directional information from a panoramic skyline. J. Exp. Biol. 219, 1689–1696. https://doi.org/10.1242/jeb.136697.

Wright, A.A., Delius, J.D., 1994. Scratch and match: pigeons learn matching and oddity with gravel stimuli. J. Exp. Psychol. Anim. Behav. Process. 20, 108–112.

Wystrach, A., Beugnon, G., Cheng, K., 2011a. Landmarks or panoramas: What do navigating ants attend to for guidance? Front. Zool. 8, 21. https://doi.org/10.1186/1742-9994-8-21.

Wystrach, A., Schwarz, S., Schultheiss, P., Beugnon, G., Cheng, K., 2011b. Views, landmarks, and routes: How do desert ants negotiate an obstacle course? J. Comp. Physiol. A 197, 167–179. https://doi.org/10.1007/s00359-010-0597-2.

Wystrach, A., Beugnon, G., Cheng, K., 2012. Ants might use different view-matching strategies on and off the route. J. Exp. Biol. 215, 44–55. https://doi.org/10.1242/jeb.059584.

Wystrach, A., Philippides, A., Aurejac, A., Cheng, K., Graham, P., 2014. Visual scanning behaviours and their role in the navigation of the Australian desert ant Melophorus bagoti. J. Comp. Physiol. A 200, 615. https://doi.org/10.1007/s00359-014-0900-8.

Zeil, J., 2012. Visual homing: an insect perspective. Curr. Opin. Neurobiol. 22, 285–293. https://doi.org/10.1016/j.conb.2011.12.008.

Zeil, J., Hofmann, M.I., Chahl, J.S., 2003. Catchment areas of panoramic snapshots in outdoor scenes. J. Opt. Soc. Am. A 20, 450. https://doi.org/10.1364/josaa.20.000450.

Zeil, J., Narendra, A., Sturzl, W., 2014. Looking and homing: how displaced ants decide where to go. Philos. Trans. R. Soc. B: Biol. Sci. 369https://doi.org/10.1098/rstb.2013.0034. 20130034–20130034.

Ziegler, P.E., Wehner, R., 1997. Time-courses of memory decay in vector-based and landmark-based systems of navigation in desert ants, *Cataglyphis fortis*. J. Comp. Physiol. A 181, 13–20. https://doi.org/10.1007/s003590050088.