

Piloting in desert ants: pinpointing the goal by discrete landmarks

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Accepted 22 September 2010

SUMMARY

The inconspicuous nest entrances of the Namibian desert ant *Ocymyrmex robustior* are located on barren sandflats often devoid of any goal-defining landmark. Foragers that have returned by path integration to the rough area of the goal need a considerable amount of time to finally pinpoint the goal. Even a single landmark decreases the search time dramatically. By using artificial landmarks placed in the neighbourhood of the goal, we show that the larger the image transformations (caused by the landmarks) in the ant's visual field, the faster the homing ants localize the goal. While approaching the goal the ants do not try to fixate the landmarks frontally. Hence, even if provided with discrete landmarks rather than extended visual scenes, *Ocymyrmex* relies on image changes occurring in wide areas of its panoramic field of view rather than those occurring in a frontal fixation area alone.

Key words: piloting, desert ants, *Ocymyrmex*, panoramic vision.

INTRODUCTION

During their far-ranging foraging journeys desert ants of the genera *Cataglyphis* in northern Africa and *Ocymyrmex* in southern Africa employ path integration as their predominant means of navigation. In fact, in featureless environments such as salt pans (in the case of *Cataglyphis fortis*) and sandflats (in the case of *Ocymyrmex robustior*), path integration is the ants' only means of finding their way back home, i.e. of returning to the point of departure. However, because of the inevitable accumulation of path integration errors, homing accuracy rapidly decreases as foraging distance increases [theoretical considerations: Benhamou et al. and Cheung et al. (Benhamou et al., 1990; Cheung et al., 2007); experimental data: Merkle et al. and Merkle and Wehner (Merkle et al., 2006; Merkle and Wehner, 2010)]. For finally pinpointing the goal – an inconspicuous nest entrance, level with the barren ground – piloting by landmarks becomes a supplementary, and actually the most effective, means of visually guided spatial orientation. As in marine navigation, in which piloting by landmarks ('pilotage') is used during the approach to land in the final stage of a voyage (Bowditch 2002) [for a similar use of the term pilotage in avian and mammalian navigation, see Bingman (Bingman, 1998) and Wallace et al. (Wallace et al., 2003), respectively], *C. fortis* and *O. robustior* use mechanisms of local landmark guidance once they have arrived by path integration close to, but not exactly at, their final destination.

Experiments using sets of artificial landmarks have already shown that desert ants store views of the landmark scene around the goal and later use these stored views in one way or another to return to the goal as directly as possible (Wehner and Räber, 1979; Wehner et al., 1996; Narendra et al., 2007) [for wood ants, see Graham et al. (Graham et al., 2004)]. A number of theoretical models have been proposed on how homing can be achieved by relating currently received visual information to stored information. Among them are various template-matching models [full or partial template matching (Cartwright and Collett, 1983; Möller et al., 1999; Nicholson et al., 1999; Lambrinos et al., 2000; Franz and Mallot, 2000; Vardy and Möller, 2005)] as well as parameter-based models such as the average landmark vector model (Möller, 2001) (for a review, see

Möller and Vardy, 2006). However, we know relatively little about the kind of information that the ants are actually deriving from the visual scene surrounding their goal.

From experiments in which parts of the eyes of *C. fortis* have been covered by light-tight caps we can already conclude that only the upper half of the eye, i.e. the part dorsal to the equator of the eye, is involved in accomplishing this task, and that 360 deg structured landmark panoramas contrasting with the sky and extending not more than 2 deg above the horizon are sufficient (Wehner et al., 1996). In open-field arena experiments performed with the Australian desert ant *Melophorus bagoti* (Muser et al., 2005), Graham and Cheng obscured parts of the ant's visual field using the walls of the arena and found that homing ants rely on the full panoramic image rather than single salient features such as discrete trees or bushes, and that the lower portions of the visual panorama (up to an elevation of about 20 deg above the horizon) are more important than the upper ones (Graham and Cheng, 2009a; Graham and Cheng, 2009b).

The more distant the terrestrial marks are that surround the goal, the less precise is the spatial information that can be derived from them. This is due to the phenomenon of motion parallax: the closer the object to the observer, the larger the image displacement caused on the observer's eye during one unit step of locomotion. Hence, rather than providing the ant with full, well-structured and – in terms of ant size – distant skyline panoramas, in the present account we focused on the significance of discrete landmarks placed in the immediate neighbourhood of the goal, the nest entrance. We first asked how important even a single landmark is in increasing the homing success of *O. robustior* (one-landmark condition), when compared with the homing accuracy under landmark-free (flat-horizon) conditions. This question is especially challenging in the extremely thermophilic *Ocymyrmex* ants, which increase their foraging efficiency on the barren sandflats of the Namib desert by exposing themselves to near-lethal temperatures (Marsh, 1985a; Wehner, 1987). Under these conditions strong selection pressures exist for reducing time outside the nest as much as possible, i.e. locating the nest entrance as quickly as possible.

Second, we investigated the visual information extracted by the ants from landmarks that are situated at short distances from the goal and the approaching animal. The prevailing hypothesis is that in such cases the ants fixate the landmarks, i.e. use their frontal visual field to acquire and use information about discrete terrestrial objects. This hypothesis has been derived from arena experiments performed in wood ants, *Formica rufa* (Nicholson et al., 1999). The emphasis placed by this hypothesis on landmark fixation has even led to a model of partial image matching that comes close to the one proposed by Möller and colleagues (Möller et al., 1999) for *Cataglyphis* [on the basis of experimental data obtained in *C. bicolor* (Wehner and Räber, 1979) and *C. fortis* (Wehner et al., 1996) (see also Möller, 2001)]. In short, Nicholson and colleagues conclude from their *Formica* experiments that the ants learn about discrete objects by employing their frontal visual fields and later use these frontal visual fields to guide them back to the goal. This conclusion contrasts with the data obtained by Müller and Wehner in *Ocymyrmex* (Müller and Wehner, 2010). In acquiring visual information about discrete objects, these ants do not fixate the objects. During their well-structured learning walks they repeatedly stop and perform small pirouettes during which they read out their path integrator and orient themselves in the direction of the invisible goal rather than towards the conspicuous landmark presented in these experiments. The obvious question, then, is whether *Ocymyrmex* ants when returning to the goal fixate the landmark as *Formica* ants do, or whether they extract visual information even from a discrete-landmark scene by employing their full field of view.

MATERIALS AND METHODS

Experiments were performed in the southern African desert ant *Ocymyrmex robustior* (Stitz, 1923), a former subspecies of *O. barbigier* raised to species rank by Marsh (Marsh, 1986). Ants of the genus *Ocymyrmex* are thermophilic scavengers and thus ecological equivalents to the northern African and Asian genus *Cataglyphis* (Wehner, 1987).

The nests selected for the present study were on bare sandflats of the Kuiseb river bed next to the Gobabeb desert station in the Namib-Naukluft area (Namibia), 23°34'S, 15°03'E. In order to record the search times needed by returning foragers to locate the inconspicuous nest entrance, level with the ground, we drew a concentric circle (radius: 0.4 m) around the entrance hole. We then observed the returning ants and used stop watches to determine the time needed by the ants from entering the recording circle to entering the nest hole.

In the majority of the experiments two artificial landmarks (polyvinylchloride cylinders, 0.15 m high and 0.11 m wide) were placed at a distance of 0.4 m from the nest entrance and an angular distance of 90 deg from each other. The recording circle was divided into four 90 deg sectors with one sector flanked by the two landmarks. Search-time data were recorded for each sector separately.

Data are presented in the form of search-time histograms (bin width: 1 s) and box-plot representations. Mann-Whitney *U*-tests were used to compare the mean values of two sets of non-normally distributed data.

RESULTS

Precision of localizing the goal in flat-horizon and discrete-landmark situations

When foragers of the desert ant species *O. robustior* return to their nest, located on open sandflats, they often need a substantial amount of time to finally pinpoint the goal, a tiny hole leading to their

subterranean colony, when the near neighbourhood of the goal is devoid of any landmark (flat-horizon scene). Even when the ants are only a few centimetres away from the goal they may miss it and start extensive search movements that are similar to the ones observed in *Cataglyphis* ants [*C. bicolor* (Wehner and Srinivasan, 1981); *C. fortis* (Müller and Wehner, 1994; Merkle et al., 2006)]. This search behaviour may lead the ants away from the goal for substantial distances (sometimes more than 5 m) and considerable amounts of time (sometimes more than 10 min). Such far-ranging search movements never occur when even a single landmark is available next to the goal (discrete-landmark scene). The difference in the ants' behaviour between the two visual scenarios is documented in Fig. 1. Under flat-horizon conditions (two nests tested), the returning foragers, having reached a distance of 0.4 m from the nest entrance, searched for 14.2 s (median value; quartiles: 7.8 s and 30.0 s; *N*=113, nest A) and 23.5 s (median value; quartiles: 8.0 s and 51.0 s; *N*=90, nest M) (Fig. 1A,B) until they reached the nest entrance and vanished underground. Given the surface temperatures prevailing during the recordings (45–60°C) and the temperature dependency of the ants' running velocity (Marsh, 1985b), the animals would have needed a mere 0.9–1.6 s to directly cover the 0.4 m distance between the recording circle and the nest entrance. There are small but not significant search-time differences between the data sets from the two flat-horizon nests (*P*>0.05, *N*=203, Mann-Whitney *U*-test), which might be due to slight differences in the structure of the sandy floor surrounding the nest openings. That such textural differences can be detected by desert ants has been shown in *Cataglyphis* (Seidl and Wehner, 2006). In sharp contrast to the search times recorded at the flat-horizon nests the ants needed just 3.3 s (median value; quartiles: 2.6 s and 5.7 s; *N*=60, year 1) and 3.0 s (median value; quartiles: 2.0 s and 4.0 s; *N*=108, year 2) (Fig. 1C,D) when the nest entrance was only 0.15 m away from a conspicuous granite stone. All differences between the search times recorded in the flat-horizon and the one-landmark situations are highly significant (*P*<0.001, *N*=371, Mann-Whitney *U*-test). The two data sets obtained in the one-landmark situation were recorded at the same nest but in two different summers. Note that at this one-landmark nest the ants needed a maximum of 17 s (one outlier 37 s) and 8 s to locate the goal, while under flat-horizon conditions 13.3 and 17.8% of the returning ants searched for more than 60 s until they finally pinpointed the nest entrance.

Significance of landmark position within the approaching ant's field of view

Next we provided the flat-horizon nest A with two cylindrical landmarks located at a linear distance of 0.4 m from the nest entrance and separated by an angular distance of 90 deg from each other (see inset of Fig. 3). One day after these landmarks had been installed the search times as defined above had decreased significantly (median value: 8.3 s; quartiles: 5.2 s and 16.3 s; *N*=110; difference from data of Fig. 1A: *P*<0.001, Mann-Whitney *U*-test), and they had decreased even more on the second day (median value: 6.2 s, quartiles: 4.4 s and 11.1 s, *N*=162; Fig. 2; difference from data obtained on the previous day: *P*<0.01, Mann-Whitney *U*-test). There might have been some further decrease of search times after 3 days of training to the goal-defining landmarks, but as we know from freely foraging *Cataglyphis* ants (R.W., unpublished data), such learning tasks are accomplished rather rapidly, and hence a plateau level of homing precision might have already been reached by day two. Nonetheless, the main purpose of this experiment was not to study learning effects but to test whether the direction from which the ants approached the nest entrance had any influence on the ants'

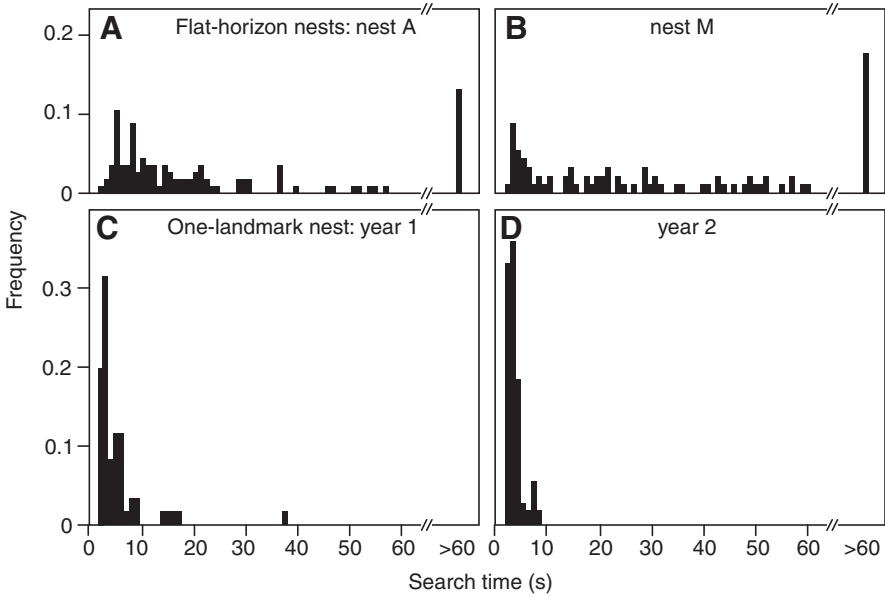


Fig. 1. Search times needed by returning ants to finally pinpoint their goal, the nest entrance, after they had crossed a recording circle with a radius of 0.4 m. (A,B) Data from two nests, in which the entrance hole was located on completely flat, barren sand surfaces devoid of any landmarks within a surrounding area of at least 10 m in diameter. $N=113$ and 90 ants, respectively. (C,D) Data obtained in two successive years at the same nest, where a single natural landmark, a large stone, lay 0.15 m from the nest entrance. $N=60$ and 108 ants, respectively. Search times are given in 1.0 s bins.

homing precision. For example, in ants that had crossed the 0.4 m recording circle in sector 1 and were running towards the nest entrance the images of the two landmarks were always located in their frontal visual field, while in ants that had entered sector 4 the landmark images shifted from the frontal (anterior) across the lateral to the caudal (posterior) parts of the visual field. As the results show (Fig. 3), sector 1 ants exhibit the longest search times (median value: 8.1 s, quartiles: 4.9 s and 13.6 s; $N=70$) and sector-3 ants the shortest ones (median value: 4.5 s, quartiles: 3.9 s and 5.5 s; $N=23$). The difference between the search times recorded in the two sectors is highly significant ($P<0.005$, Mann–Whitney U -test). The two other sectors exhibit intermediate values (sector 2: median value: 6.5 s; quartiles: 4.6 s and 11.1 s; $N=55$; sector 4: median value: 5.8 s, quartiles: 4.8 s and 8.0 s; $N=14$).

Fig. 4 depicts the azimuthal positions (angle α) and angular widths (angle β) of the two landmarks as they appear in the visual field of an ant moving towards the goal from a distance of 1 m. The smallest image transformations occur when the ants enter sector 1. Then during the approach to the goal the landmarks are always kept in the frontal visual field, with their azimuthal positions moving laterally from 12 deg to 45 deg off the forward direction, and their angular widths increasing from 5 deg to 16 deg. In contrast, if the

ants approach the goal from the opposite side, i.e. enter sector 4, the position of the landmark changes from 22 deg to 135 deg, while the widths of the landmarks first increase from 8 deg to 22 deg and then decrease again to 16 deg. Even more dramatic image transformations are experienced when the ants enter sector 3. Now the image of one landmark always remains in the frontal part of the visual field, while that of the other landmark moves from the frontal to the caudal part. These differences in the visual input parameters correspond well with the precision with which the ants localize the goal. Sector 3 ants do so most precisely, i.e. they need the shortest

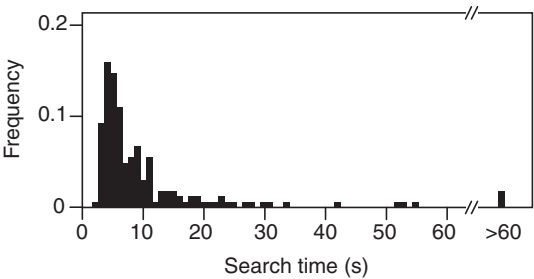


Fig. 2. Search times of ants returning to nest A (see Fig. 1A) 2 days after a pair of artificial landmarks (black cylinders at an angular distance of 90 deg from each other) had been installed 0.4 m away from the otherwise inconspicuous nest entrance. $N=162$ ants. For further conventions see Fig. 1.

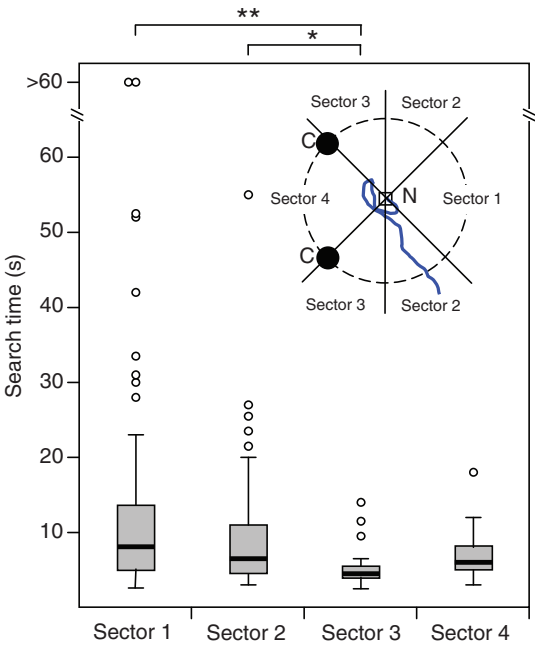


Fig. 3. Search times of ants returning to the entrance hole (N) of nest A 2 days after a pair of black cylinders (C) had been installed close to N (see Fig. 2). In the present box-plot representations the search times are given separately for the four 90 deg sectors (1–4; see inset at upper right of figure). Differences between section-specific search times are significant at the $P<0.01$ (*) or $P<0.005$ (**) level.

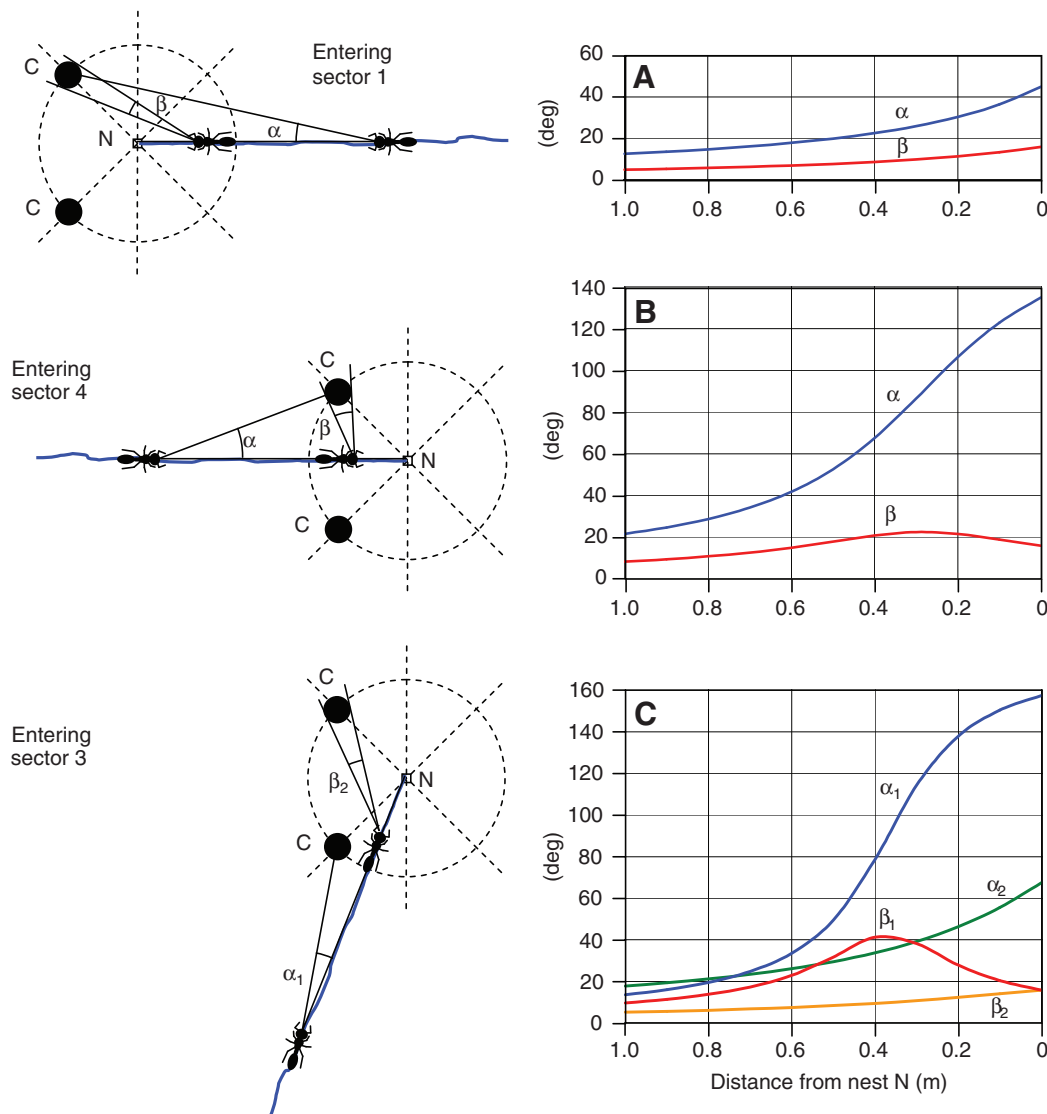


Fig. 4. Changes of angular position (α) and angular width (β) of two nest-defining landmarks (C, black cylinders) as they occur in the visual field of an ant that approaches its goal, the nest entrance (N), from a distance of 1.0 m via the centres of sector 1 (A), sector 4 (B) and sector 3 (C).

search times for pinpointing the nest entrance. Just the opposite is true for sector 1 ants.

As they approached the nest entrance, the ants ran steadily and continuously at a great pace and maintained the mode of locomotion they had exhibited farther away from the nest. In particular, they did not stop and fixate one cylinder or the other. Moreover, no differences could be detected in the approach behaviour of ants entering any of the four sectors (as far as this could be observed by the naked eye). High-speed video recordings are certainly needed to unravel details (we are currently investigating this).

DISCUSSION

In localizing a fixed goal, be it a nesting or a frequently visited feeding site, discrete near-by landmarks play a decisive role (see Wehner and R  ber, 1979; Wehner et al., 1996; Judd and Collett, 1998; Nicholson et al., 1999;   kesson and Wehner, 2002; Graham et al., 2004). Whereas more distant landmarks can guide the animal only to the wider area of the goal, landmarks that are close to the goal cause more rapid image transformations as the animal moves and hence allow the goal to be pinpointed more precisely [for experimental data obtained in honeybees, see Cheng et al. (Cheng et al., 1987)]. In the present account the significance of even a single landmark is clearly born out by a comparison of Fig. 1A–D. In the

case in which nest-defining landmarks were not available at all (flat-horizon scene, Fig. 1A,B), navigation by path integration brought the ants to the rough area of the goal, the nest entrance, so the returning foragers had to get engaged in extensive search movements (area-concentrated searches) until they reached the goal. Their search times were reduced the closer the goal was to discrete – either natural or artificial – landmarks (Fig. 1C,D, Fig. 2).

The substantial decrease in search time if even a single landmark is available in the vicinity of the nest might strongly decrease the heat and desiccation stress imposed on the highly thermophilic *Ocymyrmex* foragers, which spend large fractions of their time outside the nest when temperatures are close to their lethal limit. Hence, one might wonder whether these constraints are directly or indirectly taken into account by the ants when they choose their new nesting sites. Often nests are located close to stones, pebbles or tussocks of dried-out grass, *Cladoraphis spinosa*, but many nests are also found on completely barren ground. A systematic survey of nest sites within particular populations of *O. robustior* is certainly needed, as are detailed studies on the ants' nest-founding behaviour. At present we only know that nest relocations as well as multiplications by fission often occur, and that in the latter case a newly mated ergatoid (worker-like) female excavates – with the help of some recruited workers – a new nest at some distance from

the mother colony (Bolton and Marsh, 1989) (R.W. and S. Wehner, personal observations).

How ants could acquire information about discrete objects (artificial landmarks in the form of black cylinders) in close proximity to the goal has been studied in wood ants, *F. rufa* (Nicholson et al., 1999; Durier et al., 2003) as well as in desert ants, *O. robustior* (Müller and Wehner, 2010). When learning the location of the goal, the wood ants take snapshot images of the landmark while they fixate the landmark, i.e. keep its image in their frontal visual field. In contrast, the desert ants face in the direction of the invisible goal and do so during short stopping episodes included in graceful pirouettes, which the ants repeatedly perform during their learning walks. This means that *Ocymyrmex* must read out its path integrator in order to obtain a reference direction when taking the snapshot view of the landmark. If each of these snapshots acquired during the learning walks were correlated with a viewing direction towards the nest, the returning ants could at any one time retrieve the snapshot that is closest to their current position, and read out the corresponding direction of the nest (Zeil et al., 2003; Graham et al., 2010). At present, however, we do not know how many snapshots – and, if so, which – are stored. Nevertheless, while returning to the rough area of the nest the ants do not perform the pirouettes and stops that are so characteristic of the preceding acquisition phase; rather, they run uninterruptedly at a steady pace towards the goal. Hence it seems likely that they exploit, in one way or another, optic flow field cues rather than match static landmark memories. In honeybees approaching a familiar feeding site it has recently been shown that matching routines based on self-induced optic flow alone are sufficient for accomplishing the pinpointing task [‘optic flow matching’ (Dittmar et al., 2010)]. Close to the goal, the bees perform characteristic flight manoeuvres by proceeding in straight lines, making sharp saccadic turns, and moving sideways, so that during the lateral movements strong transitory optic flow fields are generated in the frontal field of view. In *Ocymyrmex* ants, which run straight towards the goal at rates of up to 0.35 m s^{-1} , such step-wise locomotor behaviours have not been observed yet, but it might well be that fast head movements [for honeybees, see Boeddeker et al. (Boeddeker et al., 2010)] or short, quick body saccades could be detected by high-speed video.

Whatever the self-induced motion cues are that the desert ants extract from their environment, it is worth mentioning that, similar to ants of the genera *Cataglyphis* (Wehner, 1987; Wehner et al., 2004) and *Melophorus* (Muser et al., 2005), foragers of *O. robustior* exhibit strong directional fidelity (S. Wehner, D. Weibel and R.W., personal observations). This means that on successive returns each homebound ant approaches its goal within its habitual sector and hence repeatedly experiences the same optic flow amplitudes. The overarching question, however, is how the visual information acquired during the markedly discontinuous, multi-step behaviour characterizing the learning walks (Müller and Wehner, 2010) is translated into the visual information that is later used during the obviously continuous return walks.

In conclusion, while moving towards the nest at a constant pace the ants do not keep the image of the landmarks in any preferred position within their visual field, let alone face one or the other landmark. It would be worthwhile using high time resolution recordings to study whether saccadic head and/or body movements occur in the approaching ants, and how such potential movements might be influenced by the positions of the near-by landmarks. But our present observations do not provide us with any indication that the ants included such saccadic episodes in approaching their landmark-defined goals. The data reported in the present account

are in accord with the hypothesis recently supported by Graham and Cheng in the Australian desert ant *Melophorus bagoti* that, in localizing their nest entrance, the animals take into account complete skyline contours and hence employ their full panoramic vision rather than respond to particular salient landmark features (Graham and Cheng, 2009a; Graham and Cheng, 2009b). Even if they are provided with only one or two single, though very conspicuous landmarks, close to the goal, as is the case in the present study on Namibian desert ants *O. robustior*, they do not try to fixate these landmarks frontally but rely on image transformations more likely perceived in a dynamic rather than a static way, as they occur in all parts of their visual field in which the images of the landmarks come to lie, while the ants are approaching the goal.

ACKNOWLEDGEMENTS

We thank Sibylle Wehner and Klaus Sattler for their help in the experiments and Joh Henschel as well as the team of the Gobabeb Training and Research Centre (Namibia) for infrastructural support. This work was partly financed by the Promotor Foundation.

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