

RESEARCH ARTICLE

Species-specific differences in the fine structure of learning walk elements in *Cataglyphis* ants

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ABSTRACT

Cataglyphis desert ants are famous navigators. Like all central place foragers, they are confronted with the challenge to return home, i.e. relocate an inconspicuous nest entrance in the ground, after their extensive foraging trips. When leaving the underground nest for the first time, desert ants perform a striking behavior, so-called learning walks that are well structured. However, it is still unclear how the ants initially acquire the information needed for sky- and landmark-based navigation, in particular how they calibrate their compass system at the beginning of their foraging careers. Using high-speed video analyses, we show that different *Cataglyphis* species include different types of characteristic turns in their learning walks. Pirouettes are full or partial rotations (tight turns about the vertical body axis) during which the ants frequently stop and gaze back in the direction of the nest entrance during the longest stopping phases. In contrast, voltes are small walked circles without directed stopping phases. Interestingly, only *Cataglyphis* ant species living in a cluttered, and therefore visually rich, environment (i.e. *C. noda* and *C. aenescens* in southern Greece) perform both voltes and pirouettes. They look back to the nest entrance during pirouettes, most probably to take snapshots of the surroundings. In contrast, *C. fortis* inhabiting featureless salt pans in Tunisia perform only voltes and do not stop during these turns to gaze back at the nest – even if a set of artificial landmarks surrounds the nest entrance.

KEY WORDS: Celestial compass, Central place forager, Panorama snapshot, Spatial orientation, Visual landmark, Vector navigation

INTRODUCTION

Hymenopteran central place foragers – such as bees, wasps and ants – perform so-called learning flights or walks whenever they have to memorize the landmark panorama surrounding a particular place, e.g. the location of their nest. Since the first descriptions over a century ago (Peckham and Peckham, 1898; Wagner, 1907), learning flights have been investigated in great detail in wasps (Tinbergen, 1932; Zeil, 1993a,b; Zeil et al., 1996), honeybees (Becker, 1958; Capaldi and Dyer, 1999; Lehrer, 1991, 1993; Opfinger, 1931; Vollbehr, 1975) and bumblebees (Collett et al., 2013; Hempel de Ibarra et al., 2009; Philippides et al., 2013; Robert et al., 2017) using increasingly sophisticated techniques like harmonic radar (Capaldi et al., 2000; Degen et al., 2015, 2016; Osborne et al., 2013) or high-speed cameras (Riabinina et al., 2014;

Stürzl et al., 2016). Much less is known about learning walks of ants (Fleischmann et al., 2016; Jayatilaka, 2014; Müller and Wehner, 2010; Muser et al., 2005; Nicholson et al., 1999; Stieb et al., 2012; Wehner et al., 2004). However, these few studies document that – like flying insects – some ant species exhibit a striking behavioral sequence at the beginning of their foraging life. Desert ants in particular, which are well known for their navigational performance (Ronacher, 2008; Wehner, 2008; Wehner and Rössler, 2013; Wehner et al., 1996), use a considerable amount (up to 3 days; Fleischmann et al., 2016; Stieb et al., 2012) of their short lives (often less than a week; Schmid-Hempel and Schmid-Hempel, 1984) outside the nest to perform learning walks. *Cataglyphis* ants are thermophilic scavengers searching for dead arthropods during their extensive foraging excursions. *Cataglyphis fortis* inhabiting North African chotts and sebkhas cover the largest distances compared with other desert ant species (Wehner, 1983, 1987a). Their paths can be longer than 1 km and their maximal foraging distances more than 300 m from the nest (Buehlmann et al., 2014). *Cataglyphis noda*, native to Greece, search for food closer to the nest, but still cover large distances (Wehner et al., 1983), as do *Cataglyphis bicolor* [Wehner, 1987a; note that in that publication (and others: Harkness, 1977; Wehner et al., 1983), *C. noda* belonging to the *bicolor* species group, i.e. to the same phylogenetical group as *C. bicolor*, is named *C. bicolor*]. Before the successful completion of these extensive foraging trips, *Cataglyphis* ants perform learning walks characterized by several typical features: naive ants (called ‘novices’ below) move slowly around the nest entrance and explore all directions around it in subsequent learning walks (Fleischmann et al., 2016; Wehner et al., 2004). These ants include repeated body turns in their small excursions and they do not bring back any food items (Fleischmann et al., 2016; Stieb et al., 2012; Wehner et al., 2004). However, in novices, the characteristics of the learning walks, including circular movements as well as saccadic rotations with distinct stopping phases, have not yet been analyzed in detail. Only a few studies have recorded these striking elements during learning walks in different desert ant species and report on their rotational motifs (*C. fortis*: Stieb et al., 2012; *Melophorus bagoti*: Wystrach et al., 2014; *Myrmecia croslandi*: Jayatilaka, 2014). Namibian desert ants, *Ocymyrmex robustior*, perform ‘re-learning walks’ when presented with a new landmark situation around the nest (Müller and Wehner, 2010). These walks contain marked pirouettes with well-defined nest-fixating stopping phases.

Here, we used high-speed video recordings to reveal temporal and spatial characteristics of the learning walk of novices in different *Cataglyphis* species inhabiting different types of environments (cluttered and open). Our analyses show that the ant species performed different types of turn. Only ants inhabiting a cluttered environment (namely *C. noda* and *Cataglyphis aenescens*) performed both voltes (small walked circles) and pirouettes (tight rotations about the vertical body axis). They paused during the latter to gaze in the nest direction. In contrast, ants inhabiting a featureless

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habitat (*C. fortis*) only performed voltes and did not gaze back to the nest entrance even if artificial landmarks offered a prominent panorama.

MATERIALS AND METHODS

Test animals and study sites

To compare learning walks of different *Cataglyphis* species inhabiting different environments, we performed experiments in Tunisia and Greece. The experiments with *C. noda* (Brullé 1832) were performed in July and August 2015 in the Schinias National Park near Marathon, Greece (38°08'N, 24°02'E). We used two nests located on different clearings in the surrounding pine forest. The trees around the clearings offer prominent skylines with natural landmarks (Fig. 1A). In addition, during July 2016, we recorded learning walks of a smaller species, *C. aenescens* (Nylander 1849), inhabiting the same clearings as *C. noda*. The experiments with *C. fortis* (Forel 1902) were carried out in June and July 2014 at a saltpan near Menzel Chaker, Tunisia (34°57'N, 10°24'E). The saltpan offers an almost landmark-free habitat. We used two different colonies for the video recordings, both situated towards the middle of the saltpan where almost no natural landmarks occurred (Fig. 1B).

Data acquisition: video recordings

All foragers were marked with the same color (Motip Lackstift Acryl, Motip Dupli GmbH, Haßmersheim, Germany) over a period of 3–4 days before video recordings started. We considered unmarked ants appearing on subsequent experimental days at the nest entrance as novices and recorded their learning walks for 2–3 days. As these novices are easily disturbed and disappear

immediately into the nest (Wehner et al., 2004), we usually did not mark them. Therefore, we usually could not decide whether a learning walk was the first or a subsequent one. However, as the walks were only included in the data if the ants stayed within the recording area, and the ants move further away with more experience (Fleischmann et al., 2016), these walks were most probably early learning walks. In one colony of *C. noda*, we marked some of the naive ants with an individual color code in order to record subsequent learning walks of individual ants. The experimental setup consisted of cameras mounted on one or two tripods (Manfrotto 190, Lino Manfrotto+co. Spa, Cassola, Italy) placed north of the nest entrance. A Full HD video camera (HDC-SD300, Panasonic Corp., Osaka, Japan) recorded the nest entrance and its surroundings (i.e. an area of about 100 cm×60 cm) at 25 frames s⁻¹ and minimal zoom throughout the entire day. We used these videos to trace the learning walks in the case of one individually marked ant (see Fig. 2D–F), because its paths left the high-speed recording area. The high-speed camera (Lumix DMC-FZ200, Panasonic Corp.) recorded a smaller area (about 25 cm×43 cm) at 100 frames s⁻¹ temporal and 1080×720 pixel spatial resolution. The observer sitting 5 m east of the nest watched the ants through binoculars (Condor 10×50 1821050, Bresser GmbH, Rhede, Germany), and started and stopped the high-speed recordings via a remote control (Wireless Remote Release DCCS System Base, HAMA GmbH & Co KG, Monheim, Germany) whenever learning walks occurred.

In Tunisia, we performed three experiments with *C. fortis*: no artificial landmarks, one artificial landmark or three artificial landmarks were placed near the nest entrance. In the first case, the ants did not have any additional landmarks (Fig. 1B). In the second case, one black cylinder (height: 33 cm, diameter: 20 cm) was positioned 0.4 m north of the nest entrance (vertical angular size: 48 deg, horizontal angular size: 28 deg; Fig. 1C). In the third case, three black cylinders (height: 38 cm, diameter: 22 cm) were placed 2 m from the nest at 0 deg (north), 120 deg (southeast) and 240 deg (southwest) (for each cylinder: vertical angular size: 11 deg, horizontal angular size: 6 deg; Fig. 1D).

Data analysis

We cut the videos to the length of one learning walk or one turn and converted them into image sequences using QuickTime Player Pro 7.7.5 (Apple Inc., Cupertino, CA, USA). Both learning walks and individual turns were easily identifiable and were extracted by eye. A learning walk was defined as an explorative trip, i.e. no digging or foraging, of an unmarked ant from exiting the nest entrance until its return into the nest. A turn was defined as a circular movement during which an ant changed its gaze direction until eventually re-establishing its previous walking direction. We analyzed the image sequence frame by frame with the Matlab (MathWorks, Inc., Natick, MA, USA) application Digilite (Jan Hemmi and Robert Parker, The Australian National University). We tracked the ant's position by marking the mandibles as well as the thorax. Furthermore, the position of the nest and the north direction were marked. We used these four types of coordinates to determine the ant's position and its viewing direction relative to the nest (the nest direction was defined as 180 deg). We defined a stopping phase as a period of at least 100 ms during which the ant did not move forward and gazed in one direction. Of course, the duration of 100 ms is an arbitrary criterion. However, as *O. robustior* ants pause for about 150 ms (Müller and Wehner, 2010), and both *Cataglyphis* and *Ocymyrmex* desert ants are very fast (Wehner and Wehner, 2011), we are confident that we captured the vast majority of relevant stopping

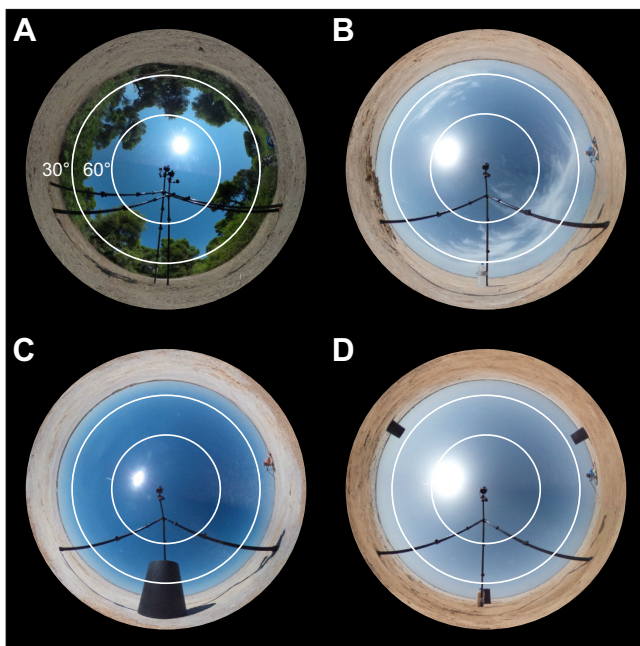


Fig. 1. Panoramic (360 deg) pictures of the different experimental setups. (A) In the pine forest in Greece, the trees and bushes offer a natural and prominent skyline. (B) In contrast, the saltpan in Tunisia lacks prominent natural landmarks. (C) One or (D) three black cylinders were offered as artificial landmarks close the nest entrance for the setup shown in B. The camera tripod stood north of the nest entrance in all setups. The experimenter sitting 5 m east of the nest watched the ants through binoculars to start high-speed recordings when naive ants performed learning walks at the nest entrance. The white lines indicate 30° and 60° latitudes above the horizon; the zenith is in the middle of the circles. The panoramic pictures in A and C are also shown in Movie 1.

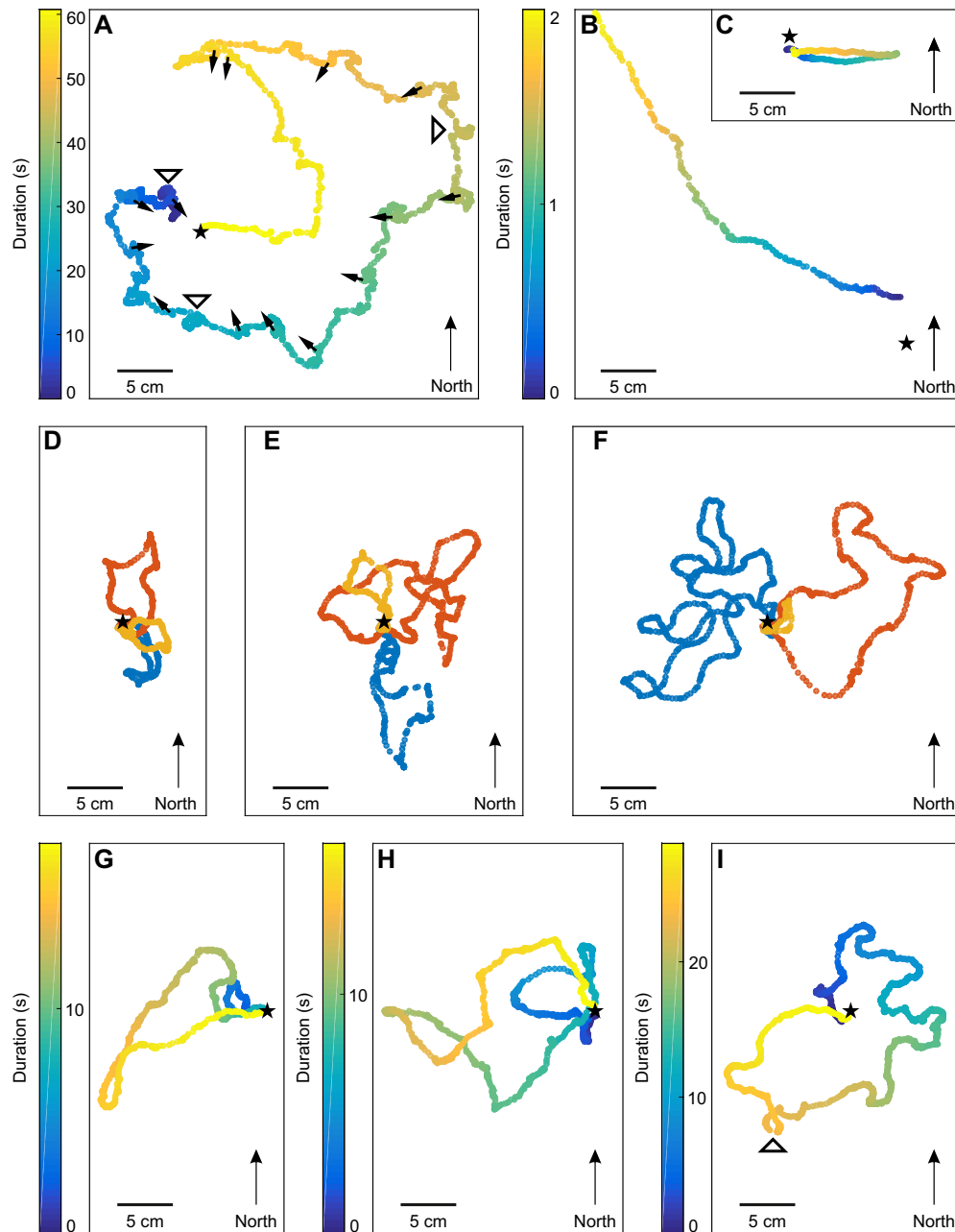


Fig. 2. Characteristics of learning walks in *Cataglyphis*. (A–C) Three paths walked by ants (*C. noda*) leaving the nest for different purposes recorded at 100 frames s^{-1} . (A) Typical learning walk circling around the nest entrance (black star), including several pirouettes, during which the ant looks back to the nest entrance (black arrows), and voltes, without stopping phases (white arrowheads). (B) An experienced forager leaves the nest in a straight line without any turns. (C) Typical path of a digger ant leaving the nest in a straight line, followed by a 180 deg turn and run back to the nest after depositing soil. Time is color coded in all traces. Note that the learning walk in A takes about 1 min, whereas the path of the forager in B and the digger in C disappears after 2 s outside the recording area or into the nest, respectively. (D–F) Successive learning walks of an individual ant (*C. noda*) during 1 day (18 July 2015) recorded at 25 frames s^{-1} . This individually marked ant was seen only once outside the nest in the morning before the recordings started. (D) The first three walks happened in short sequence at 11:05:05, 11:05:33 and 11:07:02 h local time. The durations were 14 s (yellow), 16 s (red) and 10 s (blue). After these explorative trips, the ant re-appeared outside the nest entrance at 11:07:21 h local time, became lost and searched for several minutes (4 min 55 s) to find its way back to the nest (not shown). (E) This ant immediately continued to perform learning walks at 11:12:26 h local time (7 s, yellow). The subsequent two learning walks were performed in short sequence, at 11:43:25 h (24 s, red) and 11:43:58 h (12 s, blue), respectively. (F) Three further learning walks directly followed the ones shown in E. The first of these three started at 11:45:06 h and was aborted (2 s, yellow) because the ant was frightened and returned to the nest immediately. The next learning walk occurred directly afterwards at 11:45:21 s (14 s, red). The last learning walk of this ant was recorded at 12:17:32 s (19 s, blue). During subsequent learning walks, the ant explored different sectors around the nest entrance. (G–I) Examples of three ants (*C. fortis*) performing a learning walk with no, one or three artificial landmarks recorded at 100 frames s^{-1} . (G) Without artificial landmarks. (H) One black cylinder, 0.4 m north of the nest entrance. (I) Three artificial landmarks positioned symmetrically at a 2 m distance around the nest entrance. Time is color coded in all traces. Note that the durations of learning walks depicted were slightly different (color bars). However, the learning walk durations of ants in different experimental groups were not significantly different between species and experimental setups (Fig. 3). A complete learning walk of *C. noda* recorded from the top as well as from the side is shown in Movie 1.

phases with this criterion. It is also noteworthy that the duration of the stopping phases in *Ocymyrmex* is temperature dependent (Müller and Wehner, 2010). However, the ground temperatures in Tunisia and Greece were similar [Tunisia: $41.7 \pm 9.3^\circ\text{C}$, $36.5\text{--}45.8^\circ\text{C}$; Greece: $47.2 \pm 21.6^\circ\text{C}$, $38.8\text{--}60.4^\circ\text{C}$; median \pm interquartile range (IQR: Q1–Q3), ranging from 31.3 to 51.4°C in Tunisia and from 26.6 to 66.3°C in Greece]. Concerning the gaze direction, we tolerated a deviation of 10° during a stopping phase. Multiple analyses of the same sequence showed that the accuracy for determining gaze direction is within this 10° limit. Based on these data, we also calculated the angular velocities of the turns.

Statistics

Because our data were not normally distributed, we report medians \pm IQR, calculated by subtracting the lower quartile (Q1) from the upper quartile (Q3). We compared the duration of learning walks and the number of turns per learning walk of our experimental groups using the Kruskal–Wallis test. The significance level was $\alpha=0.05$. If necessary, i.e. if there was a significant difference indicated by the Kruskal–Wallis test, we performed *post hoc* pairwise comparisons with the Mann–Whitney *U*-test with Bonferroni correction. The significance level was $\alpha=0.05$ (i.e. $\alpha=0.0084$ with Bonferroni correction, because we compared the four experimental groups: ‘*C. fortis* with no artificial landmark’, ‘*C. fortis* with one artificial landmark’, ‘*C. fortis* with three artificial landmarks’ and ‘*C. noda*’ pairwise with each other, resulting in six performed tests). We compared the number of stopping phases and the angular velocity of different types of turn pairwise within species using the Mann–Whitney *U*-test ($\alpha=0.05$). All these statistical tests were performed with Matlab R2014b (MathWorks, Inc.). To analyze gaze direction, we used the Rayleigh test to test for uniformity, i.e. whether the data were randomly distributed over the 360° deg. If the data were significantly directed ($\alpha=0.05$), we calculated the 95% confidence interval and checked whether the expected value, i.e. the direction of the nest (180° deg) was between the limits. All circular statistics were performed with Oriana (version 4.02, Kovach Computing Services, Pentraeth, UK).

RESULTS

Cataglyphis ants perform characteristic learning walks

Cataglyphis desert ants leave their nest for quite different reasons. When observing the happenings at the nest entrances of three *Cataglyphis* species (*C. noda*, *C. fortis* and *C. aenescens*) in two completely different environments (Fig. 1), three main reasons were identifiable, i.e. performing learning walks, digging/waste disposal and foraging (Fig. 2A–C). All these outdoor behaviors were clearly distinguishable. In this study, the focus was on the learning walks performed by the ants before starting their foraging careers (Fig. 2A). However, ants also left the nest to carry out nest-related tasks like waste disposal or digging behavior (Fig. 2C; see Harkness, 1977; Stieb et al., 2012), and of course to search for food (Fig. 2B). In addition, some ants carried out single nest mates or stood next to the nest entrance and guarded it from time to time as has been described in detail elsewhere (Harkness, 1977). Indoor workers that deposited soil or waste outside the nest moved very fast. They ran in a straight line outside the nest, dropped their item a few centimeters away [9.9 ± 3.7 cm, $8.5\text{--}12.2$ cm, median \pm IQR (Q1–Q3) dropping distance from the nest entrance, $n=20$], turned around by 180° deg immediately and ran back into the nest (Fig. 2C). Foragers also left the nest quickly and in a straight line. In contrast to diggers and learners, foragers moved far away from the nest entrance and left the recording area rapidly (Fig. 2B). Conversely, novices

performed their learning walks at the beginning of their foraging career in close vicinity to the nest entrance, and therefore they remained inside our selected recording area, enabling us to analyze entire learning walks using high-speed video recordings. These explorative trips were very short [*C. noda* $n=25$: 10.4 ± 9.3 s, $6.8\text{--}16.1$ s; *C. fortis* without artificial landmarks $n=12$: 12.0 ± 5.4 s, $11.2\text{--}16.6$ s, median \pm IQR (Q1–Q3); Fig. 3A, Kruskal–Wallis test: duration of learning walks $\chi^2_3=3.98$, $n=66$, $P=0.27$]. No significant differences between the durations of the learning walks of the different species or setups were apparent (Fig. 3A). We marked some individual *C. noda* ants with a unique color code at their first appearance so that we could record subsequent learning walks of the same ants (Fig. 2D–F). Typically, *C. noda* moved further away from the nest entrance with increasing experience until they eventually

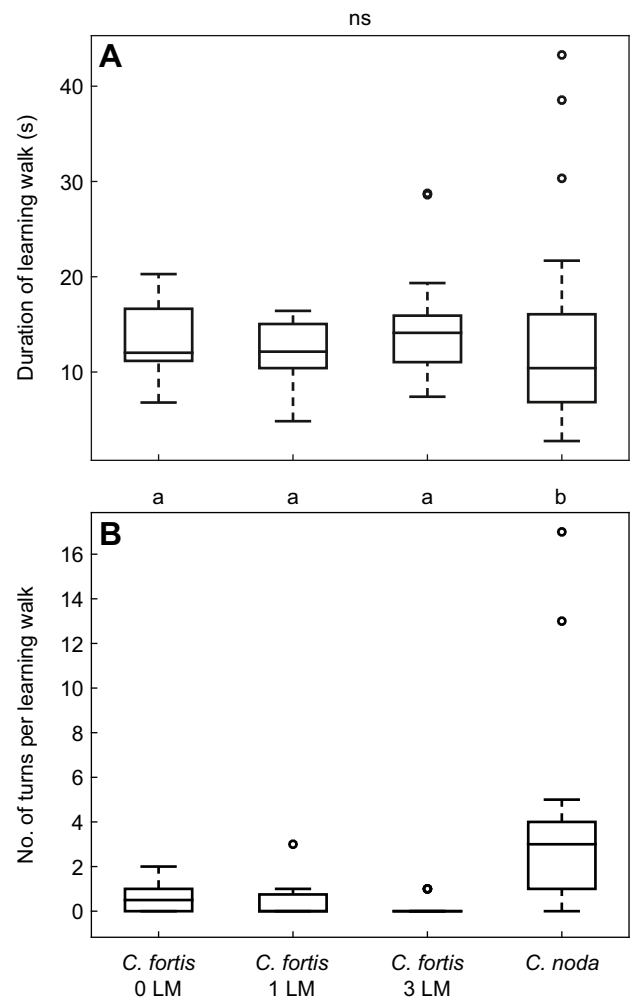


Fig. 3. Comparison of early learning walks performed by two different *Cataglyphis* species and under different conditions. The central mark of each boxplot represents the median, the edges of the boxes are the 25th and 75th percentiles, and the whiskers extend to the most extreme data points (excluding outliers). Outliers are plotted individually as open circles. Different letters indicate significant differences between the groups when compared pairwise (Mann–Whitney *U*-test with Bonferroni correction, i.e. $\alpha=0.0084$). (A) The durations of early learning walks performed within our recording areas were not significantly different between the experimental conditions (*C. fortis* with no, one or three artificial landmarks) or between the two species. (B) The number of turns per learning walk was significantly different between species. However, there was no significant difference between the three experimental setups of *C. fortis*.

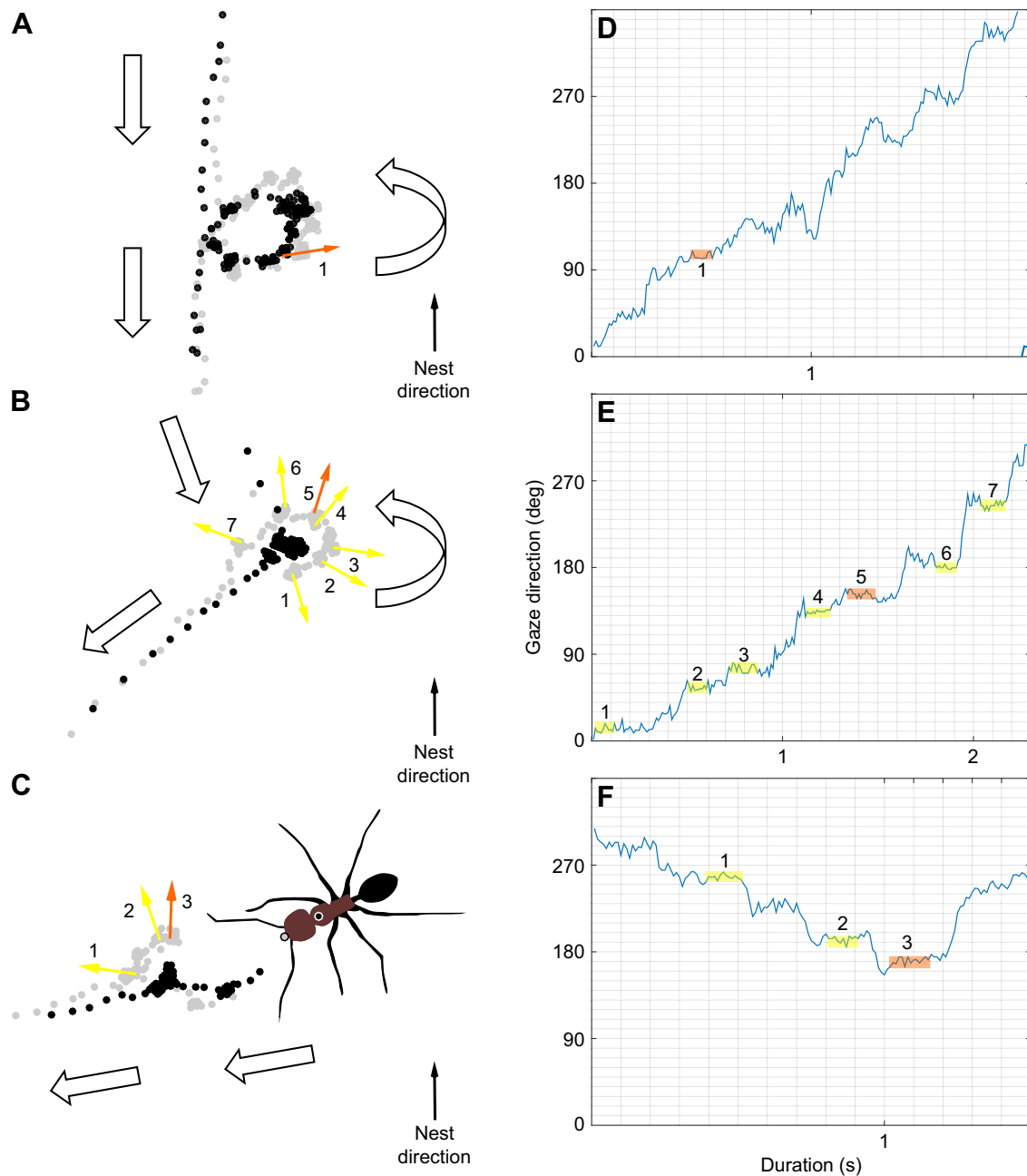
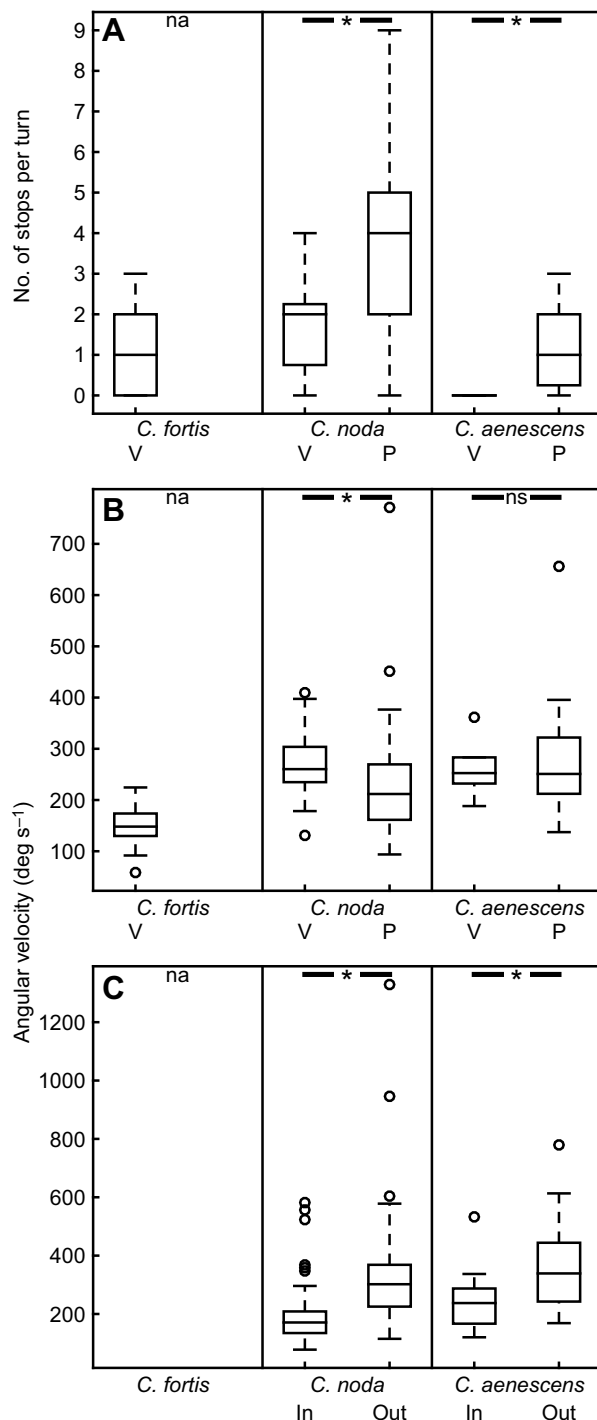


Fig. 4. Different types of turns. (A–C) The position of the mandibles (gray) and the thorax (black) recorded every 10 ms (as illustrated in C). The walking and turning directions are indicated by white arrows. Black arrows point towards the nest. (A) A volte was defined as a walked circle. The tracks of the mandibles and thorax follow the same path. In contrast, (B) full or (C) partial pirouettes were defined as turns about the ant's own axis. The tracks of the mandibles circle around the position of the thorax. Stopping phases (>100 ms) are indicated by yellow and orange arrows (see D–F), and are numbered consecutively. (D–F) Gaze directions of the ants during these three turns with regard to the nest (180 deg) is plotted over time. A stopping phase is defined as an interval of at least 100 ms during which the ant does not move forward and does not change its gaze direction for more than 10 deg. The stopping phases of the turns are highlighted in yellow, and the longest stopping phase per turn is in orange. (D) The volte has only one stopping phase (100 ms), which is not directed towards the nest. (E) The full pirouette includes seven stopping phases of which no. 5 is the longest (180 ms). Stopping phase no. 6 (132 ms) is directed towards the nest. (F) The partial pirouette has three stopping phases of which the longest (no. 3, 185 ms) is directed towards the nest. In general, pirouettes include more stopping phases than voltes (Fig. 5). The underlying data are shown in Movie 1.

became foragers. The most obvious characteristic of *C. noda* learning walks were the frequent turns, during which the ants usually looked back to the nest. The ants performed up to 17 turns per learning walk in our recording area. The average number of turns was 3 ± 3 [1–4, median \pm IQR (Q1–Q3), $n=25$; Fig. 3B]. In comparison to the Greek *C. noda* ants living in a pine forest, the Tunisian *C. fortis* ants inhabiting a saltpan performed fewer turns

during their learning walks [0.5 ± 1 , 0–1, median \pm IQR (Q1–Q3), $n=12$; Fig. 3B; Kruskal–Wallis test: number of turns per walk $\chi^2_3=30.75$, $n=66$, $P<0.05$, and *post hoc* pairwise comparison with Mann–Whitney *U*-test with Bonferroni correction: *C. noda* versus *C. fortis* without an artificial landmark (LM) $z=3.41$, $n_{Cn}=25$, $n_{Cf/LM}=12$, $P<0.0084$; *C. noda* versus *C. fortis* with one artificial landmark $z=4.03$, $n_{Cn}=25$, $n_{Cf/LM}=15$, $P<0.0084$; *C. noda* versus *C.*



fortis with three artificial landmarks $z=4.27$, $n_{Cn}=25$, $n_{C\beta LM}=14$, $P<0.0084$].

An artificial panorama in an otherwise featureless environment does not alter the learning walks in *C. fortis*

To check whether *C. fortis* did not perform frequent turns because of the absence of visual landmarks, we manipulated its natural habitat with two different settings of artificial landmarks. In one experiment, we installed a black cylinder 0.4 m north of the nest entrance (Fig. 1C; Movie 1); in another, three cylinders were placed at 2 m distance around the nest entrance (Fig. 1D). However, there was not any noticeable difference between the learning walks of

Fig. 5. Interspecies comparison of the different types of turn. The central mark of each boxplot represents the median, the edges of the boxes are the 25th and 75th percentiles, and the whiskers extend to the most extreme data points (excluding outliers). Outliers are plotted individually as open circles. Data were compared pairwise within each species using the Mann–Whitney *U*-test when applicable. *Cataglyphis fortis* did not perform any pirouettes; therefore, no statistical comparison was possible (na, not applicable). Asterisks indicate significant differences ($P<0.05$), groups labeled 'ns' are not significantly different. (A) Number of stopping phases per turn. Pirouettes (P) of *C. noda* and *C. aenescens* include more stopping phases than do voltes (V). (B) Angular velocity during turns. The angular velocity of *C. noda* voltes was significantly higher than that of pirouettes, but there was no significant difference for *C. aenescens*. However, it is noteworthy that the angular velocities were quite different depending on the turning direction relative to the nest, i.e. whether the ant turned to the nest (turning-in) or back to continue the learning walk (turning-out). This becomes especially clear when examining the fine structure of the partial pirouettes performed by the Greek *Cataglyphis* ants. (C) Angular velocity of in- and out-turns of the partial pirouettes. Both species performing partial pirouettes, i.e. *C. noda* and *C. aenescens*, turn in with less speed than they turn out, as does the Namibian desert ant *O. robustior* (Müller and Wehner, 2010).

C. fortis under the different conditions (Fig. 2G–I). The duration of the learning walks remained the same (Kruskal–Wallis test: duration of learning walks $\chi^2_3=3.98$, $n=66$, $P=0.27$; Fig. 3A), and the number of turns per learning walk of *C. fortis* did not increase [one artificial landmark: 0 ± 0.75 , $0-0.75$, median \pm IQR (Q1–Q3), $n=15$; three artificial landmarks: 0 ± 0 , $0-0$, median \pm IQR (Q1–Q3), $n=14$; Fig. 3B]. There was no significant difference between the number of turns per walk in the three conditions under which *C. fortis* ants performed their learning walks (Fig. 3B; Kruskal–Wallis test: number of turns per walk $\chi^2_3=30.75$, $n=66$, $P<0.05$, and *post hoc* pairwise comparison with Mann–Whitney *U*-test with Bonferroni correction: *C. fortis* without an artificial landmark versus *C. fortis* with one artificial landmark $z=1.09$, $n_{C\beta LM}=12$, $n_{C\beta LM}=15$, $P=0.28$; *C. fortis* without an artificial landmark versus *C. fortis* with three artificial landmarks $z=1.55$, $n_{C\beta LM}=12$, $n_{C\beta LM}=14$, $P=0.13$; *C. fortis* with one artificial landmark versus *C. fortis* with three artificial landmarks $z=0.38$, $n_{C\beta LM}=15$, $n_{C\beta LM}=14$, $P=0.71$). As stated above, *C. noda* made significantly more turns per learning walk than *C. fortis* even when artificial landmarks were available for the latter species (Fig. 3B).

Cataglyphis ants perform different types of turns with distinct features

Beside the difference in the number of turns per learning walk between *C. fortis* and *C. noda*, our high-speed recordings also revealed striking qualitative differences of turns across and within species. *Cataglyphis fortis* and *C. noda* included different types of turns in their learning walks (Fig. 4). *Cataglyphis fortis* ants performed only one type of turn during their learning walks: small walked circles, we termed voltes. During this type of turn, the ants moved forward on a circumference. Voltes were only rarely interrupted by stopping phases longer than 100 ms. The median number of stopping phases per volte of *C. fortis* was 1 ± 2 [0–2, median \pm IQR (Q1–Q3), $n=20$; Fig. 5A]. *Cataglyphis noda* also performed this type of turn (Fig. 4A,D; Movie 1). During these voltes, *C. noda* stopped 2 ± 1.5 times [0.75–2.25, median \pm IQR (Q1–Q3), $n=17$; Fig. 5A, Mann–Whitney *U*-test: *C. noda* voltes versus pirouettes $z=-3.99$, $n_{CnV}=17$, $n_{CnP}=85$, $P<0.05$]. However, *C. noda* much more frequently performed another, more saccadic, type of turn we termed pirouettes (as in Müller and Wehner, 2010). Over 80% of *C. noda* turns were pirouettes (85 out of 102 analyzed turns were pirouettes and only 17 were voltes). In contrast to a volte, a pirouette does not include any forward motion. Instead, to perform a

pirouette, an ant stops walking and turns on its vertical axis without any translation (Fig. 4B,C; Movie 1). To re-establish its former walking direction, an ant has to turn back either continuing or reversing its direction of rotation. Therefore, pirouettes may be full 360 deg turns or partial turns (Fig. 4E,F; Movie 1). Usually, the ants took the shorter way back to re-establish their initial angular position – only in 12 partial pirouettes did ants cover an angle larger than 180 deg when turning back ($n=74$). Furthermore, the angular velocities of the back-turns were usually higher than those of the in-turns (Fig. 5C). Pirouettes were frequently interrupted by stopping phases defined as phases of at least 100 ms during which the ants did not move forward and gazed in one direction (± 10 deg to compensate for tracking inaccuracies). *Cataglyphis noda* pirouettes included 4 ± 3 [2–5, median \pm IQR (Q1–Q3), $n=85$] stopping phases, significantly more than their voltes (Fig. 5A). In addition, *C. noda* pirouettes had a lower angular velocity than their voltes (Fig. 5B, Mann–Whitney *U*-test: *C. noda* voltes versus pirouettes $z=2.84$, $n_{CnV}=17$, $n_{CnP}=85$, $P<0.05$). Interestingly, a smaller *Cataglyphis* species (*C. aenescens*) inhabiting the same clearings as *C. noda* in the Greek pine forest also performed both types of turns. Similar to *C. noda*, pirouettes in *C. aenescens* contained more stopping phases than voltes (Fig. 5A, Mann–Whitney *U*-test: *C. aenescens* voltes versus pirouettes $z=-2.50$, $n_{CaV}=5$, $n_{CaP}=15$, $P<0.05$); however, there was no significant difference in their angular velocity (Fig. 5B, $z=0.00$, $n_{CaV}=5$, $n_{CaP}=15$, $P=1$). In both *C. noda* and *C. aenescens*, the turning-in movements of the partial pirouettes were slower than the turning-out movement (Fig. 5C, Mann–Whitney *U*-test: *C. noda* turning-in versus turning-out $z=-6.79$, $n_{Cni}=74$, $n_{Cno}=74$, $P<0.05$; *C. aenescens* turning-in versus turning-out $z=-2.04$, $n_{Cai}=14$, $n_{Cao}=14$, $P<0.05$).

Only *Cataglyphis* species inhabiting cluttered environments perform pirouettes during which they turn back to the nest entrance

The striking feature of the saccadic pirouettes is that the ants turn back and look towards the nest entrance. As has been described for other desert ants (see *C. bicolor*: Wehner et al., 2004; *O. robustior*: Müller and Wehner, 2010), *C. noda* ants turned back to the nest (defined as the direction 180 deg), faced the nest entrance (which was invisible to them) and paused for a few hundred milliseconds [longest stopping phase per turn: 162 ± 68 ms, 134–202 ms, median \pm IQR (Q1–Q3); minimum by definition 100 ms, maximum 469 ms, $n=83$]. However, *C. noda* ants only paused and fixated the position of the nest entrance during one type of turn, i.e. during pirouettes (Rayleigh test: $z=30.48$, $n=83$, $P<0.05$; 187.5 deg, mean vector, 174.7–200.2 deg, 95% confidence interval; Fig. 6A). In contrast, the gaze direction of *C. noda* ants during the voltes was randomly distributed (Rayleigh test: $z=1.29$, $n=13$, $P=0.28$; Fig. 6B). The same was true for *C. fortis* ants – they also did not fixate the nest direction during voltes (Rayleigh test: $z=2.46$, $n=11$, $P=0.08$; Fig. 6C). In contrast to *C. noda*, *C. fortis* never performed any pirouettes during which they stopped to look back to the nest entrance (Fig. 5). *Cataglyphis aenescens* ants inhabiting the same clearings in the Greek pine forest as *C. noda* also performed pirouettes and looked back to the nest entrance during the longest stopping phases (Rayleigh test: $z=10.17$, $n=11$, $P<0.05$; 183.5 deg, mean vector, 172.5–194.4 deg, 95% confidence interval; Fig. 6D).

DISCUSSION

Conspicuous turns have been observed in several desert ant species (*C. fortis*: Fleischmann et al., 2016; Stieb et al., 2012; *C. bicolor*: Wehner et al., 2004; *C. aenescens*: Petrov, 1993; *Cataglyphis bombycina*: Wehner, 1994; Wehner and Wehner, 1990; *M. bagoti*:

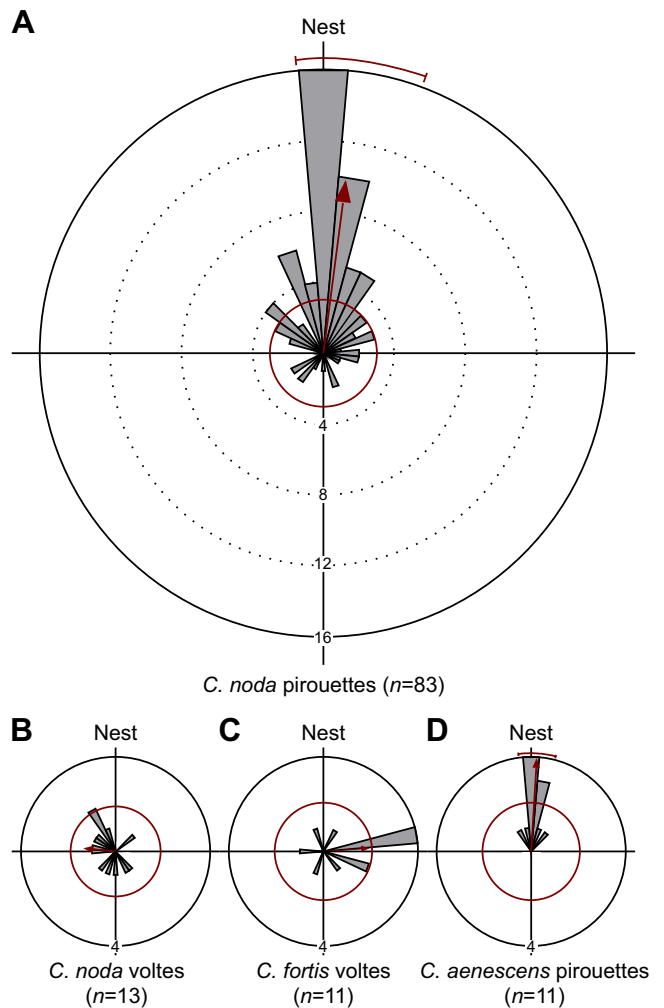


Fig. 6. Viewing directions during the longest stopping phases. Data are shown in gray and the corresponding statistics are shown in red. The width of the circular histogram bins was 10 deg. The red circle indicates Rayleigh's critical value $\alpha=0.05$. The red arrow indicates the *r*-vector pointing in the mean direction. If the red arrow exceeds the red circle, the data are directed and not randomly distributed. In that case, the 95% confidence interval is also shown (red circular line). If the expected direction (nest) lies between the confidence interval limits, we assume that the ants look back at the nest entrance. (A) *Cataglyphis noda* mean gaze direction during the longest stopping phases of their pirouettes was not significantly different from the nest direction. (B) In contrast, *C. noda* volte gaze was non-directional. (C) The same was true for the gaze direction of *C. fortis* during the longest stopping phases of their voltes – there was no preferred viewing direction towards the nest. (D) *Cataglyphis aenescens* ants inhabit the same clearings as *C. noda* ants, and also looked back to the nest entrance during the longest stopping phases of their pirouettes. In these diagrams, only the turns that had at least one stopping phase (>100 ms) were included – all turns without stopping phases were disregarded here (see Fig. 5).

Wystrach et al., 2014; *O. robustior*: Müller and Wehner, 2010). However, these turns have never been directly compared with each other. In this study, we showed that both *C. noda* and *C. aenescens* inhabiting a pine forest in Greece (Fig. 1A) performed voltes as well as pirouettes during their learning walks. These different types of turns can be easily distinguished qualitatively – the former is a walked circle whereas the latter consists of a full or partial rotation about the body axis. However, there were also quantitative differences – the number of stops per turn was higher in pirouettes than in voltes in both species. Most importantly, *C.*

noda as well as *C. aenescens* only stopped to gaze back at the nest entrance during the pirouettes. Furthermore, in partial pirouettes, the turning-in rotations were slower than the turning-out rotations as is the case in *O. robustior* (Müller and Wehner, 2010). In contrast, *C. fortis* inhabiting a featureless saltpan in Tunisia (Fig. 1B) did not perform any pirouettes and did not look back at the nest. We manipulated the natural panorama around the nest entrance using artificial landmarks (Fig. 1C,D). However, even this enrichment of the visual environment did not induce the performance of pirouettes in *C. fortis* with pauses directed to the nest entrance, even though experiments showed that the ants learn these landmarks reliably during their learning walks (Fleischmann et al., 2016). It is noteworthy, however, that the artificial landmarks did not enrich the visual panorama comparable to the natural environment of *C. noda* (Fig. 1A versus B). Therefore, one might speculate that the panorama was not visually enhanced enough to induce the performance of pirouettes. We think this is unlikely, because other desert ants that live in cluttered but less structured environments than the pine forest of the Greek *Cataglyphis* ants in this study also perform turns and look back to the nest entrance repeatedly during their learning walks (Müller and Wehner, 2010; Wehner et al., 2004). Why is it that *C. fortis* does not invest any time in stopping and looking back at the nest entrance? As its natural habitat usually does not offer a prominent panorama and all directions look alike, it may not be worth making distinct snapshots of the panorama, as has been suggested for the Namibian desert ant *O. robustior* (Graham et al., 2010). These ants only stop once or twice during their back turns (Müller and Wehner, 2010). This suggests a possible correlation between the richness of the visual scene in the natural environment and the number of stopping phases during the frequent turns of the desert ants performing learning walks [i.e. *C. fortis*: no landmarks (salt pans and chotts) – exclusively voltes without stopping phases, *O. robustior*: few landmarks (a skyline of distant dunes and acacia trees) – only nest-centered stopping phases during pirouettes; Müller and Wehner, 2010; *C. noda* and *C. aenescens* (forest): many landmarks, i.e. a lot of visual information available – two types of turns with several stopping phases during pirouettes]. Further analyses should investigate whether fixation directions are associated with panorama features. Wood ants (*Formica rufa*), for example, look back to fixate a landmark when becoming familiar with a new feeder (Nicholson et al., 1999). Therefore, it is possible that desert ants might fixate prominent landmarks during the other stopping phases. However, systematic fixations of specific landmarks could not be observed by qualitative judgments, whereas the look back to the nest entrance behavior was as obvious in the Greek *Cataglyphis* species as in the Namibian *O. robustior*.

Besides the question of the purpose of the other stopping phases during the pirouettes, there are two other pressing questions: (1) what enables the ants to look back precisely towards the nest entrance?; and (2) why do *Cataglyphis* desert ants perform different types of turns? Concerning the first question, it has been proposed that the main navigational tool, i.e. path integration, offers the reference system needed to precisely gaze at the nest (Graham et al., 2010; Müller and Wehner, 2010). Further experiments need to be conducted to verify that path integration enables the Greek *Cataglyphis* ants in their landmark-rich habitat to turn back to the nest, as opposed to another mechanism, such as landmark guidance. Concerning the second question, it may be that there are anatomical reasons for performing different types of turn (Wehner, 1994). However, the behavioral trait to perform pirouettes is independent from morphological traits enabling different desert ant species to

raise their gasters to improve their mobility (McMeeking et al., 2012). This indicates that the habitat, rather than anatomical constraints or phylogenetic relationships, exerts a selection pressure on the performance of the different types of turns.

Therefore, the second question has to be reformulated: what might be the function of the voltes performed exclusively (*C. fortis*) or in addition to other turns (*C. noda*, *C. aenescens*)? As mentioned above, the main navigational toolkit of *Cataglyphis* is path integration (Ronacher, 2008; Wehner, 2008). To determine the direction of their home vectors, the ants mainly rely on celestial cues, especially the polarization pattern and the azimuthal position of the sun (Wehner and Müller, 2006). In principle, compass information can be deduced from the polarization pattern by either a sequential or an instantaneous method (Wehner and Labhart, 2006). Voltes could provide the rotatory component necessary for the sequential method (Wehner, 1987b, 1994). Moreover, voltes may be used by desert ants to learn the configuration of landmarks close to the nest entrance even though they do not include stopping phases like pirouettes. Regardless, *C. fortis* ants learn the artificial landmarks surrounding the nest entrance even though they do not perform any pirouettes or other turns with distinct stopping phases (Fleischmann et al., 2016). It is not known how ants – or other animal species – store snapshots or other visual information in their brains. However, it was shown that short-term light exposure at the beginning of the ants' foraging careers has long-term effects on the synaptic architecture in visual subregions of the mushroom bodies, high order sensory integration and learning and memory centers (Stieb et al., 2010, 2012). Similarly, microglomerular synapses in the lateral complex, the last synaptic relay station in the neural pathway of the sky compass are influenced by light particularly in the UV region of the spectrum during first exposure (Schmitt et al., 2016). We hypothesize that visual information gained by different types of turns during learning walks may represent crucial elements triggering neuroplastic calibrations in visual pathways.

Interestingly, circular movements and rotatory motifs are important not only in the learning walks of desert ants but also in the orientation behavior of other arthropods. Learning flights of flying hymenoptera include repeated arcs, loops and turn-backs (honeybees: Becker, 1958; Capaldi and Dyer, 1999; Capaldi et al., 2000; Degen et al., 2015, 2016; Lehrer, 1991, 1993; Opfinger, 1931; Vollbehr, 1975; wasps: Peckham and Peckham, 1898; Stürzl et al., 2016; Tinbergen, 1932; Zeil, 1993a,b; Zeil et al., 1996; bumblebees: Collett et al., 2013; Hempel de Ibarra et al., 2009; Philippides et al., 2013; Riabinina et al., 2014; Robert et al., 2017; Wagner, 1907). Dung beetles perform rotations about their vertical axis before rolling a ball away from the dung pile (Baird et al., 2012), during which they take a snapshot of the celestial scenery (el Jundi et al., 2016). Desert spiders also perform learning walk-like behavior: they leave their burrows in sinusoidal paths when departing to unfamiliar terrains (Nørgaard et al., 2012).

In conclusion, different types of turns performed by desert ants (and other arthropods) during learning walks (or flights) are likely to serve different functions. Pirouettes during which the desert ants look back to the nest entrance are only performed by ants inhabiting cluttered environments (*C. noda* and *C. aenescens*). The stopping phases during pirouettes are most suited to taking snapshots (Graham et al., 2010; Müller and Wehner, 2010), suggesting that the ants take snapshots of the distant panorama around the nest entrance. Additionally, all *Cataglyphis* species investigated so far performed voltes, which may provide the rotational movement needed to successfully calibrate the celestial cues as compass tools or serve other navigational purposes like memorizing the configuration of nearby landmarks.

Acknowledgements

We thank the Tunisian and the Greek governments for the permits to conduct our experiments in these two wonderful home countries of *Cataglyphis*. We especially want to thank the management board of the Schinias National Park for permission to perform our research in the Schinias National Park in Marathon. Furthermore, we are deeply grateful for the indispensable support on site by Maria Trivourea and Olga Papigioti. We also want to thank Christos Georgiadis for introducing us to the Greek *Cataglyphis* ants and for his help with administrative issues. In addition, Christos made contact with two students from the University of Athens, Thanos Tsiatouras and Tom Zisis, who kindly enriched our field team in 2016 and helped to record the learning walks of *C. aenescens*. We also want to thank all members of the field teams of 2014, 2015 and 2016, without whom the experiments could not have been performed in this way. We thank Bernhard Ronacher, who supported our research excursions with his expertise concerning *Cataglyphis* fieldwork and by lending us his VW bus, Jochen Zeil for help with data analysis and the introduction to the Digilite application, for many discussions during the project and for his remarks concerning the manuscript, and Martin Strube-Bloss for helping to solve Matlab problems. We thank two anonymous reviewers for their very helpful comments.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: P.N.F., R.G., R.W., W.R.; Methodology: P.N.F., R.G., R.W., W.R.; Software: P.N.F., R.G.; Validation: P.N.F., R.G.; Formal analysis: P.N.F., R.G.; Investigation: P.N.F., R.G.; Resources: W.R.; Data curation: P.N.F., R.G.; Writing - original draft: P.N.F.; Writing - review & editing: P.N.F., R.W., W.R.; Visualization: P.N.F.; Supervision: P.N.F., R.W., W.R.; Project administration: P.N.F., R.W., W.R.; Funding acquisition: R.W., W.R.

Funding

This study was supported by the Deutsche Forschungsgemeinschaft (DFG), Collaborative Research Center SFB1047 'Insect Timing' [Project B6 to W.R. and R.W.].

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.158147.supplemental>

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