

## RESEARCH ARTICLE

# Desert ants benefit from combining visual and olfactory landmarks

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### SUMMARY

The desert ant, *Cataglyphis fortis*, uses both visual and olfactory cues to guide its return to the nest. The ants use vision-based path integration for long-distance navigation and memorize the visual and olfactory surrounding of the nest to finally locate the entrance. In the present study we investigated how the visual and the olfactory navigation systems interact. In field experiments ants were trained to associate the nest with a visual cue, an olfactory cue or a combination of both cues. We tested ants after one, five and 15 training runs, to investigate whether the ants would make use of the training cues to pinpoint the nest. We found that they were slow to learn the location of the nest when it was specified by just an olfactory or a visual cue. However, the ants focused their nest search after the first training run with the combined cue. Equally experienced ants responded to the individually presented visual or olfactory cues with the same high accuracy as they did to the combined cue. After 15 training runs, the combined cue still evoked an accurate response in the test, whereas the individually presented cues no longer did. Apparently, *C. fortis* benefit from combining their visual and olfactory navigational tools, because the bimodal sensory input accelerates the acquisition of landmark information.

Key words: desert ants, landmark, navigation, olfaction, vision.

### INTRODUCTION

Landmark ambiguity during navigation can be reduced either by increasing sensory sensitivity or by integrating information deriving from several modalities (Wessnitzer and Webb, 2006). The desert ant *Cataglyphis fortis* Fabricius 1793 has, so far, been a model organism for studying mainly visual orientation (Wehner, 2003). The individually foraging ants leave their nests for long-range foraging trips. Once they encounter a food item they return to the inconspicuous nest entrance on a straight path following their home vector. The ant's home vector is the continuously updated and reversed sum of all directional and translational movements (Wehner, 2003; Wittlinger et al., 2006). Owing to the egocentric nature of the ants' path integration system, errors accumulate and the home vector leads the ants only to the approximate vicinity of the nest. However, for the survival of the foragers it is essential to return to the nest as fast as possible and to minimize the time spent outside the nest in the hostile habitat. Therefore, to reliably locate the nest entrance the ants make use of visual landmarks (Wehner, 2003). The ants learn the visual surroundings of the nest and use this knowledge when returning from their foraging trips. Unlike in, for example trail-laying ant species, olfactory orientation was thought to play no major role in *C. fortis*, with the exception of when locating food sources (Wolf and Wehner, 2000). Only recently, it was shown that, in addition to the visual panorama, *C. fortis* also memorizes environmentally derived olfactory cues and uses this information for close-range navigation (Steck et al., 2009; Steck et al., 2010).

This study investigated whether *C. fortis* is able to use the combination of visual and olfactory cues and whether combined cues improve the homing performance of *C. fortis*.

### MATERIALS AND METHODS

#### Experimental site

Field experiments were performed in the ants' natural habitat, the dried-out salt lakes in Northern Africa. The experimental site was located near the village of Menzel Chaker, Tunisia (Sebkhet Bou Jemel, 34°96'N, 10°41'E).

#### Experimental protocol

Foraging ants were trained to associate the nest entrance with an olfactory cue, a visual cue or a combination of both cues. Each training and test was conducted in linear channels with a U-shaped cross section. The channels were composed of aluminium modules (length, 1 m; width, 7 cm; height, 7 cm). The channel walls were covered with a homogeneous light-coloured adhesive tape and the channel floor was coated with quartz sand to eliminate reflections. The training and the test channel were aligned in parallel, with the wind blowing from the nest entrance to the feeder (Fig. 1A).

#### Training

We enclosed an ants' nest with a low bucket and connected it *via* a tube to the training channel (Fig. 1A). The ants were trained to visit a feeder positioned 1 m downwind of the inconspicuous nest entrance in the channel floor. The entrance hole was marked by one of the following nest-defining cues.

#### Visual cue

As a visual cue we used two pieces of black cardboard (each 10 cm wide, 7 cm high) that were placed adjacent to the nest entrance on the channel walls (Fig. 1B). Because *C. fortis* has a visual resolution of approximately 3 deg (Labhart, 1986; Zollikofer et al., 1995) the

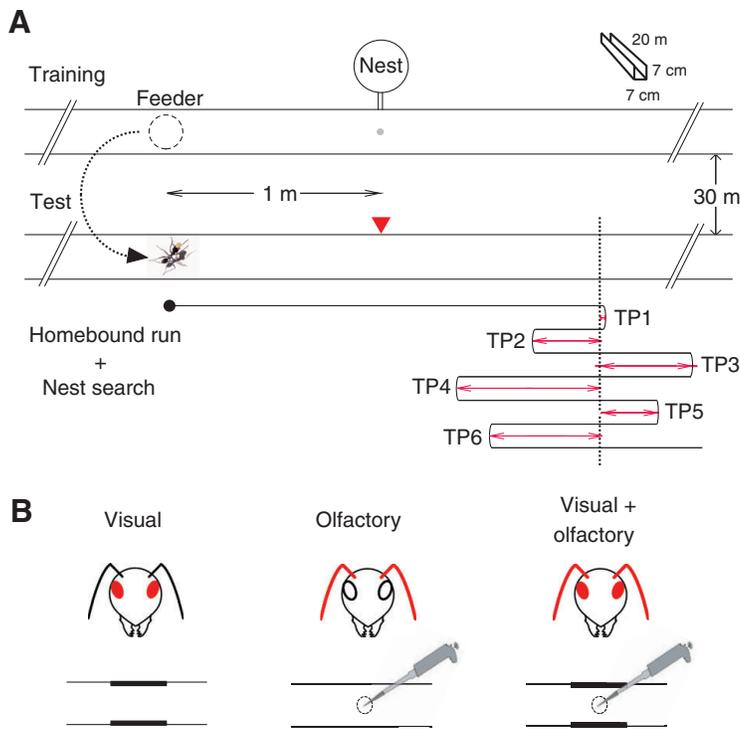


Fig. 1. Training, test protocol, schematic homebound run, nest search and data acquisition. (A) Top diagram: ants were trained to visit a feeder 1 m downwind of the nest entrance (grey dot) in linear channels (grey lines; sizes given in inset). The exit from the training channel to the nest was marked by a nest-defining cue. Bottom diagram: example specimen homebound run and nest search (zigzag line; for simplicity projected outside the channel). Black dot, point of release; red arrowhead, position of fictive nest as defined by the path integrator. Dotted vertical line, position of nest-defining cue in test channel. For additional specimen runs see Fig. 2. TP1–TP6: the first six turning points of the nest search were recorded and their distances to the nest-defining cue were calculated (red double-headed arrows). (B) The test situations and the symbols used in subsequent figures. Visual cue: two black odourless pieces of cardboard attached to the channel walls; olfactory cue: an invisible drop of diluted indole applied at the entrance hole (reapplied every 20 min); combined cue: visual and olfactory cues presented together.

black cardboard became visible to an approaching ant from a distance of approximately 35 cm. The pieces of cardboard covered the largest part of the ant's visual field (i.e. were most salient) at the position of the nest entrance. We tested whether the visual cue provided additional olfactory information by analyzing the air above the cardboard using gas chromatographic analysis (Agilent Technologies, Santa Clara CA, USA; model 7890A GC-MS). We did not detect any cardboard-derived olfactory cues (data not shown).

#### Olfactory cue

As an olfactory cue we applied 2  $\mu$ l of diluted indole (1:50 in hexane) directly at the nest entrance. In order to ensure the presence of the cue at all times during the training, the olfactory cue was reapplied every 20 min; for a detailed description see Steck et al. (Steck et al., 2009). The range of the olfactory cue was determined using a photoionization detector (Aurora Scientific Inc., Ontario, Canada; model 200A). Using this device we detected the volatiles until 50 cm downwind of the odour source, with the olfactory cue being strongest directly at the odour source, i.e. at the nest entrance. For a detailed description of the plume structure in the channel see Steck et al. (Steck et al., 2010).

#### Combined cue

The combined cue consisted of the visual cue (two pieces of black cardboard) and the olfactory cue (2  $\mu$ l of diluted indole).

After the nest had been connected to the training channel the ants located the feeder usually within a few minutes. Food crumbs were provided in a feeder trap, i.e. a cup placed in a hole in the ground in the centre of the channel. The ants could enter the feeder trap but were not able to leave it without assistance. Having entered the feeder trap for the first time, the ants were marked individually with a two-colour code (dots of enamel paint applied on the gaster) and were released from the feeder trap. For each marked ant we counted how many training runs it had conducted. For each training situation

we used a different nest. That means that a nest that had been used for training with, e.g. a visual cue, was never used for training with another nest-defining cue again.

#### Test, data collection and analysis

For the test, marked ants were caught at the feeder and were released for their homebound run in a test channel 2 m downwind of one of the nest-defining cues (Fig. 1). Only ants that had gathered a food item were caught and tested. The test channel was not connected to a nest and therefore, did not contain an exit hole. The ants started their homebound run and then began a systematic nest search. The ants' home vector was 1 m in length, because they had covered the distance from the nest to the feeder (i.e. 1 m) before being displaced from the feeder to the test channel (Fig. 1A). This experimental setup ensured that there was a conflict between the path integrator information and the landmark navigation information. Therefore, we were able to tell which information the ants were relying on: would the ants run off their home vector and search at the nest position as defined by the path integrator, or did they learn to associate the nest entrance with one of the landmarks that was positioned 1 m behind the path integrator position?

An ant having run off its home vector without encountering the nest switches to a systematic and well-investigated nest search (Mueller and Wehner, 1994; Wehner and Srinivasan, 1981). During this nest search *C. fortis* carries out loops around the position where it assumes the nest entrance to be, returning at regular intervals to the estimated position of the nest (Wehner and Wehner, 1986).

As a result of the linear channels the ants' systematic nest search is reduced to one dimension and therefore, is characterized by subsequent turning points (Fig. 1A and Fig. 2) (Cheng and Wehner, 2002). We recorded the first six turning points with an accuracy of 5 cm by placing a measuring tape alongside the test channel. To display the search pattern we calculated search density plots for each experimental situation (Fig. 3). Therefore, we divided the total distance of the test channel into virtual 5 cm bins. The visits per bin

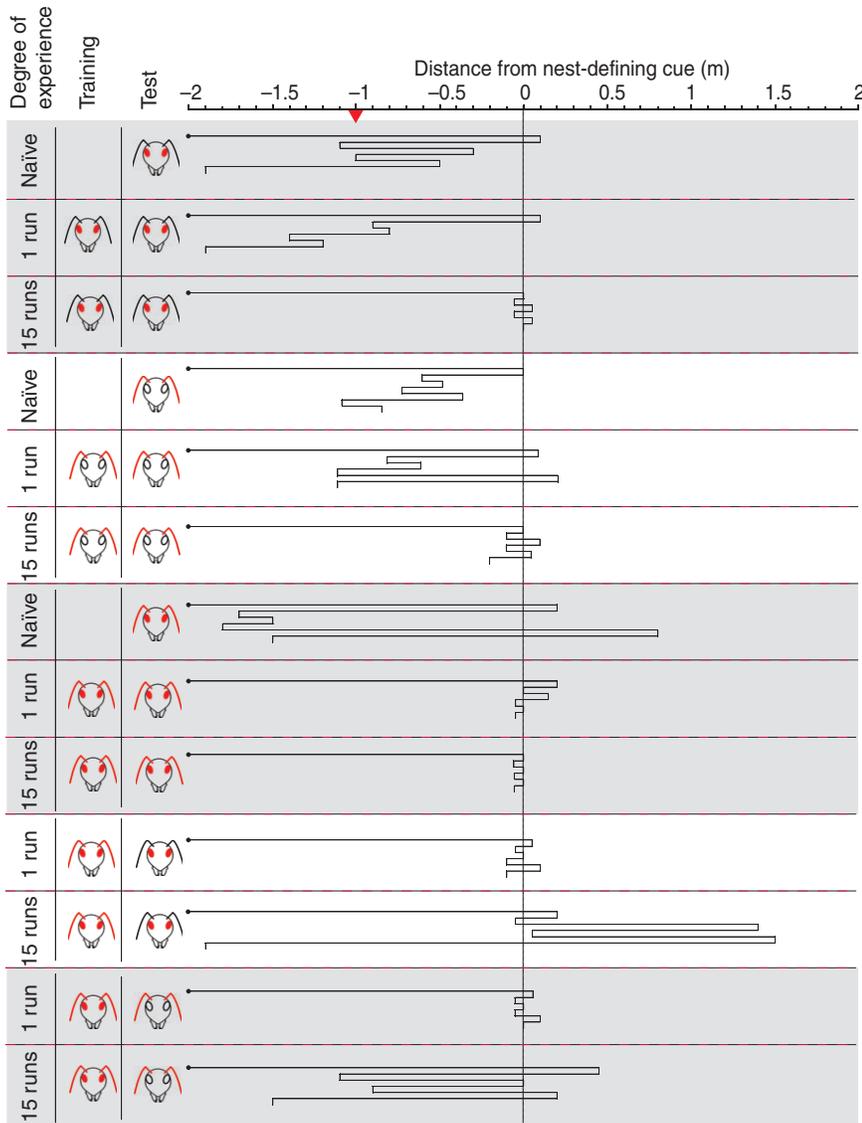


Fig. 2. Example specimen runs. Schematic nest searches of naïve ants and ants trained and tested with either the individual or the combined cues. Degrees of experience: naïve ants (i.e. tested before the cues were installed in the training channel); 1-run ants (i.e. tested after their first outbound run with the installed cue, but before they could accomplish their first inbound run); and 15-run ants [i.e. trained and tested with the installed visual cue (black ant with red eyes), olfactory cue (black ant with red antennae) or combined cue (black ant with red eyes and red antennae)]. Black dot, the point of release for each homebound run at position  $-2\text{ m}$  from nest-defining cue; red arrowhead, position of fictive nest as defined by the path integrator; dotted vertical line, position of nest-defining cue in the test channel. The first six turning points after the ants passed the cue for the first time were taken for analysis, i.e. for search density plots (see Fig. 3) and search accuracy plots (see Fig. 4). For simplicity, runs are projected two-dimensionally with the time course for each run going from top to bottom.

were cumulated for each ant during its nest search and summed up for each experimental group. Consequently, the peak of the search density plot depicts the bin most often visited, i.e. the estimated position of the nest entrance. The search density plots were normalized to the total number of bin visits.

Apart from the position of the assumed nest entrance, the shape of the search density plots reveals additional information. The ‘sharpness’ of the peak, i.e. the narrowness of the nest search reflects the ants’ confidence in the nest position, as the loops decrease in size with increasing confidence in the estimated position of the nest (Merkle et al., 2006). We used the median distance between the first six turning points and the position of the nest-defining cue as a measure of confidence in the estimated position of the nest, i.e. the search accuracy (Fig. 1). A nest search centred closely around the position of the nest-defining cue results in a short median distance between turning points and cue, whereas a broad search pattern is reflected in a long median distance.

In order to investigate how experience affects the homing performance, we tested naïve ants (i.e. ants that arrived at the feeder before the nest-defining cues had been installed) 1-run ants (i.e. ants that arrived for the first time at the feeder after the nest-defining cues had been installed), 5-run ants and 15-run ants.

### Statistics

Statistical differences between the experimental groups were based on the median distances between the first six turning points and the position of the nest-defining cue, i.e. the search accuracy, and were calculated with GraphPad InStat (GraphPad Software Inc., La Jolla, CA, USA).

## RESULTS

### How do naïve ants respond to the cues?

We first tested how naïve animals respond to the visual, the olfactory or the combined cues. The turning points of naïve ants were ranged widely around the path integrator position (naïve ants in Fig. 2) and search patterns were broad (naïve ants in Fig. 3). Moreover, animals that were confronted with the olfactory cue for the first time seemed to be slightly repelled as the search density plot exhibits a local minimum at the position of the nest-defining cue (Fig. 3).

### Do ants rely on information derived from the path integrator or on landmarks?

Having experienced one of the cues, be it the visual, the olfactory or the combined cue, at least once in the training, the search density

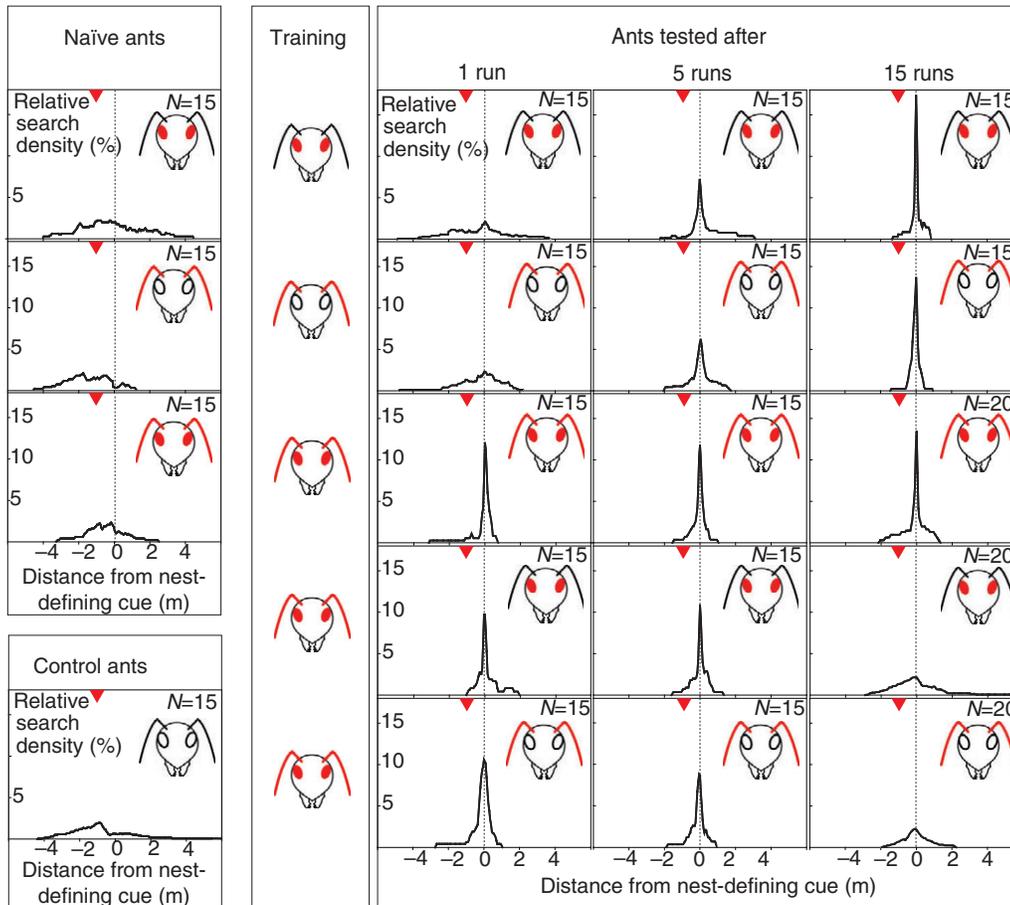


Fig. 3. Search densities of differently trained and tested ants. (Left top) Naïve ants tested with a visual (black ant with red eyes), an olfactory (black ant with red antennae) or a combined cue (black ant with red eyes and red antennae). (Left bottom) Control ants trained and tested without any cue. Right, relative search densities of differently experienced ants, trained and tested with the individual or the combined cues. First column, training cue; second to fourth columns, degree of experience; diagram rows, experimental group; black dotted line, position of nest-defining cue; red arrowhead, fictive nest defined by the path integrator; point of release,  $-2$  m. The search plots include the first six turning points after the ants had passed the cue for the first time.

plots exhibit the maximum at the position of the cue and not at the path integrator position (Fig. 3).

#### Does a combined olfactory and visual nest-defining cue improve the homing performance of *C. fortis*?

Ants that were tested with an olfactory or a visual cue after they had experienced it only once displayed broad search patterns (1-run ants in Fig. 3) with low search accuracies, i.e. long median distances between turning points and the nest-defining cues (1-run ants in Fig. 4A,B). With increasing experience of the cue the ants exhibited an increased search density at the position of the cue (Fig. 3), and displayed the most focused search after 15 training runs (Fig. 3). Accordingly, the median distances between the turning points and the cues became shorter with increasing experience (Fig. 4A,B), i.e. the ants became more confident about the position of the nest. At no experiential stage did the search accuracies of visually trained and tested ants differ from those of olfactory trained and tested ants (Fig. 4A,B). In contrast, when trained with the combined visual and olfactory cue, the animals displayed a focused search at the position of the combined cue after the very first training run (Fig. 3). Despite the ants' single experience with the combined cue their searches were as focused as after 15 training runs with the individual cues (Fig. 4, compare 15-run ants in A and B with 1-run ants in C). Although the ants needed 15 training runs with the single cues to reach the same accuracy as ants trained once with a combined cue, the final accuracy was the same irrespective of whether the ants were trained and tested with the individual or the combined cues (15-run ants in Fig. 3 and Fig. 4A–C).

We finally investigated whether the ants would recognize a single olfactory or visual cue when they had been trained with a combination of both cues. Therefore, we again trained ants to associate their nest entrance with a combined cue, but now tested them either with the single olfactory cue or the single visual cue. Even after one single training experience with the combined cue the ants concentrated their search on the single test cues (Fig. 3 and 1-run ants in Fig. 4C–E). However, having experienced the combined cues several times, the ants lost their confidence in the singly presented cues, i.e. displayed a broad search pattern with long distances between the turning points and the cues (Fig. 3 and 15-run ants in Fig. 4D,E).

#### DISCUSSION

Desert ants have been shown to use visual and olfactory cues for navigation. Although the visual system has been well studied (Bisch-Knaden and Wehner, 2003a; Wehner, 2003), the use of olfactory landmarks has been described only recently (Steck et al., 2009; Steck et al., 2010). In the present study we examined whether and how the visual and the olfactory navigation systems interact. We investigated whether the ants benefit from nest-defining cues that combine visual and olfactory information or only relied on single visual or olfactory cues.

#### Ants are not innately attracted to the cues

All nest-defining cues used in this study did not attract naïve ants (naïve ants in Fig. 3). Moreover, the ants that had never experienced the olfactory cue before appeared to pass the olfactory cue less

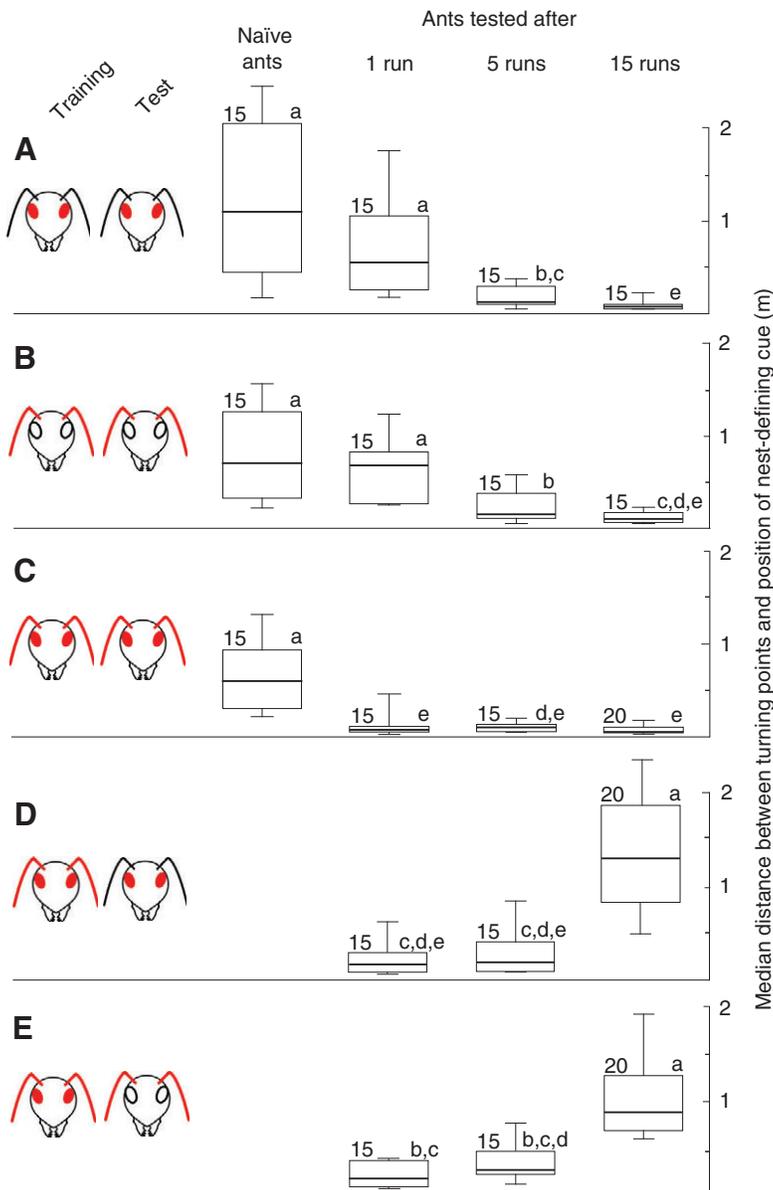


Fig. 4. Search accuracies of differently experienced ants trained and tested with the individual or the combined cues. For the degree of experience and for the training and test protocols (A–E) see Figs 1 and 2. Box plots are the median distances between turning points and the nest-defining cues. Bold black line, median; box, interquartile range; whiskers, 90th and 10th percentiles. Numbers on the upper left corner of the box are sample sizes. Letters on the upper right of the boxes indicate statistical differences (same letter,  $P > 0.05$ ; different letters,  $P < 0.05$ ; Kruskal–Wallis test with Dunn's *post hoc* analysis). Each ant was tested only once.

frequently (Fig. 3). Because naïve ants had no external cue, i.e. visual and/or olfactory landmarks, they could rely solely on the information derived from the path integrator. Therefore, the maxima of the search density plots for these experimental groups were at the position as calculated by the path integrator (control ants and naïve ants in Fig. 3).

#### Ants that had been trained to associate their nest with a landmark rely on landmark information rather than on path-integrator-derived information

The ants' responses to the cues in the test changed considerably when there had been a cue installed during training and the ants were asked to associate their nest entrance with the cues. We observed a shift of the maxima of the search density plots towards the position of the nest-defining cue even after the very first training run (1-run ants in Fig. 3). However, the search accuracies of the visual- or olfactory-trained and tested 1-run ants did not differ significantly from the search accuracies of naïve ants (Fig. 4A,B). It needed five to 15 experiences with the individual cues before the ants started to focus their search on the cues, with

the highest accuracy being reached only after 15 experiences (Fig. 4A,B). This acquisition rate is comparable to findings in desert ants that had to learn visual landmarks in the open field (Bisch-Knaden and Wehner, 2003b; Narendra et al., 2007). It is difficult to precisely quantify the salience and the operating distance of the visual and the olfactory cues that we used in the present study. However, both cues could be detected by the ants at a distance of between 35 and 50 cm from the nest entrance and, most important, both cues reached their highest intensity directly at the nest. Our findings that the ants learned the association between their nest entrance and the visual or the olfactory cue equally fast (Fig. 4A,B) points at a comparable salience of these two cues. Furthermore, they show that *C. fortis*, which so far was considered to be a mainly visually guided navigator, is able to make use of olfactory cues equally well.

#### Ants benefit from combined visual and olfactory cues

The ants that were trained with the combined visual and olfactory cues exhibited a search accuracy that did not differ from ants that had repeatedly experienced individual cues. However, being

trained with the combined cues the ants focused their search on the combined test cue after just a single training experience (1-run ants in Fig. 4C). The rapid location of the nest entrance after a long-lasting foraging trip in the inhospitable desert is crucial for an ant. Therefore, faster acquisition of the combined cue might be of significant benefit for *C. fortis*, especially as ants of the genus *Cataglyphis* usually conduct only 20–50 foraging runs during their brief lifetime (Harkness, 1977; Schmid-Hempel and Schmid-Hempel, 1984). The benefit of multisensory training in subsequent unimodal tests has been shown for humans (Shams and Seitz, 2008) and *Drosophila* (Guo and Guo, 2005). The ants' accelerated acquisition of the combined cue thus supports the enhanced perception (Chow and Frye, 2008; Goyret et al., 2007; van Swinderen and Greenspan, 2003) and learning (Reinhard et al., 2006; Rowe, 2002; Waeckers and Lewis, 1994) of bimodal signals.

We also tested how ants that had been trained with the combined cue responded to the single olfactory or visual cues. We found that after only one single outbound run with the combined cue the ants concentrated their search on the single olfactory or visual cues as accurately as on the combined cue (1-run ants in Fig. 4C–E). Hence, although being trained to a combination of both cues, the ants accepted the single cues as nest-defining landmarks. The finding that the ants learned the single cues faster in a bimodal background (1-run ants in Fig. 4A,B,D,E) again supports the enhanced perception and learning of bimodal signals (Chow and Frye, 2008; Goyret et al., 2007; Pearce and Bouton, 2001; Reinhard et al., 2006; Rowe, 2002; van Swinderen and Greenspan, 2003; Waeckers and Lewis, 1994).

However, after extended training with the combined cue the ants displayed a broad search pattern when tested with the individual cues (Fig. 3, and 15-run ants in Fig. 4D,E). Apparently, with increasing experience the ants had realized that the single cues were only valid when detected in combination. Navigating subjects are often confronted with similar, i.e. ambiguous visual landmarks (Wessnitzer and Webb, 2006), which could become unequivocal if a second modality is added. In the habitat of *C. fortis* visual landmark information can be ambiguous, i.e. several landmarks (e.g. different shrubs of halophytic plants) can be similar in shape and size. Therefore, the use of bimodal cues could prevent confusion arising from environmental ambiguity. *C. fortis* has previously been a model organism in which to study orientation because of its recognized visually based navigation system. However, we found that olfactory cues are learned as fast as visual cues, whereas combined visual and olfactory landmarks are learned much faster. Apparently, the hostile habitat of *C. fortis* pushes the evolution of a sophisticated navigational machinery, exploiting and combining input deriving from different sensory modalities.

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## REFERENCES

- Bisch-Knaden, S. and Wehner, R.** (2003a). Landmark memories are more robust when acquired at the nest site than en route: experiments in desert ants. *Naturwissenschaften* **90**, 127–130.
- Bisch-Knaden, S. and Wehner, R.** (2003b). Local vectors in desert ants: context-dependent landmark learning during outbound and homebound runs. *J. Comp. Physiol. A* **189**, 181–187.
- Cheng, K. and Wehner, R.** (2002). Navigating desert ants (*Cataglyphis fortis*) learn to alter their search patterns on their homebound journey. *Physiol. Entomol.* **27**, 285–290.
- Chow, D. M. and Frye, M. A.** (2008). Context-dependent olfactory enhancement of optomotor flight control in *Drosophila*. *J. Exp. Biol.* **211**, 2478–2485.
- Goyret, J., Markwell, P. M. and Raguso, R. A.** (2007). The effect of decoupling olfactory and visual stimuli on the foraging behavior of *Manduca sexta*. *J. Exp. Biol.* **210**, 1398–1405.
- Guo, F. Z. and Guo, A. K.** (2005). Crossmodal interactions between olfactory and visual learning in *Drosophila*. *Science* **309**, 307–310.
- Harkness, R. D.** (1977). Quantitative observations on the foraging of nests of an ant *Cataglyphis bicolor* in Greece. *Acta Entomol. Jugoslavica* **13**, 21–34.
- Labhart, T.** (1986). The electrophysiology of photoreceptors in different eye regions of the desert ant, *Cataglyphis bicolor*. *J. Comp. Physiol. A* **158**, 1–7.
- Merkle, T., Knaden, M. and Wehner, R.** (2006). Uncertainty about nest position influences systematic search strategies in desert ants. *J. Exp. Biol.* **209**, 3545–3549.
- Mueller, M. and Wehner, R.** (1994). The hidden spiral: systematic search and path integration in desert ants, *Cataglyphis fortis*. *J. Comp. Physiol. A* **175**, 525–530.
- Narendra, A., Si, A., Sulikowski, D. and Cheng, K.** (2007). Learning, retention and coding of nest-associated visual cues by the Australian desert ant, *Melophorus bagoti*. *Behav. Ecol. Sociobiol.* **61**, 1543–1553.
- Pearce, J. M. and Bouton, M. E.** (2001). Theories of associative learning in animals. *Annu. Rev. Psychol.* **52**, 111–139.
- Reinhard, J., Srinivasan, M. V. and Zhang, S. W.** (2006). Complex memories in honeybees: can there be more than two? *J. Comp. Physiol. A* **192**, 409–416.
- Rowe, C.** (2002). Sound improves visual discrimination learning in avian predators. *Proc. R. Soc. Lond. B Biol. Sci.* **269**, 1353–1357.
- Schmid-Hempel, P. and Schmid-Hempel, R.** (1984). Life duration and turnover of foragers in the ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Insect Soc.* **31**, 345–360.
- Shams, L. and Seitz, A. R.** (2008). Benefits of multisensory learning. *Trends Cogn. Sci.* **12**, 411–417.
- Steck, K., Hansson, B. S. and Knaden, M.** (2009). Smells like home: desert ants, *Cataglyphis fortis*, use olfactory landmarks to pinpoint the nest. *Front. Zool.* **6**, 5.
- Steck, K., Knaden, M. and Hansson, B. S.** (2010). Do desert ants smell the scenery in stereo? *Anim. Behav.* **79**, 939–945.
- van Swinderen, B. and Greenspan, R. J.** (2003). Saliency modulates 20–30 Hz brain activity in *Drosophila*. *Nat. Neurosci.* **6**, 579–586.
- Waeckers, F. L. and Lewis, W. J.** (1994). Olfactory and visual learning and their combined influence on host site location by the parasitoid *Microplitis croceipes* (Cresson). *Biol. Control* **4**, 105–112.
- Wehner, R.** (2003). Desert ant navigation: how miniature brains solve complex tasks. *J. Comp. Physiol. A* **189**, 579–588.
- Wehner, R. and Srinivasan, M. V.** (1981). Searching behavior of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J. Comp. Physiol.* **142**, 315–338.
- Wehner, R. and Wehner, S.** (1986). Path integration in desert ants – approaching a long-standing puzzle in insect navigation. *Ital. J. Zool.* **20**, 309–331.
- Wessnitzer, J. and Webb, B.** (2006). Multimodal sensory integration in insects – towards insect brain control architectures. *Bioinspir. Biomim.* **1**, 63–75.
- Wittlinger, M., Wehner, R. and Wolf, H.** (2006). The ant odometer: stepping on stilts and stumps. *Science* **312**, 1965–1967.
- Wolf, H. and Wehner, R.** (2000). Pinpointing food sources: olfactory and anemotactic orientation in desert ants, *Cataglyphis fortis*. *J. Exp. Biol.* **203**, 857–868.
- Zollikofer, C. P. E., Wehner, R. and Fukushi, T.** (1995). Optical scaling in conspecific *Cataglyphis* ants. *J. Exp. Biol.* **198**, 1637–1646.