ORIGINAL PAPER

Wind and sky as compass cues in desert ant navigation

Martin Müller · Rüdiger Wehner

Abstract While integrating their foraging and homing paths, desert ants, *Cataglyphis fortis*, depend on external compass cues. Whereas recent research in bees and ants has focused nearly exclusively on the polarization compass, two other compass systems—the sun compass and the wind (*anemo*) compass—as well as the mutual interactions of all these compass systems have received little attention. In this study, we show that of the two visual compass systems, it is only the polarization compass that invariably outcompetes the wind compass, while the sun compass does so only under certain conditions. If the ants are experimentally deprived of their polarization compass system, but have access simultaneously to both their sun compass and their wind compass, they steer intermediate courses. The intermediate courses shift the more towards the wind compass course, the higher the elevation of the sun is in the sky.

Keywords Skylight compass · Wind compass · Cataglyphis fortis · Polarized skylight

Introduction

When desert ants of the genus *Cataglyphis* forage over distances of several thousand times their body length, they employ path integration as their main means of navigation. As far as the compass component of the path integrator is concerned, recent research has focused nearly exclusively

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on the ant's—and the bee's—polarization compass. In particular, it has been shown that a specific part of the ant's and bee's visual system, the dorsal rim area (DRA), is devoted exclusively to detect and use polarized skylight for recording the insect's angular components of movements (for reviews, see Wehner and Rossel 1985; Rossel 1989; Wehner 1994). In addition, some decisive neural properties of the insect's polarization channel have been unraveled (for reviews, see Labhart and Meyer 1999; Wehner and Labhart 2006).

On the other hand, the sun compass, albeit having been the first compass system to be discovered in any animal species—and in fact, in ants (Santschi 1911)—has recently attracted much less attention. It is only in a few studies that its optical characteristics have been the focus of more recent research in honeybees (Edrich et al. 1979; Brines and Gould 1982; Rossel and Wehner 1984) as well as desert ants (Lanfranconi 1982; Fent 1985).

Finally, in *Cataglyphis*, wind direction has turned out to be a potential compass cue at least under conditions, in which wind is blowing from constant directions over considerable periods of time, as it is the case at our Maharès field site in southern Tunisia (Wehner and Duelli 1971). *Cataglyphis* ants even rely on such a wind-based system of navigation in efficiently approaching a familiar food source. Upon leaving the nest, they do not head directly towards the food source, as they would do under wind-free conditions, but steer some angular distance downwind of the food source and, when picking up the odor filaments emanating from it, follow these odor plumes upwind until they hit the feeding site (Wolf and Wehner 2000, 2005). Hence, the ants must be able to include wind-derived directional information into their path integration system. In this study, we focus on the role that the hitherto much neglected wind (*anemo*) compass plays in desert ant navigation.

Materials and methods

The experiments were performed in the coastal inundation plains at our habitual Tunisian field site near Maharès, Tunisia (34.56°N, 10.50°E). Individual specimens of the salt-pan species of *Cataglyphis*, i.e., *Cataglyphis fortis*, were trained to run back and forth within tube-like plastic (polyvinylchloride) channels cut open at their upper sides (diameter of channels 65 mm, nest–feeder distance 15 m). The channels were provided with a horizontal plywood floor coated with a mixture of sand and glue. The ants running on this floor (usually in the center of the channel, Heusser and Wehner 2002) were provided with a 90° wide slit-like view of the sky. Furthermore, the training channel was oriented with respect to the direction of the prevailing winds in such a way that the homebound (feeder-to-nest directed) ants experienced tailwind conditions.

Inside the narrow training channels, the wind direction was only either from-nest-to-feeder or from-feeder-to-nest. Which of the two directions prevailed depended on how the ambient wind hit the channel. If the direction of the ambient wind formed an acute angle with, say, the feeder-to-nest axis ($\alpha < 90°$), it was deflected inside the channel such that it blew from feeder to nest. On the other hand, if $\alpha > 90°$, the wind was deflected in the opposite direction, i.e., blew from nest to feeder. In the training paradigms used in the present account, the channel was aligned such that the former condition ($\alpha < 90°$) applied, so that the homebound ants ran downwind. In the open test field, the ants were exposed to the natural (ambient) wind direction, which deviated by various (test-specific) amounts to the left or right from the direction of the wind that the ants had experienced inside the training channel. The latter could be easily determined by the direction in which small sand grains were moving across the channel floor. Of course, the wind did not flow smoothly in a laminar way down the tube, but this applies to the natural open-field situation as well. However, as shown by Wolf and Wehner (2000), who actually visualized the degree of turbulence appearing close to the desert floor (Fig. 10, literature cited), the ants are, nevertheless, able to record mean wind directions under the wind conditions prevailing at our experimental study sight.

In the coastline area near Maharès, the wind continually blows from a rather constant direction during the course of the day especially during the time at which the experiments were performed (10–16 h, solar time): While the total variation over this time period was about ±12°, during an individual homebound run of any particular ant, the variation was much smaller, i.e., about ±1.5° about the mean direction (Wehner and Duelli 1971 and recent unpublished recordings by S. Sommer and R. Wehner). Wind speed covered the range of 2–6 m s^{-1} rather evenly

(Wehner and Duelli 1971; Wolf and Wehner 2005, and the recent recordings mentioned above).

Trained ants were captured at the feeder, displaced to an open test field, and released there within a rectangular grid of white lines (mesh width 1 m) painted on the hard salt-pan ground. Standard techniques (e.g., Wehner 1982) were used to record the ants' homing trajectories. In particular, straight lines were fitted to the (rather straight) trajectories of the ants' paths, and the azimuthal directions of the fitted lines were recorded. These angular data were further processed by applying circular statistics (Batschelet 1981) and testing for uniformity (Rayleigh test).

In experiment 2, the ants' polarization compass was shut off by covering the polarization-sensitive DRAs of both compound eyes (and the ocelli, Fent and Wehner 1985) with black acrylic paint (Lascaux Studio). These ants could then use only their sun and wind compasses. At this juncture, it should be mentioned that in the upward looking part of each eye, the DRA, and only the DRA, looks contralaterally. Hence, although separate parts of the eye are tuned to detect polarized skylight (DRA) and direct sunlight (dorsal retina), from each pixel of the celestial hemisphere, both aspects of visual information are received simultaneously: information about direct sunlight by the dorsal retina of the ipsilateral eye and information about polarized skylight by the contralateral DRA. In an additional (control) experiment, we investigated the performance of the ants' sun compass in isolation by excluding not only the polarization compass (see above) but also the wind compass. We did so by letting the ants run under an experimental trolley that shielded off any influence of the wind (for details, see Wehner 1982).

Results

We first asked whether ants tested under full-sky conditions, i.e., under conditions, in which they had both polarized skylight and direct sunlight at their disposal, changed their directional courses, if the direction of the prevailing wind was shifted experimentally. We know already that, under these conditions, the polarization compass dominates the sun compass in so far that the ants do not pay attention to the sun at all (Wehner and Müller 2006). Hence, in our first experimental paradigm, the wind compass was made to compete with the polarization compass. This was achieved by training the ants inside a channel to tailwind conditions and then providing them in the open test field with the prevailing wind direction, which deviated either by 80° to the left (group 1) or by 30° to the right (group 2) from what the channel-bound ants had experienced during training. Nevertheless, the ants of both groups invariably selected courses that were determined
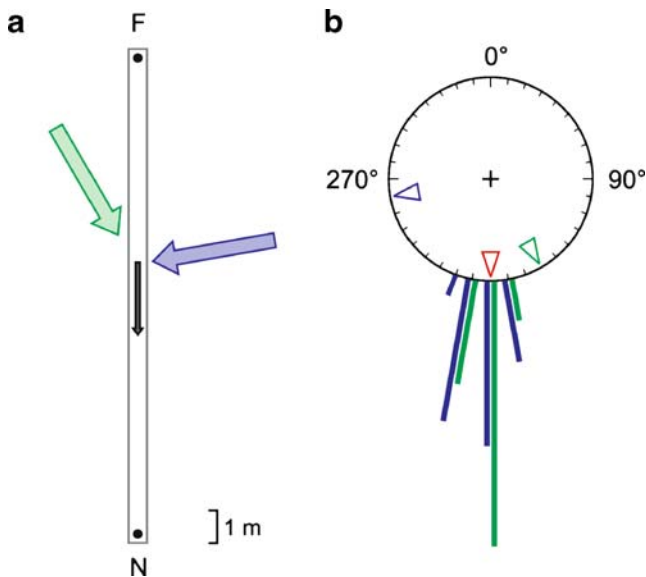
Fig. 1 Competition experiment: polarization compass vs wind compass. **a** Experimental setup during training. The *blue and green arrows* mark the directions of the prevailing winds in subsequent open-field tests. The *black arrow* depicts the resulting wind direction inside the channel. *F* feeder; *N* nest. The dimensions of the channel are not drawn to scale. **b** Directions taken by the ants in the open-field test situation. The trained ants were displaced from the feeder to the test field. Their directional choices are shown for the two wind conditions depicted in **a** (*blue and green bars*, *n*=20 for each group). The *blue and green open arrowheads* mark the directions that the ants should have taken, if they had used their wind compass. Correspondingly, the *red open arrowhead* marks the direction to be taken by the ants, if they had used the polarization pattern in the sky as their compass cue. The two test series (*blue and green data bars*) have been performed at the same times of day with the training channels oriented in the same direction

exclusively by their polarization compass (Fig. 1b). Group 1 ants and group 2 ants were trained in the channel under the same skylight conditions, so that the polarization-induced systematic errors (Wehner and Müller 2006) were the same in both cases. In either group, the means of the ants' directional choices did not significantly deviate from each other (group 1 vs group 2, Watson Williams test (Batschelet 1981), *n*=20 for each group; $F_{1,38}=0.187$, $p=0.668$). Nor was there any significant deviation ε from the course as determined by the skylight cues (group 1: $\varepsilon=1.7\pm7.0°$, *n*=20; group 2: $\varepsilon=1.5\pm4.4°$, *n*=20). Hence, in selecting their homeward courses, the ants fully relied on polarized skylight and completely neglected the change in wind direction that had occurred in the test situation.

The second question was whether the sun compass, if experimentally isolated as the only celestial compass mechanism available to the ants, would be as inert to changes in the direction of the wind as the polarization compass had turned out to be. To tackle this question, the polarization-sensitive DRAs of the ants' compound eyes were covered with light-tight paint, so that during both training and testing, the ants could derive compass information only from the azimuthal position of the sun and the direction of the wind. In the training situation inside the channel, the ants again experienced tailwind conditions (in this case, the angle between the axis of the channel and the direction of the wind outside the channel was 45°). As a consequence, in the subsequent experimental test situation, the homeward course determined by the direction of the wind deviated by 45° from the homeward course determined by the azimuthal position of the sun. Now with their polarization compass shut off, the ants behaved quite differently from what they had done in experimental paradigm 1. They selected courses that were uniformly distributed about an intermediate direction (Fig. 2a). This intermediate direction ($\alpha=210.0°$) differed significantly ($p<0.001$, Stephens test, Stephens 1962) from the direction that the ants should have chosen, if they had relied on either the solar azimuth or the direction of the wind alone. Both directions, i.e., the sun-derived and the wind-derived compass courses, lie outside the 99% confidence limits (202.5°–217.5°) of the ants' mean course (Batschelet 1981).

As tests performed under finer time resolution showed, these intermediate directions shifted the more towards the wind-derived navigational course, i.e., away from the sun-derived navigational course, the higher the sun was in the sky (Fig. 2b,c). Under conditions of high sun elevations, the compass input to the ant's path integrator seemed to become dominated more and more by the directional information provided by the prevailing winds.

Control experiments in which the ants were deprived of any wind-borne information indeed showed that the accuracy of the ants' compass courses deteriorated the more, the higher the sun had risen in the sky. This result was obtained in ants in which the DRAs of the eyes had been occluded (to inactivate the ants' polarization compass) and in which the ants had to walk underneath a wind-proof experimental trolley. Under these conditions, the ants could derive the direction of their navigational courses only from the azimuthal position of the sun. They did so less precisely for higher ($\mu_s=72.7°\pm1.1°$) than for lower ($\mu_s=53.8°\pm4.3°$) elevation of the sun (SD=12.5°, *n*=31 and SD=8.5°, *n*=29, respectively; $p<0.025$, F-test). The ants' directional choices were determined at a 4-m distance from the point of release. Furthermore, the ants exhibited much more tortuous trajectories when tested under conditions of 72.7° rather than 53.8° elevation of the sun (straightness index $d/l=0.66\pm0.16$, *n*=31, and $d/l=0.83\pm0.12$, *n*=29, respectively.). The straightness index is defined as the ratio of the beeline distance (*d*) to the total path length (*l*) of the ant's walking trajectory.
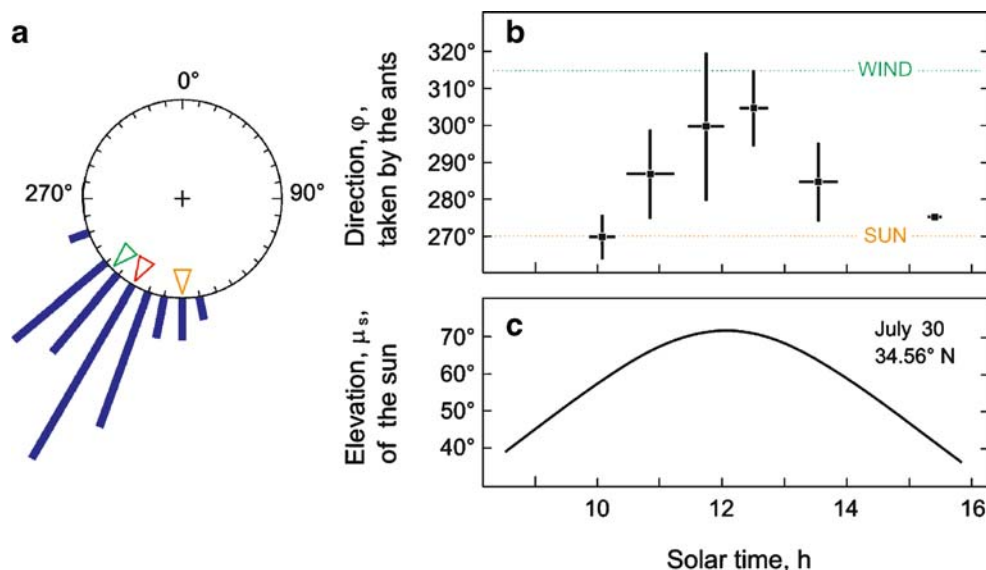
Fig. 2 Competition experiment: sun compass vs wind compass. Directional choices of channel trained ants in which the polarization compass had been excluded by painting out the DRAs of the ants' eyes. The experiments of Figs. 1 and 2 have been performed during the same times of day, i.e., under the same elevations of the sun. **a** Directional choices taken by a group of ants tested within the time period 11–13 h. The *green and orange arrowheads* mark the homing directions based on the wind compass and the sun compass, respectively. The mean direction taken by the ants is indicated by the *red arrowhead*; n=34. **b** Tests performed under a finer time resolution over the entire daytime foraging period of *C. fortis*. The *green and orange dotted lines labelled Wind and Sun* indicate the directions to be taken by ants if they relied exclusively on their wind compass or their sun compass, respectively. The *vertical bars* depict the standard deviations of the azimuthal directions chosen by the ants in the test field. In all cases, the directions of the ant's straight homeward courses were orientated about one mean direction (see Fig. 2a). The *horizontal bars* depict the standard deviations of the times at which the individual runs where recorded. The angular mean and the circular standard deviation are indicated for each time of testing; overall sample size n=45. **c** Daily course of the elevation of the sun during the time of year at which the experiments were performed

Discussion

If an animal navigating over large distances relied entirely on path integration to keep track of its current position relative to its point of departure, it would have to continuously monitor all its angular and linear components of movement (Mittelstaedt 1983; Wehner and Srinivasan 2003). Some animals do so by relying exclusively on self-generated motor signals (for reviews dealing with arthropods and mammals, see Wehner 1992 and Etienne 2003, respectively). However, if path integrating systems relied exclusively on internal signals, e.g., proprioceptive signals, they would be heavily constrained by the rapid accumulation of errors. Theoretical considerations indeed show (Benhamou et al. 1990) that such cumulative errors would rapidly build up and that it is especially the rotatory component of movement that imposes severe limitations on the accuracy of the path integration system, if this component were recorded merely by internal means. Hence, it comes as no surprise that long-distance navigators such as bees and ants rely entirely on external compass cues.

In the present account, we show that the *Cataglyphis* path integrator receives its information about the angular components of movement not only from one, but from (at least) three compass systems: Two of them depend on visual cues, in particular on direct sunlight and scattered (polarized) skylight, while the third one relies on mechanoreceptive cues, i.e., on the direction of the prevailing wind. The by far dominating compass system employed by *Cataglyphis* is the polarization compass, against which the sun compass dwindles in importance (Wehner and Müller 2006). This is certainly due to the amount of information provided by direct sunlight and polarized skylight. While the sun is a local point light source, which at any one time is seen only by a single ommatidium, and can easily be obscured by clouds, polarized skylight forms a global pattern spanning the entire celestial hemisphere. In the present account, we focus on the relative importance of celestial cues (both polarized skylight and direct sunlight) vs wind in the ant's compass system. The main result is that changes in wind direction do not affect the ants' courses, if the animals have access to the pattern of polarized light (Fig. 1), but that they severely do so if (1) the animals are experimentally deprived of their polarization compass and if (2) the sun had risen to high elevations in the sky (Fig. 2). Unfortunately in the diurnally foraging *Cataglyphis* ants, the wind compass could not be tested in isolation. We tried to do so by testing ants, which had been trained the

previous day, long before sunrise, when the wind direction systematically deviated from daytime conditions (Wehner and Duelli 1971). In this nocturnal, low-temperature situation, which normally is never experienced by any *Cataglyphis* forager, the ants relied exclusively on their wind compass, but moved extremely slowly and in a highly tortuous way, so that these data cannot be compared with the daytime data obtained in the present account.

The effect that the elevation of the sun has on the accuracy of the ant's sun compass might be astounding at first, but can easily be explained in functional terms: The lower the elevation of the sun in the sky, the higher the accuracy with which the azimuthal position of the sun can be determined. Just consider two adjacent ommatidia in the ant's compound eye and let the optical axes of these two ommatidia deviate from each other horizontally by the angular difference $\Delta\varphi$ (divergence angle). As in the sky, the meridians converge towards the zenith, the azimuthal range covered by $\Delta\varphi$ within the celestial hemisphere becomes the larger, and hence, the accuracy of the compass readings becomes the smaller, the higher the elevation of the sun is in the sky. In addition to this effect, which follows from purely geometrical reasoning, $\Delta\varphi$ is not constant across the *Cataglyphis* compound eye. It varies especially with the elevation μ above the ant's visual horizon. In *Cataglyphis bicolor*, for example, it ranges from $\Delta\varphi=5.0°$ for $\mu=30°$ to $\Delta\varphi=7.0°$ for $\mu=70°$ (Zollikofer et al. 1995) and, by this, again guarantees a higher accuracy of compass readings for lower elevations of the sun. This prediction has been confirmed by our experiments in which the ants were prevented from using their polarization compass as well as their wind compass and, hence, were left alone with their sun compass system. Under these conditions, their directional choices scattered the more, and their walking trajectories became the more circuitous, the higher the sun was in the sky. The same result had previously been obtained by Lanfranconi (1982), who had applied another experimental paradigm in another species, *C. bicolor*. In Lanfranconi's as well as in our test situation, the ants had to walk underneath the experimental trolley, so that they were deprived of any wind-based system of navigation, but in Lanfranconi's experiments, the polarization compass was shut off by providing the trolley with an ultraviolet absorbing filter rather than by occluding the DRAs of the ants' eyes (the ant's polarization compass operates only in the ultraviolet range of the spectrum: Duelli and Wehner 1973). In the critical tests, the elevation of the sun was changed by means of mirrors. When *C. bicolor* was trained under a mean sun elevation of $\mu=49°$ and was later tested with apparent sun elevations of either $\mu=35$ or $75°$, the standard deviations of the ants' compass bearings were SD=11.2 and 26.3°, respectively ($p<0.01$, F-test for differences between standard deviations).

One of the most striking results of the present account is the role that the wind (*anemo*) compass can play in the ant's path integration system (the term "anemomenotactic orientation" much applied in former times refers to the outdated taxis concept— Kühn (1919), Fraenkel and Gunn (1961)– and nowadays should be avoided). Earlier work had already shown that beetles can maintain straight courses by keeping a constant angle to the direction of the wind (Linsenmair 1969, 1970) and that *C. bicolor* can use the wind as a compass cue if tested under nighttime conditions, when neither the sun nor polarized skylight cues are available, or if tested during daytime, but with its compound eyes and ocelli painted out (Wehner and Duelli 1971). As shown in the present account, under certain conditions, the wind compass can even preside over the sun compass. Wind direction is monitored by the antennae, especially by the pedicellar Johnston organ. This follows from the fact that wind orientation in *Cataglyphis* can be completely abolished by cutting off (Duelli and Wehner, unpublished observations) or immobilizing (Wolf and Wehner 2000) the antennae. The latter was achieved by glueing the scape, the pedicel, and the proximal parts of the flagellum to the head capsule.

In conclusion, the path integration system of *Cataglyphis* desert ants receives its information about the angular components of movement from a set of compass mechanisms. Each compass—the polarization compass, the sun compass, and the wind compass—suffices to provide the integrator with the necessary information. If the whole range of sensory cues is available, i.e., polarized skylight, direct sunlight, and wind, the polarization compass clearly dominates. This has been shown in experimental paradigms in which the polarization compass and the sun compass (Wehner and Müller 2006) or the polarization compass and the wind compass (present account, Fig. 1) provided conflicting directional information. In either case, the ants relied exclusively on the information provided by polarized skylight. However, intermediate courses were steered when the polarization compass was experimentally shut off and when a high elevation sun was made to compete with the direction of the wind (Fig. 2). In this context, our present investigation leads to the hypothesis that the sun compass originally discovered in ants as the first compass system in any animal (Santschi 1911) plays only a subordinate role if compared to the polarization compass and that it might not even be robust enough to dominate the wind compass under all possible conditions.

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