The learning walks of ants (Hymenoptera: Formicidae)

Jochen ZEIL & Pauline N. FLEISCHMANN

Abstract

When transitioning from in-nest duties to their foraging life outside the nest, ants perform a series of highly choreographed learning walks around the nest entrance, before leaving to forage for the first time. These learning walks have been described in detail only for a few species of ants, but a pattern of similarities and differences is emerging that we review here with an emphasis on understanding the functional significance of this learning process for efficient homing in ants. We compare the organization of learning walks in ants with that of the learning flights in bees and wasps and provide a list of key research questions that would need to be tackled if we are to understand the role of learning walks in the acquisition of nest-location information, the evolution of this highly conserved learning process, and how it is controlled.

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Introduction

There comes a moment in the life of every social insect when it first ventures outside its nest or hive. In many ants and bees this happens after several weeks spent inside the dark nest, conducting duties such as tending to the queen and her eggs or feeding and cleaning larvae (e.g., SEELEY 2009, ROBINSON & al. 2009). The first confrontation with the outside world must have dramatic consequences for the activity of sensory systems, such as the eyes, with photoreceptors for the first time being exposed to daylight intensities, to the spectral properties of sunlight, skylight and the landmark panorama and to the polarized light pattern of the sky. Chemosensory systems will equally be confronted for the first time with wind, turbulence and the chemical composition of fresh air and of the surface outside the nest. The only potential senses that are not confronted with new activity patterns during this transition between inside and outside the nest are those systems involved in sensing gravity and the magnetic field. It is currently not known whether visual and chemosensory systems are being slowly adapted to this new sensory world by naïve insects spending time sitting at the nest or hive entrance, or in the case of ants during short excursions

away from the nest depositing excavation material (see below).

We are concerned here with the processes involved in navigation that are first engaged or are confronted with a new set of inputs when an ant leaves the nest for the first time but that will also need to be updated when the environment has changed. One of the most fundamental is path integration, which in ants involves a stride integrator as a measure of distance walked and an external compass reference (reviewed by HEINZE & al. 2018). We do not know at present whether path integration is already active (or even useful) inside the nest, with magneto- and graviception possibly serving as horizontal and vertical directional references. But even without path integration, tactile, airborne and surface chemical landmarks may have already guided ants during their movements inside the nest. What is completely new for an ant exiting the nest, however, is the experience of the non-uniform distribution of radiant and reflected light and the changing activity patterns of her light sensitive systems, the compound eyes and ocelli, when she moves. For both view-based navigation and path integration this means that there are new sensory activity
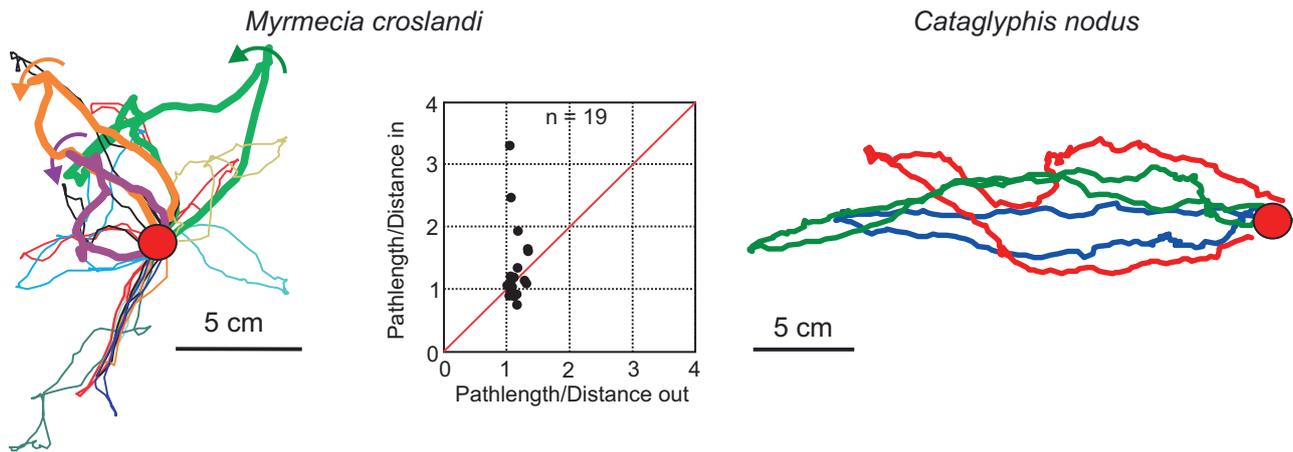
Fig. 1: Ant movements close to the nest. Examples of the paths taken by ants which exit the nest to deposit excavate. Left panel shows such **"digging paths"** by *Myrmecia croslandi* ants (from JAYATILAKA & al. 2018, adapted with permission). Three paths are highlighted to emphasize that returns to the nest are not straight. Centre panel: Path length in divided by the maximum distance reached vs path length out divided by the maximum distance for 19 *M. croslandi* digging paths demonstrating that out paths are fairly straight (path length / distance close to 1) while return paths can be much less direct (path length/distance > 1). Right panel: Three example digging paths of *Cataglyphis nodus* ants (see also FLEISCHMANN & al. 2017).

patterns associated with translation, such as translational optic flow in addition to stride integration (WITTLINGER & al. 2007, PFEFFER & WITTLINGER 2016), and with rotation, which generates rotational optic flow, but also changing activity patterns of photoreceptors with different spectral sensitivities, and activation of polarization sensitive sensor arrays in the dorsal rim of the compound eyes and in the ocelli. All these rotation induced activity patterns are correlated with activity patterns in magneto-sensitive receptors and associated neuropils that are likely to exist in ant brains (WAJNBERG & al. 2010, FLEISCHMANN & al. 2018a).

With this in mind, it is interesting to note that the transition to life outside the nest is accompanied by distinct changes in brain organization in ants (reviewed by RÖSSLER 2019) and that ants before becoming foragers engage in a series of distinctly choreographed learning walks in the vicinity of the nest (WEHNER & al. 2004, MUSER & al. 2005, MÜLLER & WEHNER 2010, STIEB & al. 2012, FLEISCHMANN & al. 2016, 2017, 2018b, JAYATILAKA & al. 2018, COLLETT & ZEIL 2018), which are the topic of this review.

The learning walks of ants

Excursions close to the nest: In the ants the authors work with, namely *Cataglyphis* and *Myrmecia*, we observe three kinds of distinct movement patterns around the nest entrance. The first is the straight paths of ants heading out to forage, which we assume to be performed by experienced ants.

The second movement pattern we see is the paths of "digging" ants which exit the nest in seemingly random directions in a straight line for a few centimetres and deposit nest excavate. Digging ants return to the nest immediately, sometimes in a straight line, but often not (Digging paths;

Fig. 1; FLEISCHMANN & al. 2017, JAYATILAKA & al. 2018). We do not know at present whether digging ants form a distinct developmental stage, but if digging forays are made by "naïve" ants they would provide these ants with their first experience of the outside world and require of them to keep track of the nest entrance location.

The third pattern we observe is ants walking relatively slowly in loops around the nest while performing distinct scanning movements, which we will describe in detail below. These loops all end up at the nest and we know now that they are performed by naïve ants (FLEISCHMANN & al. 2016, 2017, JAYATILAKA & al. 2018). Naïve ants have been observed to conduct up to 7 such learning walks over several days before going on their first foraging trip (JAYATILAKA & al. 2018; Fig. 2, inset bottom row centre). Interestingly, successive walks of individually identified ants tend to explore different compass directions around the nest (Fig. 2), although we do not know yet whether this is based on a random choice of directions or whether it indicates that ants remember where they had been before (FLEISCHMANN & al. 2016, 2017, JAYATILAKA & al. 2018). Successive learning walks also extend further and further out from the nest, reaching distances of up to 4 m (Fig. 2, bottom row right). The data at hand show large inter-individual variation in these aspects of learning behaviour and it will be important in future to investigate what determines the number of walks an ant performs and their directions before she decides to leave on foraging excursions.

Movements and gaze directions of ants during learning walks: The first descriptions of learning walks of wood ants, *Formica rufa*, at a feeder (NICHOLSON & al. 1999) and of the Namibian desert ant, *Ocymyrmex robustior*, at the nest (MÜLLER & WEHNER 2010), both stressed the fact that ants repeatedly turned back to face the goal or
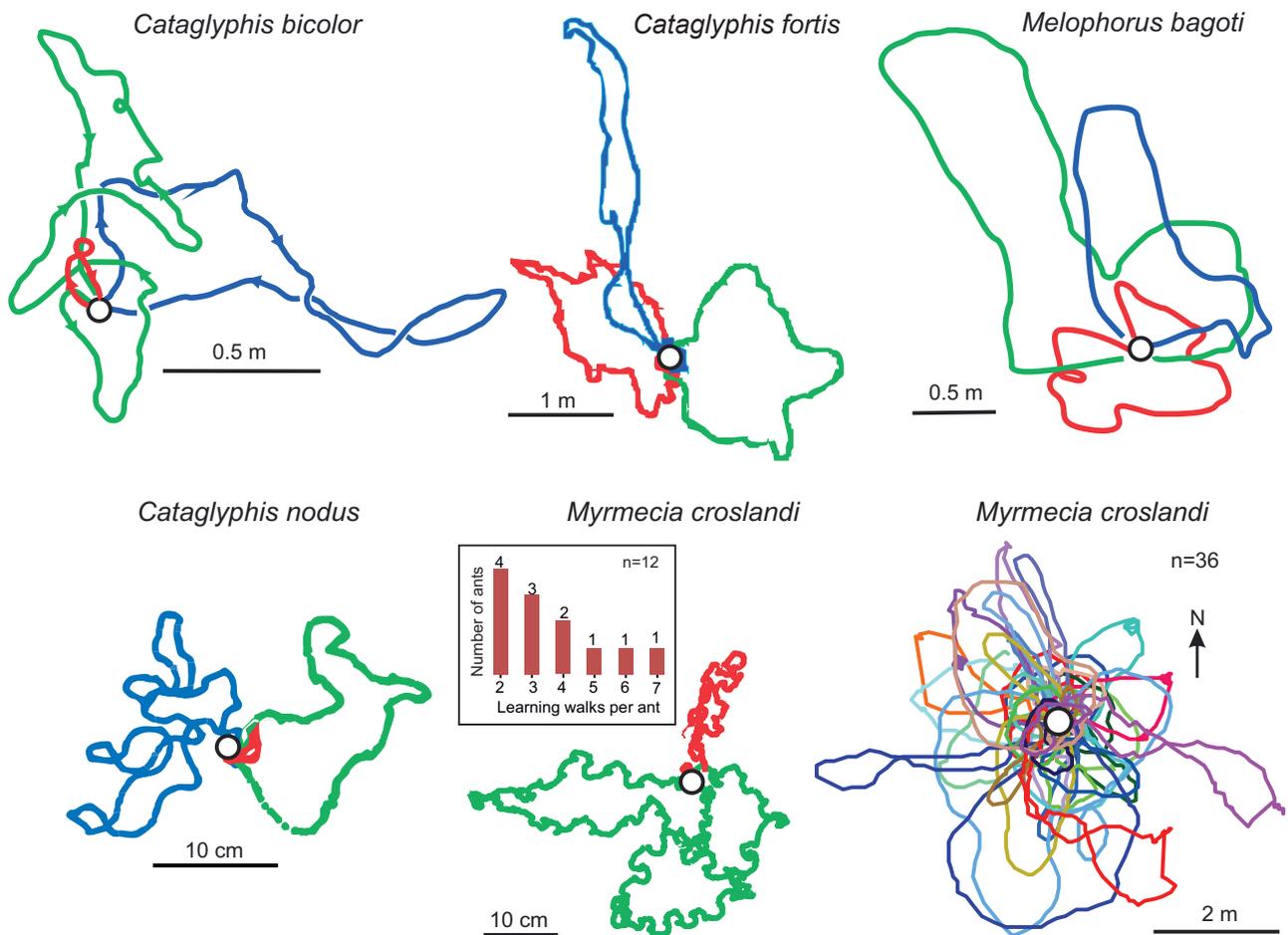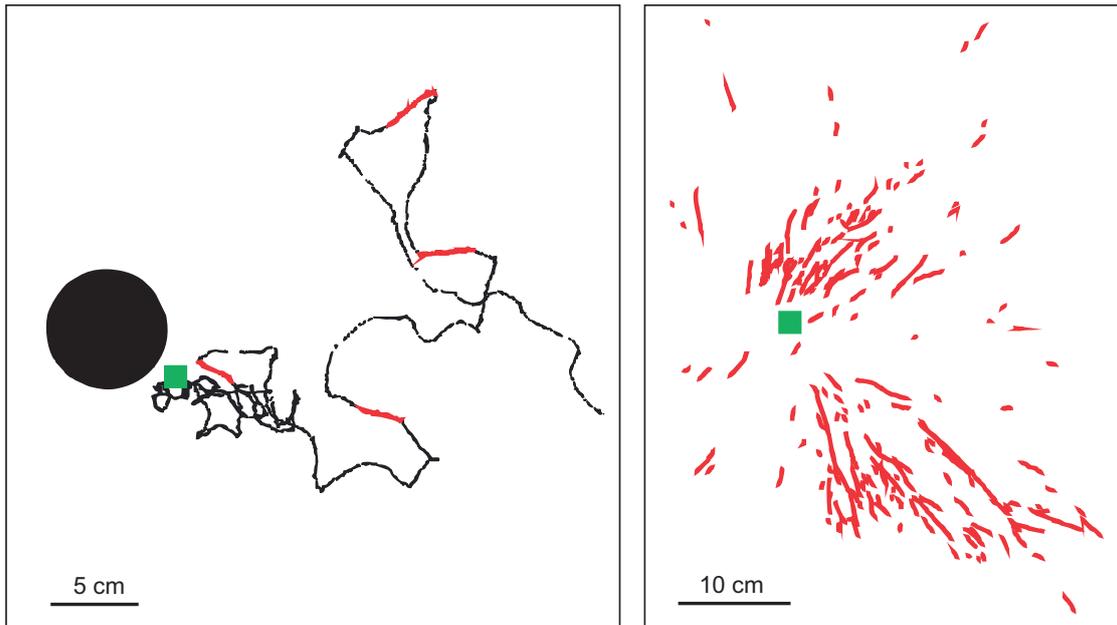
Fig. 2: Examples of the first successive learning walks of different ant species. With the exception of bottom right panel, paths are from individually identified ants with first learning walk: red; second learning walk: green; third learning walk: blue. Bottom right panel shows the learning walk loops of 36 different ants as recorded with differential GPS at the same nest over two years. Note that learning walks can reach distances of several metres from the nest. (*Cataglyphis bicolor*, modified from WEHNER & al. 2004; *C. fortis*, from FLEISCHMANN & al. 2016, adapted with permission; *Melophorus bagoti*, modified from MUSER & al. 2005 with permission from CSIRO Publishing; *C. nodus*: from FLEISCHMANN & al. 2017, adapted with permission; *Myrmecia croslandi* (from JAYATILAKA & al. 2018, adapted with permission).)

a prominent landmark from different compass directions, in the case of wood ants even walking a small distance towards it (Fig. 3A & B). These learning walks were made by ants in response to discovering a new food location (wood ants) and to the introduction of a new landmark close to the nest (desert ants). Such walks differ from those made by naïve ants around the nest by eventually leading away from the goal, not immediately returning to it (Fig. 3A & B). Such "re-learning walks" by presumably experienced foragers have recently also been described for the bull ant *Myrmecia croslandi* (see JAYATILAKA & al. 2018). Despite this difference, re-learning walks share many of the distinct scanning movements naïve ants perform in the course of their learning walks at the nest. The details of these movements, common properties and interesting differences between species have now been documented for desert ants and bull ants.

The choreography of learning walks at the nest of naive desert ants (*Cataglyphis nodus*, Fig. 4, *Melophorus*
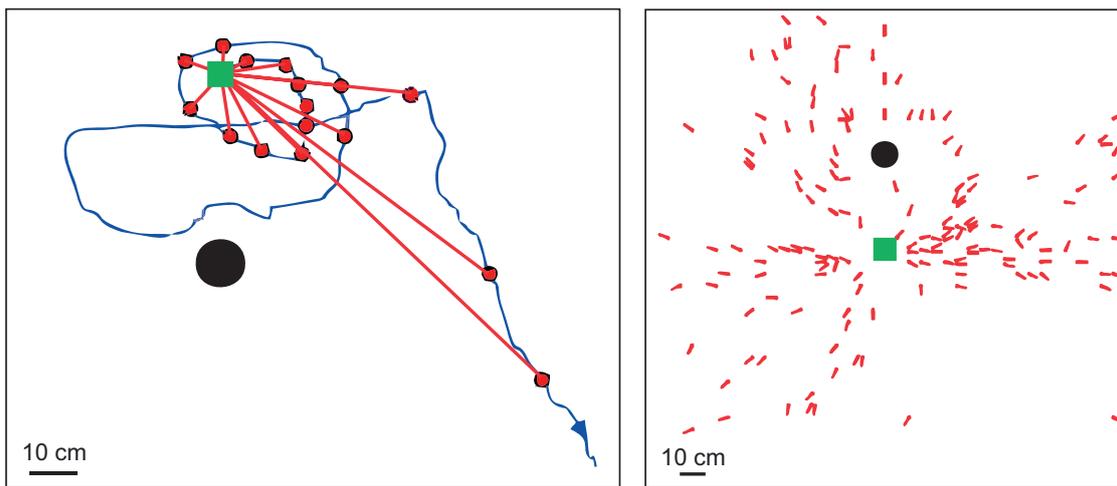
bagoti, Fig. 5) and naïve Australian bull ants (*Myrmecia croslandi*, Fig. 6) have the following common features: learning ants walk along an arc around the nest entrance and eventually return to it. As they walk along they perform regular rotational scanning movements oscillating between home vector (marked in red in Figs. 4 - 6) and anti-home vector directions (marked in blue in Figs. 4 - 6). This is emphasized by the time series plots of body axis direction or gaze direction relative to the nest direction at 0° in Figs. 4 - 6, which also demonstrate that the reversals of turning direction tend to cluster around the nest direction (at 0°) and the direction away from the nest at ± 180°. The distribution of gaze directions relative to the nest direction at over 500 of such reversals during 13 learning walks of *M. croslandi* shows peaks close to 0°, 90° and 180° (inset bottom right panel Fig. 6; see also JAYATILAKA & al. 2018). More often in desert ants than in bull ants, these scanning movements are interspersed with full 360° rotations (marked by black circles in the path and body axis
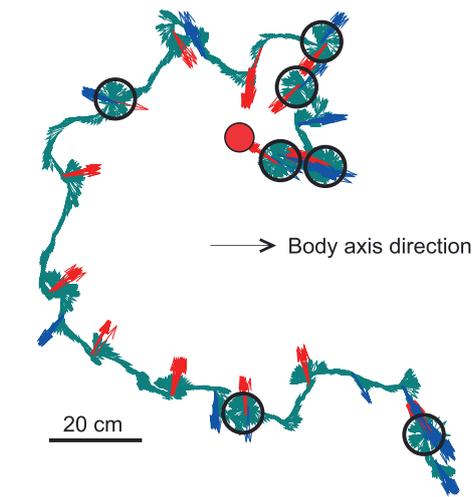
Formica rufa: Learning walks at feeder

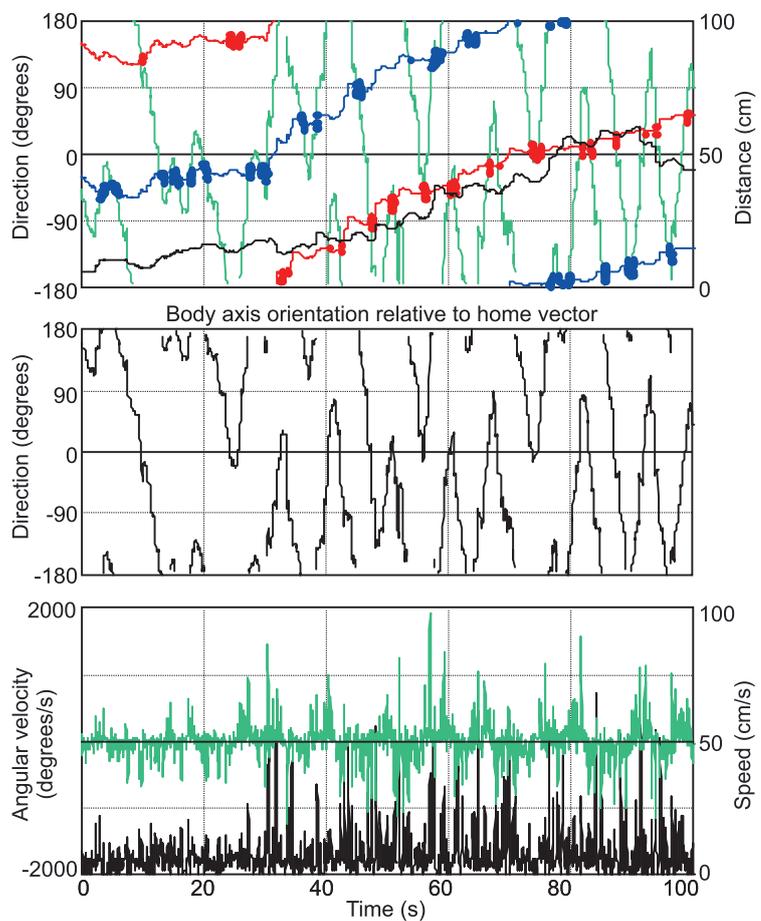**A**
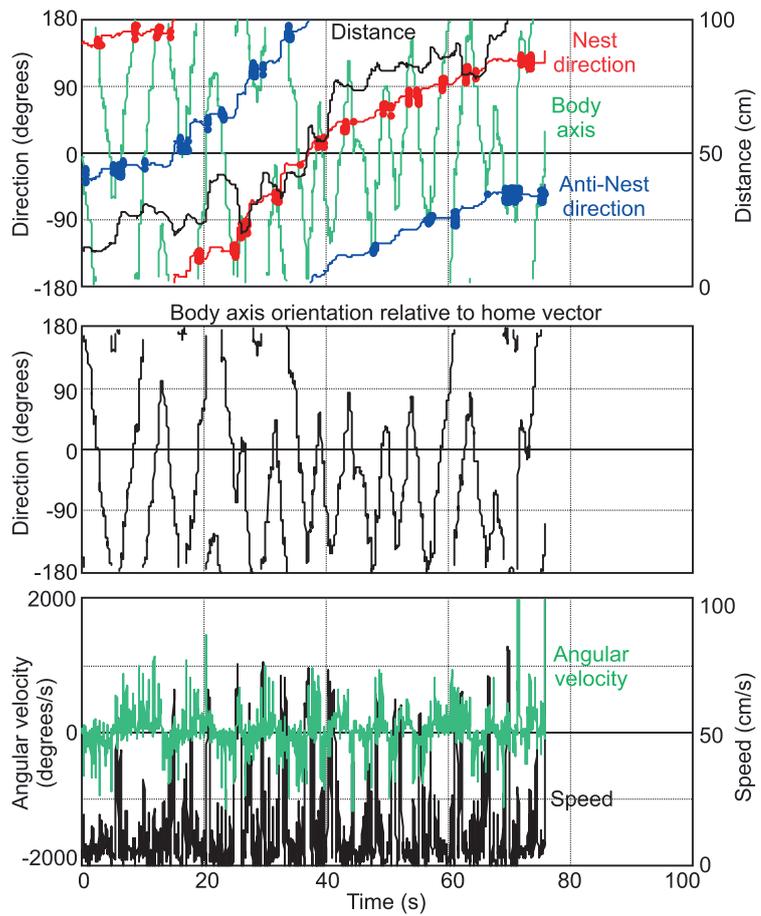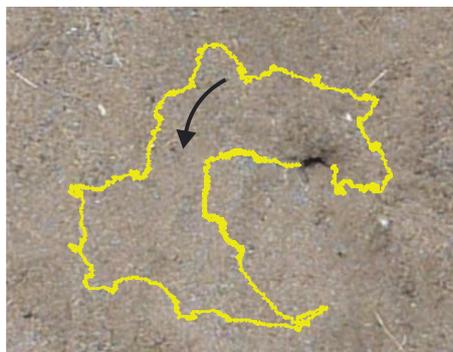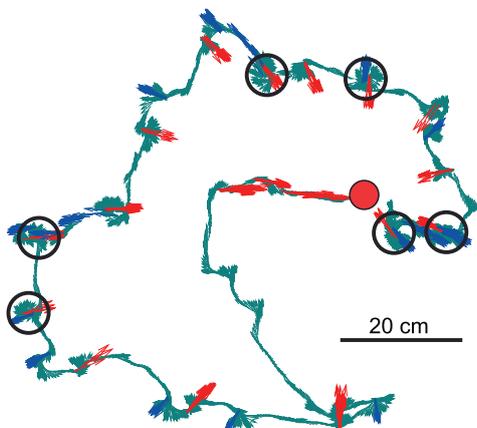
Ocymyrmex robustior: Learning walks at nest

B

Fig. 3: First descriptions of the learning walks of *Formica rufa* at a feeder (A) and *Ocymyrmex robustior* at the nest (B) with landmark-directed (A) and nest-directed turn-backs (B) marked in red. Black circles mark the positions and sizes of cylindrical landmarks and green squares the feeder (A) or nest position (B). (Figures adapted with permission from Nicholson & al. 1999 (A) and Müller & Wehner 2010 (B).)

Fig. 4: The choreography of learning walks in *Cataglyphis nodus*. Two examples of the learning walks of *C. nodus* ants recorded at 50 frames per second. Viewing directions (red, green and blue) in left and right panels are represented by the orientation of the longitudinal body axis, because head orientation could not be resolved. Longitudinal body axis orientation (indicated by arrows) is shown in the top left panels and paths over video images on the bottom left. Instances in which the longitudinal body axis of ants points into the nest direction to within ± 10° are marked red in top left and top right panels and instances in which it points directly away from the nest are marked blue. Full 360° rotations, including both "voltes" and "pirouettes" are indicated by black circles in the top left panels; red circles mark the nest entrance. Top right panels show the time course of longitudinal body axis orientation (green), distance from the nest (black), home vector direction (red) and anti-home vector direction (blue) relative to the horizontal x-axis of video frames with north at approximately 90°. Centre right panels show the time course of longitudinal body axis orientation relative to the nest direction at zero degrees. Bottom right panels show the time course of angular velocity (green) and of walking speed (black).

Body axis direction

20 cm

Cataglyphis nodus

20 cm

Distance
Nest direction
Body axis
Anti-Nest direction

Body axis orientation relative to home vector

Angular velocity
Speed

Body axis orientation relative to home vector

Angular velocity
Speed

plots in Fig. 4 and seen as loops in the path plots of Fig. 5). The rotational scanning movements during the learning walks of desert ants have been called "pirouettes" when the ants stop still and perform turns around their yaw axis (see Fig. 7A; Müller & Wehner 2010, Fleischmann & al. 2017, 2018a, Grob & al. 2017) and "voltes" when the ants walk in loops or circles (Fleischmann & al. 2017, 2018a). Time series plots of angular velocities (green) and walking speeds (black) indicate that desert ants (Figs. 4 & 5) generally walk and turn faster than bull ants during their learning walks (Fig. 6).

Finally, both desert and bull ants increase their rate of turning immediately after they reverse scanning direction. Such instances are in the case of *Myrmecia croslandi* marked by red dots in Fig. 7B for an example time series of gaze direction relative to the nest direction at zero degrees and shown in Fig. 7C for three species of desert ants as the summary statistics of the turning rates before (in) and after reversal of turning direction (out). At this stage, it remains unclear what this common feature signifies, but we offer the hypothesis that finding the alignment with the home vector may require from the ants to perform relatively slow scanning movements, while once this alignment is found, the ants can turn rapidly away from this alignment to continue walking roughly perpendicular to the home vector direction.

In listing these features of learning walk choreography and their potential significance for the acquisition of visual memories that can guide homing (see detailed discussion below) we need to add a word of caution. It is important to point out that ants of at least *Myrmecia croslandi* make significant head movements during their learning walks, which means that their true gaze direction (shown in green in Fig. 7D) can deviate from the orientation of their longitudinal body axis (shown in blue in Fig. 7D) by up to 40° as documented by the frequency distributions of head orientation relative to body axis orientation for 5 learning walk sequences in Fig. 7E. In desert ants, being much smaller than bull ants, it is often difficult to accurately measure head orientation, except when the recording area is kept small and only short-ranging learning walks are recorded (e.g., Fleischmann & al. 2017). In many cases, however, the longitudinal body axis orientation has to be taken as a proxy for gaze direction (as for *Cataglyphis nodus* and *Melophorus bagoti* in Figs. 4 & 5 here and in Müller & Wehner 2010 for *Ocymyrmex robustior*).
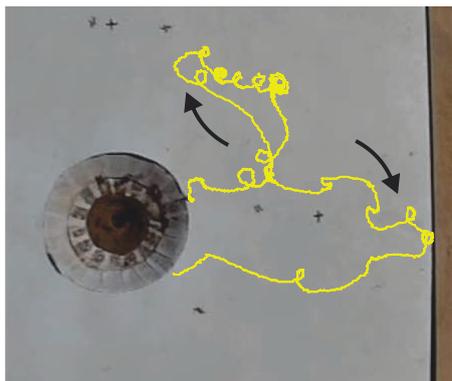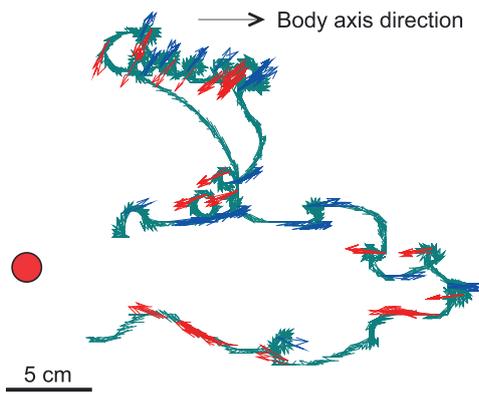
There are a number of reasons why the extent of head movements during the learning walks of different ant species need more detailed attention in future work: for relating learning walk choreographies to homing performance it will be important to analyse in detail where exactly ants

look during learning and during their homing walks and how this correlates with the navigational decisions they make when pinpointing the nest. To accurately determine in which direction they look during prolonged "fixations" and when they decide to reverse turning direction during learning walks will help to understand the control and function of learning walks. Given the evidence that naïve ants rely on a magnetic compass reference during their learning walks (Fleischmann & al. 2018a; see below), investigating head and body orientation relative to the ambient magnetic field may also contribute to answering the question whether the transduction mechanism of magneto-sensitivity is located in the head or in the thorax. We note that some of the manoeuvres of learning ants, such as saccadic head movements between "stops" or "fixations" (Fleischmann & al. 2017) are quite fast and moments of fixations are short, so that their detailed analysis will require camera equipment with high frame rates (higher than the 25 frames per second offered by standard video cameras).
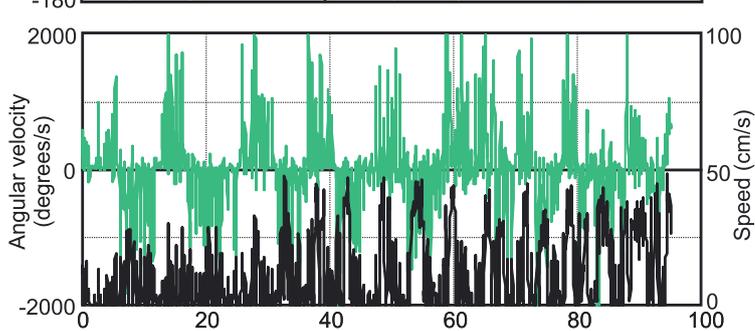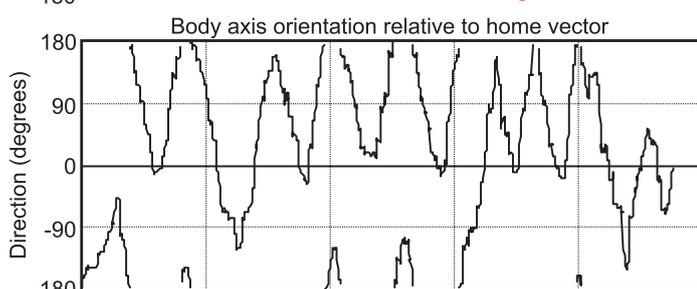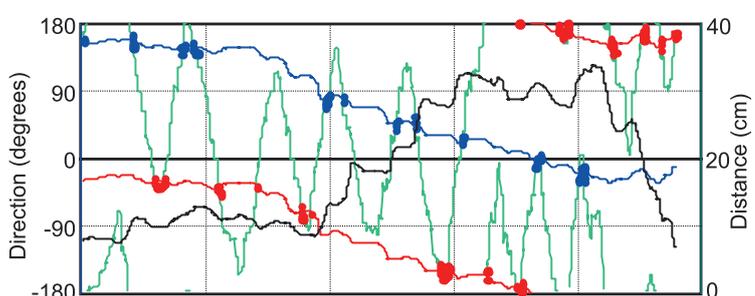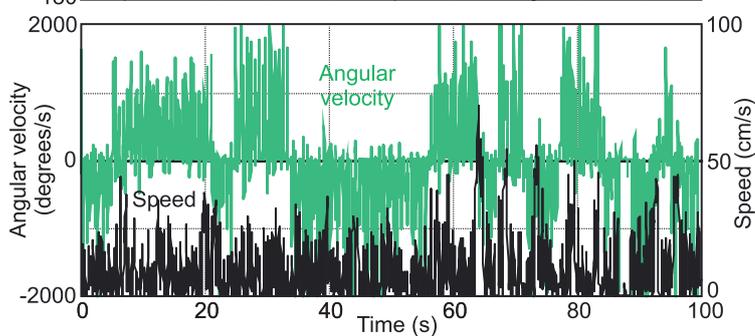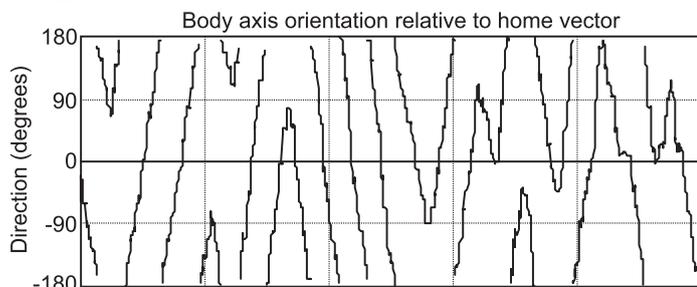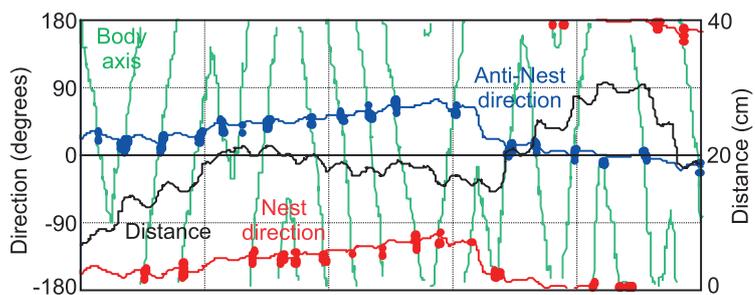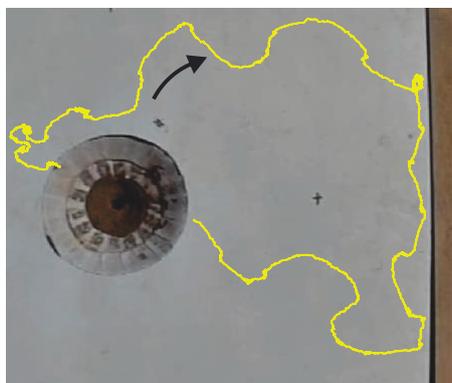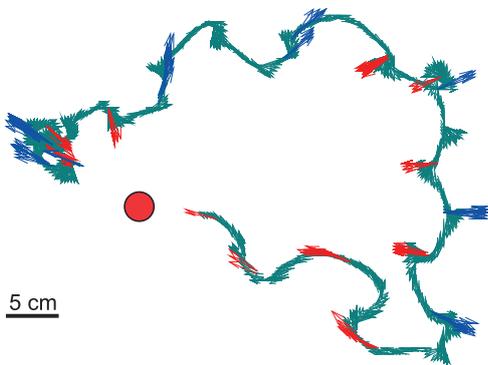
The regular scanning movements between the nest direction and away from the nest and in particular the prolonged fixations of the nest direction in *Ocymyrmex robustior* and *Cataglyphis nodus* must be guided by path integration, because the nest entrance is in most cases not visible to the learning ants (Müller & Wehner 2010, Fleischmann & al. 2017). Surprisingly, the path integration process that guides the prolonged, nest-directed fixations in *C. nodus* relies on a magnetic compass reference, as has been demonstrated by Fleischmann & al. (2018a), providing to our knowledge the first example of path integration involving a magnetic compass reference (Fig. 8). The authors monitored the first "pirouette" or "turn-back-and-look" movements (see Fig. 7A) of learning *C. nodus* ants under normal conditions and when the local magnetic field was rotated about 90°, -90°, or 180° (Fig. 8A,B) The nest-directed fixations of ants were consistently deflected towards a virtual nest direction defined by the direction of the magnetic field by these treatments (Fig. 8B). Given that *Cataglyphis* foragers rely on celestial compass information, involving the pattern of polarized skylight, the sun and spectral gradients (e.g., Wehner & Labhart 2006, Wehner & Müller 2006) there must, therefore, be a transition from the use of a magnetic compass reference in naïve ants to a celestial compass reference at some stage in the foraging life of *Cataglyphis* ants. It will be interesting to see when this transition occurs and whether it is also occurring in other ant species.

The function of learning walks: The regular scanning and translational movements of learning ants have the consequence that they experience views in the nest

Fig. 5: The choreography of learning walks in *Melophorus bagoti*. Two examples of the learning walks of the Australian desert ant *M. bagoti* recorded at 100 frames per second. Viewing directions (red, green and blue) in left and right panels are represented by the orientation of the longitudinal body axis, because head orientation could not been resolved. Otherwise conventions as in Fig. 4. Note the frequent full rotations (**"voltes"**) performed by the ant shown in the top left panel. Video recordings courtesy of Antoine Wystrach.

Body axis direction

5 cm

Melophorus bagoti

Body axis orientation relative to home vector

Body axis orientation relative to home vector

5 cm

direction and views away from the nest at regularly spaced locations in different compass directions from the nest (Figs. 4 - 6). This has led to the suggestion that ants learn both "attractive" or "positive" views when aligned with the home vector direction and "repellent" or "negative" views when aligned with the anti-home vector direction (Jayatilaka & al. 2018). However, it remains unclear at this stage whether views are only memorized when ants are aligned parallel to the home vector or whether views are learnt continuously and tagged with the nest direction. The observation that *Ocymyrmex robustior* and *Cataglyphis nodus* ants gaze into the nest direction slightly longer compared to other directions may be an indication that learning happens during such fixations (Müller & Wehner 2010, Fleischmann & al. 2017). *Myrmecia croslandi* ants, however, do not show such a distinct difference in fixation durations (Jayatilaka & al. 2018), possibly because their overall movement and scanning speed is slower (see Fig. 6).
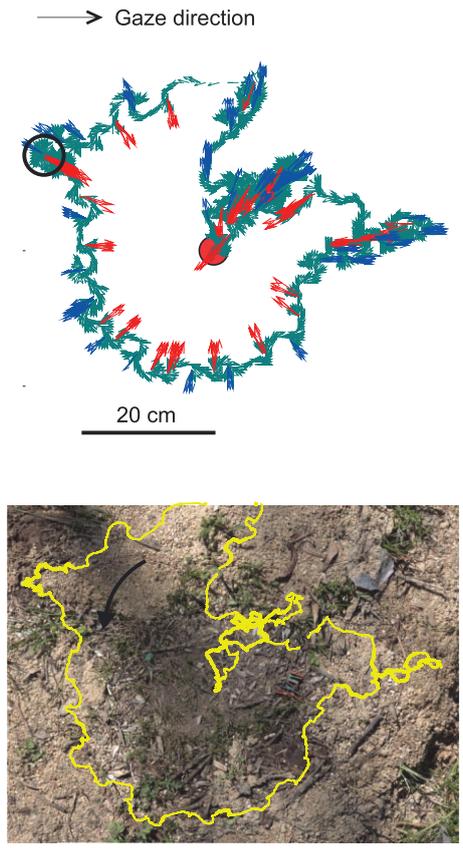
The learning walks of ants clearly serve to acquire and to update cues to the location of the nest or a newly discovered food source relative to the landmark panorama (Nicholson & al. 1999, Müller & Wehner 2010, Jayatilaka & al. 2018, Fleischmann & al. 2016, 2018b). Evidence for this is indirect, because experiments are lacking in which learning walks are interrupted at different times and in which the navigational knowledge of ants is tested by systematically displacing them to different distances from where they performed their learning walks. However, it is indicative that the landmark-guided homing performance of *Cataglyphis fortis* ants does depend on their level of experience outside the nest: Fleischmann & al. (2016) caught ants at different stages in their foraging life and released them in a test field close to an identical array of landmarks that the ants had experienced around their nest (Fig. 9A). They found that the degree to which released ants were guided by the landmark array to search for their fictive nest depended on whether or not they had performed learning walks, on the range over which they did so and on whether they had gone on foraging excursions or not. Fig. 9B shows example paths and a heat map of search movements by naïve ants that were caught at their first appearance outside the nest and when released at the test site searched close the release site just outside the landmark array. Individually marked ants that had performed long learning walks extending more than 0.7 m away from the nest and that may have had some foraging experience searched closer to the centre of the landmark array when released at the test site (Fig. 9C). Finally, experienced foragers are clearly guided by the landmark array when searching at its centre for the fictive nest entrance (Fig. 9D). In a follow-up study, Fleischmann & al. (2018b)

trained three groups of naïve ants along a 5 m corridor from the nest to a feeding site (Fig. 9E, inset at top). The groups differed in the area they had available around the nest in which they could move during learning and foraging. One group was restricted to the corridor (marked red in Fig. 9E), a second group had an additional 1 m² area to move around the nest (marked green) and the third group could move within a 4 m² area around the nest (marked blue). Trained ants that had only experienced the accessible terrain around the nest and along the corridor to the "right" of the nest were then displaced 5 m to the "left" of the nest at a location where they have never been before and their search paths back to the nest were monitored. The larger the area of exploration, the more direct was the ants' return to the nest (Fig. 9E). The space available to ants for moving and learning clearly has an impact on the range over which they are able to home from unfamiliar places.
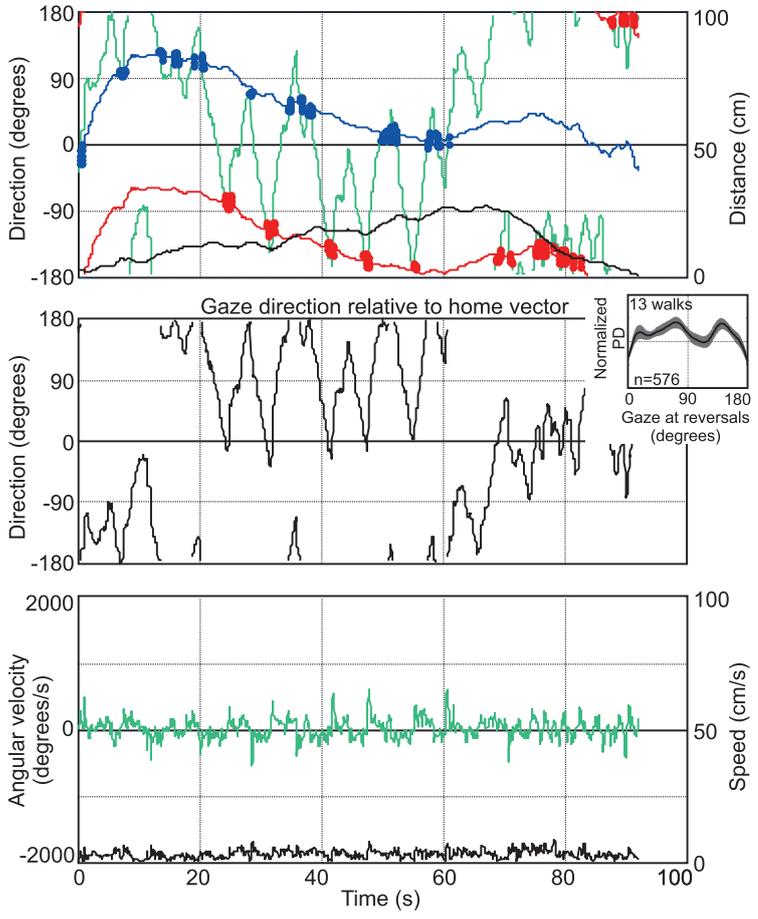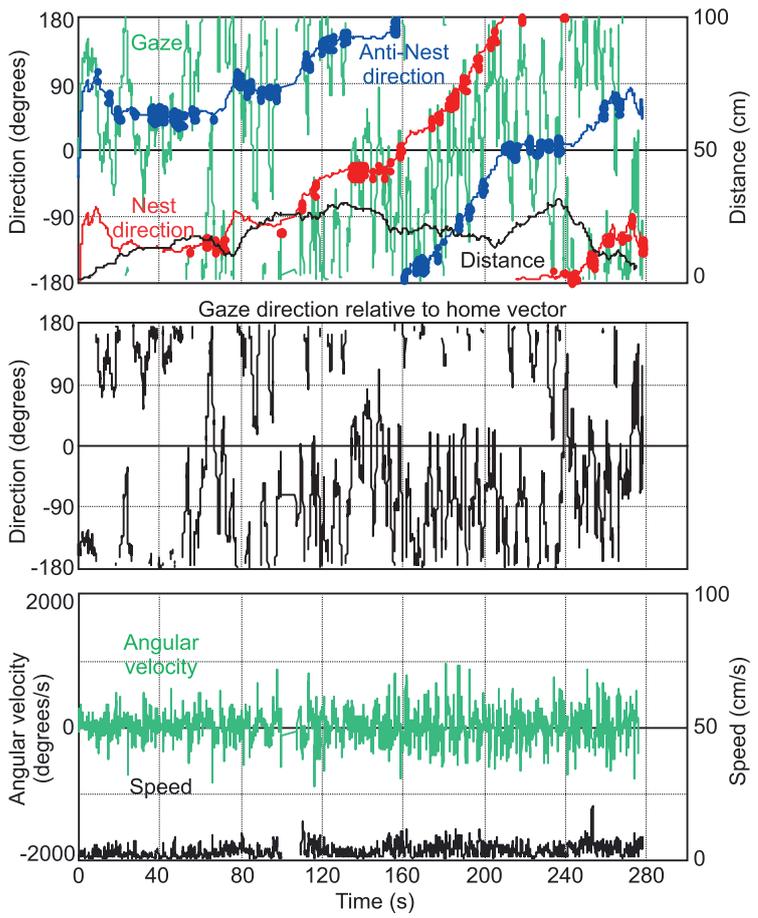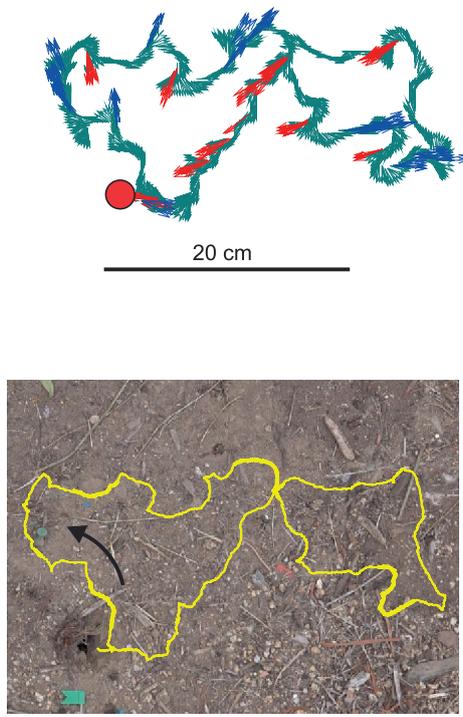
One possible explanation is that the area and the viewing directions covered by learning (and foraging) walks determine the range over which learnt panoramic views can provide guidance (Fig. 9F and Narendra & al. 2013, Dewar & al. 2014, Stürzl & al. 2015). In general, depending on the particular distribution of objects and on the visual structure of habitats, a comparison between a current view and a nest-directed memorized view provides a measure of familiarity when there is a detectable minimum of the rotational image difference function (see inset Fig. 9F; Stürzl & Zeil 2007, Zeil 2012, Dewar & al. 2014, Murray & Zeil 2017, Zahedi & Zeil 2018). The compass direction, at which this minimum lies, corresponds to the orientation of the memorized snapshot (Zeil & al. 2003, Graham & al. 2010, Narendra & al. 2013, Stürzl & al. 2015). The effective range of guidance provided by such panoramic views depends on the catchment area of the translational image difference function that describes the image differences due to the distance between views and reference images (see Murray & Zeil 2017).

This said, it is important to point out that so far there is no direct experimental evidence showing how views experienced during learning are related to the navigational decisions made by homing ants. What is required is a detailed analysis comparing the scanning movements of individually identified ants during learning walks with the scanning movements and path corrections they make when returning home. In this context it will be particularly interesting to investigate the potential importance of ants learning both attractive, nest-directed and repellent views when pointing away from the nest and the possibility that all views encountered during learning walks are memorized together with path integration information on the nest direction (e.g., Jayatilaka & al. 2018).

Fig. 6: The choreography of learning walks in *Myrmecia croslandi*. Two examples of the learning walks of the Australian bull ant *M. croslandi* recorded at 25 frames per second. Here, viewing directions (red, green and blue) in left and right panels are true gaze directions, because the orientation of the head can be resolved in *M. croslandi* ants. Note different time scale of top example. Otherwise conventions as in Fig. 4.

> Gaze direction

Myrmecia croslandi

20 cm

20 cm

Gaze

Anti-Nest direction

Nest direction

Distance

Direction (degrees)

Distance (cm)

Gaze direction relative to home vector

Direction (degrees)

Angular velocity

Speed

Angular velocity (degrees/s)

Speed (cm/s)

Time (s)

Gaze direction relative to home vector

Direction (degrees)

13 walks

Normalized PD

n=576

Gaze at reversals (degrees)

Angular velocity (degrees/s)
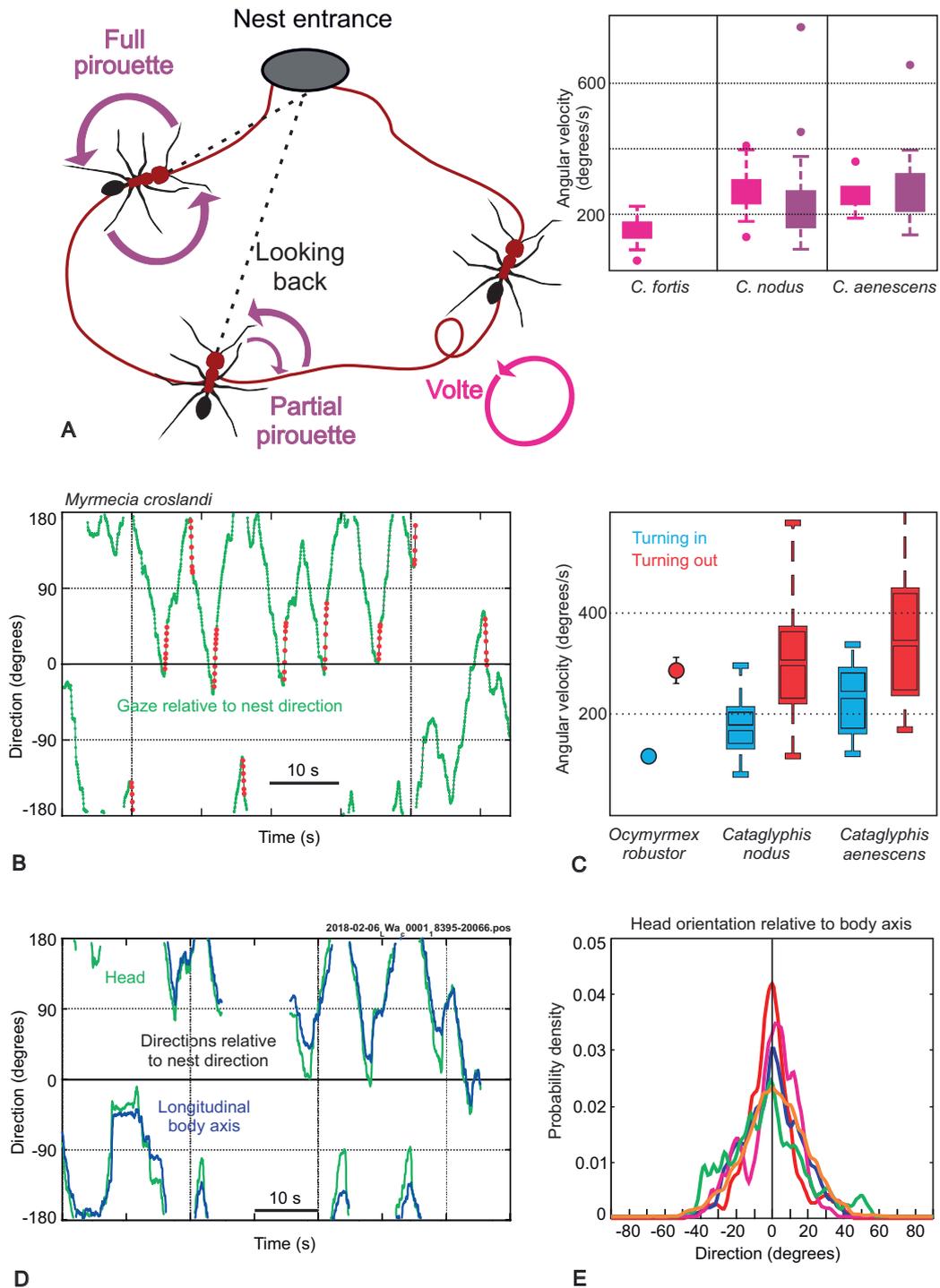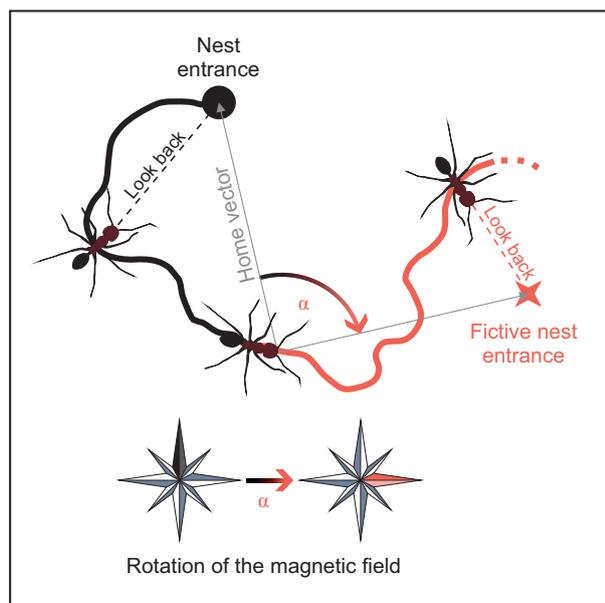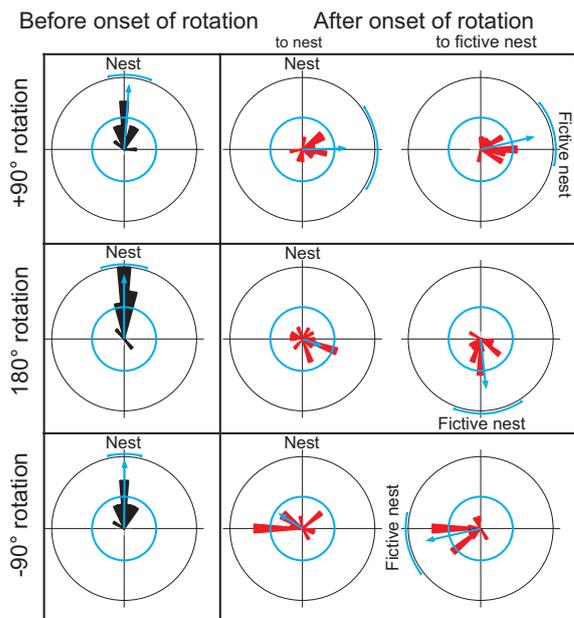
Speed (cm/s)

Time (s)

Fig. 7: The different scanning movements performed by learning ants. (A) Schematic definitions for the **"pirouettes"** (the partial or full rotations of *Cataglyphis nodus* and *C. aenescens*) and for **"voltes"** (the walked circles of *C. fortis, C. nodus and C. aenescens*) (modified from FLEISCHMANN 2018). Box and whisker plots on the right show the angular velocities of **"voltes"** and **"pirouettes"** for three species of *Cataglyphis* (from FLEISCHMANN & al. 2017, adapted with permission). (B) *Myrmecia croslandi* ants turn faster after reversing scanning direction. These instances are marked in red in the time series of gaze direction relative to the nest direction (green) for one learning walk. (C) The same is true for *O. robustior, C. nodus* and *C. aenescens* with mean angular velocities before (**"in"**) being consistently lower compared to mean angular velocities after reversal of scanning direction (**"out"**). Data for *Ocymyrmex robustior* from MÜLLER & WEHNER 2010; data for *C. nodus* and *C. aenescens* from FLEISCHMANN & al. 2017. (D) The time course of true gaze direction (head orientation, green) and the orientation of the longitudinal body axis (blue) during a learning walk of *M. croslandi*. Note the significant head movements made by these ants in particular before the reversal of scanning direction. (E) Frequency distributions of head orientation relative to the longitudinal body axis during 5 learning walks of *M. croslandi*, demonstrating that true gaze direction can deviate from body axis orientation by up to 40°.

Fig. 8: Naïve learning ants rely on a magnetic compass reference to guide nest-directed turn-backs. (A) A schematic representation of how *Cataglyphis nodus* turn-back orientation is changed by changes in the orientation of the ambient magnetic field. (B) Direction of turn-back fixations before and after different experimental rotations of the ambient magnetic field. (From FLEISCHMANN & al. 2018a, with permission, (B) in modified form.)

It has only recently been recognized how important it is for view-based navigation that insects control head orientation around pitch and roll axes. This is true for both the acquisition of views during learning walks and for the comparison of memorized and currently experienced views during guidance. The analysis of head pitch (ARDIN & al. 2015) and head roll (RADERSCHALL & al. 2016) has shown that foraging ants only partially compensate for body pitch and roll movements. It would thus be interesting, but admittedly difficult, to determine how accurately ants during their learning walks keep the roll and pitch orientation of their head constant.

Finally, it remains to be seen whether the full rotations ("voltes") performed in particular by the desert ants *Cataglyphis nodus*, *C. fortis* (Fig. 4 and FLEISCHMANN & al. 2017), and *Melophorus bagoti* (Fig. 5) serve a different purpose than the scanning movements oscillating between gaze directions that are aligned parallel to the home vector ("pirouettes"). The question is whether these full 360° rotations reflect the need to calibrate celestial and magnetic compass systems rather than the need for the acquisition of panoramic views (see FLEISCHMANN & al. 2017, GROB & al. 2017, RÖSSLER 2019). Eminently testable predictions for this would be that these full rotations become rarer with successive learning walks and that they are absent from the re-learning walks performed by experienced foragers in response to visual changes around the nest (e.g., MÜLLER & WEHNER 2010, JAYATILAKA & al. 2018). It is interesting to note in this context that in contrast to the desert ants *C. nodus* and *C. aenescens* (and *M.*

bagoti, Fig. 5) that inhabit landmark-rich environments, *C. fortis* ants, operating in the particularly sparse visual environment of salt pans, only perform "voltes", but no "pirouettes" (Fig. 7A; FLEISCHMANN & al. 2017). Whether this reflects species differences or a direct influence of panoramic view complexity on scanning movements remains to be investigated.

Brain re-organization during and after learning walks: The transition from early life in the dark colony to foraging life in the outside world is associated with major changes in the brains of ants (reviewed by RÖSSLER 2019). Most interestingly, some of these changes are conditional upon an ant performing learning walks under natural conditions: GROB & al. (2017) showed that reorganization of synaptic complexes in both the central complex (subserving compass systems and possibly also path integration (STONE & al. 2017, HEINZE & al. 2018, COLLETT 2019)) and the mushroom bodies (hypothesized to providing associative networks receiving visual input (ARDIN & al. 2016, HOINVILLE & WEHNER 2018, WEBB 2019)) could only be detected in naïve *Cataglyphis* ants that had experienced a changing pattern of natural polarized skylight in the presence of the Earth's magnetic field (reviewed in RÖSSLER 2019). All naïve ants investigated so far perform learning walks over several days (FLEISCHMANN & al. 2016, JAYATILAKA & al. 2018) and this may reflect the dynamics of long-term memory consolidation, which requires several days in both ants and honey bees (MENZEL 2001, FALIBENE & al. 2015, RÖSSLER 2019). The degree to which the short-term, oscillating dynamics of learning

walk choreographies also reflect the timing of learning and memory processes in the brain remains to be investigated. It is intriguing to note that in the visual system of *Cataglyphis* ants 1200 to 2400 ommatidia (pixels) (600 - 1200 per eye, Menzel & Wehner 1970, Zollikofer & al. 1995) feed information into equivalent numbers of cartridges in the lamina and columns in the medulla and lobula which in turn project to 400,000 synaptic complexes in the visual subregions of the mushroom body calyces (Rössler 2019). This constitutes a massive spread of visual information into an associative network providing the potential for a very sparse code for navigation-relevant visual information, considering that neural modelling has shown that at least 600 images can be safely stored in a mushroom body inspired network of 20,000 Kenyon cells (Ardin & al. 2016, Webb & Wystrach 2016). Given that we do not know what the memory requirements are for successful navigation in natural environments, it would be interesting to systematically study these requirements at the scale of ant foraging ranges most promisingly using visually navigating legged robots that can approximate the viewpoint of ants and negotiate rugged terrain (e.g., Dupeyroux & al. 2018).
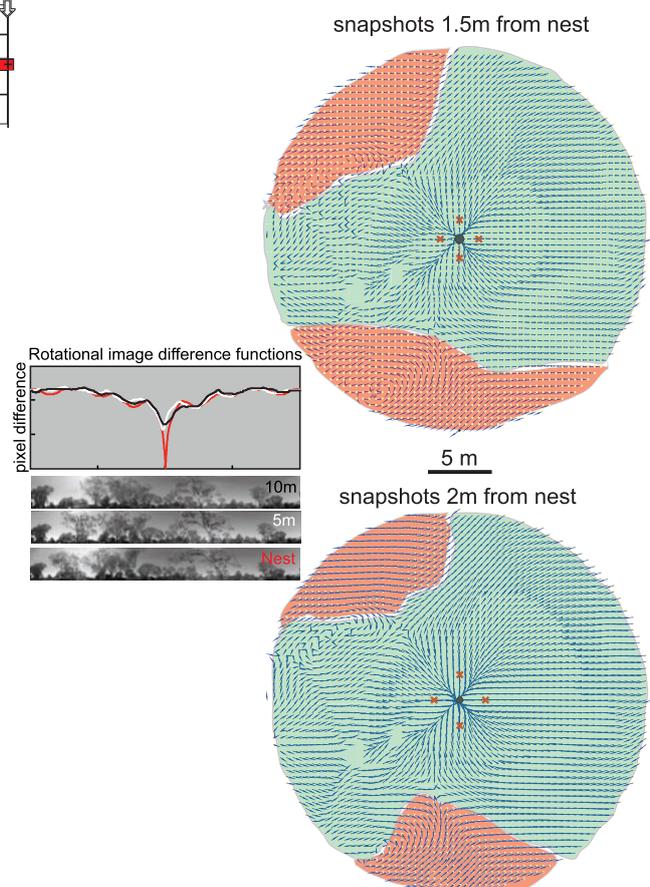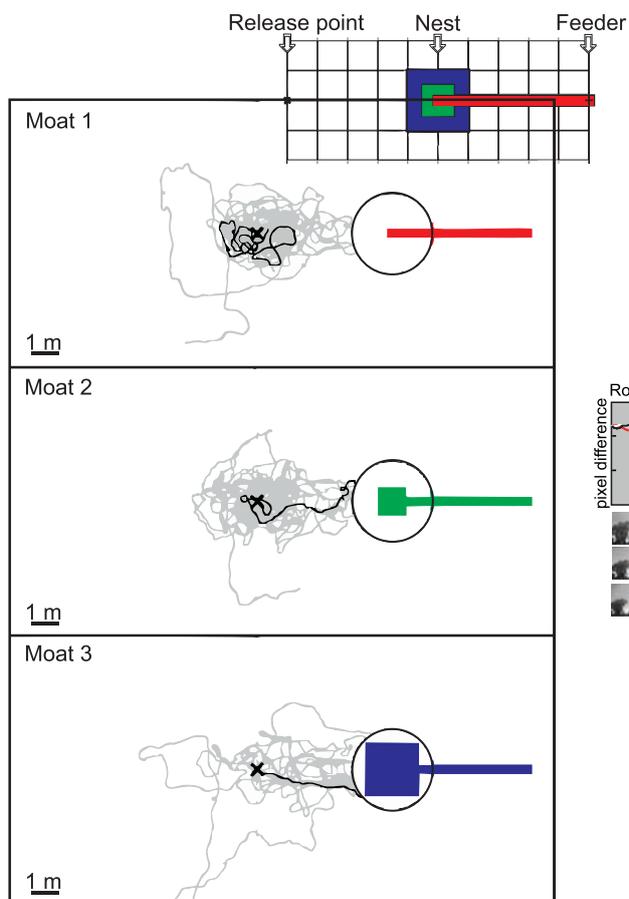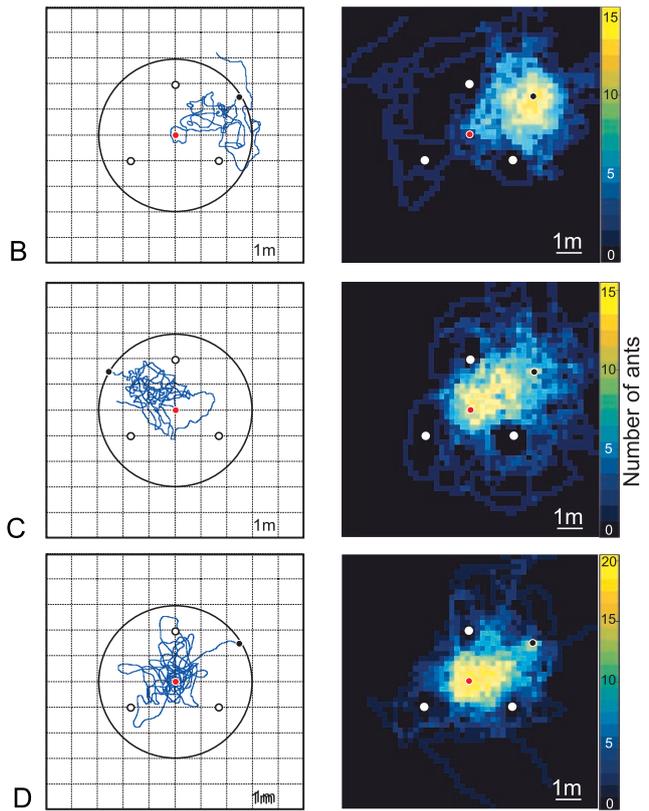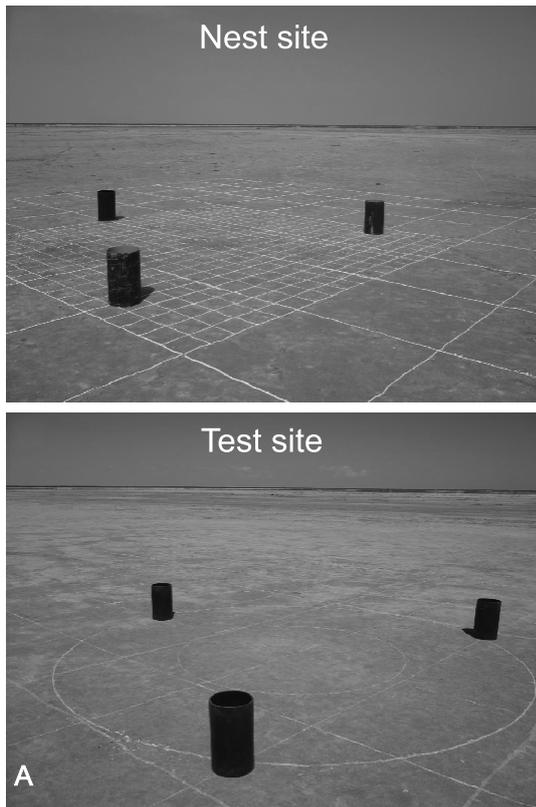
Learning walks and learning flights compared

From a phylogenetic and a functional perspective we would expect that there must be similarities between the learning flights of wasps and bees and the learning walks of ants, despite differences that are to be expected due to different modes of locomotion (Collett & Zeil 2018). Our present state of knowledge suggests at least four common features:

Learning insects move along arcs around the nest (or goal) which means that the direction of their movements is roughly perpendicular to the goal direction. Flying insects do this by moving sideways which allows them to continue to face towards the goal (Fig. 10A, see also Zeil 1993a, Philippides & al. 2013, Stürzl & al. 2016). Ants cannot or do not move sideways, except when carrying heavy prey (Schwarz & al. 2017), so instead at times need to turn away from the goal to walk in a direction roughly perpendicular to it. Note that in the examples of the learning flights close to the goal shown in Fig. 10, the insects tend to move through relatively small arcs and subsequently leave the area, much like the examples of "re-learning walks" we show in Fig. 3 (see also Jayatilaka & al. 2018).

Both flying and walking insects carefully "monitor" the nest direction during learning. Flying insects can in principle see the nest or its immediate environment and therefore track its position visually, as can be shown by experimentally moving a visual pattern around the nest during a learning flight (Zeil 1993a) and by simulating visual tracking of the nest entrance using reconstructed natural scenes (Samet & al. 2014). From their pedestrian perspective, learning ants cannot see the nest and thus must be using information from their path integration system to identify the nest direction (Müller & Wehner 2010, Fleischmann & al. 2018a). They thus would be able in principle, to tag the views they experience during learning with the home direction. Two observations are difficult to explain without the assumption that ants are constantly aware of the nest direction: they would otherwise not be able to move along arcs around the nest, or repeatedly from different compass directions turn into the nest direction and either "fixate" it (Müller & Wehner 2010, Fleischmann & al. 2017), or change scanning direction after alignment in both nest- and anti-nest direction parallel to the home vector (Figs. 4 - 6; Jayatilaka & al. 2018).

The very regular spatio-temporal organization of both learning walks and learning flights has all the hallmarks of a systematic scanning process that leads to regularly spaced and oriented views across the nest from different compass directions (see Figs. 4 - 6 & 10A, B). Whenever a homing insect encounters one of these views it would thus be associated with the direction towards the nest (Graham & al. 2010, Dewar & al. 2014, Stürzl & al. 2016). However, because these views are taken from different locations, a comparison between them would in principle also allow animals to determine relative distances of salient objects due to pivoting parallax (Zeil 1993a,b, Riabinina & al. 2014, Dewar & al. 2014): objects close to the nest (the pivoting centre) experience relatively less displacements in successive images taken along an arc, compared to distant objects. In fact, such sequences of overlapping views could in principle be used to generate a 3D model of the nest environment (Baddeley & al. 2009, Stürzl & al. 2015). This, however, would require not only a global image comparison, but the localizing and tracking of image features depending on their stability from one view to the next (see also Dittmar & al. 2010, Dittmar 2011).

Fig. 9: Experience dependent homing performance in *Cataglyphis fortis* ants. (A) The landmark array at a nest and a test site. (B) Example paths (left) and 2D search histograms (right) for inexperienced ants released just outside the landmark array at the test site. (C) Same for ants that had performed learning walks, but had not gone on foraging excursions. (D) Same for experienced foragers. Release point black circle, nest position red circle. (From Fleischmann & al. 2016, adapted with permission.) See text for details. (E) Example search paths of ants released 5 m to the "left" of the nest, the foraging experience of which had previously been restricted to varying degrees (see inset): to a narrow corridor (red Moat 1, top), to the same corridor but in addition a 1 m² area around the nest (green Moat 2, middle) and to the same corridor but in addition to a 4 m² area around the nest (blue Moat 3, bottom). Modified from Fleischmann & al. 2018b. (F) The catchment area (green) of 4 nest-directed panoramic snapshots (marked by red x) acquired at distances of 1.5 m (top) and 2 m from the nest (bottom). Nest marked by black dot. Areas from where a simulated agent would not be able to home to the nest are marked in red. Modified from Stürzl & al. 2015. Inset shows rotational image difference functions of nest views compared with views 5 and 10 m away from the nest. (Modified from Narendra & al. 2013).

Nest site

Test site

A

B

C

D

Number of ants

1m

Release point   Nest   Feeder

Moat 1

1 m

Moat 2

1 m

Moat 3

1 m

E

Rotational image difference functions

pixel difference

10m

5m

Nest

snapshots 1.5m from nest

5 m

snapshots 2m from nest

F

105

Box 1: Key questions regarding the functional significance of learning walks in ants.

- Do different ant species make head movements during their learning walks?
- What are the species-specific and ecological differences of learning walks in ants (cf. Fleischmann & al. 2017, Jayatilaka & al. 2018), including how do gaze directions relate to panorama features and the home vector direction?
- Do all naïve ants rely initially on a magnetic compass reference during their learning walks and if so, when does the transition to using celestial compass cues occur?
- What are the differences between the first learning walks of naïve ants and re-learning walks of experienced ants, in particular regarding the occurrence of full rotations and the use of magnetic compass cues?
- What triggers re-learning walks (see van Iersel & van den Assem 1964)?
- How are the views experienced during learning walks related to the navigational decisions made by homing ants?
- Do learning walks differ in ants with different visual resolution?
- Do learning walks differ when the view of the landmark panorama is blocked or not?
- What would be a necessary and sufficient set of rules for the control of learning walks which could be tested on a legged robot (see Dupeyroux & al. 2018)?
- What determines "the end of learning" and the transition to foraging?
- What kind of learning is involved during learning walks, perceptual learning or imprinting (Jayatilaka & al. 2018) and/or associative learning (Freas & al. 2019)?
- What are the memory requirements for successful navigation in any given natural environment (see Webb 2019)?
- Are the visual input regions in the mushroom bodies of ants living in landmark-rich and landmark-poor habitats organized differently?

We do not know at present whether ants segment scenes in this way or not (but see Buehlmann & al. 2016), the viewing directions of learning *Myrmecia croslandi* at least do not appear to be associated with particular panorama features (Jayatilaka & al. 2018). Most importantly in contrast to learning flights (e.g., Zeil 1993b, Philippides & al. 2013, Stürzl & al. 2016) we lack detailed data on the relationship between the learning walks of ants and the navigational decisions they make when returning home.
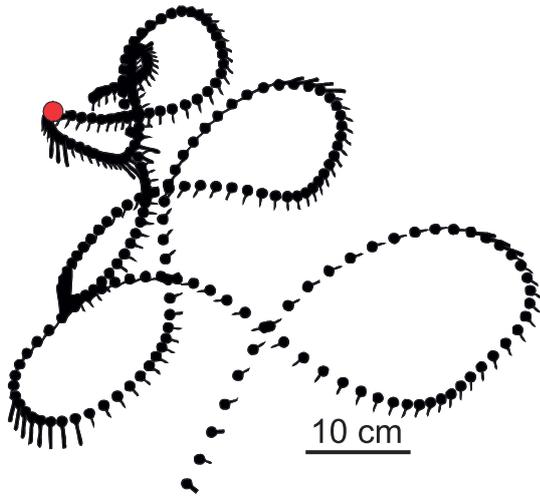
Exploration (learning) walks (Muser & al. 2004, Fleischmann & al. 2016, Jayatilaka & al. 2018) and flights (Capaldi & Dyer 1999, Capaldi & al. 2000, Osborne & al. 2013, Degen & al. 2015, Woodgate & al. 2016) are characterized by the insects returning to the nest after excursions during which they do not seem to forage. Ants, honeybees and bumblebees systematically cover different compass directions around the nest in a series of such excursions (e.g., Degen & al. 2015, Fleischmann & al. 2016, Woodgate & al. 2016, Jayatilaka & al. 2018). In contrast, all other examples of learning at the nest and at a feeder show that insects then depart after turning back and looking at the goal (Zeil 1993a, Lehrer 1993, Collett &

Lehrer 1993, Lehrer & Collett 1994, Collett 1995, Nicholson & al. 1999, Hempel de Ibarra & al. 2009, Müller & Wehner 2010, Collett & al. 2013, Philippides & al. 2013, Riabinina & al. 2014, Stürzl & al. 2016, Jayatilaka & al. 2018, Robert & al. 2018) which appears to be a different process that does not serve to explore the wider goal environment, but to acquire or update existing local memories. These re-learning actions have a very similar choreography to the one performed by insects that exit the nest for the first time (e.g., Robert & al. 2018) and are triggered by changes in the visual environment (e.g., van Iersel & van den Assem 1964, Müller & Wehner 2010), by the need to learn new locations (e.g., Lehrer 1993, Collett & Lehrer 1993, Lehrer & Collett 1994, Nicholson & al. 1999) and by difficulties finding the goal during the preceding return (e.g., Zeil 1993a,b).
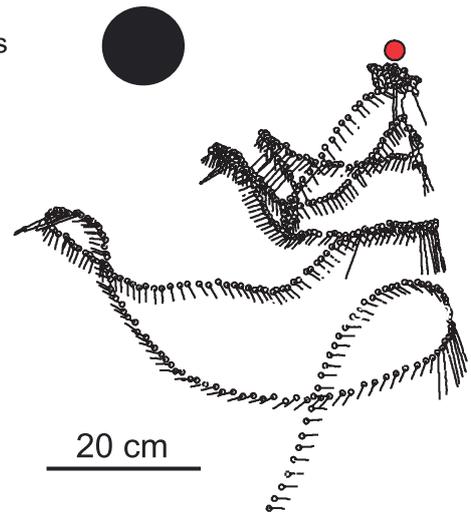
The only non-hymenopteran central place forager we are aware of that performs stereotypical movements on its departure from a burrow in unfamiliar terrain is the nocturnal desert spider, *Leucorchestris arenicola* (see Nørgaard & al. 2012). Interestingly, the spiders do not move along arcs around the burrow, but in a sinusoidal path oscillating around a constant compass direction.

Fig. 10: The learning flights of bees and wasps. (A) Flight paths and body axis directions of wasps and bees during their learning flights. (Bumble bee: reproduced from Philippides & al. 2013, adapted with permission; social wasp: modified from Collett & Lehrer 1993 with permission from the Royal Society; weevil wasps (*Cerceris*): J. Zeil, unpubl.; honeybee: modified from Lehrer & Collett 1994.) (B) Left panel: The learning flight path of a *Cerceris* wasp as seen from the side. White rectangle marks the path for which the top-down view is shown above. Right panel: The time course of gaze direction (green), bearing relative to the nest (blue) and the retinal position of the nest entrance (red) for the flight shown on the left.
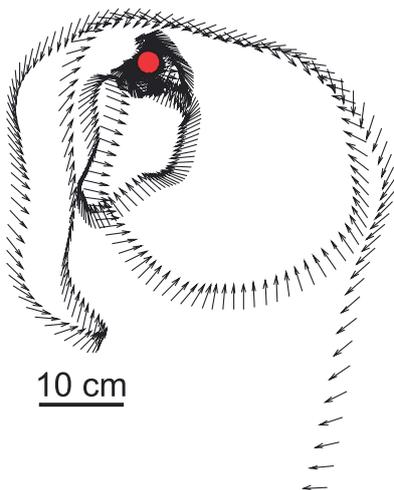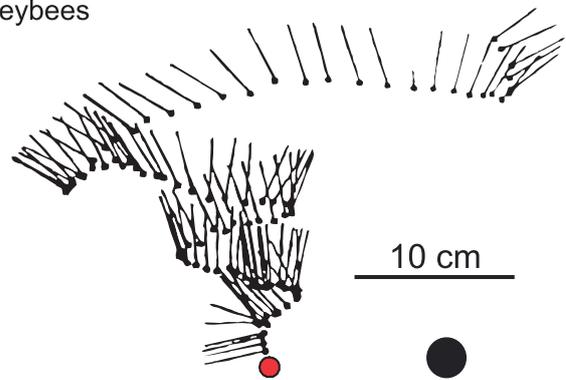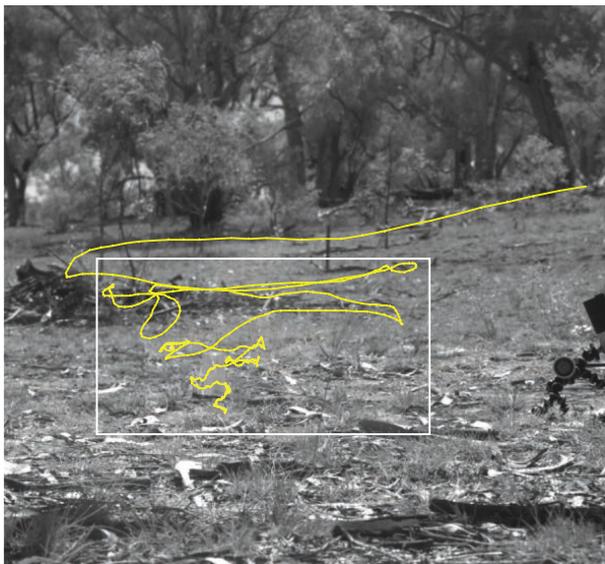
Bumblebees

10 cm

Social wasps

20 cm

Weevil wasps *(Cerceris)*

10 cm

Honeybees

10 cm

A

B

180

Gaze

Retinal position of nest

90

0

-90

Bearing

-180

Direction (degrees)

0   1   2   3   4   5   6   7   8
Time (s)
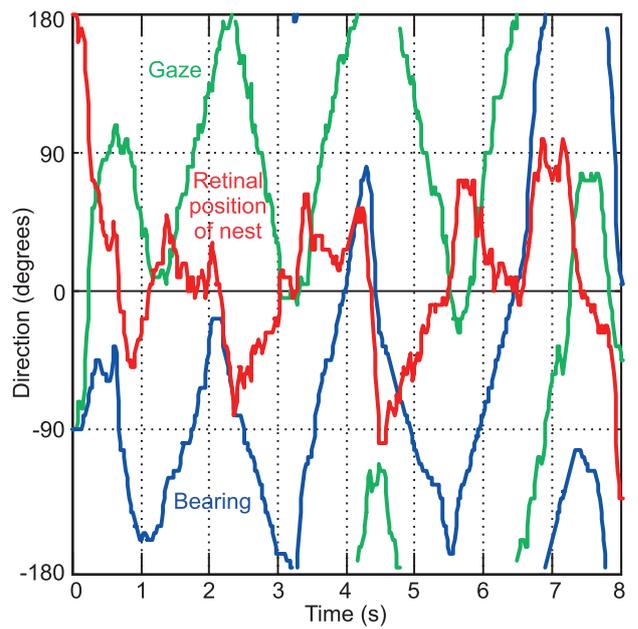
However, a feature in common with the learning walks of ants and the learning flights of bees and wasps is that the spiders appear to keep careful track of the home direction. They view the burrow direction sideways in the overlapping visual fields of their lateral eyes, alternating on their left and their right side, depending on their direction of movement relative to the home direction, in some respects much like wasps during their learning flights (Stürzl & al. 2016).

Future research needs and opportunities

Throughout this review we have already identified a number of research questions and issues that need attention in future, such as the need to monitor head movements around the yaw axis and head orientation around roll and pitch axes or the need to analyse the relationship between viewing directions of individual ants during learning walks and the navigational decisions they make when returning to the nest. We list these in Box 1 together with further suggestions for a number of fruitful research topics that would help us understand the functional significance, the evolution and the control of learning walks.

At the level of behavioural analysis, on which we have concentrated here, we clearly need to understand more about the memory requirements for navigation under natural conditions and how and when in detail memories are acquired and used for guidance. A start would be to investigate and simulate a set of rules for the control of learning walks, as has been done for learning flights (Schulte & al. 2019) which could then be tested on a legged robot (Dupeyroux & al. 2018). At the neurobiological level, rapid progress is being made to characterize the brain centres that are involved in navigation (e.g., Stone & al. 2018, Heinze & al. 2018) and to document in detail the changes and memory traces in the brains of ants following learning walks (Rössler 2019, Grob & al. 2019), in particular relating to celestial compass cues (Grob & al. 2017). However, it remains to be identified how and when particular visual scenes are encoded in the brains of ants during learning walks and how they are recalled for navigational guidance. To tackle these questions regarding the neurobiological basis of visual navigation in insects will require the development of sophisticated, closed-loop visual stimulation techniques combined with optical and electrophysiological recordings of neural network activities in navigating insects.

Acknowledgments

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