

Path integration as the basic navigation mechanism of the desert ant *Cataglyphis fortis* (FOREL, 1902) (Hymenoptera: Formicidae)

Bernhard RONACHER



Abstract

This review describes recent progress in the analysis of the fascinating navigation abilities of desert ants. On their foraging excursions, ants of the genus *Cataglyphis* cover distances up to hundred thousand body lengths. Having found a prey item they return to their inconspicuous nests with high precision, using path integration as their major navigation aid. This account focuses on the question of how these ants measure their travelling distances, information that is an essential constituent of path integration. Recently it has been shown that *Cataglyphis* uses a stride integrator to measure walking distances. Remarkably, the ants' path integration module works precisely even when the animals forage in undulating terrain, e.g., when climbing over walls or hills. This indicates that the ants are able to measure the inclination of ascents or descents, and do integrate this information into their distance estimates. Navigation by means of path integration is error prone due to its susceptibility to accumulate errors. *Cataglyphis* and other desert ant species use landmarks – if present – as additional navigational aid. Many studies were devoted to the interactions between the path integration system and landmarks. There are no indications that by combining vector and landmark information ants would acquire a representation of their environs in the sense of a "cognitive map". A lesson that we may learn from the small-brain navigator *Cataglyphis* is how complex, "high-level" behaviour is achieved by the interaction of rather simple, "low-level" subroutines.

Key words: Desert ants, *Cataglyphis*, navigation, dead reckoning, path integration, 3-D orientation, review.

Myrmecol. News 11: 53-62 (online 28 May 2008)
ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 5 February 2008; revision received 10 April 2008; accepted 10 April 2008

Prof. Dr. Bernhard Ronacher, Institut für Biologie, Humboldt Universität zu Berlin, Invalidenstraße 43, D-10015 Berlin, Germany. E-mail: bernhard.ronacher@rz.hu-berlin.de

It seems to me that in the matter of intellect the ant must be a strangely overrated bird. ... I have not yet come across a living ant that seemed to have any more sense than a dead one. I refer to the ordinary ant, of course; I have had no experience of those wonderful Swiss and African ones which vote, keep drilled armies, hold slaves, and dispute about religion. Those particular ants may be all that the naturalist paints them, but I am persuaded that the average ant is a sham. I admit his industry, of course; he is the hardest-working creature in the world – when anybody is looking – but his leather-headedness is the point I make against him. He goes out foraging, he makes a capture, and then what does he do? Go home? No – he goes anywhere but home. He doesn't know where home is. His home may be only three feet away – no matter, he can't find it.

Mark Twain, A tramp abroad. XXII The Black Forest and its treasures

Introducing *Cataglyphis*, a race horse among ants

Most animals actively search for food and this requires an ability to navigate efficiently in their habitat. A most important navigational task is to return to a certain place, be it the nest, a food source, or a place for mating. This ability is crucial for animals that exhibit repeated parental care for their offspring as, for example, solitary bees and wasps (TINBERGEN 1932, TINBERGEN & KRUYT 1938). To find the way back to a certain point in space was certainly a quite essential precondition for the evolution of social insects as central place foragers.

This account focuses on the spectacular and fascinating orientation abilities of desert ants of the genus *Cataglyphis*. These elegant, long-legged animals live in flat and rather hostile habitats, with high ambient temperatures, where they search for prey, mostly insects that have succumbed to the heat. In contrast to other ant species they do not rely on

pheromones to mark their trail. Obviously, the lack of scent trails is due to constraints of their habitat. Scent marks would constitute rather unreliable cues in view of the heat induced evaporation of volatile hydrocarbons and the perpetual turnover of the sand surface by wind. Since the position of prey is patchy and unpredictable, each individual performs large excursions on its own, on meandering paths until it finds a food item. From this point the ant returns to her nest on a rather straight way. Not only is the navigational feat quite remarkable – also in flat salt pans devoid of landmarks that could be used to pinpoint the inconspicuous nest entrance the ants steer very precisely towards their underground nests – but also the physical endurance is fascinating. Foraging excursions can extend as far as some hundred meters, corresponding to ten-thousands of body lengths, and the ants move at the astonish-

ing average speed of 50 cm/s and even more (WEHNER & WEHNER 1990, WEHNER 1994a). We can compare this to a Marathon course, over a distance of 23,000 to 25,000 body lengths, for which the women's record is around 2 hours and 20 minutes, corresponding to a marvellous average speed of 18 km per hour (5 m/s). If we linearly extrapolate the ant's performance to human size we would, however, arrive at the absurd expected speed of 180 km/h. Even if one scales the ant's speed according to the power law exponent proposed for optimal running speed of insects ($0.3 * \text{bodymass}^{0.29}$; PETERS 1983: fig. 6.5), a human athlete would have to run at ~ 14.5 m/s (or ~ 52 km/h) to be a match for *Cataglyphis*. This extrapolated speed is far beyond the world record in human sprint. In contrast, 50 cm/s is the cruising speed of *Cataglyphis*.

Three basic strategies for homing

There are three principal strategies to solve the problem of returning to a specific point in space, e.g., the nest (WEHNER & WEHNER 1990, WEHNER 1991, see also BIEGLER 2000). The first, **route following** (Fig. 1, left), has been applied in Grimm's tale of Hansel and Gretel, and is found in animal species as diverse as Polyplacophora, gastropods, *Formica* wood ants, and mammals (CHELAZZI 1992, PAPI 1992). It consists of applying some marks, often chemical trail pheromones, to the outward trail, and to follow these marks back to the starting point. This strategy does not necessarily involve a sophisticated representation of the surrounding area. Visual "snap shots" of conspicuous objects (CARTWRIGHT & COLLETT 1983) instead of chemical marks could also be remembered and used as marks defining a route, but the ordered storage and recall of landmarks obviously is a rather demanding strategy (COLLETT 1996, WEHNER & al. 1996b, KOHLER & WEHNER 2005).

An even more sophisticated navigational performance is to build up an internal representation of the surroundings, in which the geometrical relations of prominent locations are stored, and to use this internal "**cognitive map**" as a reference system to navigate in known areas, by comparing external cues with their internal counterparts (Fig. 1, right). While such map-like orientation has been demonstrated in various vertebrate species (see, e.g., GALLISTEL & CRAMER 1996, MCNAUGHTON & al. 2006), it is a matter of dispute whether insects use such a strategy (DYER 1991, WEHNER & MENZEL 1990, GIURFA & CAPALDI 1999). The use of novel shortcuts after a displacement is often considered as evidence for a map-like representation. Recent results obtained with bees have been interpreted as evidence for a map-like organization of spatial memories (MENZEL & al. 2005) – but see COLLETT & al. (2007) for a different interpretation of novel route evidence. In contrast, data obtained with the Australian ant *Melophorus bagoti* LUBBOCK, 1883 are not compatible with the assumption of a cognitive map (WEHNER & al. 2006).

The North-African ant *Cataglyphis fortis* (FOREL, 1902) follows the third strategy, which is termed **path integration, vector navigation or dead reckoning** (WEHNER & SRINIVASAN 2003). An animal relying on path integration continuously updates a vector that points to the location of its starting position, the nest (Fig. 1, middle, stippled red arrow). To perform a vector addition of path segments, information about their direction, relative to a reference system, and distance is needed (see below and

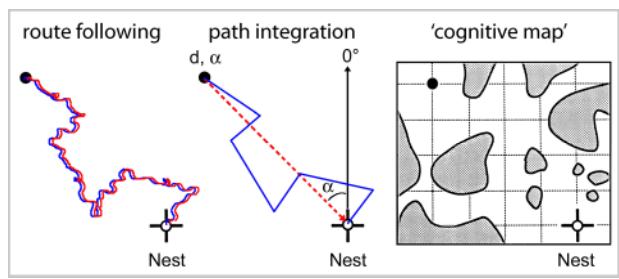


Fig. 1: Three orientation strategies to return to a point in space. Left: route following; middle: path integration, 0° indicates a reference system, α the angle between home vector and reference direction, d distance; right: cognitive map. Explanations in text. Modified after WEHNER & WEHNER (1990).

MÜLLER & WEHNER 1988, WEHNER & WEHNER 1990). This type of orientation strategy probably involves a complexity of neuronal mechanisms that lies between the route following and the map strategies mentioned above. However, navigating according to path integration appears still demanding enough for a brain that weighs only a tenth of a milligram.

Cataglyphis – a champion in path integration

Cataglyphis ants are prime examples for the efficient use of path integration. By observing an excursion of a single *Cataglyphis* forager it becomes clear that these ants do not employ the first strategy, to retrace their outbound path: upon having found a food item, in open terrain they return on the direct, short cut way to their nest. The strong heat load in their habitats implies the danger of desiccation, thus the ability to find back to the nest on a short cut entails a valuable reduction in heat stress (cf. WEHNER & al. 1992). On the other hand, *Cataglyphis* ants often live in very flat salt pans without much vegetation. Such a surrounding without any conspicuous landmarks would not be particularly suited to develop a cognitive map of the surroundings. In contrast to the conspicuous anthills we know from forests in more northern latitudes, the entrance to the subterranean *Cataglyphis* nest is frequently inconspicuous. However, desert ants could still adhere to the map strategy and use cues for their navigation, that we are unable to perceive, say magnetic cues. Therefore, displacement experiments were used to decide between the different hypotheses (Fig. 2). An ant that made a typical meandering foraging excursion (Fig. 2A) was given a food item at point F and at the same time it was captured and released at some distance (point R in Fig. 2B). If undisturbed, the ant would have returned directly from point F to the nest on a straight path (dotted line). According to the route following strategy (cf. Fig. 1) one would expect that after the displacement the animal behaves as if lost (e.g., CHELAZZI 1992). With a cognitive map, one would expect that the animal heads from the release point R directly to the nest (N in Fig. 2A), by comparing features of the external world with their internal representations. However, after the displacement the ant performed a homebound run in exactly the direction of the – now fictive – nest (open square in Fig. 2B). At this point the running behaviour changed abruptly, marked by a sharp turn (T), and the ant performed search loops of increasing diameter. This search behaviour is a

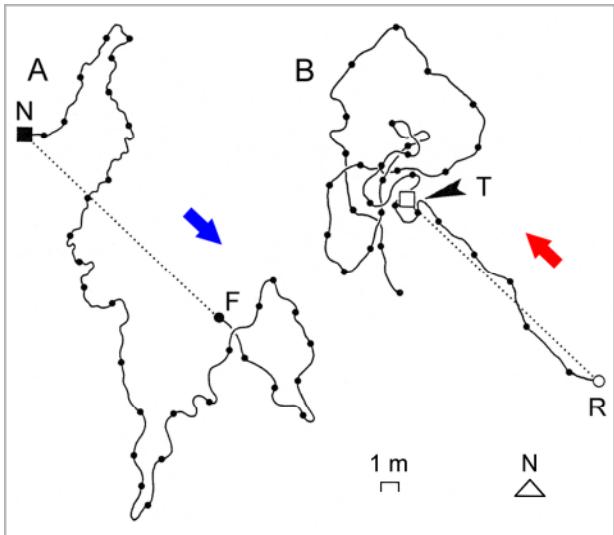


Fig. 2: Displacement experiments reveal path integration strategy. (A) Outbound path of an ant, starting at the nest N. At F the ant was captured, provided with a food morsel and released at some distance. Black dots on the path indicate 10-s time intervals. Stippled line gives the direction of the home vector. (B) From the release point R the ant performed its homebound run, heading in a straight path to the – now fictive – position of the nest (open square). T marks the typical U-turn that indicates the start of the search loop programme. From WEHNER & WEHNER (1986).

kind of safety mechanism by which the ant will eventually reach the nest, even if the home vector did not lead the ant back to the exact nest position, e.g., due to a displacement of the animal by a wind gust (WEHNER & SRINIVASAN 1981, WEHNER & WEHNER 1986, MÜLLER & WEHNER 1994). Figure 2B suggests that the presumed home vector does not only comprise the direction but also the distance to the nest, as the searching behaviour begins at the fictive nest position. Nevertheless, and in spite of this safety programme, a high accuracy of the path integrator is most important: when returning to the nest from a 100 m distance, an error of only 5° in the home vector direction would lead to a ~9 m lateral deviation of the path from the nest, which would be difficult to compensate for by the time-consuming search loops.

Directional and distance information are necessary constituents of path integration

The experiment of Figure 2 (and many additional tests) demonstrated that on each point of a foraging excursion the ant has quite precise information about the current direction and the distance of the nest. This home vector constitutes a kind of invisible safety line (WEHNER & WEHNER 1986, 1990). But how can such a small brain – of ~ 0.1 mg mass – calculate this home vector from a tortuous path like that in Figure 2A, and, in particular, how can it achieve the required accuracy in these calculations? Obviously, the ants need two kinds of information to determine the home vector. They must combine information about the actual direction of the path – relative to a reference system – with information about the distance travelled in a certain direction. The directional information alone is not sufficient as can be seen from a simple example: the re-

spective home vectors would be entirely different if one walks either 200 m to the East and 50 m to the North, or 50 m to the East and 200 m to the North.

The ants' compass uses the polarization pattern of the sky as reference

Several studies have provided evidence that ants obtain directional information from a celestial compass. *Cataglyphis* uses predominantly the sky's polarization-pattern and to a lesser degree the sun's position, spectral gradients and wind direction (WEHNER 1992, WEHNER & MÜLLER 2006, MÜLLER & WEHNER 2007). Since there exist many excellent reviews on this topic (WEHNER 1994a, b, 1997, WEHNER & SRINIVASAN 2003, HOMBERG 2004, WEHNER & LABHART 2006, see also HEINZE & HOMBERG 2007), I will not dwell on the compass problem. For the moment we can take for granted that the ants can determine their walking direction by virtue of their celestial compass. The main focus of this review will be laid on the question of how travelling distances are measured, and how directional and distance information are combined in the path integrator.

Nevertheless, a few general problems of the compass orientation should be mentioned briefly. First, the sky's polarization pattern is highly complex, and changes considerably with the height of the sun and thus with the time of the day. By ingeniously designed experiments on honey bees, WEHNER & ROSSEL (1985; see also ROSSEL & WEHNER 1986) have shown that these insects use a single, simplified internal template that encompasses the different polarization patterns occurring during different times of the day and the year. Later, this template concept was confirmed in *Cataglyphis* as well. Under most conditions this simplifying mechanism allows to determine the travelling direction with sufficient precision. However, under artificial experimental conditions it may lead to errors – indeed exactly such errors have been used to predict the internal template's structure (WEHNER & ROSSEL 1985). Another drawback, apart from the complexity of the polarization pattern, is that the celestial reference system is not fixed relative to the Earth's coordinates but shifts during the day. Hence, during longer excursions, or if they intend to visit the same place on different times of the day, these insects have to take into account the course of the sun, by means of their internal clock. To solve this problem, they adhere to a simplified rule as well (WEHNER & MÜLLER 1993, see also DYER & DICKSON 1994).

How do ants measure travelling distances?

As emphasized above, path integration requires not only information about travelling directions but also on the respective travelling distances. In contrast to the rather well understood compass, the mechanism by which ants could measure travelling distances, their odometer, remained elusive until 2006. Since the 1950s there existed three classes of hypotheses of how insects could measure travelling distances: (i) by measuring energy consumption (HERAN & WANKE 1952), (ii) by measuring optic flow (FRISCH 1965), and (iii) by relying on idiothetic parameters (MITTELSTAEDT & MITTELSTAEDT 1973, 1980). The latter are cues that result from monitoring the output of a central pattern generator for locomotion or using cues derived from the actual movements, for example a kind of stride counter. Based on data obtained with honey bees (HERAN & WANKE 1952,

see also FRISCH 1965), for a long time the energy hypothesis has been favoured – although it remained a bit mysterious how the necessary accuracy could be achieved. Only a decade ago, strong evidence against the energy hypothesis has been provided in a beautiful experiment by ESCH & BURNS (1996). These authors trained bees to visit a feeder at 70 m distance from the hive, and then lifted this feeder slowly, by means of a helium balloon, up to a height of 90 m. The bees followed the uplifted feeder, and by their dances in the hive indicated the estimated distance of the feeder. The expectation was that the bees would signal to their nest mates a distance of at least 114 m (the shortest distance between hive and elevated feeder), or even more, as the upwards directed flight arguably is energetically more demanding. Surprisingly enough, quite the opposite happened. The bees indicated a much shorter distance (~25 m) than the 70 m ground distance! This result was not compatible with the proposed use of energy cues but was in accord with the optic flow hypothesis: with increasing distance from the ground, the image speed of ground structures moving across the retina slows down – which leads to an underestimation of the distance flown. The optic flow hypothesis has been elegantly confirmed by Srinivasan and coworkers. They trained bees to fly to a food source that was located at the end of a 6 m tunnel of small diameter. The tunnel's inside was covered with random patterns of high contrast so that the foragers experienced an unusually strong, high-speed optic flow. When the authors analysed video sequences of the dances they found that a 6 m flight within the tunnel was treated by the bees as equivalent to a ~180 m distance flown in the field (SRINIVASAN & al. 2000). These and later experiments strongly indicate that honey bees rely predominantly on optic flow to measure travelling distances (see also ESCH & al. 2001, BARRON & SRINIVASAN 2006).

Remarkably, the odometer of *Cataglyphis* relies on different cues to infer distances. We have tested the optic flow hypothesis by training ants to walk to a food source in a 10 m channel in which we could manipulate the optic flow in the ventral eye region (RONACHER & WEHNER 1995). In a second, independent experiment, we manipulated the lateral optic flow (RONACHER & al. 2000). The testing principle was to transfer the ant for their return run into a much longer test channel in which the optic flow cues were different from the training channel, and to record at which point the ants would switch from their steady straight run to nest search behaviour (see Fig. 2B). The typical 180° turn (first U-turn) was then taken as an indicator of the ants distance estimate. Manipulation of the lateral optic flow had no influence at all on the distance estimation (RONACHER & al. 2000), while high-contrast ventral optic flow had a small influence. However, additional tests, in which the ventral parts of the compound eyes were occluded with black paint, demonstrated that the ants still could measure their walking distance rather well, even if all optic flow cues were excluded (RONACHER & WEHNER 1995). Obviously, *Cataglyphis* relies on a different mechanism to infer travelling distances than honeybees – although both belong to the taxon Hymenoptera. Probably the type of locomotion, walking or flying, induces the use of different odometric cues. For flying insects, optic flow constitutes the best or only available cue (see, e.g., SRINIVASAN & al. 1997), while for walking insects other cues appear to be



Fig. 3: *Cataglyphis fortis* on stilts. Preparation and photo: M. Wittlinger.

more reliable. It would be interesting to see whether ants living in more cluttered habitats do weigh optic flow cues more strongly than *C. fortis*.

Energy could be excluded as the relevant cue by experiments in which heavy loads were put onto ants (only for their return run). Loads up to four times the ant's weight did not influence distance estimates (SCHÄFER & WEHNER 1993, see also WOHLGEMUTH & al. 2002, LIPP & al. 2005). Hence, for *Cataglyphis* we were left with the third hypothesis, a stride counting mechanism (cf. also THIÉLIN-BESCOND & BEUGNON 2005). However, it proved to be very difficult to provide conclusive evidence for such a "pedometer". Only most recently, a breakthrough has been reached. Matthias Wittlinger succeeded to put ants on stilts after they had arrived at the feeder, located at a distance of 10 m from the nest (Fig. 3). The knack of these experiments was to perform this manipulation so gently that the ants, after the stilts were attached, were still inclined to exhibit their normal homing behaviour. An ant on stilts now stopped and searched for her nest at ~15 m distance, corresponding to the increased stride length, while ants with shortened legs underestimated the nest distance considerably (WITTLINGER & al. 2006, 2007a). Remarkably, ants showed this overshoot – or undershoot in case of shortened legs – only on their homebound trip after the manipulation. When tested after their next foraging excursion, the ants stopped at the correct 10 m distance in the test channel. Now an ant on stilts needed a smaller number of strides already on her way from nest to feeder. These data provide convincing evidence that *C. fortis* indeed uses a stride integrator to measure walking distances (WITTLINGER & al. 2007a).

Path integration uses an approximate mechanism

How is the sensory information about compass directions and walking distances combined and processed within the ant's brain, to obtain a precise home vector from the meandering path segments?

The problem of vector navigation can be solved exactly with the aid of sine and cosine functions (MITTELSTAEDT & MITTELSTAEDT 1973). How well did *Cataglyphis* pay attention in evolutionary math courses dealing with trigonometric functions? Probably not too well, as demonstrated

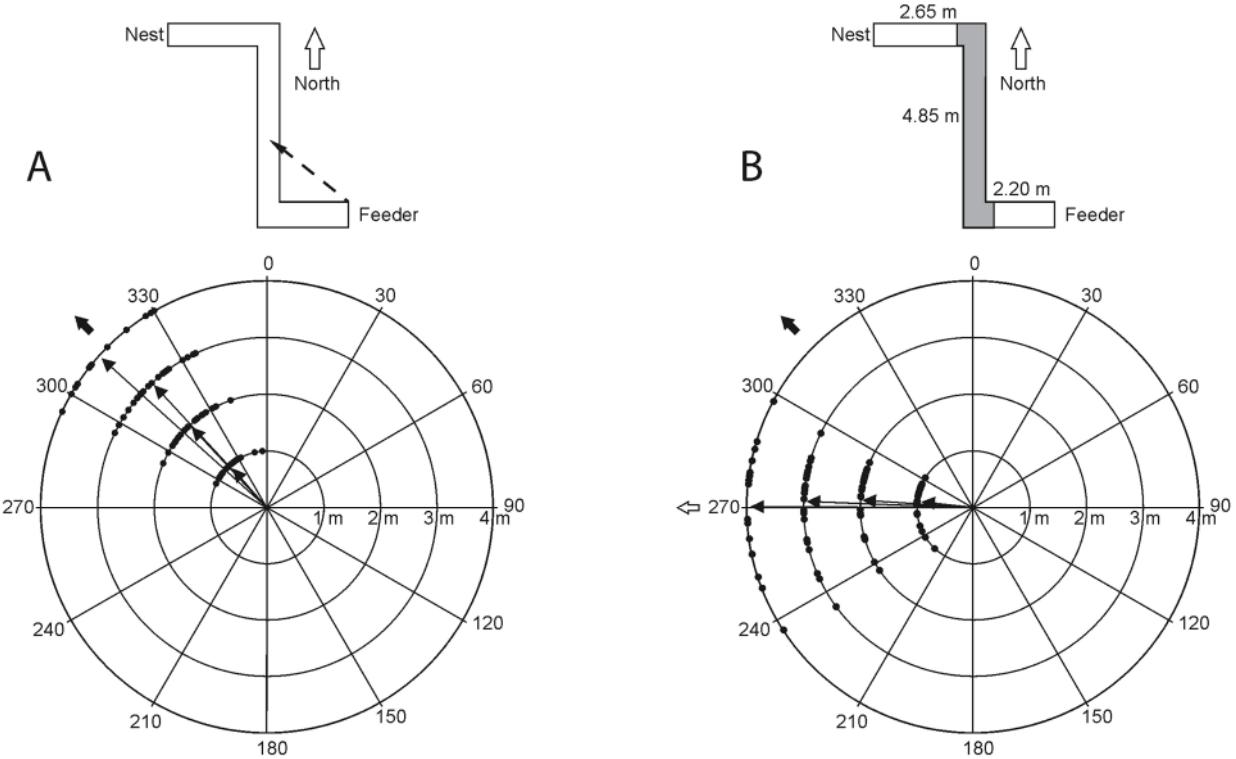


Fig. 4: How is distance information processed in the absence of celestial compass information? Ants were trained to visit a feeder in a Z-like channel system. From the feeder individuals were transferred to a distant test field where their homing behaviour could be recorded. Stippled arrow in the inset of A indicates expected homing direction. Arrows indicate the observed mean homing directions at 1 m, 2 m, 3 m, and 4 m distance from the release point, filled circles indicate individual data (intersection of the path with the respective circle). 22 and 25 ants were tested for A and B, respectively. The mean homing directions in A are not significantly different from the expectation (thick black arrow at 315°). In B the middle segment of the channel was covered with orange perspex that precluded the perception of polarized light patterns. Now the ants headed in a Western direction (270°), indicating that the middle segment of the path – where sky compass information was not available – was not included into their path integration. Adapted from RONACHER & al. (2006).

by MÜLLER & WEHNER (1988) in a series of elegant experiments. Ants were trained to visit a food source in a channel system that allowed view of a large part of the sky – to allow for a functional sky compass. After a 10 m straight path a sharp bend forced the ants to change their walking direction, and to continue in the new direction for another 5 m, to arrive at the feeder. At the food source, ants were captured and transferred to a distant test field, covered with a painted grid, on which the homing direction could be recorded precisely. In different training series, ants experienced different bending angles. Depending on the size of the bending angle during training the ants showed systematic deviations from the expected home direction. A thorough analysis of these error angles led to the interpretation that the ants do not solve the problem by using the exact trigonometric procedure, but rather apply an approximate iterative strategy, by which they incrementally update the home vector (MÜLLER & WEHNER 1988). Although this approximate path integration results in errors under some restricted experimental conditions, it normally yields sufficiently accurate directional information to guide the ants safely home.

The next experiment was designed to further elucidate the interplay between directional and distance information: how is distance information processed in the path integrator if at the same time compass information is not avail-

able? Ants were trained in a Z-shaped channel system, the three segments of which joined at right angles (see insets in Fig. 4). From the feeder they were transferred to a test field where their homing paths could be observed. In the crucial test the middle segment of the maze was covered by orange Perspex that precluded the perception of polarization patterns (which in *Cataglyphis* is based on the UV-part of the spectrum). Direct view of the sun was also precluded (RONACHER & al. 2006). In this paradigm, any change of the ant's processing of odometric information while walking within this occluded channel segment will directly translate into a change in homing direction on the test field. The results indicate that the odometric information about distance travelled is largely ignored for path integration, if there is no simultaneous input from the sky-view based compass. In addition these results demonstrate that idiothetic information alone cannot substitute for the polarization compass to infer travelling directions (RONACHER & al. 2006).

Ants on their way to higher dimensions

As mentioned above, and as can be inferred from Figure 5, *C. fortis* occupies rather flat habitats. However, a related species, *C. bicolor*, lives also in vertically structured habitats and even in towns and there manages to navigate across structures extending in the vertical plane, such as

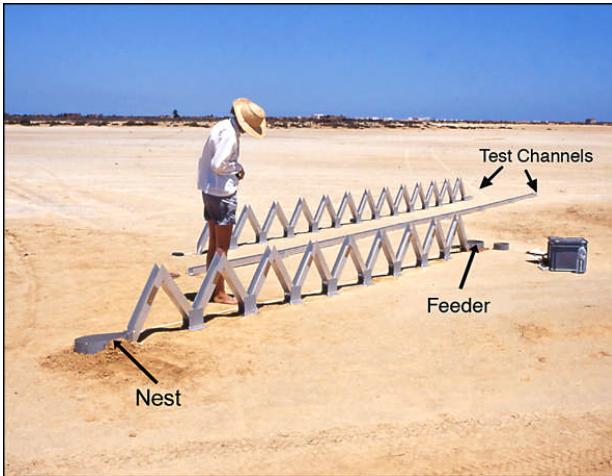


Fig. 5: Top: Testing *Cataglyphis*' orientation in 3-D. Training channel in the foreground. The nest site on the left was surrounded by an enclosure in order to lead the ants into the hill channel. The feeder was situated at the end of the 9th hill. Also visible are the two longer test channels, laid out in parallel to the training course, to which the ants were transferred from the feeder and released at the far end. For details see Fig. 6 and WOHLGEMUTH & al. (2002).

walls. We prompted *C. fortis* to walk over several artificial hills to a feeder, and recorded their homing distances (measured by occurrence of the first U-turns, as mentioned before) both over hills and on flat terrain (Fig. 5). Ants that were trained over hills and then transferred for their homebound run into a hill channel exhibited their nest search behaviour at the correct distance (5.2 m ground distance – control in Fig. 6a). However, ants that were released into the flat test channel did not reel off their training walking distance (8.7 m) but rather stopped at 4.7 m, i.e., approximately at the ground position where the nest should have been. Even more conclusive was the reverse experiment (Fig. 6b). Ants trained to the 5.2 m distant feeder in a flat channel, which were then transferred for their return run into the hill channel, now searched for the nest at 4.8 m ground distance, which, however, was equivalent to an actual walking distance of ~8 m. That is, these ants showed a ~50 % overshoot in their walking behaviour (WOHLGEMUTH & al. 2001, 2002). The conclusion from these results (and additional controls) was that ants that walk over hills somehow perceive the inclines and integrate this information into their odometric distance estimate – a quite unexpected capacity. By some mechanism they must be able to convert their actual walking distances in undulating terrain into the respective ground distances, and thereby can avoid navigational errors when foraging in undulating terrain. Using a different paradigm, in which ants were trained in a three-dimensional maze, we could confirm that ants do indeed compute ground distances for their path integration also in a complex 3-D task (GRAH & al. 2005).

However, so far these experiments do not allow to discriminate whether in solving a 3-D task *Cataglyphis* operates in a virtual 2-D projection, or to what extent the ants have access to true 3-D information (e.g., that a food source is situated at a different height, say 2 m above the nest). In other words, the question was whether *Cataglyphis* does

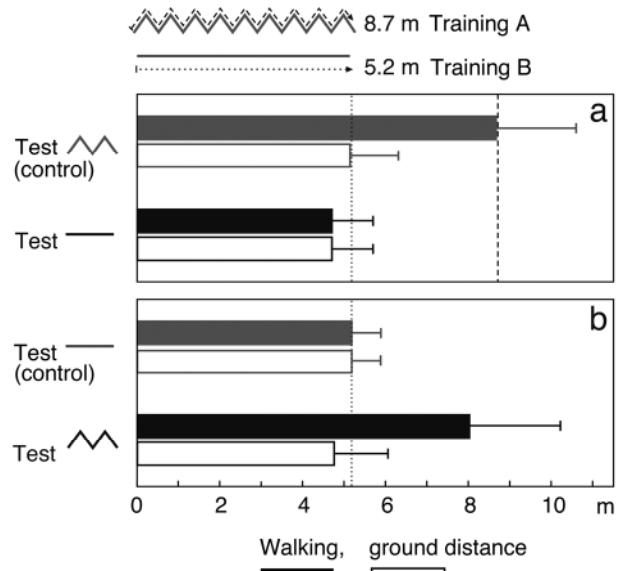


Fig. 6: Results of the experiments shown in Fig. 5. (a) Homing distances of ants after training over hills (training A, see insets). Ants ($n = 21$) were trained to walk over nine symmetric hills: walking distance 8.7 m, ground distance 5.2 m. Filled bars indicate the actual walking distances (mean \pm SD), open bars the corresponding ground distances. Dotted vertical line: expected ground distance; broken vertical line: expected walking distance. (b) Homing distances after flat training (Training B). When transferred to the hill channel, the ants covered a ground distance of ~4.8 m, which was, however, equivalent to a much larger walking distance than experienced during training (training distance: 5.2 m, $n = 17$). Adapted from WOHLGEMUTH & al. (2002).

indeed compute a true 3-D home vector, which includes the vertical dimension, or whether they reduce the 3-D problem completely to a projection on the horizontal plane. Recent observations argue against this latter hypothesis that the 3-D orientation problems are reduced to a 2-D task in the (virtual) horizontal plane (GRAH & al. 2007). On the other hand, several lines of evidence made it unlikely that the ants rely on a fully functional 3-D vector when travelling in undulating terrain (GRAH & al. 2007). Rather, *Cataglyphis* seems to rely on a kind of procedural knowledge about the vertical extensions of their paths, while performing path integration in the horizontal plane only (GRAH & al. 2007, GRAH & RONACHER 2008).

It should be emphasized, however, that, how coarse or how fine their 3-D representation might be, the ants must have a means of measuring the inclination of their path when walking over hilly terrain (see below), and must be able to feed this information into their path integration module to compute the base line distance from the respective slopes and walking distances (WOHLGEMUTH & al. 2001, GRAH & al. 2005). These results thus underline the notion that the ant's odometer module must be still more complex than the stride integrator described by WITTLINGER & al. (2006, 2007a). In spite of intensive efforts it is still not clear how the ants actually measure the slopes of ascending or descending path segments. A likely hypothesis was that *Cataglyphis* uses hair fields as graviceptors and

monitors changes in the relative positions of body parts (e.g., head, alitrunk, and gaster) that are induced when walking on different inclinations. However, an investigation of the potential contribution of several groups of hair sensors, by shaving or immobilizing hair fields, so far has not revealed any clue of the mechanism used by these ants (WITTLINGER & al. 2007b).

Accumulation of errors – a fundamental problem of path integration

Path integration is inherently error-prone. Even small systematic errors tend to accumulate in the iterative, egocentric process as described above (WEHNER & MÜLLER 1988, WEHNER & SRINIVASAN 2003). Indeed, ants that were trained to cover large distances in a linear channel showed increasing errors in their distance estimates (SOMMER & WEHNER 2004). How can *Cataglyphis* avoid a – potentially disastrous – long term accumulation of errors? One solution is to reset the path integrator to a zero state at certain places (cf. BIEGLER 2000). Indeed, *Cataglyphis* resets its path integrator to zero, when reentering the nest after a foraging trip – and thereby avoids error accumulation to carry over across repeated foraging excursions. Remarkably, coming very close to the nest entrance, while not entering the nest, is not sufficient to start the reset process (KNADEN & WEHNER 2005, 2006).

Nonetheless, it is still not well understood how the ants obtain the necessary accuracy of the path integrator in excursions over ten thousands of body lengths. Indeed, ants do employ two kinds of safety programmes that help to compensate for errors of the navigational tool kit, as well as in case of accidental displacements of an animal by wind gusts. The first is the systematic search strategy that ants apply if they do miss the nest after having run off the home vector (see Fig. 2, and WEHNER & SRINIVASAN 1981, MÜLLER & WEHNER 1994). Ants can even adjust their search programme to the uncertainty that increases with distance (WOLF & WEHNER 2005, MERKLE & al. 2006, WOLF 2008).

Interaction between landmarks and vector navigation

As a second mechanism to improve navigational accuracy, ants also rely on landmarks, if present, which allow to correct potential errors by means of stable geocentric information. Landmarks are stored as "snap shots" (CARTWRIGHT & COLLETT 1983), in a retinotopically fixed manner (WEHNER & al. 1996), and are memorized for much longer time periods than vector information (ZIEGLER & WEHNER 1997). Landmarks therefore may help to find back to the nest if an individual is displaced, e.g., by a gust of wind (WEHNER & al. 1996, NARENDRA 2007). Landmarks also serve as beacons to pinpoint exactly a food source or the nest entrance (WEHNER 1991, WOLF & WEHNER 2000, BISCH-KNADEN & WEHNER 2003, GRAHAM & al. 2003, WEHNER & al. 2006, KNADEN & WEHNER 2005), and with multiple excursions to a rich food source landmark-based route information gains in importance (WOLF & WEHNER 2000, WOLF 2008).

A plethora of experiments have been performed with artificial landmarks, and it is beyond the scope of this review to present these experiments in detail (for reviews see, e.g., WEHNER & al. 1996b, COLLETT & al. 2006, 2007). Here, I will focus only on a few recent experiments that investigate the interactions of landmark and vector based

navigation in the natural habitat. Several of these papers have focused on the Australian ant *Melophorus bagoti*. The foraging ecology of this thermophilic species is basically similar to that of *Cataglyphis* (MUSER & al. 2005), and similar orientation mechanisms as described here for *Cataglyphis* were found in *M. bagoti* (and another thermophilic ant species, the Namibian *Ocymyrmex barbiger* EMERY, 1886). *Melophorus bagoti* occupies more cluttered habitats compared to *C. fortis*. Hence, landmarks are likely to play a more important role for the navigation of this species. Indeed, individual *M. bagoti* foragers follow highly stereotypic, idiosyncratic routes to a permanent food source (KOHLER & WEHNER 2005) – as do *C. fortis* (WEHNER & al. 1996). Ants that were placed halfway on their usual routes followed their idiosyncratic route with high accuracy. This was true both for full-vector ants (i.e., ants that were taken from the feeder) as for zero-vector ants (i.e., ants that had already completed their home run), demonstrating that landmark memories can be retrieved independently from the current state of their home vector (KOHLER & WEHNER 2005). A follow up study showed that individual *M. bagoti* foragers are able to store and recall at least three different route memories (SOMMER & al. 2008). A most conclusive result was obtained in experiments, in which the ants were induced to use different paths on their way towards a distant feeder and on their way home, respectively (WEHNER & al. 2006). As in the earlier experiments (KOHLER & WEHNER 2005), an inbound ant followed its individual home route without hesitation when hitting this route after a displacement. However, if an *inbound* ant was displaced to its *outbound* route it behaved as if lost, and was unable to follow this – equally well known – route. This result demonstrates that landmark memories are not completely decoupled from the original context, and provides strong evidence against the assumption that ants would acquire a map-like representation of their environment when visiting a food source repeatedly. Hence, there is no indication that the combination between these two orientation mechanisms, path integration and landmark orientation leads to an extended representation of space in the sense of a "cognitive map" (WEHNER & al. 2006, COLLETT & al. 2007).

Concluding remarks

A lesson that we may learn from the small-brain navigator *Cataglyphis* is how complex, "high-level" behaviour is achieved by the interaction of rather simple, "low-level" subroutines. From studies on 2-D path integration by WEHNER & MÜLLER (1988) we know that *Cataglyphis* does not employ a perfect vector summation mechanism but rather uses a rule-of-thumb strategy well adapted to its particular navigational needs.

Also in other respects, e.g., for the polarization compass (WEHNER & ROSSEL 1985), and the daily ephemeris function (WEHNER & MÜLLER 1993), bees and ants do use a simplified approximate approach. These approximation rules have been deduced experimentally from systematic navigational errors displayed by the ants within particular test paradigms that do not readily occur under natural conditions, while such approximations obviously are sufficiently robust for the ant's daily life. These fascinating animals may thus offer an experimental approach to the general problems of brain functioning: how complex compu-

tational tasks can be boiled down to simpler approximate solutions, and how brains can avoid the accumulation of errors across repeated computations.

Acknowledgements

It is a special pleasure to thank Rüdiger Wehner for many years of friendship and fruitful collaborations. He made possible the encounter with these fascinating desert ants. Thanks to him for the permission to reproduce figures from his publications, and to Harald Wolf and Matthias Wittlinger for the collaboration and agreeable stays at Maharès, as well as for the photo of an ant on stilts. Sandra Wohlgegmuth initiated the hill experiments during her diploma thesis and helped with the layout of the figures. Thanks also to Harald Wolf and two referees for helpful comments on the manuscript. The Volkswagen Foundation provided generous financial support for the 3-D projects (grant No. I/78 574) and the Tunisian Ministère de l'Agriculture granted the permission to carry out these investigations near the village Maharès.

Zusammenfassung

Dieser Übersichtsartikel beschreibt einige neuere Ergebnisse zu den faszinierenden Navigationsleistungen von Wüstenameisen. Ameisen der Gattung *Cataglyphis* legen bei ihrer Futtersuche Strecken von bis zu hunderttausend Körperlängen zurück, und kehren dann – mittels Wegintegration – auf geradem Weg zu ihrem unauffälligen Nesteingang zurück. Hier soll die Frage im Vordergrund stehen, auf welche Weise die Tiere die zurückgelegten Wegstrecken mit hinreichender Genauigkeit messen können. Seit langem existierten verschiedene Hypothesen in der Literatur, aber erst 2006 wurde gezeigt, dass die Entfernungsmessung von *Cataglyphis* auf einer Schritt-Integration beruht. Allerdings ist immer noch unklar, wie die Tiere damit die nötige Präzision erreichen – Wegintegration ist ja besonders anfällig gegen Akkumulation systematischer Fehler. Erstaunlicherweise funktioniert die Wegintegration auch dann noch genau, wenn die Ameisen in hügeligem Terrain unterwegs sind. Die Entfernungsmessung scheint also noch wesentlich komplexer zu sein, als bloß Schritte zu zählen. Offenbar können die Tiere die Steigung von Wegstrecken messen und diese Information in ihre Wegintegration mit einbeziehen. Als weitere Navigationshilfen nutzen die Tiere auch Landmarken, soweit vorhanden. Viele Studien beschäftigten sich mit den Wechselwirkungen zwischen dem Wegintegrationssystem und Landmarken, speziell auch mit der Frage, ob die Tiere aus mehrfachen Begegnungen mit Landmarken eine Art "kognitive Karte" der Umgebung herzuleiten imstande sind. Mehrere kürzlich publizierte Ergebnisse sprechen jedoch klar gegen die Verfügbarkeit einer derartigen Karte. Die Wüstenameisen können als Musterbeispiele dafür dienen, wie scheinbar hoch komplexe Verhaltensleistungen auf recht einfache approximative Verfahren zurückgeführt werden können.

References

- BARRON, A. & SRINIVASAN, M.V. 2006: Visual regulation of ground speed and headwind compensation in freely flying honey bees (*Apis mellifera* L.). – Journal of Experimental Biology 209: 978-984.
- BIEGLER, R. 2000: Possible uses of path integration in animal navigation. – Animal Learning & Behaviour 28: 257-277.
- BISCH-KNADEN, S. & WEHNER, R. 2003: Local vectors in desert ants: context-dependent landmark learning during outbound and homebound runs. – Journal of Comparative Physiology A 189: 181-187.
- CARTWRIGHT, B.A. & COLLETT, T.S. 1983: Landmark learning in bees. Experiments and models. – Journal of Comparative Physiology 151: 521-543.
- CHELAZZI, G. 1992: Invertebrates (excluding arthropods). In: PAPI, F. (Ed.): Animal homing. – Chapman & Hall, London, pp. 19-43.
- COLLETT, T.S. 1996: Insect navigation en route to the goal: multiple strategies for the use of landmarks. – Journal of Experimental Biology 199: 227-235.
- COLLETT, T.S., GRAHAM, P. & HARRIS, R.A. 2007: Novel landmark-guided routes in ants. – Journal of Experimental Biology 210: 2025-2032.
- COLLETT, T.S., GRAHAM, P., HARRIS, R.A. & HEMPEL-DE-IBARRA, N. 2006: Navigational memories in ants and bees: memory retrieval when selecting and following routes. – Advances in the Study of Behavior 36: 123-172.
- DYER, F.C. 1991: Bees acquire route-based memories but not cognitive maps in a familiar landscape. – Animal Behaviour 41: 1-8.
- DYER, F.C. & DICKINSON, J.A. 1994: Development of sun compensation by honey bees. How partially experienced bees estimate the sun's course. – Proceedings of the National Academy of Sciences of the United States of America 91: 4471-4474.
- ESCH, H.E. & BURNS, J.E. 1996: Distance estimation by foraging honeybees. – Journal of Experimental Biology 199: 155-162.
- ESCH, H.E., ZHANG, S. & SRINIVASAN, M.V. 2001: Honeybee dances communicate distances measured by optic flow. – Nature 411: 581-583.
- FRISCH, K. von 1965: Tanzsprache und Orientierung der Bienen. Berlin: Springer, 578 pp.
- GALLISTEL, C.R. & CRAMER, A.E. 1996: Computations on metric maps in mammals: getting oriented and choosing a multi-destination route. – Journal of Experimental Biology 199: 211-217.
- GIURFA, M. & CAPALDI, E.A. 1999: Vectors, routes and maps: new discoveries about navigation in insects. – Trends in Neuroscience 22: 237-242.
- GRAH, G., RONACHER, B. 2008: Three-dimensional orientation in desert ants: Context-independent memorisation and recall of sloped path segments. – Journal Comparative Physiology A 194 in press (DOI 10.1007/s00359-008-0324-4)
- GRAH, G., WEHNER, R. & RONACHER, B. 2005: Path integration in a three-dimensional maze: ground distance estimation keeps desert ants *Cataglyphis fortis* on course. – Journal of Experimental Biology 208: 4005-4011.
- GRAH, G., WEHNER, R. & RONACHER, B. 2007: Desert ants do not acquire and use a three-dimensional global vector. – Frontiers in Zoology 4: 12.
- GRAHAM, P., FAURIA, K. & COLLETT, T.S. 2003: The influence of beacon-aiming on the routes of wood ants. – Journal of Experimental Biology 206: 535-541.
- HEINZE, S. & HOMBERG, U. 2007: Map like representation of celestial E-vector orientations in the brain of an insect. – Science 315: 995-997.
- HERAN, H. & WANKE, L. 1952: Beobachtungen über die Entfernungsmeldung der Sammelbienen. – Zeitschrift für Vergleichende Physiologie 34: 383-393.
- HOMBERG, U. 2004: In search of the sky compass in the insect brain. – Naturwissenschaften 91: 199-208.

- KNADEN, M. & WEHNER, R. 2005: Nest mark orientation in desert ants *Cataglyphis*: what does it do to the path integrator. – *Animal Behaviour* 70: 1349-1354.
- KNADEN, M. & WEHNER, R. 2006: Ant navigation: resetting the path integrator. – *Journal of Experimental Biology* 209: 26-31.
- KOHLER, M. & WEHNER, R. 2005: Idiosyncratic route-based memories in desert ants, *Melophorus bagoti*: how do they interact with path integration vectors? – *Neurobiology of Learning and Memory* 83: 1-12.
- LIPP, A., WOLF, H. & LEHMANN, F.O. 2005: Walking on inclines: energetics of locomotion in the ant *Camponotus*. – *Journal of Experimental Biology* 208: 707-719.
- MCNAUGHTON, B.L., BATTAGLIA, F.P., EDWARD, O.J. & MOSER, M.B. 2006: Path integration and the neural basis of the "cognitive map". – *Nature Reviews Neuroscience* 7: 663-678.
- MENZEL, R., GREGGERS, U., SMITH, A., BERGER, S., BRANDT, R., BRUNKE, S., BUNDROCK, G., HÜLSE, S., PLÜMPE, T., SCHAUPEL, F., SCHÜTTLER, E., STACH, S., STINDT, J., STOLLHOFF, N. & WATZL, S. 2005: Honey bees navigate according to a map-like spatial memory. – *Proceedings of the National Academy of Sciences of the United States of America* 102: 3040-3045.
- MERKLE, T., KNADEN, M. & WEHNER, R. 2006: Uncertainty about nest position influences systematic search strategies in desert ants. – *Journal of Experimental Biology* 209: 3545-3549.
- MITTELSTAEDT, H. & MITTELSTAEDT, M.-L. 1973: Mechanismen der Orientierung ohne richtende Außenreize. – *Fortschritte der Zoologie* 21: 46-58.
- MITTELSTAEDT, M.-L. & MITTELSTAEDT, H. 1980: Homing by path integration in a mammal. – *Naturwissenschaften* 67: 566-567.
- MÜLLER, M. & WEHNER, R. 1988: Path integration in desert ants, *Cataglyphis fortis*. – *Proceedings of the National Academy of Sciences of the United States of America* 85: 5287-5290.
- MÜLLER, M. & WEHNER, R. 1994: The hidden spiral: systematic search and path integration in desert ants, *Cataglyphis fortis*. – *Journal of Comparative Physiology A* 175: 525-530.
- MÜLLER, M. & WEHNER, R. 2007: Wind and sky as compass cues in desert ants navigation. – *Naturwissenschaften* 94: 589-594.
- MUSER, B., SOMMER, S., WOLF, H. & WEHNER, R. 2005: Foraging ecology of the thermophilic Australian desert ant, *Melophorus bagoti*. – *Australian Journal of Zoology* 53: 301-311.
- NARENDRA, A. 2007: Homing strategies of the Australian desert ant, *Melophorus bagoti*. II. Interaction of the path integrator with visual cue information. – *Journal of Experimental Biology* 210: 1804-1812.
- PAPI, F. (Ed.) 1992: Animal homing. – Chapman & Hall, London, 390 pp.
- PETERS, R.H. 1983: The ecological implications of body size. – Cambridge University Press, Cambridge, 329 pp.
- RONACHER, B., GALIZZI, K., WOHLGEMUTH, S. & WEHNER, R. 2000: Lateral optic flow does not influence distance estimation in the desert ant *Cataglyphis fortis*. – *Journal of Experimental Biology* 203: 1113-1121.
- RONACHER, B. & WEHNER, R. 1995: Desert ants *Cataglyphis fortis* use self-induced optic flow to measure distances travelled. – *Journal of Comparative Physiology A* 177: 21-27.
- RONACHER, B., WESTWIG, F. & WEHNER, R. 2006: Integrating two-dimensional paths: do desert ant process distance information in the absence of celestial cues? – *Journal of Experimental Biology* 209: 3301-3308.
- ROSSEL, S. & WEHNER, R. 1986: Polarization vision in bees. – *Nature* 323: 128-131.
- SCHÄFER, M. & WEHNER, R. 1993: Loading does not affect measurement of walking distance in desert ants *Cataglyphis fortis*. – *Verhandlungen der Deutschen Zoologischen Gesellschaft* 86: 270.
- SOMMER, S., VON BEEREN, C. & WEHNER, R. 2008: Multiroute memories in desert ants. – *Proceedings of the National Academy of Sciences of the United States of America* 105: 317-322.
- SOMMER, S. & WEHNER, R. 2004: The ant's estimation of distance travelled: experiments with desert ants, *Cataglyphis fortis*. – *Journal of Comparative Physiology A* 190: 1-6.
- SRINIVASAN, M.V., ZHANG, S., ALTWEIN, M. & TAUTZ, J. 2000: Honeybee navigation: nature and calibration of the "odometer". – *Science* 287: 851-853.
- SRINIVASAN, M.V., ZHANG, S. & BIDWELL, N.J. 1997: Visually mediated odometry in honeybees. – *Journal of Experimental Biology* 200: 2513-2522.
- THIÉLIN-BESCOND, M. & BEUGNON, G. 2005: Vision-independent odometry in the ant *Cataglyphis cursor*. – *Naturwissenschaften* 92: 193-197.
- TINBERGEN, N. 1932: Über die Orientierung des Bienenwolfs (*Philanthus triangulum* FABR.). – *Zeitschrift für Vergleichende Physiologie* 16: 305-334.
- TINBERGEN, N. & KRUYT, W. 1938: Über die Orientierung des Bienenwolfs (*Philanthus triangulum* FABR) III Die Bevorzugung bestimmter Wegmarken. – *Zeitschrift für Vergleichende Physiologie* 25: 292-334.
- WEHNER, R. 1991: Visuelle Navigation: Kleinstgehirn-Strategien. – *Verhandlungen der Deutschen Zoologischen Gesellschaft* 84: 89-104.
- WEHNER, R. 1992: Homing in arthropods. In: PAPI, F. (Ed.): *Animal homing*. – Chapman & Hall, London, pp. 45-144.
- WEHNER, R. 1994a: The polarization-vision project: championing organismic biology. In: SCHILDBERGER, K. & ELSNER, E. (Eds.): *Neural bases of behavioural adaptations*. – G. Fischer, Stuttgart, New York, pp. 103-143.
- WEHNER, R. 1994b: Himmelsbild und Kompassauge – Neurobiologie eines Navigationssystems. – *Verhandlungen der Deutschen Zoologischen Gesellschaft* 87: 9-37.
- WEHNER, R. 1997: The ant's celestial compass system: spectral and polarization channels. In: LEHRER, M. (Ed.): *Orientation and communication. Arthropods*. – Birkhäuser, Basel, pp. 145-185.
- WEHNER, R., BOYER, M., LOERTSCHER, F., SOMMER, S. & MENZEL, U. 2006: Desert ant navigation. One-way routes rather than maps. – *Current Biology* 16: 75-79.
- WEHNER, R. & LABHART, T. 2006: Polarization vision. In: WARWICK, E. & NILSSON, D.E. (Eds.): *Invertebrate vision*. – Cambridge University Press, Cambridge, UK, pp. 291-348.
- WEHNER, R., LEHRER, M. & HARVEY, W.R. (Eds.) 1996b: Navigation. – *Journal of Experimental Biology* 199.
- WEHNER, R., MARSH, A.C. & WEHNER, S. 1992: Desert ants on a thermal tightrope. – *Nature* 357: 586-587.
- WEHNER, R. & MENZEL, R. 1990: Do insects have cognitive maps? – *Annual Review of Neuroscience* 13: 403-414.
- WEHNER, R., MICHEL, B. & ANTONSEN, P. 1996a: Visual navigation in insects: coupling of egocentric and geocentric information. – *Journal of Experimental Biology* 199: 129-140.
- WEHNER, R. & MÜLLER, M. 1993: How do ants acquire their celestial ephemeris function? – *Naturwissenschaften* 80: 331-333.
- WEHNER, R. & MÜLLER, M. 2006: The significance of direct sunlight and polarized skylight in the ant's celestial system of navigation. – *Proceedings of the National Academy of Sciences of the United States of America* 103: 12575-12579.
- WEHNER, R. & ROSSEL, S. 1985: The bee's celestial compass – a case study in behavioural neurobiology. – *Fortschritte der Zoologie* 31: 11-53.

- WEHNER, R. & SRINIVASAN, M.V. 1981: Searching behavior of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). – Journal of Comparative Physiology 142: 325-338.
- WEHNER, R. & SRINIVASAN, M.V. 2003: Path integration in insects. In: JEFFERY, K.J. (Ed.): The neurobiology of spatial behaviour. – Oxford University Press, Oxford, pp. 11-30.
- WEHNER, R. & WEHNER, S. 1986: Path integration in desert ants. Approaching a long standing puzzle in insect navigation. – Monitore Zoologico Italiano (N.S.) 20: 309-331.
- WEHNER, R. & WEHNER, S. 1990: Insect navigation: use of maps or Ariadne's thread? – Ethology, Ecology & Evolution 2: 27-48.
- WITTLINGER, M., WEHNER, R. & WOLF, H. 2006: The ant odometer: stepping on stilts and stumps. – Science 312: 1965-1967.
- WITTLINGER, M., WEHNER, R. & WOLF, H. 2007a: The desert ant odometer: a stride integrator that accounts for stride length and walking speed. – Journal of Experimental Biology 210: 198-207.
- WITTLINGER, M., WOLF, H. & WEHNER, R. 2007b: Hair plate mechanoreceptors associated with body segments are not necessary for three-dimensional path integration in desert ant, *Cataglyphis fortis*. – Journal of Experimental Biology 210: 375-382.
- WOHLGEMUTH, S., RONACHER, B. & WEHNER, R. 2001: Ant odometry in the third dimension. – Nature 411: 795-798.
- WOHLGEMUTH, S., RONACHER, B. & WEHNER, R. 2002: Distance estimation in the third dimension in desert ants. – Journal of Comparative Physiology A 188: 273-281.
- WOLF, H. 2008: Desert ants adjust their approach to a foraging site according to experience. – Behavioral Ecology and Sociobiology 62: 415-425.
- WOLF, H. & WEHNER, R. 2000: Pinpointing food sources: olfactory and anemotactic orientation in desert ants, *Cataglyphis fortis*. – Journal of Experimental Biology 203: 857-868.
- WOLF, H. & WEHNER, R. 2005: Desert ants, *Cataglyphis fortis*, compensate for navigation uncertainty. – Journal of Experimental Biology 208: 4223-4230.
- ZIEGLER, P.E. & WEHNER, R. 1997: Time-courses of memory decay in vector-based and landmark-based systems of navigation in desert ants, *Cataglyphis fortis*. – Journal of Comparative Physiology A 181: 13-20.