

The architecture of the desert ant's navigational toolkit (Hymenoptera: Formicidae)

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Abstract

In the last decades North African desert ants of the genus *Cataglyphis* FOERSTER, 1850 – and more recently their ecological equivalents in the Namib desert (*Ocymyrmex* EMERY, 1886) and Australia (*Melophorus* LUBBOCK, 1883) – have become model organisms for the study of insect navigation. While foraging individually over distances of many thousand times their body lengths in featureless as well as cluttered terrain, they navigate predominantly by visual means using vector navigation (path integration) and landmark-guidance mechanisms as well as systematic-search and target-expansion strategies as their main navigational tools. In vector navigation they employ several ways of acquiring information about directions steered (compass information) and distances covered (odometer information). In landmark guidance they rely on view-based information about visual scenes obtained at certain vantage points and combined with certain steering (motor) commands of what to do next. By exploring how these various navigational routines interact, the current position paper provides a hypothesis of what the architecture of the ant's navigational toolkit might look like. The hypothesis is built on the assumption that the toolkit consists of a number of domain-specific routines. Even though these routines are quite rigidly preordained (and get modified during the ant's lifetime by strictly task-dependent, rapid learning processes), they interact quite flexibly in various, largely context-dependent ways. However, they are not suited to provide the ant with cartographic information about the locations of places within the animal's foraging environment. The navigational toolkit does not seem to contain a central integration state in which local landmark memories are embedded in a global system of metric coordinates.

Key words: *Cataglyphis*, *Melophorus*, *Ocymyrmex*, path integration, landmark guidance, systematic search, target expansion, associative networks, cognitive mapping, review, position paper.

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Introduction

Among the most remarkable insect navigators are desert ants belonging to the genus *Cataglyphis* FOERSTER, 1850. The rich repertoire of navigational mechanisms, which they display during their far-ranging outdoor journeys, and the multiple associative links between these mechanisms provide a vivid example of the complexity and versatility of spatial behaviours that one can observe in social hymenopterans. In the present account I outline the main navigational strategies and discuss how they might be combined and linked. My aim is not to provide a comprehensive review of the subject, or even of parts of it (for such reviews, see WEHNER 1992, GIURFA & CAPALDI 1999, COLLETT & COLLETT 2000, WEHNER 2003a, COLLETT & al. 2006, COLLETT & al. 2007, RONACHER 2008, WEHNER 2008), but to propose some – potentially provoking – hypotheses about how the animal's navigational toolkit might be organized. By doing so I hope to enter into a discussion upon this architectural issue, and by the same token into one upon the map hypothesis so much *en vogue* today.

There are two main navigational strategies employed by ants as well as bees: path integration (vector navigation) and view-based landmark guidance. In principle, path integration could provide the animal with a global coordinate system centred on the nest and capable of assigning metric

coordinates to landmark-defined places. If this were actually the case, the animal would have the potential of acquiring a "cognitive map" *sensu* TOLMAN (1948) and O'KEEFE & NADEL (1978) of its foraging terrain (see also GALLISTEL 1990, BENNETT 1996, SAMSONOVICH & MC NAUGHTON 1997, BIEGLER 2000). Whether insects are really able to exploit this possibility has fuelled some quite controversial literature since the map hypothesis has been proposed for honey bees first by GOULD (1986) and later in more detail by MENZEL & al. (2000) and MENZEL & al. (2005) (for critical discussions, see DYER 1994, BENNETT 1996, WEHNER 2003a, COLLETT & al. 2006, RONACHER 2008, WEHNER 2008).

The question of how the path-integration and the landmark-guidance systems interact is all the more intriguing as in the mammalian brain the recently discovered cortical (entorhinal) arrays of grid cells provide the animal with an intrinsic, environment-independent metric that results from path-integration inputs (HAFTING & al. 2005, FYHN & al. 2007, MOSER & al. 2008). Integrated with environmental landmark cues this internal coordinate system allows for the formation of spatial representations as found downstream in the hippocampal system of place cells (MC NAUGHTON & al. 2006, SOLSTAD & al. 2006). The latter is supposed to

form the neural basis of the cognitive map (NADEL 1991, WILSON & MC NAUGHTON 1993, ULANOVSKY & MOSS 2007). Given this upsurge of interest in the neurobiology of the mammalian cognitive map, and the concomitant claim that bees, too, integrate spatial information into "a common spatial memory of geometric organization (a map)", "a map-like memory ... as in other animals and humans" (MENZEL & al. 2007: 429), the present account on the organization of the ant's navigational toolkit will certainly have to bear on such claims as well. Mainly, however, I shall focus on the particular navigational routines employed by *Cataglyphis* and its ecological equivalents *Ocymyrmex* EMERY, 1886 and *Melophorus* LUBBOCK, 1883 in southern Africa and central Australia, respectively, and what the potentialities and constraints of these routines are in contributing to one or another representation of the animal's foraging space. Figure 1 portrays two phylogenetically quite unrelated species of these long-legged and highly speedy desert ants, which occupy the unique ecological niche of a thermophilic scavenger (WEHNER 1987, WEHNER & al. 1992). Members of both genera are strictly diurnal, solitary foragers searching over large distances for arthropods that have succumbed to the environmental stress of their desert habitats.

Vector navigation

Path integration (MITTELSTAEDT & MITTELSTAEDT 1980), i.e., vector navigation (WEHNER 1982), is an ongoing process enabling the animal to keep a running total of its direction and distance from its starting point. In central place foragers such as bees, ants and many other hymenopterans this starting point is usually the nest opening. Hence at any one time *Cataglyphis* is endowed with a vector pointing from its present location back to the nest. Once it has returned to the nest, actually once it has vanished into it (KNADEN & WEHNER 2006), the path-integration vector is reset to zero, but a copy of the full vector pointing from the foraging site, from which the ant has just successfully returned, to the nest is stored in memory. Later, when the ant sets out for another foraging run to that site, the memorized reference vector is retrieved and used again, reversed in sign, to steer the animal to the previously visited site (for reviews and arguments, see WEHNER 1992, COLLETT & al. 1998, COLLETT & COLLETT 2000, WEHNER & al. 2002, WEHNER & SRINIVASAN 2003). As in the preceding inbound (homing) run it is now also during the outbound (foraging) run that *Cataglyphis* continuously compares the state of its current vector with the memorized reference vector and walks until both vector states match. The path integrator is then said to be in its zero state. I shall return to this way of reasoning later in more detail when possible interactions between path integration and landmark guidance are discussed.

The necessary information about the angular and linear components of movement that are combined in the path integrator is provided by compass and odometer routines, respectively. Among the various compass systems employed by *Cataglyphis* the polarization compass is by far the dominating one (WEHNER & MÜLLER 2006), but some early remarks made by SANTSCHI (1913, 1923) could let one assume that in other genera of ants, e.g., *Messor* FOREL, 1890, the sun compass is more important. It would be a worthwhile research project in sensory ecology to disen-

tangle the navigational roles which the various but closely related skylight cues – sun, polarization and spectral gradients – play in different species.

The polarization compass relies on information provided by the polarization of scattered skylight and processed by a small specialized part of the ant's visual system (WEHNER 1994, LABHART & MEYER 1999). However, there is a snag in it. The direction which the polarization compass records for a given course taken by the ant depends on the parts of the cloudless (polarized) sky currently available to the animal. For example, if the ants are trained to perform their outbound (foraging) runs under the full skylight pattern, but have then to perform their subsequent inbound (homing) runs under restricted views of the sky, or *vice versa*, systematic errors occur (WEHNER & MÜLLER 2006). Depending on the experimental circumstances these errors can be quite substantial. Under natural conditions this potential source of error is reduced by (I) the fact that the pattern of the angles of polarized light continues even underneath clouds, if – but only if – the air space underneath the clouds is directly hit by the sun (POMOZI & al. 2001), (II) the observation made in crickets (HENZE & LABHART 2007) and in technical models of polarization-sensitive interneurons (LABHART 1999) that a wide-field polarized-light detecting system can be quite robust against irregular perturbations of the polarization pattern as caused by haze, clouds or vegetation, and (III) the extremely wide fields of view and other physiological properties of the polarization-sensitive interneurons in the optic lobes and central complex (as deduced from work on crickets and locusts: WEHNER & LABHART 2006, HEINZE & HOMBERG 2007, SAKURA & al. 2008, LABHART 2008). As the latter two arguments refer to crickets and locusts rather than ants and bees, and as we do not know yet whether these orthopterans have a true polarization compass or use polarized skylight just for maintaining their courses (for a discussion, see WEHNER & LABHART 2006), at present these arguments should not be frankly applied to the hymenopteran case. More experiments on how the ant's and bee's polarization compass performs under naturally varying skylight conditions are certainly needed to better understand the significance of the systematic navigational errors which can readily be induced under controlled experimental conditions. (The way of how the compass mechanism compensates for the daily rotation of the skylight pattern is not considered here. A brilliant analysis of the bee's way to acquire the appropriate solar ephemeris function has been provided by DYER & DICKINSON [1994]; for *Cataglyphis*, see WEHNER & MÜLLER [1993] and WEHNER [2008].)

The *Cataglyphis* odometer depends mainly on idiothetic cues, i.e., works as a pedometer (stride integrator, WITTLINGER & al. 2006), and to a much lesser extent on self-induced optic flow-field cues perceived by the downward looking parts of the eye (RONACHER & WEHNER 1995). Under normal walking conditions *Cataglyphis* keeps a rather constant walking speed (ZOLLIKOFER 1988), but we do not know yet how robust the ant's odometer is against changes in walking speed and hence against changes in stride length and stride frequency – two locomotor parameters that in walking ants are quite tightly coupled (ZOLLIKOFER 1988, WITTLINGER & al. 2007).

In flying bees, in which a visually driven odometer time-integrates self-induced optic flow experienced during flight

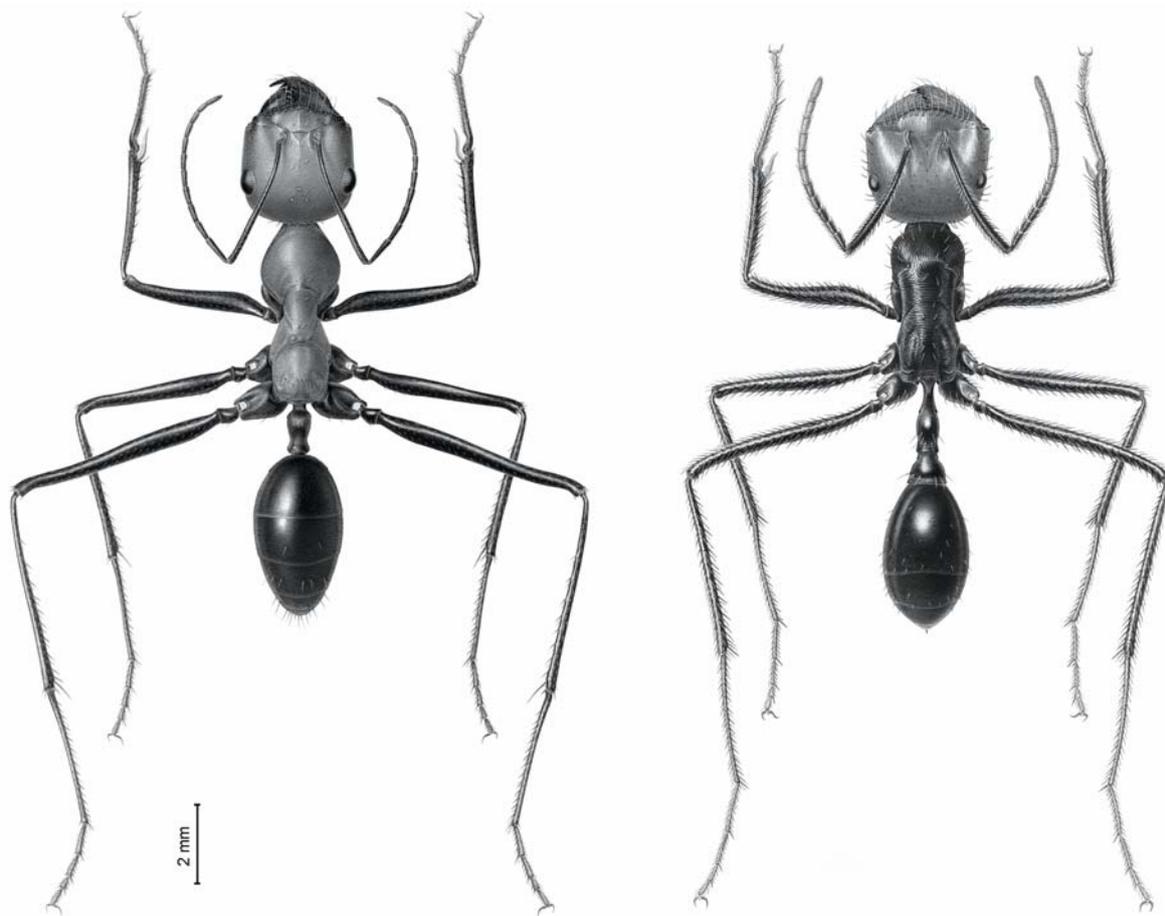


Fig. 1: *Cataglyphis bicolor* (left) and *Ocymyrmex velox* (right), a striking example of parallel evolution. The species shown are representatives of two genera of desert ants which belong to different subfamilies (formicines and myrmicines, respectively) and inhabit different faunal regions, but exhibit the same suite of morphological and physiological adaptations to long-distance foraging in barren terrain: extremely long legs, slender alitrunks and high running speeds. Because of these characteristics they have been dubbed the race horses of the insect world (WEHNER 2003b). In fact, their legs are highly significantly longer (relative to body size) than those of phylogenetically closely related ants that inhabit more mesic habitats.

(ESCH & BURNS 1995, SRINIVASAN & al. 1996, SRINIVASAN & al. 1997, SRINIVASAN & al. 2000), the information acquired by the bees about distances travelled depends on the visual properties of the terrain across which the bees fly, and hence is not environment-invariant. Although the bee's visual odometer has been shown to be quite robust against variations in visual texture (spatial frequency) and contrast (SI & al. 2003), at least above certain threshold levels (TAUTZ & al. 2004), the amount of image motion experienced during flight is largely affected by the distances to the various objects that the bee passes *en route*. This argument is the more compelling as the bee's visual odometer used in path integration seems to rely primarily on the motion that is perceived by the lateral rather than ventral regions of the visual field (SRINIVASAN & al. 1997), so that the amount of perceived image motion depends on the distances of vertical landmarks such as trees and bushes in the bees' environment. Of course, as a bee follows a fixed route to a familiar foraging site, and as a recruited bee, which has followed the forager's waggle dance inside the hive, flies along the same route, both bees – recruiter and recruit - will experience the same terrain and hence the same optic flow-field cues. But the path-integration vector that a scout bee is computing while performing a tortuous

foraging flight will certainly depend on how heterogeneously the visual objects encountered by the bee are distributed within the foraging area.

Further analysis of the *Cataglyphis* path integrator has shown that odometric information is disregarded whenever there is no concurrent input from the skylight compass (SOMMER & WEHNER 2005, RONACHER & al. 2006). When ants are trained in a tunnel that is partially occluded, i.e., consists of a sequence of open-topped and closed-topped segments, and when they are subsequently tested in a tunnel that is open along its entire length, they search at a distance corresponding only to the distance previously travelled under sky-view conditions. The same result has recently been obtained in honey bees (DACKE & SRINIVASAN 2008). The bee story, however, has a curious twist. The result is valid only under the experimental conditions mentioned above, i.e., when an experienced forager returns to a previously visited food source. When instead the forager performs its recruitment dance inside the hive, it encodes information about the total (hive-to-feeder) distance flown, even if it has experienced skylight compass cues only during part of the journey. Hence the authors suggest that bees may possess two visually driven odometers: a "community odometer" alongside a "personal odometer".

There is yet another aspect of the path integrator that has been analysed in *Cataglyphis* and will have important implications for any use of the path integrator in map-based navigation. As again shown by channel experiments, but later also confirmed by recording foraging and homing paths in the field, the courses computed by the ant's path integrator deviate from the true vector courses whenever the outbound paths are biased towards one-sided (left-sided or right-sided) turns (MÜLLER & WEHNER 1988, MÜLLER & WEHNER 1994; for a hypothesis of the functional significance of this behaviour, see WEHNER 2008). In open, landmark-free terrain the frequency distribution of an ant's angular movements (the angular deviations of the ant's (n+1)th step from the vector acquired after the (n)th step) is symmetrical in shape (WEHNER & WEHNER 1990), but in cluttered environments, to which the map concept especially applies, one-sided detours enforced by landmarks do often occur (see, for instance, SANTSCHI 1913: fig. 7). This implies that path integration coordinates attached to a particular foraging site are not independent of how the animal has reached that site. Such independence, however, is an indispensable requirement for allocentric map-based navigation.

Landmark guidance

Desert ants studied in North Africa (*Cataglyphis fortis* [FOREL, 1902]: e.g., WEHNER & al. 1996) and central Australia (*Melophorus bagoti* LUBBOCK, 1883: e.g., KOHLER & WEHNER 2005, WEHNER & al. 2006, NARENDRA 2007, SOMMER & al. 2008) as well as wood ants of holarctic regions (*Formica rufa* LINNAEUS, 1761, *F. japonica* MOTSCHOUJSKY, 1866: e.g., NICHOLSON & al. 1999, GRAHAM & COLLETT 2002, COLLETT & al. 2003b, FUKUSHI & WEHNER 2004) and tropical ants (*Gigantiops destructor* FABRICIUS, 1804: MACQUARDT & al. 2006) acquire and use rich navigational memories of landmark-defined places and routes. They can learn and store in memory even a number of routes and sequences of motor commands associated with these routes, and later retrieve these memories alternately in correct route-specific sequences (SOMMER & al. 2008). However, there is no indication at all that the ants have learned anything about the spatial relationships among different routes, for instance, about the angles separating these familiar routes.

The upshot of all investigations on place and route learning is that landmark navigation turns out to be an exclusively view-based routine. Ants (and bees) behave as if they took two-dimensional views ("snapshots") of the landmark scenes seen from particular vantage points, stored these views, and later when again approaching the goal, in particular when entering the catchment area surrounding the goal, compared the stored views with the current ones. Multiple views can be stored of the same scene (JUDD & COLLETT 1998, NICHOLSON & al. 1999). By applying one or another kind of image matching strategy several authors have tried to simulate the animal's behaviour (CARTWRIGHT & COLLETT 1983, LAMBRINOS & al. 2000, MÖLLER & VARDY 2006). Some of them have even done the step from simulation to the real world by constructing an autonomous agent, a mobile robot (Sahabot: LAMBRINOS & al. 2000). In all these simulations the animal is thought to move in such a way that the currently perceived image would gradually be transformed into the one stored at the

acquisition point. The local views, or individual signposts within these views, can be associated with "local vectors" (COLLETT & al. 1998), i.e., local movement commands (BISCH-KNADEN & WEHNER 2003), that tell the animal in what direction to move after image matching has been achieved (for *Myrmica sabuleti* MEINERT, 1861, see CAMMAERTS & LAMBERT 2008; for honey bees, see COLLETT & al. 1993, COLLETT & al. 1997, SRINIVASAN & al. 1997). Although network models have been designed that are based on associations between local views and local movements (SCHÖLKOPF & MALLOT 1995, FRANZ & MALLOT 2000), the important point to be emphasized here is that all these view-based mechanisms of landmark guidance do not, *eo ipso*, provide the animal with metric information about absolute distances and sizes. Whether and how these local views and associated local movement commands could get globally connected, is one of the most pressing questions in the study of landmark guidance in insects, and in animals in general. A first step in trying to answer such questions is to record the spatial behaviour of individual ants during successive foraging and homing runs as completely as possible. For example, desert ants departing from the nest acquire visual information about the landmark scene around their nest by performing highly structured learning runs, similar to the learning flights performed by wasps and so beautifully analysed by Jochen Zeil and his co-workers (e.g., ZEIL & al. 2007; for wood ants leaving a feeding site, see NICHOLSON & al. 1999). On the basis of such records hypotheses can be developed and experiments can be designed (for current hypotheses on landmark-based navigational strategies in ants and bees, see WEHNER 1992, MENZEL & al. 2005, COLLETT & al. 2006, WEHNER 2008). Although flying bees and walking ants differ in the sizes of their foraging ranges and the ways of how they travel through these ranges, the tasks they have to accomplish in acquiring, storing and using information about spatial relationships among visually separated sites are rather similar indeed. Hence let me hypothesize that any difference in the navigational strategies that might exist between bees and ants is one of degree rather than kind. By all means, joint investigations on the differences and conformities in ant and bee navigation are highly recommended. Again, a crucial task, though not easily to accomplish, would be to get more detailed information about the visual inputs actually experienced and acquired by the insects as they negotiate their ways through their foraging grounds, at best starting with the time at which the animals commence foraging. Reconstructing the optic flow experienced by the insect as it moves through its environment – either by computer simulations (after having recorded the spatial layout of the insect's path and the 3-D structure of the surrounding landscape) or, better yet, by moving a camera along the insect's path (for flies, see BOEDDEKER & al. 2005, ZANKER & ZEIL 2005) – would be a first step in analysing what navigationally relevant information the insect might extract from the visual scenes. Ideally, a second step would then be to play such natural flow-field scenes back to particular interneurons known to be involved in one or another kind of navigation, and to record the neuronal responses to these natural stimuli (for the wide-field motion-sensitive interneurons in the lobula plate of flies, see BOEDDEKER & al. 2005, VAN HATEREN & al. 2005, KARMEIER & al. 2006).

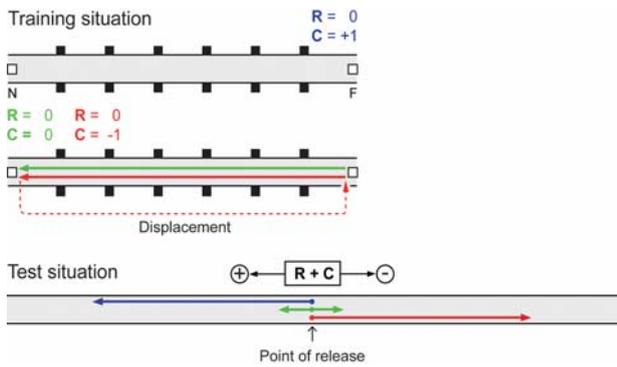


Fig. 2: Outline of an experiment demonstrating that the ant's path integrator is running continuously even if its output is temporarily suppressed by landmark-guidance routines (for full data sets, see ANDEL & WEHNER 2004).

N nesting site, F feeding site. Path-integration vector: R_{in} and C denote the memorized reference vector of the homebound ant and the state of the current vector, respectively, with $[+]$ and $[-]$ meaning the inbound (feeder-to-nest) and outbound (nest-to-feeder) direction, respectively, and the value 1 defining the unit vector length (feeder-nest distance). $R_{in} + C$ represents the output of the path integrator. In the assumption made here the reference vector retrieved by the homebound ant is always the zero vector ($R_{in} = 0$).

Training situation: Ants, *Cataglyphis bicolor*, are trained to run back and forth between N and F within a channel provided with an alley of landmarks (black pillars). The channels are not drawn to scale.

Test situation: At various stages of their homing runs (see coloured arrows inside the training channel) the ants are displaced to a landmark-free test channel, which is aligned with the training channel and within which the homing paths of the ants are recorded. Displacement occurs (I) after the outbound ants have reached F (blue signatures: $[+1]$ -vector ants), (II) after the inbound ants have arrived at N , but not yet entered the nest (green signatures: zero-vector ants), and (III) after the ants having arrived at N and having been displaced back to F have arrived at N a second time (red signatures: $[-1]$ -vector ants). As indicated by the coloured arrows inside the test channel, upon release the ants, which all are in their homing motivational state, (I) run in the homeward (inbound) direction, (II) search symmetrically around the point of release, and (III) run in the outbound direction, i.e., away from home.

The figure depicts the situation for the homebound ant. For the sake of clarification let us further assume (what is not shown here) that an ant having returned home would set out for another foraging journey to the previously visited feeding site. It then would download its nest-to-feeder reference vector $R_{out} = -1$ and move until its current vector, which is $C = 0$ at the nest, has reached the state $C = +1$, so that $R_{out} + C = 0$. Note that in the assumptions made here the current vector is always pointing from the ant to the nest. When later starting to return to the nest the ant would again download $R_{in} = 0$ and continue as described above.

Possible interactions between vector navigation and landmark-guidance

When a *Cataglyphis* worker leaves its colony for its first foraging run into then still unfamiliar terrain, path inte-

gration is its only navigational means. Later, when it gets increasingly familiar with the landmarks within its nest environment, it could associate particular landmark views with particular states of its path integrator. These associations, however, do not seem to be very strong indeed. One could assume that memories of nest-defining landmarks would be activated only after the ants have run off their home vector. But this is not the case. When trained foragers are displaced from the feeder to a distant test area, where they experience a nest-defining landmark at various positions sideways of their vector course, they slightly drift towards the landmark even right from the start of their homeward run, but then resume their homebound vector course. This drifting towards the landmark and the subsequent rejoining of the vector course occurs wherever the landmark appears further down the homing course (BREGY & al. 2008, see also MICHEL & WEHNER 1995). Hence, nest-mark memories are effective during the entire vector-based homeward run, but are either activated or used only partly unless the state of the ant's path integrator is close to zero.

Furthermore, sequences of landmark scenes can be stored and used, like pearls on a string, independently of the state of the path integrator that was running while the ants were acquiring their route memories. If zero-vector ants, i.e., homing ants that have already arrived at the nest but have been prevented from entering it, are displaced to a location sideways of their habitual homing route, they can rejoin this route at any one point at which they come to hit it (KOHLER & WEHNER 2005, WEHNER & al. 2006, WEHNER 2008). Obviously, the retrieval of the appropriate sequence of landmark memories does not depend on the state of the path integrator. Path integration and view-based landmark guidance seem to represent rather independent modules of navigation. The former is used to establish the latter, but once established, landmark guidance can work independently of path integration. In establishing route memories the ants could monitor how views change, and acquire new ones when the image differences become large (e.g., CARTWRIGHT & COLLETT 1987). In robotics such procedures have been used when mapping new environments (GAUSSIER & al. 2000).

Striking evidence that landmark memories are strongly coupled to the context within which they have been acquired, and that they are not knitted together in a more general, say, map-like way comes from displacement experiments performed in the Australian red honey ant, *Melophorus bagoti*. Within their landmark-rich foraging environments these ants establish idiosyncratic routes travelled between nest and a frequently visited feeding site. If in a particular experimental paradigm they are forced to select different one-way routes for their outbound and inbound journeys, inbound ants displaced to their outbound route do not follow this route in the reverse direction back to the nest, but start their search programme; nor do they compute the direct course from any site of a familiar route to the landmark-defined nesting site (WEHNER & al. 2006).

There is yet another important point to be mentioned here. The path integrator is continuously running whenever the ant has left its colony and is moving about in its foraging environment. Even if the ant is currently relying exclusively on landmark-based systems of navigation, the path integrator keeps operating in the background (SASSI & WEHNER 1997, KNADEN & WEHNER 2005). This can be

shown most dramatically in an experiment, in which ants trained to run within a channel from feeder to nest along a landmark alley are forced to follow the landmark-defined feeder-to-nest route several times before they are allowed to enter the nest and to reset their path integrator (Fig. 2, for details, see ANDEL & WEHNER 2004). If then displaced to a landmark-free test channel, the ants still carrying their food items and thus still being in their homing mood run in the counter direction of their homebound course. This is because due to the repeated runs in the feeder-to-nest direction their current vector is now pointing in the nest-to-feeder direction. It is as if in a natural situation the homebound ants had considerably overshot their goal, the nest, and had now to move in the counter direction of the feeder-to-nest direction in order to approach the nest again.

In Figure 2 it is assumed that in the ant's path-integration system a current vector C is continually compared with a stored reference vector R (see the section on path integration and references cited therein). It is further assumed that for the inbound (homebound) ants $R_{in} = 0$, while for the outbound (feederbound) ants R_{out} is pointing at the feeder (for details, see legend of Fig. 2). At the nest and at the feeder $R_{in} + C = 0$ and $R_{out} + C = 0$, respectively. At these two sites the path-integrating system is in its zero state ("zero-vector ants"). Other assumptions depending on whether resetting occurs only at the nesting site (as assumed here) or at other sites as well, or to what sites R and C can be anchored, will lead to other models of how the path integrator might work. Actually, in discussing the results on which Figure 2 is based ANDEL & WEHNER (2004) have used a model in which resetting occurs at both the nesting and the feeding site. Irrespective of such modelling attempts, the results schematically shown in Figure 2 also mean that during their more than 50 training runs the ants had not acquired the cartographic information that running, say, west would always bring them home.

When the negative state of the path integrator was experimentally increased to an extent that an ant would never experience in nature, the ant once displaced to the test channel would suddenly stop walking, drop its food item and, as if paralysed, remain motionless. When approached by the experimenter, it would hardly display any escape behaviour. For the otherwise witty and vivacious *Cataglyphis* ants, this is a completely unusual state of affairs.

Systematic search and target expansion

As shown in the previous section, *Cataglyphis* does not assign path-integration coordinates to landmarks it encounters *en route* and hence cannot take positional fixes while winding its way through its foraging grounds. As a consequence, errors are inevitably accumulating during the path-integration process: the tip of the path-integration vector is not pointed but blurred, with the "blur circle", the uncertainty range, getting the larger, the longer the path integrator has run (WEHNER & WEHNER 1986, MERKLE & al. 2006). The systematic search behaviour displayed when the path integrator has reached its zero state, but the ant has not yet arrived at its nest (WEHNER & SRINIVASAN 1981, MÜLLER & WEHNER 1994) is adapted to this variable uncertainty range, or target probability function, in so far as the search density profile gets the broader, the larger the uncertainty range is (WEHNER 1992, MERKLE & al. 2006). It is as if the homing ant expected a particular uncertainty in pin-point-

ing its goal, and adjusted its search behaviour accordingly (see also WOLF & WEHNER 2005, WEHNER 2008). It is also in honey bees trained to forage inside an optically well textured tunnel that the width of the search distribution, one-dimensional in this case, increases systematically with the distance of the feeder from the tunnel entrance. However, when the bees while flying towards the feeder experience a prominent landmark *en route*, the search distribution is narrowed substantially (SRINIVASAN & al. 1997). This result suggests that when passing a known landmark the bees re-commence the computation of their distance flown, i.e., reset their odometer.

We can regard the systematic search routine as some kind of emergency plan that comes into play especially in featureless terrain, where landmarks are not available to serve as final guides. In such terrain nest mates in the immediate vicinity of the nest might provide another cue informing the returning foragers that the goal is within reach. This type of goal-expansion strategy has apparently been adopted by *C. bombycina* (ROGER, 1859), the silver ant. This *Cataglyphis* species, which inhabits the Saharan seas of sand, is characterized by mostly inconspicuous entrance holes leading to large subterranean colonies. Within an area of several square metres around these nest entrances about five to ten individuals would stay motionless on the ground ready to approach any returning ant, contact it intensively with its antennae, and then let it go again. At the colonial level, this behaviour can certainly be regarded as a means to enhance the goal area for the returning foragers. The fast running foragers, which due to their long legs keep their bodies well above the flat sand surface, will be conspicuous targets even for the visual system of formicine ants (STÄGER 1931, STURDZA 1942). This capability has already been discussed for *C. bicolor* (FABRICIUS, 1793) in the context of a particular kind of "visual recruitment" behaviour (WEHNER 1987).

In *Ocymyrmex robustior* STITZ, 1923, which inhabits the sand-dune and sand-field areas in southern Africa, a similar type of behaviour occurs. At times of high foraging activity one or two workers would run frantically around the nest entrance and contact as many returning foragers as possible. As these "contactors" exhibit brighter red heads than the foragers, they could be workers just in the state of starting their outdoor activities. These observations suggest that even in individually foraging, visually navigating rather than pheromone-guided ants inter-individual interactions might contribute to improving navigational accuracy – a hypothesis certainly worthy of further investigation. For example, does the search density profile of a returning forager get more focussed after the forager has been approached by a contactor?

Proposing a cognitive architecture

What can we learn from the organization of the ant's navigational performances about the architecture of the underlying neural toolkit? As outlined above, *Cataglyphis* comes programmed with an amazingly rich repertoire of navigational routines, of which only the most fundamental ones have been mentioned. These routines generate quite rigidly preordained behavioural outcomes shaped by species-specific evolutionary experience and modified individually by pre-programmed, strictly task-specific, rapid learning processes; for example, in learning local landmark sceneries

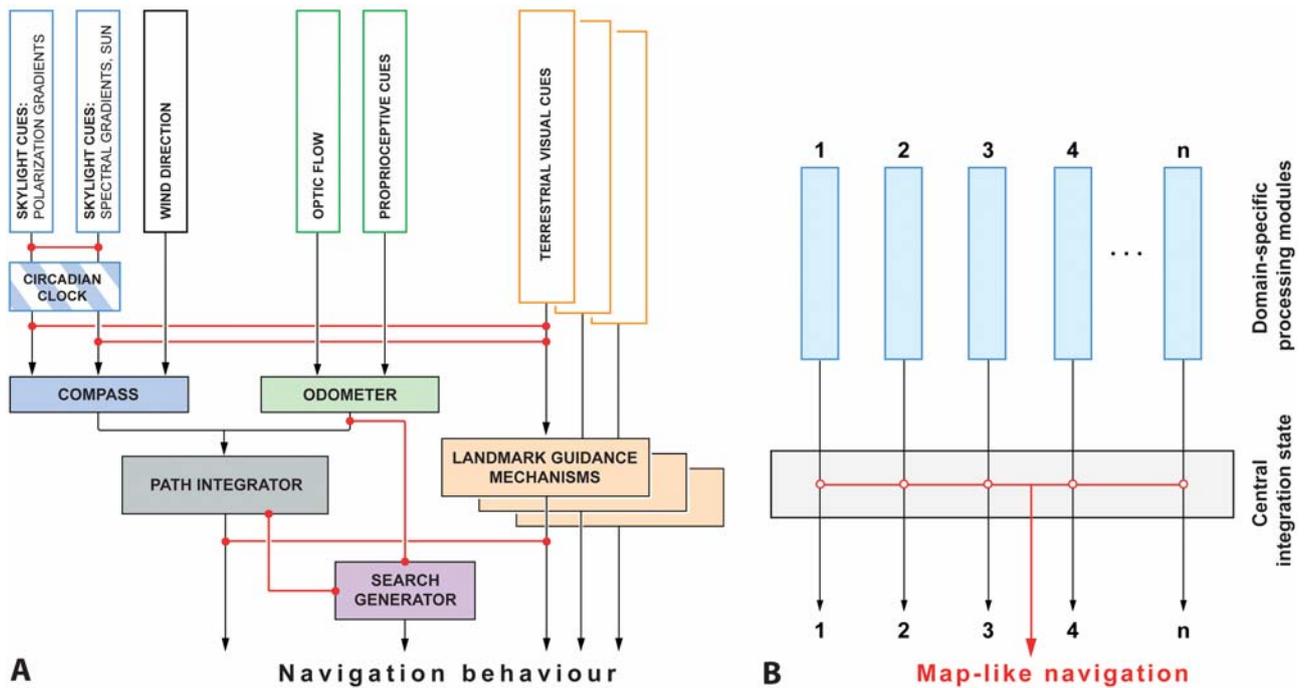


Fig. 3: The architecture of the insect's navigational toolkit: two hypotheses.

(A) Domain-specific modules are interlinked within a distributed system. Some interactions supported by experimental evidence are indicated, tentatively though, by red lines. Depending on the external stimulus situation and the internal (motivational) state of the animal they can come into play simultaneously or successively, and can be reinforcing, modulating or inhibiting. Hierarchical organizations, even though they do exist, are not explicitly shown in this diagram. Inside the boxes representing the sensory processing modules (upper part of figure) the processed sensory cues are given. Among the landmark-guidance modules are mechanisms of, e.g., view-based image matching, flow-field detection, and beacon aiming.

(B) (proposed by MENZEL & GIURFA 2001). Spatial information is processed in a central integration state, where a coherent map-like memory is formed. According to this concept of "vertical modularity" and "central integration" there are no horizontal interactions between the domain-specific processing modules (1, 2, ... n) outside the central stage. As emphasized by the authors, vertical processing is mandatory. Examples given for the modules 1, 2, ... n are the polarization compass, distance estimation, and path integration during search flights. The horizontal interactions within the central processing unit result in map-like navigation and other kinds of "new behaviours". – Inputs from motivational states or value-specific modules are omitted in (A) and (B).

(WEHNER & al. 2004), in acquiring the local celestial ephemeris function (DYER & DICKINSON 1994), or in learning and re-adjusting path-integration vectors (WEHNER & al. 2002, CHENG & WEHNER 2002, CHENG & al. 2006, NARENDRA & al. 2007, MERKLE & WEHNER 2008) and search patterns (WEHNER & al. 2002). The time courses and the extent of these rapid, pre-structured learning processes will be promising topics of future research.

In general, what we can conclude from the potentialities and constraints of the domain-specific routines is that *Cataglyphis* accomplishes its grand navigational tasks certainly not by starting out from first principles, not by handling geometrical relations in any graph-like way, but by flexibly interlocking a number of particular routines. This hypothesis is sketchily portrayed in Figure 3A. Rather than feeding their information into a central processing unit, in which a unified global representation of the insect's outside world is formed, as suggested, for instance, by MENZEL & GIURFA (2001) (Fig. 3B), the individual routines interact, simultaneously or successively, in flexible and largely context-dependent ways. What we observe is an assemblage of interacting distributed systems. Some of these interac-

tions have facilitating functions, others have inhibiting effects, some occur at more peripheral, others at more central levels.

In the present account the particular kinds of interactions cannot be outlined in detail. They will be the focus of future study. Nevertheless let me make a few remarks. In the ant's and bee's celestial compass system information about the polarization and spectral gradients in the sky are picked up and processed by different parts of the insect's peripheral visual system (WEHNER 1994, 1997, LABHART & MEYER 1999), but might converge at some quite early stage of data processing (see the properties of a particular type of polarization-sensitive interneuron studied in locusts, PFEIFFER & HOMBERG 2007). This makes sense as under natural conditions all these skylight parameters are closely correlated. As to another point, the skylight compass is an integral part of the path integrator (SOMMER & WEHNER 2005, RONACHER & al. 2006, DACKER & SRINIVASAN 2008), but it can separately interact with landmark memories in so far as it assigns directional motor commands to stored landmark scenes and helps in snapshot matching (AKESSON & WEHNER 2002). Most likely it is also odometric informa-

tion that can be used in more than one way (DACKE & SRINIVASAN 2007, DACKE & SRINIVASAN 2008). Furthermore, and probably at a more central level, landmark-guidance routines can inhibit the output of the path integrator without preventing the integrator from running uninterrupted all the time the animal is on its way. Finally, the search generator is switched on only after the path integrator has been reset to zero and goal-defining landmarks have not been encountered.

To a certain extent the hypothesis outlined in Figure 3A corresponds to a competing agent model. As all the agents act on the same motor programme where they compete for motor output, one might argue that there should be a gating or comparator stage that decides which output line drives the behaviour at any one time. For the sake of argument let me instead propose that there is no such central decision stage, but that the properties of the associative links within the network have evolved so as to generate efficient and meaningful navigational performances adapted to the animal's species-specific ecological requirements. If the natural conditions under which the system normally works are experimentally distorted, less efficient or even aberrant behaviour results. Then, a homing ant will run away from home (ANDEL & WEHNER 2004), and a nest-defining landmark appearing earlier than expected during an ant's homeward run will deflect the ant from its straight course, but will not let it abandon the vector course (BREGY & al. 2008). It is the intricacy of the interactions between the various modules as they have been shaped by natural selection that defines the read-out of the associative network, with coincidence and salience playing perhaps a major role in the final result.

The particular navigational routines might well have become established in the insect's nervous system at various evolutionary times depending on the prevailing ecological and behavioural needs. In accord with the general evolutionary principle of duplicating and subsequently modifying structures, already existing types of neural networks might have become integrated into new modules, in which they now serve new functions. In various forms of navigation some kind of template matching occurs: in path integration a current vector is continually compared with a memorized reference vector, while in landmark guidance current images of landmark scenes are compared with images of scenes that have been stored at previously visited sites. At a more peripheral level, similar coding principles might be involved in processing polarization and spectral skylight information. A hot spot for future research, and a fascinating project in comparative evolutionary biology, is to inquire about differences that might exist between desert ant species that are closely related phylogenetically but differ ecologically in the types of environment they inhabit: featureless or cluttered ones, two- or three-dimensional ones. We have started such a project, and exciting results are already beginning to emerge.

Of course, as in this position paper I have painted my picture with a rather broad brush, the characterization of the architecture of the ant's navigational toolkit must be avowedly sketchy. Even though the structural details of this architecture are neither conclusive nor complete, and have been implemented for the mere purpose to stimulate discussion, the basic conceptual difference between the concepts depicted in Figures 3A and B should have become ap-

parent. Contrary to the hypothesis proposed here (Fig. 3A), authors adhering to the cognitive-map hypothesis (GOULD 1986, MENZEL & al. 2000, MENZEL & GIURFA 2001, MENZEL & al. 2005) have argued for a more centralized architecture, in which spatial information is globally integrated within a central processing unit, or central integration state (Fig. 3B). It is in this central unit that the map computations are supposed to take place. According to this central-unit hypothesis there are no interactions between the various navigational routines outside the central integration state.

At present it would be rash to assign specific neural centres to particular navigational modules, but let me nevertheless hypothesize, a bit daringly though, that the neural pathway involved in path integration by-passes the mushroom bodies – the multimodal integration centre in the insect brain – and mainly includes neuropiles of the ventral protocerebrum such as the lateral and central complexes (STRAUSS 2002, HEINZE & HOMBERG 2007, SAKURA & al. 2008, TRÄGER & al. 2008), while the mushroom bodies are most likely a higher-order centre involved in visual place learning (MIZUNAMI & al. 1998, SCOTTO-LOMASSESE & al. 2003, PAULCK & GRONENBERG 2008).

As shown in the previous sections of this essay, neither the path integrator nor the landmark-guidance routines provide *Cataglyphis* with correct metric information about directions and distances. Recall that the coordinates, which the ant might associate with particular environmental sites, depend on the structure of the multi-leg path along which the ant has reached that site (MÜLLER & WEHNER 1988). Furthermore, path-integration coordinates fade away in the integrator memory rather quickly (ZIEGLER & WEHNER 1997, CHENG & al. 2006, NARENDRA & al. 2007), while landmark memories are long-lived and may last for the entire lifetime of a forager (WEHNER 1981: fig. 64; ZIEGLER & WEHNER 1997). Until now there is no evidence whatsoever that the ant's path integrator and the landmark memories interacted in such a way that site-specific landmark memories were combined with (correct and persistent) metric coordinates. Most importantly, ants displaced to one of these familiar sites are not able to retrieve the path-integration coordinates of that site: *Cataglyphis* performs all its path integration with reference to the nest, and it is only there – and not at any other place – that the path integrator can be reset (SASSI & WEHNER 1997, COLLETT & al. 2003a, ANDEL & WEHNER 2004, KNADEN & WEHNER 2005, KNADEN & WEHNER 2006). In an intriguing paper ETIENNE & al. (2004) argue that mammals, hamsters in their case, can reset their path integrator at places encountered *en route*, but the evidence is not very strong. *Cataglyphis*, however, is not able to lay acquired path-integration vectors – metaphorically speaking – down on the ground and use the resulting vector network for computing, say, novel shortcuts between familiar sites, but such computations are at the heart of what acquiring and using a map would imply (BENNETT 1996, TRULLIER & al. 1997).

The most interesting experiments to which the proponents of the map hypothesis of insect navigation refer are the ones in which honey bees were displaced from a feeder to arbitrary points in their foraging environment, and in which their subsequent flight paths were recorded by harmonic radar (MENZEL & al. 2005). Upon release the bees would first follow their path-integration vector ("capture-vector flights"), then perform looping "search flights", and

having reached a particular point ("homing point") finally fly straight back to the hive or, in a few instances, to the feeder. In contrast to the claim "that all bees returned to the hive along fast and straight flights from all regions around the hive" (MENZEL & al. 2007: 428), the original data on which this claim is based only show that different bees returned from different homing points. The most likely interpretation of these results, and the one that is in accord with what has been described in the preceding sections of this article, is that a bee while performing its search flights has come across a particular site (its homing point as defined, e.g., by a particular arrangement of ground landmarks), which during previous flights it had associated with a hive-directed steering command, or local vector *sensu* COLLETT & al. (1998). This local vector would then bring the bee quickly in the immediate neighbourhood of the hive.

Without labouring such points further, let me conclude by emphasizing again that the scheme shown in Figure 3A should serve as nothing but an operational working hypothesis helping us to elucidate the properties, connections and functional interactions between the neural modules involved in navigation. Along the same lines, for those who claim that a coherent map-like memory exists at a central integration state (Fig. 3B) the next step must be to inquire about the structure, acquisition and use of this map-like memory. After all we should not get involved too much in semantic arguments about maps and map-like representations, but try to unravel step by step how small-brain navigators such as bees and ants obtain, process, handle and use the various kinds of spatial information provided by their foraging environments. In tackling such questions we should take advantage of all the conceptual and technical tools nowadays provided by neurobiology, neuroinformatics, autonomous-agent robotics, experimental behavioural biology and evolutionary theory – and embark on a joint *Cataglyphis* Cockpit Project in the neurosciences. There is hope for success, because given the insect navigators' tiny brains and short life expectancies (0.1 mg and 6.1 days, respectively, in *Cataglyphis bicolor*, see WEHNER & al. 2007 and SCHMID-HEMPEL & SCHMID-HEMPEL 1984, respectively), *Cataglyphis* and its companion hymenopteran foragers provide us with promising model organisms for such an enterprise: for analysing how complex spatial information is acquired and used by a limited amount of nervous matter within a limited span of time.

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Zusammenfassung

In den letzten Jahrzehnten sind die nordafrikanischen Wüstenameisen der Gattung *Cataglyphis* FOERSTER, 1850 – und in jüngster Zeit auch ihre ökologischen Äquivalente in der Namib-Wüste (*Ocymyrmex* EMERY, 1886) und Zentralaustralien (*Melophorus* LUBBOCK, 1883) – zu Modellorganismen der Navigationsforschung avanciert. Als thermophile, rein tagaktive Fourageure jagen diese schlanken, langbeinigen Rennameisen weiträumig über die Wüstenböden. Vorwiegend optisch navigierend, bedienen sie sich dabei eines Arsenalns verschiedener Orientierungsmechanismen (Vektornavigation, Bildvergleichsverfahren bei Orts- und Routenerkennung, zielpunktorientierte Suchstrategien und ein Verfahren der Zielpunkterweiterung). Diese Mechanismen werden in der Arbeit kurz skizziert. Der Schwerpunkt liegt jedoch auf den möglichen Interaktionen zwischen diesen Navigationsmodulen, speziell auf der Frage, ob die Interaktionen eher distributiv innerhalb eines assoziativen Netzwerks auf verschiedenen Ebenen der Datenverarbeitung erfolgen oder ob die eingehenden Informationen zunächst in einen Zentralprozessor einfließen, in dem dann – z.B. anhand einer zuvor erstellten metrischen Karte – der Navigationsentscheid fällt. Aufgrund einer kritischen Diskussion der vorliegenden Experimentalbefunde plädiert der Autor für erstere Hypothese.

References

- AKESSON, S. & WEHNER, R. 2002: Visual navigation in desert ants *Cataglyphis fortis*: are snapshots coupled to a celestial system of reference? – *The Journal of Experimental Biology* 205: 1971-1978.
- ANDEL, D. & WEHNER, R. 2004: Path integration in desert ants, *Cataglyphis*: how to make a homing ant run away from home. – *Proceedings of the Royal Society of London Series B, Biological Sciences* 271: 1485-1489.
- BENNETT, A.T.D. 1996: Do animals have cognitive maps? – *The Journal of Experimental Biology* 199: 219-224.
- BIEGLER, R. 2000: Possible use of path integration in animal navigation. – *Animal Learning and Behavior* 28: 257-277.
- BISCH-KNADEN, S. & WEHNER, R. 2003: Local vectors in desert ants: context-dependent learning during outbound and inbound runs. – *Journal of Comparative Physiology A, Sensory, Neural, and Behavioral Physiology* 189: 181-187.
- BOEDDEKER, N., LINDEMANN, J.P., EGELHAAF, M. & ZEIL, J. 2005: Responses of blowfly motion-sensitive neurons to reconstructed optic flow along outdoor flight paths. – *Journal of Comparative Physiology A, Sensory, Neural, and Behavioral Physiology* 191: 1143-1155.
- BREGY, P., SOMMER, S. & WEHNER, R. 2008: Nest-mark orientation versus vector navigation in desert ants. – *The Journal of Experimental Biology* 211: 1868-1873.
- CAMMAERTS, M.-C. & LAMBERT, A. 2008: Maze negotiation by a myrmicine ant (Hymenoptera: Formicidae). – *Myrmecological News* 12: 41-49.
- CARTWRIGHT, B.A. & COLLETT, T.S. 1983: Landmark learning in bees: experiments and models. – *Journal of Comparative Physiology A, Sensory, Neural, and Behavioral Physiology* 151: 521-543.
- CARTWRIGHT, B.A. & COLLETT, T.S. 1987: Landmark maps for honeybees. – *Biological Cybernetics* 57: 85-93.

- CHENG, K., NARENDRA, A. & WEHNER, R. 2006: Behavioral ecology of odometric memories in desert ants: acquisition, retention, and integration. – *Behavioral Ecology* 17: 227-235.
- CHENG, K. & WEHNER, R. 2002: Navigating desert ants (*Cataglyphis fortis*) learn to alter their search patterns on their homebound journey. – *Physiological Entomology* 27: 285-290.
- COLLETT, M. & COLLETT, T.S. 2000: How do insects use path integration for their navigation? – *Biological Cybernetics* 83: 245-259.
- COLLETT, M., COLLETT, T.S., BISCH, S. & WEHNER, R. 1998: Local and global vectors in desert ant navigation. – *Nature* 394: 269-272.
- COLLETT, M., COLLETT, T.S., CHAMERON, S. & WEHNER, R. 2003a: Do familiar landmarks reset the global path integration system of desert ants? – *The Journal of Experimental Biology* 206: 877-882.
- COLLETT, T.S., FAURIA, K., DALE, K. & BARON, J. 1997: Places and patterns – a study of context learning in honeybees. – *Journal of Comparative Physiology A, Sensory, Neural, and Behavioral Physiology* 181: 343-353.
- COLLETT, T.S., FRY, S.N. & WEHNER, R. 1993: Sequence learning by honeybees. – *Journal of Comparative Physiology A, Sensory, Neural, and Behavioral Physiology* 172: 693-706.
- COLLETT, T.S., GRAHAM, P. & DURIER, V. 2003b: Route learning by insects. – *Current Opinion in Neurobiology* 13: 718-725.
- COLLETT, T.S., GRAHAM, P. & HARRIS, R.A. 2007: Novel landmark-guided routes in ants. Commentary. – *The Journal of Experimental Biology* 210: 2025-2032.
- COLLETT, T.S., GRAHAM, P., HARRIS, R.A. & HEMPEL-DE-IBARA, N. 2006: Navigational memories in ants and bees: memory retrieval when selecting and following routes. – *Advances in the Study of Behavior* 36: 123-172.
- DACKE, M. & SRINIVASAN, M.V. 2007: Honeybee navigation: distance estimation in the third dimension. – *The Journal of Experimental Biology* 210: 845-853.
- DACKE, M. & SRINIVASAN, M.V. 2008: Two odometers in honeybees? – *The Journal of Experimental Biology* 211: 3281-3286.
- DYER, F.C. 1994: Spatial cognition and navigation in insects. In: REAL, L.A. (Ed.): *Behavioral mechanisms in evolutionary ecology*. – Chicago University Press, Chicago, pp. 66-98.
- 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. 1995: Honeybees use optic flow to measure the distance of a food source. – *Naturwissenschaften* 82: 38-40.
- ETIENNE, A.S., MAURER, R., BOULENS, V., LEVY, A. & ROWE, T. 2004: Resetting the path integrator: a basic condition for route-based navigation. – *The Journal of Experimental Biology* 207: 1491-1508.
- FRANZ, M.O. & MALLOT, H.A. 2000: Biomimetic robot navigation. – *Robotics and Autonomous Systems* 30: 133-153.
- FUKUSHI, T. & WEHNER, R. 2004: Navigation in wood ants, *Formica japonica*: context dependent use of landmarks. – *The Journal of Experimental Biology* 207: 3431-3439.
- FYHN, M., HAFTING, T., TREVES, A., MOSER, M.-B. & MOSER, E.I. 2007: Hippocampal remapping and grid realignment in entorhinal cortex. – *Nature* 446: 190-194.
- GALLISTEL, C.R. 1990: *The organization of learning*. – MIT Press, Cambridge, MA, 648 pp.
- GAUSSIER, P., JOULAIN, C. BANQUET, J., LEPRETRE, S. & REVEL, A. 2000: The visual homing problem: an example of robotics/biology cross fertilization. – *Robotics and Autonomous Systems* 30: 155-180.
- GIURFA, M. & CAPALDI, E.A. 1999: Vectors, routes and maps: new discoveries about navigation in insects. – *Trends in Neurosciences* 22: 237-242.
- GOULD, J.L. 1986: The locale map of honey bees: do insects have cognitive maps? – *Science* 232: 861-863.
- GRAHAM, P. & COLLETT, T.S. 2002: View-based navigation in insects: how wood ants (*Formica rufa*) look at and are guided by extended landmarks. – *The Journal of Experimental Biology* 205: 2499-2509.
- HAFTING, T., FYHN, M., MOLDEEN, S., MOSER, M.-B. & MOSER, E.I. 2005: Microstructure of a spatial map in the entorhinal cortex. – *Nature* 436: 801-806.
- HEINZE, S. & HOMBERG, U. 2007: Map-like representation of celestial E-vector orientations in the brain of an insect. – *Science* 315: 995-997.
- HENZE, M.J. & LABHART, T. 2007: Haze, clouds and limited sky visibility: polarotactic orientation of crickets under difficult stimulus conditions. – *The Journal of Experimental Biology* 210: 3266-3276.
- JUDD, S.P.D. & COLLETT, T.S. 1998: Multiple stored views and landmark guidance in ants. – *Nature* 392: 710-714.
- KARMEIER, K., VAN HATEREN, J.H., KERN, R. & EGELHAAF, M. 2006: Encoding of naturalistic optic flow by a population of blowfly motion sensitive neurons. – *Journal of Neurophysiology* 96: 1602-1614.
- 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. – *The 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.
- LABHART, T. 1999: How polarization-sensitive interneurons of crickets see the polarization pattern of the sky: a field study with an opto-electronic model neurone. – *The Journal of Experimental Biology* 202: 757-770.
- LABHART, T. 2008: The sensitive and robust polarized-skyline navigation system of crickets. – *Proceedings of the Conference on Invertebrate Vision* 2: 72.
- LABHART, T. & MEYER, E.P. 1999: Detectors for polarized skylight in insects: a survey of ommatidial specializations in the dorsal rim area of the compound eye. – *Microscopy Research and Technique* 47: 368-379.
- LAMBRINOS, D., MÖLLER, R., LABHART, T., PFEIFER, R. & WEHNER, R. 2000: A mobile robot employing insect strategies for navigation. – *Robotics and Autonomous Systems* 30: 39-64.
- MACQUARDT, D., GAMIER, L., COMBE, M. & BEUGNON, G. 2006: Ant navigation *en route* to the goal: signature routes facilitate way-finding of *Gigantiops destructor*. – *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology* 192: 221-234.
- MC NAUGHTON, B.L., BATTAGLIA, F.P., JENSEN, O., MOSER, E.I. & MOSER, M.-B. 2006: Path integration and the neural basis of the "cognitive map". – *Nature Reviews Neuroscience* 7: 663-678.
- MENZEL, R., BRANDT, R., GUMBERT, A., KOMISCHKE, B. & KUNZE, J. 2000: Two spatial memories for honeybee navigation. – *Proceedings of the Royal Society of London, Biological Sciences* 267: 961-968.

- MENZEL, R., BREMBS, B. & GIURFA, M. 2007: Cognition in invertebrates. In: KAAS, J.H. (Ed.): Evolution of nervous systems. Volume 2: Evolution of nervous systems in invertebrates. – Academic Press, New York, pp. 403-442.
- MENZEL, R. & GIURFA, M. 2001: Cognitive architecture of a mini-brain: the honeybee. – Trends in Cognitive Sciences 5: 62-71.
- MENZEL, R., GREGGERS, U., SMITH, A., BERGER, S., BRANDT, R., BRUNKE, S., BUNDRICK, G., HÜLSE, S., PLÜMPE, T., SCHAUPP, F., SCHÜTTLER, E., STACH, S., STINDT, J., STOLLHOFF, N. & WATZL, S. 2005: Honey bee navigation 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. – The Journal of Experimental Biology 209: 3545-3549.
- MERKLE, T. & WEHNER, R. 2008: Repeated training does not improve the path integrator in desert ants. – Behavioral Ecology and Sociobiology DOI 10.1007/s 00265-008-0673-6.
- MICHEL, B. & WEHNER, R. 1995: Phase-specific activation of landmark memories during homeward-bound vector navigation in desert ants, *Cataglyphis fortis*. – Proceedings of the Neurobiological Conference Göttingen 23: 41.
- MITTELSTAEDT, M.-L. & MITTELSTAEDT, T. 1980: Homing by path integration in a mammal. – Naturwissenschaften 67: 566-567.
- MIZUNAMI, M., WEIBRECHT, J.M. & STRAUSFELD, N.J. 1998: Mushroom bodies of the cockroach: their participation in place memory. – The Journal of Comparative Neurology 402: 520-537.
- MÖLLER, R. & VARDY, A. 2006: Local visual homing by matched-filter descent in image distances. – Biological Cybernetics 95: 413-430.
- MOSER, E.I., KROPFF, E. & MOSER, M.-B. 2008: Place cells, grid cells, and the brain's spatial representation system. – Annual Review of Neuroscience 31: 69-89.
- 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, Neuroethology, Sensory, Neural, and Behavioral Physiology 175: 525-530.
- NADEL, L. 1991: The hippocampus and space revisited. – Hippocampus 1: 221-229.
- NARENDRA, A. 2007: Homing strategies of the Australian desert ant *Melophorus bagoti*. II. Interaction of the path integrator with visual cue information. – The Journal of Experimental Biology 210: 1804-1812.
- NARENDRA, A., CHENG, K. & WEHNER, R. 2007: Acquiring, retaining and integrating memories of the outbound distance in the Australian desert ant *Melophorus bagoti*. – The Journal of Experimental Biology 210: 570-577.
- NICHOLSON, D.J., JUDD, S.P., CARTWRIGHT, B.A. & COLLETT, T.S. 1999: Learning walks and landmark guidance in wood ants (*Formica rufa*). – The Journal of Experimental Biology 202: 1831-1838.
- O'KEEFE, J. & NADEL, L. 1978: The hippocampus as a cognitive map. – Oxford University Press, Oxford, 570 pp.
- PAULCK, A.C. & GRONENBERG, W. 2008: Higher order visual input to the mushroom bodies in the bee, *Bombus impatiens*. – Arthropod Structure and Development 37: 443-458.
- PFEIFFER, K. & HOMBERG, U. 2007: Coding of azimuthal directions via time-compensated combination of celestial compass cues. – Current Biology 17: 960-965.
- POMOZI, I., HORVÁTH, G. & WEHNER, R. 2001: How the clear-sky angle of the polarization pattern continues underneath clouds: full-sky measurements and implications for animal orientation. – The Journal of Experimental Biology 204: 2933-2942.
- RONACHER, B. 2008: Path integration as the basic navigation mechanism of the desert ant *Cataglyphis fortis* (FOREL, 1902) (Hymenoptera: Formicidae). – Myrmecological News 11: 53-62.
- RONACHER, B. & WEHNER, R. 1995: Desert ants, *Cataglyphis fortis*, use self-induced optic flow to measure distances travelled. – Journal of Comparative Physiology A, Sensory, Neural, and Behavioral Physiology 177: 21-27.
- RONACHER, B., WESTWIG, E. & WEHNER, R. 2006: Integrating two-dimensional paths: do desert ants process distance information in the absence of celestial compass cues? – The Journal of Experimental Biology 209: 3301-3308.
- SAKURA, M., LAMBRINOS, D. & LABHART, T. 2008: Polarized skylight navigation in insects: model and electrophysiology of e-vector coding by neurons in the central complex. – Journal of Neuroscience 99: 667-682.
- SAMSONOVICH, A. & MCNAUGHTON, B.L. 1997: Path integration and cognitive mapping in a continuous attractor neural network model. – Journal of Neuroscience 17: 5900-5920.
- SANTSCHI, F. 1913: Comment s'orientent les fourmis. – Revue Suisse de Zoologie 21: 347-425.
- SANTSCHI, F. 1923: L'orientation sidéral des fourmis, et quelques considérations sur leurs différentes possibilités d'orientation. – Mémoires de la Société Vaudoise des Sciences Naturelles 4: 137-175.
- SASSI, S. & WEHNER, R. 1997: Dead reckoning in desert ants, *Cataglyphis fortis*: can homeward-bound vectors be reactivated by familiar landmark configurations? – Proceedings of the Neurobiology Conference Göttingen 25: 484.
- SCHMID-HEMPEL, P. & SCHMID-HEMPEL, R. 1984: Life duration and turnover of foragers in the ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). – Insectes Sociaux 31: 345-360.
- SCHÖLKOPF, B. & MALLOT, H.A. 1995: View-based cognitive mapping and path planning. – Adaptive Behavior 3: 311-348.
- SCOTTO-LOMASSESE, S., STRAMBI, C., STRAMBI, A., AOUANE, A., AUGIER, R., ROUGON, G. & CAYRE, M. 2003: Suppression of adult neurogenesis impairs olfactory learning and memory in an adult insect. – Journal of Neuroscience 23: 9289-9296.
- SI, A., SRINIVASAN, M.V. & ZHANG, S. 2003: Honeybee navigation: properties of the visually driven "odometer". – The Journal of Experimental Biology 206: 1265-1273.
- SOLSTAD, T., MOSER, E.I. & EINEVOLL, G.T. 2006: From grid cells to place cells: a mathematical model. – Hippocampus 16: 1026-1031.
- 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. 2005: Vector navigation in desert ants, *Cataglyphis fortis*: celestial compass cues are essential for the proper use of distance information. – Naturwissenschaften 92: 468-471.
- 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. – The Journal of Experimental Biology 200: 2513-2522.
- SRINIVASAN, M.V., ZHANG, S., LEHRER, M. & COLLETT, T.S. 1996: Honeybee navigation en route to the goal: visual flight control and odometry. – The Journal of Experimental Biology 199: 155-162.
- STÄGER, R. 1931: Über das Mitteilungsvermögen der Waldameise beim Auffinden und Transport eines Beutestücks. – Zeitschrift für wissenschaftliche Insektenbiologie 26: 125-137.

- STRAUSS, R. 2002: The central complex and the genetic dissection of locomotor behaviour. – *Current Opinion in Neurobiology* 12: 633-638.
- STURDZA, S.A. 1942: Beobachtungen über die stimulierende Wirkung lebhaft beweglicher Ameisen auf träge Ameisen. – *Bulletin de la Section Scientifique de l'Academie Roumaine* 24: 543-546.
- TAUTZ, J., ZHANG, S., SPAETHE, J., BROCKMANN, A., SI, A. & SRINIVASAN, M.V. 2004: Honeybee odometry: performance in varying natural terrain. – *PLoS Biology* 2: 915-923.
- TOLMAN, E.C. 1948: Cognitive maps in rats and men. – *Psychological Review* 55: 189-208.
- TRÄGER, U., WAGNER, R., BAUSENWEIN, B. & HOMBERG, U. 2008: A novel type of microglomerular synaptic complex in the polarization vision pathway of the locust brain. – *The Journal of Comparative Neurology* 506: 288-300.
- TRULLIER, O., WIENER, S.I., BERTHOZ, A. & MEYER, J. 1997: Biologically based artificial navigation systems: review and prospects. – *Progress in Neurobiology* 51: 483-544.
- ULANOVSKY, N. & MOSS, C.F. 2007: Hippocampal cellular and network activity in freely moving echolocating bats. – *Nature Neuroscience* 10: 224-233.
- VAN HATEREN, J.H., KERN, R., SCHWERDTFEGER, G. & EGELHAAF, M. 2005: Function and coding in the blowfly H1 neuron during naturalistic optic flow. – *The Journal of Neuroscience: the Official Journal of the Society for Neuroscience* 25: 4343-4352.
- WEHNER, R. 1981: Spatial vision in arthropods. In: AUTRUM, H. (Ed.): *Handbook of sensory physiology* Vol. VII/6c. – Springer-Verlag, Berlin, Heidelberg, New York, pp. 287-616.
- WEHNER, R. 1982: Himmelsnavigation bei Insekten. *Neurophysiologie und Verhalten*. – *Neujahrsblatt der Naturforschenden Gesellschaft Zürich* 184: 1-132.
- WEHNER, R. 1987: Spatial organization of foraging behavior in individually searching desert ants, *Cataglyphis* (Sahara Desert) and *Ocymyrmex* (Namib Desert). In: PASTEELS, J.M. & DENNEUBOURG, J.L. (Eds.): *From individual to collective behavior in social insects*. – Birkhäuser, Basel, pp. 15-42.
- WEHNER, R. 1992: Arthropods. In: PAPI, F. (Ed.): *Animal homing*. – Chapman and Hall, London, pp. 45-144.
- WEHNER, R. 1994: The polarization-vision project: championing organismic biology. In: SCHILDBERGER, K. & ELSNER, N. (Eds.): *Neural basis of behavioural adaptations*. – Gustav Fischer Verlag, Stuttgart, New York, pp. 103-143.
- WEHNER, R. 1997: The ant's celestial compass system: spectral and polarization channels. In: LEHRER, M. (Ed.): *Orientation and communication in arthropods*. – Birkhäuser Verlag, Basle, pp. 145-185.
- WEHNER, R. 2003a: Desert ant navigation: how miniature brains solve complex tasks. Karl von Frisch Lecture. – *Journal of Comparative Physiology A, Sensory, Neural, and Behavioral Physiology* 189: 579-588.
- WEHNER, R. 2003b: Blick ins Cockpit von *Cataglyphis* – Hirnforschung en miniature. – *Naturwissenschaftliche Rundschau* 657: 134-140.
- WEHNER, R. 2008: The desert ant's navigational toolkit: procedural rather than positional knowledge. – *Navigation* 55: 101-114.
- WEHNER, R., BOYER, M., LOERTSCHER, F., SOMMER, S. & MENZI, U. 2006: Desert ant navigation: one-way routes rather than maps. – *Current Biology* 16: 75-79.
- WEHNER, R., FUKUSHI, T. & ISLER, K. 2007: On being small: ant brain allometry. – *Brain, Behavior and Evolution* 69: 220-228.
- WEHNER, R., GALLIZZI, K., FREI, C. & VESELY, M. 2002: Calibration processes in desert ant navigation: vector courses and systematic search. – *Journal of Comparative Physiology A, Sensory, Neural, and Behavioral Physiology* 188: 683-693.
- WEHNER, R. & LABHART, T. 2006: Polarization vision. In: WARRANT, E. & NILSSON, D.E. (Eds.): *Invertebrate vision*. – Cambridge University Press, Cambridge, UK, pp. 291-348.
- WEHNER, R., MARSH, A.C. & WEHNER, S. 1992: Desert ants on a thermal tightrope. – *Nature* 357: 586-587.
- WEHNER, R., MEIER, C. & ZOLLIKOFER, C. 2004: The ontogeny of foraging behaviour in desert ants, *Cataglyphis bicolor*. – *Ecological Entomology* 29: 240-250.
- WEHNER, R., MICHEL, B. & ANTONSEN, P. 1996: Visual navigation in insects: coupling of egocentric and geocentric information. – *The 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. & SRINIVASAN, M.V. 1981: Searching behaviour 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. 9-30.
- WEHNER, R. & WEHNER, S. 1986: Path integration in desert ants. Approaching a long-standing puzzle in insect navigation. – *Monitore Zoologica Italiano (N.S.)* 20: 309-331.
- WEHNER, R. & WEHNER, S. 1990: Insect navigation: use of maps or Ariadne's thread? – *Ethology Ecology and Evolution* 2: 27-48.
- WILSON, M.A. & MCNAUGHTON, B.L. 1993: Dynamics of the hippocampal ensemble code for space. – *Science* 261: 1055-1058.
- 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. 2007: The desert ant odometer: a stride integrator that accounts for stride length and walking speed. – *The Journal of Experimental Biology* 10: 198-207.
- WOLF, H. & WEHNER, R. 2005: Desert ants, *Cataglyphis fortis*, compensate navigation uncertainty. – *The Journal of Experimental Biology* 208: 4223-4230.
- ZANKER, J.M. & ZEIL, J. 2005: Movement-induced motion signal distribution in outdoor scenes. – *Comparative Neural Systems* 16: 357-376.
- ZEIL, J., BOEDDEKER, N., HEMMI, J.M. & STÜRZL, W. 2007: Going wild: toward an ecology of visual information processing. In: NORTH, G. & GREENSPAN, R. (Eds.): *Invertebrate neurobiology*. – Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, pp. 381-403.
- 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, Sensory, Neural, and Behavioral Physiology* 181: 13-20.
- ZOLLIKOFER, C.P.E. 1988: Vergleichende Untersuchungen zum Laufverhalten von Ameisen. – PhD Thesis, University of Zurich, 103 pp.