Orientation and Search Strategies of Desert Arthropods: Path Integration Models and Experiments with Desert Ants, *Cataglyphis fortis* (Forel 1902)

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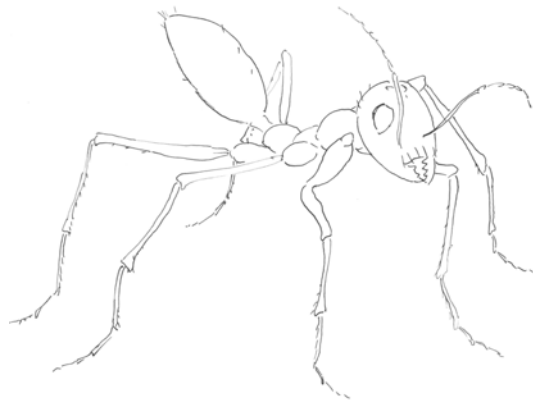
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Gewidmet sei diese Arbeit meiner Mutter

Anna Maria Merkle (1944 - 1987)

Contents

Part I
Introduction

How can a little insect find its way through the desert in search for food and, especially, return to its nest on an almost straight path after a long and tortuous foraging excursion? On which physiological and neuronal mechanisms does this ability rely? What is happening at the neuronal level to reveal such performances that have astonished observers for a long time?

Within the wide and fascinating range of orientation behavior of animals (Rodrigo 2002), the ability of desert arthropods to return to their nest on a straight path after foraging surely is one of the most intriguing. Since a successful home run to the nest is essential for the survival of desert arthropods in the heat of a desert, it is no surprise that they had to develop a number of tools that play together and back each other up. It is also not surprising that as early as 134 years ago Ch. Darwin and J.J. Murphy discussed this striking behavior (Darwin 1873; Murphy 1873). About a century later, the first detailed investigations concerning arthropods (Frisch 1950; Jander 1957, 1970; Görner 1958, 1966; Wehner 1968) were conducted. During the last 35 years, the general interest has more and more focused on the return path to the nest after foraging, and many investigations with both arthropods (e.g. Wehner and Wehner 1986; Müller and Wehner 1988; Collett and Baron 1994; Collett et al. 1999) and mammals (e.g. Mittelstaedt and Mittelstaedt 1980; Séguinot et al. 1993; Benhamou 1996, 1997; Séguinot et al. 1998) were conducted. These investigations resulted in today's knowledge on the described ability, which is most often referred to as *path integration*, and allow us to understand many details of the whole orientation process.

This work mainly aims at two things: (1) Within the theoretical part, a new model of egocentric path integration is introduced (part II). Although the system of linear differential equations upon which this model is based may be used for path integration of different animals, i.e. not exclusively for desert arthropods, here it will be especially applied to them. After presenting this model and modelling foraging excursions as well as home runs, I turn to systematic errors that many arthropods exhibit during path integration. They are described in the theoretical part and, afterwards, will be applied for the new model of egocentric path integration in arthropods. (2) The experimental part aims at getting a deeper understanding of the global vector of desert ants *Cataglyphis fortis* (part III). Thus, different factors are investigated, which may affect the accuracy of the path integration system and the systematic search behavior. In doing so, natural outbound runs are investigated in order to differentiate between the potential influence of different critical factors, and specific training procedures are applied to test specific factors by excluding all other influences.

Within this introductory part (I), the principles, upon which path integration is based, are introduced. Thereby, I also explain and discuss global and local vectors and how they interact with each other (I.1.1). Then, the information that is required to successfully perform path integration is outlined

and the mechanisms, how the arthropod receives these underlying information from various signals, are presented (I.1.2). During the description of such signals, I focus on desert arthropods and here, in particular, on desert ants *Cataglyphis fortis* and *Cataglyphis bicolor*, respectively, because more is known about them as compared to other arthropods. The biological mechanisms used by *C. fortis* are explicated predominantly, since experiments on *C. fortis* are presented in part III of this work. Nevertheless, I also mention similar investigations on other arthropods, mainly because neurobiological analyses have been performed on larger and more easily accessible arthropods (Wehner 1983). Within the next subsection (I.1.3), I focus on the use of path integration for a successful return to known feeding sites. Afterwards, I focus on errors that occur during path integration (I.1.4). These errors are important indicators how the path integration process might work. The experimental part of this work is based upon such errors: several critical factors and their influence on the path integration process are tested via the errors the ants display when faced with these factors.

In the following section (I.2), I give a short introduction to the systematic search behavior, illustrated mainly by desert ants and desert isopods. Although this work is not focused on modelling the systematic search, the experiments described later will investigate this behavior of desert ants in more detail than it has been done before.

1 Path integration

1.1 General

Desert arthropods, such as the ant *C. fortis* (Wehner 1987), the beetle *Parastizopus armaticeps* (Rasa 1990) or the woodlouse *Hemilepistus reaumuri* (Hoffmann 1978) return to their nest after foraging on a straight way, often called the *home vector*. The ability to make a beeline to the nest (or another location, such as a feeding site) without reference of visible markers or other cues, such as olfactory marks, is based on an internal mechanism of 'dead reckoning'. This mode of navigation has been called *path integration* by Mittelstaedt and Mittelstaedt (1973, 1982), who provided the first systematic studies on this phenomen, and *vector navigation* by Wehner (1982, 1983). Thereby, the arthropods perform a continuous integration of walking speed and angular variation along their walking route during foraging, i.e. during their *outbound runs*. From that integration results a so-called 'global vector' that enables the arthropod to determine distance and direction of its nest at any position and time. After detecting and loading up the food, the arthropod just unreels this vector and, therefore, performs a home run, most often referred to as *inbound run*, that leads it on the right and shortest track to its nest.

Apart from path integration, it has been shown that many species are capable of using 'landmarks' to get and improve their bearings (Hoffmann 1985; Collett et al. 1998; Biegler 2000; Graham and Collett 2002; Bisch-Knaden and Wehner 2003b; Wehner 2003). These landmarks, often referred to as 'local vectors', even seem to be preferred to the global vectors (Wehner

et al. 1996; Collett et al. 1998) as navigational tool. However, before these vectors can be applied successfully, some information about their position in relation to the nest has to be stored by the arthropod and for that purpose a different tool must be available, at least for the first foraging excursions in an arthropod's lifetime. Moreover, orientation with the aid of local vectors is error-prone, since landmarks can disappear or change their appearance during foraging excursions, and, of course, is out of question for nests with no visible landmarks nearby.

The global vector gets updated during the complete foraging trip of an arthropod including its return path (Schmidt et al. 1992), even if the orientation is obviously conducted by using landmarks (local vectors) (e.g. Wehner et al. 1996; Sassi and Wehner 1997; Collett et al. 1998, 2003a; Andel and Wehner 2004). Moreover, it has been demonstrated that, after a sudden failure of the stored landmarks, desert ants *Cataglyphis fortis* revert to their global vector for orientation and, consequently, are in a position to switch between both systems (Collett et al. 1998). Even if prevented from using the global vector for several days, desert ants keep it stored in their memory (time constant of exponential memory decay function $\tau = 4.5$ days for direction and $\tau = 2.5$ days for distance, see Ziegler and Wehner 1997). Thus, the relevance of global vectors as the underlying principle and main toolkit for path integration seems as clear as the evolutionary necessity to develop mechanisms and abilities to measure the angular and linear components of the movements and the skill to integrate them for having a home vector available whensoever.

1.2 Required information for path integration

To perform path integration successfully, an arthropod has to measure its speeds or walking distances and its rotations during the entire foraging or outbound excursion. Whereas the principles how desert ants measure the changes of directions, i.e. rotations, have been known for a longer time (for reviews, see Wehner 2003; Wehner and Srinivasan 2003), the question how they measure the lengths of runs could only be answered recently (Wittlinger et al. 2006).

In general, we can divide the signals that an arthropod processes into two groups: allothetic, i.e. external, signals, and idiothetic, i.e. internal, signals.

1.2.1 Allothetic signals

Without doubt, the various possible visual inputs have to be considered as the main allothetic signals. This evaluation applies not just for desert ants, but certainly for all other species that are able to perform path integration, both within and beyond the phylum of the arthropods. Amongst them are landmarks which can be situated in the immediate vicinity of the nest, but also en route between nest and feeder. They do not help ants to determine a speed or rotation or even provide the information about the actual position of the ant (Collett et al. 2003a), but rather indicate a specific direction (the local vector) that an ant has to steer to head for the nest, the feeder or even the next landmark (Collett et al. 1998, 2003a) and therefore are considered

to be 'contextual cues' (Wehner 2003; Wehner and Srinivasan 2003). From an evolutionary point of view, that makes sense, as landmarks can disappear during inbound or outbound journey for several reasons and, therefore, seem not exactly suitable to be a component of the principal path integration respective 'positioning system'; particularly with regard to the necessity of the path integration system working somehow as a 'standby system' that enables the ant to determine its position if all other systems fail.

Beyond dispute is the meaning of objects that happen to be indefinitely far away: with regard to desert ants, spectral skylight gradient, position of the sun, and the pattern of the polarized light of the sky are the most important cues (Duelli and Wehner 1973; Wehner 1997a,b,c, 2001, 2003; Wehner and Srinivasan 2003; Wehner and Müller 2006). These three systems can work without help of each other, as was shown in experiments where one or even two of them had been made inoperative (Duelli and Wehner 1973; Müller and Wehner 1988; Wehner 1997a). In all three the ants continuously use the sky as a reference to determine their body axis' orientation.

Whenever the ant applies *spectral cues*, it makes use of the fact that the light waves with their different wavelengths are not distributed equally over the illuminated sky. This was shown by Wehner (1997a) for ants and Rossell and Wehner (1984) for bees in experiments where sun and polarization compass had been eliminated.

Direct orientation with respect to the azimuthal position of the sun (or any other light source) has been found in ants and many other arthropods (e.g. bees, von Frisch 1950, or spiders, Görner 1958).

Wehner and Srinivasan (2003) consider both the sun and spectral cues as forms of additional navigation tools that are preferably implemented in case of ambiguities in the polarization compass, which is the standard navigation tool. Orientation with respect to the sun as a point light source may fail if it gets covered by clouds (which, of course, can also be a problem when using the polarization compass) or other objects and becomes inaccurate at high elevation around noon. Spectral cues, in contrast, are coarser and suffer more from interference with clouds and other external factors than the polarization pattern of the sky (for more details, see Wehner and Srinivasan 2003).

The skylight polarization pattern, also referred to as 'skylight compass', represents the most effective and stable means for orientation in desert ants (Wehner 2003; Wehner and Srinivasan 2003; Wehner and Müller 2006). Desert ants are able to see the so called e-vector pattern that is produced by scattering of the sunlight at air molecules in the atmosphere (Wehner 1982, 1989). They do this by using specialized UV-receptors located in the dorsal part of their compound eye (Duelli 1975; Wehner et al. 1975; Labhart 1986; Fent 1986). This ability has been found in other arthropods and vertebrates as well, first of all in bees (Frisch 1949), but also, for instance, in desert locusts *Schistocerca gregaria* (Eggers and Gewecke 1993), desert isopods *Hemilepistus reaumuri* (Hoffmann 1984), or even Savannah sparrows *Passerculus sandwichensis* (Able and Able 1995).

When using the polarization compass, desert ants measure the difference between their orientation and that of the e-vectors in the polarized light pattern. Although this pattern is changing with the elevation of the sun at a non-uniform speed, desert ants use only one template of the e-vector

pattern. More precisely, they have stored a stereotypical projection that resembles the skylight pattern at dawn or dusk, respectively, i.e. when the sun is at the horizon, in their memory. This was concluded from a number of different experiments, which pinpointed systematic errors performed by bees and ants under experimentally modified skylight patterns, such as different visible sections of the sky during outbound and inbound journeys (for more details, see Wehner 1997a,b,c, 1998, 2001). Since their strategy is to match this template with the actual, i.e. normally different, e-vector pattern in the sky, they measure their rotations by the use of the degree of concordance with the current e-vector pattern. The result of each rotation of the ant's body axis results in an increase or decrease, respectively, of this concordance, thus indicating to the ant not only the direction (in mathematical terms one can speak of the 'sign') of the performed rotation, but also its value. Thus, the ant's template of the skylight pattern obviously enables it to measure all rotations.

Moreover, it is sufficient for the individuals to have a small section of the sky available to detect their rotations. The size of that section is of little or no importance with regard to the accuracy of the determination of directions as long as the individuals are allowed to see the same section during inbound and outbound journey (Fent 1986; Wehner 1994, 1997b). More details of this principle and its working mechanism has been described by Wehner (1994, 1997c, 2001).

In order to completely understand the polarization compass, one last factor has to be mentioned: the problem of compensating the westward movement of the sun during the day. Homing ants do not really need an internal clock to compensate the moving of the sun during an excursion, since the usual foraging excursions normally last only a few minutes, so that the error resulting from that movement of the sun is negligible. For ants that are heading towards a known feeding site, the situation is a different one; this problem will be discussed later (see I.1.3).

Although bees measure the distance *flown* by integrating the images they have passed on their way, the so called optic flow (Esch and Burns 1995; Esch et al. 2001; Srinivasan et al. 1989, 1996, 2000; Tautz et al. 2004), optic flow resp. visual signals obviously are of minor importance for the ant's odometer, as Ronacher and Wehner (1995) and Ronacher et al. (2000) demonstrated. Thus, there must be at least one additional tool available that enables desert ants to measure the lengths of the walked paths.

1.2.2 Idiothetic signals

Compared to allothetic signals, for desert ants idiothetic signals seem to be of minor or no importance for detecting directions. In contrast, some species of spiders can navigate without allothetic signals, i.e. the idiothetic signals they receive enable them to measure directional changes as well as walked path lengths (Seyfarth and Barth 1972; Seyfarth et al. 1982). Different experiments with ants have shown that it is possible to predict navigational errors by manipulating the section of the sky that is visible (Fent 1986; Wehner 1994, 1997a). Hence, the ants obviously do not even revert to proprioceptive

signals if the polarization compass as standard tool provides strange results (which, under natural conditions, is unlikely anyway). In contrast, the ants rather use the position of the sun and the spectral gradient of the light, as described above. Desert beetles *Parastizopus armaticeps* also rely on the position of the light source and the polarisation compass and do not revert to proprioceptive cues in the case of ambiguities (Bisch 1999). Desert ants *C. fortis*, when captured at a feeder, and transferred to a test area in a dark flask without any allothetic signals available, do reorientate immediately after their release and set out into their stored homing direction (personal observation). Thus, idiothetic signals seem not have an effect on the ant's reorientation under such conditions.

On the other hand, Ronacher and Wehner (1995) and Ronacher et al. (2000) found that desert ants are able to estimate their walked path lengths without allothetic signals. Therefore, they proposed that their odometers mainly rely on proprioceptive signals. This claim is backed by investigations that could eliminate energy consumption as a possible cue for measuring walked distances, when ants walk along slopes (Wohlgemuth et al. 2001, 2002) or with heavy load (Schäfer and Wehner 1993). It seemes quite obvious that such proprioceptive signals derive from movements of the legs (for bristles as mechanoreceptors see Keil, 1997). Just recently, it could be shown how desert ants measure their walked distances: Wittlinger et al. (2006, 2007) manipulated the lengths of the legs of desert ants and, by doing so, could prove that a simple 'step counter' is applied for determing distances by desert ants *C. fortis*. Also, Seidl et al. (2006) showed that *C. fortis* requires active locomotion to measure distances correctly.

Although the idiothetic, i.e. proprioceptive signals are the most important tool for *C. fortis* to measure path lengths, it needs celestial compass information to apply this tool correctly (Sommer and Wehner 2005). The authors conclude that the ants' path integrator is correctly updated only if it has directional information available. This result is in concordance with studies on honeybees (Collett et al. 1996). However, *Cataglyphis cursor* is able to measure distances correctly even if celestial cues are excluded by specific experimental paradigms (Thielin-Bescond and Beugnon 2005).

1.3 Returning to a feeding site

Desert ants use their ability to perform path integration also in order to return to known feeding sites (Wolf and Wehner 2000; Wehner et al. 1983). If they have encountered such a location, they approach it over and over again on a straight path, similar to the global vector they use when returning to their nesting site (Wehner et al. 1983). The same holds for many other species of ants (e.g. Hölldobler and Wilson 1990; Wehner 1992; Wehner et al. 2004), arthropods (e.g. for bees, see Frisch 1965), and even mammals (e.g. hamsters, see Etienne et al. 1991, 1996). Many studies have shown that species of the genus *Cataglyphis* often rely on landmarks, i.e. they develop landmark-guided foraging routes to approach a feeder again in a straight way (Collett 1992; Collett et al. 1992, 1998; Bisch and Wehner 1998; Bisch-Knaden and Wehner 2003b); similar observations were made with Australian desert ants *Melophorus bagoti* (Kohler and Wehner 2005). On the other hand,

C. fortis that mainly inhabits landmark-free environments in the Saharan desert, is able to develop such foraging routes even if no externel orientation cues, as e.g. landmarks, are present (Wehner et al. 2004).

Other means that are employed for relocating a feeder are olfactoric and anemotactic cues (Wolf and Wehner 2000).

Cataglyphis is able to successfully remember feeding sites and to approach them at different daytimes (even after not foraging for quite a time) without additional help of landmarks (Wehner et al. 1983; Wehner 1987; Collett et al. 1999). In addition, *C. bicolor*, even if not trained to a specific feeder, remembers the success rate of former foraging excursions, starting with the first foraging excursion of their lifetime, and unambigously use this knowledge to decide which direction to head towards after leaving the nest for following foraging trips (Wehner et al. 1983; Wehner 1987; Wehner and Srinivasan 2003).

To accomplish this task, an individual worker must know about the position of the sun, in particular, since workers of *Cataglyphis* sometimes stay in the nest for hours or even days and, at the start of their new foraging excursion, without any trace of hesitation know which direction to head to in order to find the feeder again (Wehner et al. 1983 and Merkle, personal observation). That is, they stay in the nest for a time span during which the sun is wandering (at a non-uniformation speed). Thus, without any knowledge about the sun's movement, the ants would make (systematic) errors of a high amount and would surely not be able to find a particular feeder again. The question of how accurately desert ants are informed about the movement and speed of the wandering sun and, in particular, how they acquire this knowledge, has been approached by different experiments, conducted on both ants and bees (Dyer 1987; Wehner and Lanfranconi 1981): they showed that these species seem to have a detailed knowledge about the daily movements of the sun. In subsequent studies the daytimes at which ants (Wehner and Müller 1993) and bees (Dyer and Dickinson 1994) were allowed to forage have been manipulated from the beginning of their lifetimes. The results of both studies revealed that both ants and bees exhibit some innate knowledge about the sun's movements during the entire day. Indeed, the results of both investigations argue for the assumption that this knowledge is more general than detailed: it does not represent the correct ephemeris-time function, but rather some general differences between the position of the sun during morning and afternoon, or, as Wehner and Müller (1993) argue, the ant or bee, respectively, is aware that the solar positions at dawn and dusk lie opposite to each other. Based on these investigations, Wehner and Srinivasan (2003) argue that bees and ants are born with an approximate ephemeris function and improve this function during their lifetimes as foragers and, therefore, adapt it to the true ephemeris function.

Questions yet to be answered with regard to this behavior are, above all, whether desert ants improve their bearings during repeated foraging runs and whether individual ants are able to generate individual routes to the feeding site.

1.4 Errors during path integration

As described in I.1.1, animals perform path integration by measuring and summing up all angular changes and distances covered during walking (Mittelstaedt and Mittelstaedt 1980). Errors concerning the determination of the correct homing direction (Wehner and Wehner 1986; Müller and Wehner 1988; Müller 1989) as well as errors due to misestimation of the correct nest distance (Sommer and Wehner 2004) have been shown to exist for desert ants and also for other invertebrates such as honey bees (Srinivasan et al. 1997; Cheng et al. 1999). These *systematic errors* were discovered by means of specific experimental paradigms and exist of significant, one-sided, deviations or tendencies from the correct homing direction or distance. The other error type that might influence the accuracy of the path integrator comprises *random errors*. In general, no tendencies can be observed whenever random errors come into play; i.e. they are two-sided variations from correct directions or distances that show no tendencies (Benhamou et al. 1990). Both error types as well as their most likely origin will be described in detail in the theoretical part of this work (II.3). In general, inaccuracies happen not only during the measurement of rotations performed and distances covered, but also during their (*algorithmic*) integration, and should therefore lead to a route-dependent overall error, which should be correlated with the overall length of the foraging excursion. As feasible as this hypothesis appears, it has not been investigated yet.

Furthermore, it is not known which factors might influence the ants' path integrator during natural foraging excursions, i.e. not biased by experimental paradigms, and whether the systematic errors, which hitherto have only be shown during specific experimental setups, can influence desert ants during natural foraging excursions.

Even small deviations within the path integration system may lead to overall errors that might result in remarkable discrepancies between the tip of the home vector, i.e. the nest position as computed by the path integrator, and the actual position of the nest. This may lead to an increasing uncertainty about the destination with increasing errors. That such an uncertainty can cause changes in behavior has already been shown by Wolf and Wehner (2005): they demonstrated that desert ants, when leaving the nest, deviate from the direct global vector course with the direction of the blowing wind, and then head towards a food source against the wind direction, i.e. they approach the feeder in a way that enables them to head straight upwind towards the feeder by following the odor plume emanating from it. The upwind approach distance depends on the length of the foraging trip. Wolf and Wehner interpret this behavior as being an error compensation strategy due to navigation uncertainty, and regard it as one tool that foraging desert ants apply to deal with the errors they perform during path integration.

2 Systematic search behavior

If a desert arthropod fails to find the nest after having 'run off' its home vector, it terminates its almost straight inbound run at the assumed nest position computed via path integration and starts a systematic search for

the nest (Wehner and Srinivasan 1981; Hoffmann 1983b; Müller and Wehner 1994). Several models describe the search behavior of desert arthropods as mathematical functions (Hoffmann 1978; Wehner and Srinivasan 1981; Hoffmann 1983b,c; Pollklesener 1993; Alt 1995). During this search, the arthropod performs loops of ever increasing radius around the suspected nest position (Hoffmann 1983b,c; Wehner and Wehner 1986). At more or less regular intervals, it reverts to the starting point of the search, and then changes the direction in which it heads off next. Desert ants as well as desert isopods spatially broaden their search the farther they have ventured out during their foraging trips (Hoffmann 1983b, fig. 3.35 in Wehner 1992). The ultimate reason for this change of the search pattern with increasing distance of their foraging journeys could be an ongoing accumulation of errors during the path integration process. However, whether these errors increase with foraging distance and the arthropods adapt to these errors during their systematic search, remains to be elucidated.

Part II

Path integration models and their application to desert arthropods

This part of the work has been published in Journal of Theoretical Biology (Merkle et al. 2006b).

In this part (II), I turn to the path integration *per se*, that is the question how an arthropod integrates the received information to have a home vector available at any time. Therefore, in section II.1 I systematically review previous models of path integration. This review serves as background for section II.2, where a new model approach is presented and compared to the models developed hitherto. Section II.3 is devoted to systematic and random errors, which have been studied extensively and may give hints about internal information processing. In the final sections II.4 and 5 the model is discussed and applied to natural foraging and return runs of desert ants *C. fortis*.

1 Previous models of path integration

1.1 Geocentric models

When Mittelstaedt and Mittelstaedt (1973) established the term 'path integration', they referred to a simple and evident mathematical algorithm, namely to determine the ant's current position P by integrating its moving direction $\theta(s)$ along the migration path or, equivalently, by integrating its velocity vector $V(t) = v(t)\,\theta(t)$ over time t, where $v(t)$ denotes the ant's forward speed. This yields the estimated final positional vector P from start to end point of the path. The estimated global *home vector* is then the inverse vector $G = -P$, provided that the nest is situated at the origin.

1.1.1 Cartesian coordinates.

Mittelstaedt and Mittelstaedt (1973, 1982) use *cartesian coordinates* to represent the integrated positional vector $P = (x, y)$ and the current directional vector $\theta = (\cos\phi, \sin\phi)$, where the animal's angular orientation ϕ is given relative to some reference direction, e.g. skylight polarization. This is chosen as the initial moving direction of the arthropod, in their case the spider *Agelena labyrinthica*. In their model the arthropod is supposed to estimate the current angle ϕ in two different ways (see also Fig. II.1): by using an *idiothetic azimuth storage* as integrated value of its proprioceptively measured turning rates $\omega(t)$ along the previous path (this idea of azimuth integration is related to the earlier theory by Jander 1957), or by directly measuring the *allothetic azimuth value* ϕ of the current body axis with respect to an

allothetic direction. Then, the resulting two inputs of the directional vector θ are weighted and summed up for path integration. With the aid of this model the authors could reproduce typical two–segment experiments, during which a light source had been turned by 90°.
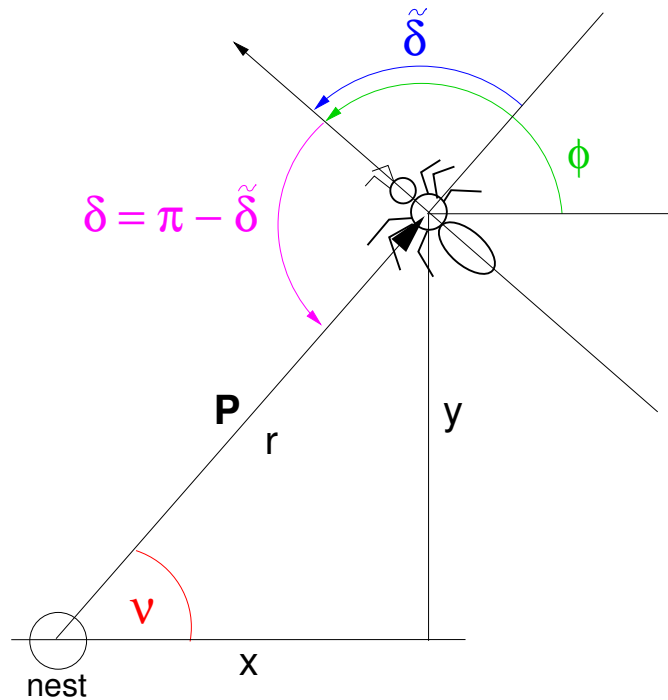
Figure II.1: Theoretical scheme of geocentric path integration. ϕ: orientation angle with respect to an allothetic reference direction, respresented by the x-axis. Both the cartesian coordinates (x, y) and the polar coordinates (r, ν) specifiy the position of the arthropod relative to the nest. P: positional vector. For more details: see text.

It should be noticed that the described model of Mittelstaedt and Mittelstaedt (1973) also contains a closed-loop control system (*'Wirkungsgefüge'*) providing reorientation with respect to the global vector, applicable to any excursion of an arthropod, including the outbound route towards a food source position P_0, whose cartesian coordinates have to be internally stored, or the homing route towards the origin $P_0 = (0, 0)$. In both cases the control system produces an efferent motor signal for the turning angle ω being negatively proportional to $|P_0 - P| \sin \delta$, where δ is the deviation angle between current moving direction ϕ and the global vector $G = P_0 - P$. By this steering algorithm, the arthropod will turn into the direction of the global vector and walk towards P_0 until the global vector is zero. Thus, the path integration mechanism is supposed to work during the whole excursion.

This comprehensive navigation model has been adapted to experiments with rodents (Mittelstaedt and Mittelstaedt 1980; Benhamou 1997) or humans (Mittelstaedt and Mittelstaedt 2001) and recently updated to be consistent with results on neural activity patterns in the hippocampus of mammals (Mittelstaedt 2000). It provides important principles of information processing, path integration, and motor control, and is mathematically easily

realizable in computer simulation programs. Nevertheless, it remains open, whether and how the necessary computational steps of calculating trigonometric functions are physiologically performable within the neural nets of arthropods or mammals. Moreover, this model supposes two successive integrating mechanisms including the necessity to store the computed variables, first $\phi = \int \omega \, dt$ (in case of proprioceptive measurement) and then $P = \int (\cos\phi, \sin\phi) \, ds$, if integration is over walked distance, s denoting arc length, or, $P = \int (v\theta)(t) \, dt$, if integration is over time. In the last case, besides determination of the turning speed ω, also that of forward speed v is required (see Table II.1).

1.1.2 Polar coordinates.

Geocentric models in *polar coordinates* have been developed and applied during the last 20 years by Wehner and Wehner (1986) and Müller and Wehner (1988), taken up by Hartmann and Wehner (1995) in connection with dynamical representations by cyclical neural chains. In order to represent the actual position vector $P = r \, (\cos\nu, \sin\nu)$ of the arthropod, the proposed model algorithms require the animal to compute, at least approximately, distance r from the nest and angle ν of the position vector relative to an allothetic reference direction, determined by the sun or, most frequently, by polarised skylight (Fig. II.1). Then, the global home vector is $G = -P = r \, (\cos(\nu + \pi), \sin(\nu + \pi))$.

For a segmented path with step length s_n (taken to be 1 for simplicity), Müller and Wehner (1988) derive approximate recursive formulas for updating the polar coordinates (r_n, ν_n) after the nth moving step. The only additional input needed during each step, besides knowing step length (or measuring forward speed), is the angle $\tilde{\delta}_n = \phi_n - \nu_n$ between moving direction ϕ_n and the direction ν_n of the positional vector. In a continuous description the corresponding general path integration formulas read $r = \int \cos(\phi - \nu) \, ds$ and $\nu = \int \sin(\phi - \nu)/r \, ds$, and they are equivalent to a system of nonlinear ordinary differential equations (see also Table II.1)

$$\frac{dr}{dt} = v \, \cos(\phi - \nu) \tag{II.1}$$

$$\frac{d\nu}{dt} = \frac{v}{r} \, \sin(\phi - \nu). \tag{II.2}$$

Again this mathematical integration algorithm requires the ability to calculate nonlinear trigonometric functions and, in addition, to perform the division by distance r. Müller and Wehner (1988) and Hartmann and Wehner (1995) suggested the trigonometric functions could be approximated by piecewise linear or polynomial functions (see also II.4). This leads to a systematic misestimation of increments in both variables, r and ν, for moving directions not parallel or antiparallel to the position vector, i.e. for $\tilde{\delta} = \phi - \nu \neq \pm\pi$ (Fig. II.1). Using this approximate algorithm, Müller and Wehner (1988) could remarkably well reproduce systematic errors in the angular component ν of the global vector, observed in the classical two–segment experiments, not only for desert ants but also for most arthropods and mammals (e.g. Bisetzky 1957; Görner 1958; Müller and Wehner 1988; Séguinot et al. 1993).

		Input variables	Internal variables	Global vector
Geocentric	Cartesian (II.1.1.1)	ω, v or ω_n, s_n	ϕ, $P = (x, y)$ ⟨lin./nonlin. ODE⟩	$G = -P$
	Polar (II.1.1.2)	ϕ s_n or v	r and ν ⟨nonlinear ODE⟩	$G = -r\,(\cos\nu, \sin\nu)$
Egocentric	Polar (II.1.2)	ω, v or ω_n, s_n	r and δ ⟨nonlinear ODE⟩	$G = r\,(\cos\delta, \sin\delta)$
	Cartesian (II.2.1)		X and Y ⟨linear ODE⟩	$G = (X, Y)$

Table II.1: Path integration models with the parameters and variables used for input, internal calculation and output as global vector. For notations and more details see the various model descriptions in the text.

1.2 Egocentric models

Another approach, which appears to be more adequate but came into consideration much later, is to model the path integration process of a moving animal in terms of a moving coordinate frame centered around the animal's body, thus reflecting the fact that it perceives all sensory inputs relative to its own position and orientation. Benhamou et al. (1990) chose *polar coordinates* to represent the global vector $G = r\,(\cos\delta, \sin\delta)$, where now G is given in egocentric coordinates with the reference direction for $\delta = 0$ being the body axis, serving as X–axis of the corresponding cartesian coordinate frame (see Fig. II.2). Although the distance variable r is the same as in the geocentric polar model, the derived recursion formulas for updating r_n and δ_n turn out to be much more complicated than any other formula used before. First, egocentric cartesian coordinates (X_n, Y_n) are updated in terms of the former polar ones,

$$X_{n+1} = r_n\cos(\delta_n - \omega_n) - s_n \tag{II.3}$$
$$Y_{n+1} = r_n\sin(\delta_n - \omega_n) \tag{II.4}$$

where ω_n denotes the change of the direction and s_n the length of the subsequent step. (An interchange of the order of stepping and turning would give s_{n+1} in equ. (II.3) but no fundamental change). Then, these equations are transformed into the new egocentric polar coordinates:

$$r_{n+1} = \sqrt{X_{n+1}^2 + Y_{n+1}^2} \tag{II.5}$$

$$\delta_{n+1} = \arctan\left(\frac{Y_{n+1}}{X_{n+1}}\right) \tag{II.6}$$

(in order to calculate the correct values of δ_{n+1} the signs of X_{n+1} and Y_{n+1} have to be considered, see Benhamou and Séguinot 1995).

The advantage of this egocentric model is that now the only *input variables* are step length s_n and turning angle ω_n, or, in the corresponding continuous path integration model, forward speed v and angular turning rate ω. Gallistel (1990) considered the corresponding differential equation using egocentric polar coordinates in the continuous limit of infinitely small time

steps which, in the corrected formulation by Benhamou and Séguinot (1995), are

$$\frac{dr}{dt} = -v \, \cos \delta \qquad (II.7)$$

$$\frac{d\delta}{dt} = v \, \frac{\sin \delta}{r} - \omega. \qquad (II.8)$$

These equations can be obtained directly from the corresponding geocentric polar coordinate equations, eqs. (II.1) and (II.2), by performing a simple angular transformation, $\delta = \nu + \pi - \phi$, so that they again require to compute division by r and trigonometric functions (see also Table II.1).

In their simulation analysis, Benhamou et al. (1990) studied the influence of random errors on the estimation of changes of direction and walked distance. With regard to directional changes, they distinguished between allothetic and idiothetic orientation: they considered idiothetic estimation as 'measuring the change of direction itself', whereas the allothetic estimation is defined as 'a comparison between the heading of current and previous step relative to some exteroceptive compass' (Maurer and Séguinot 1995). The different estimation procedures were realized by providing the actual values with normal distributed errors.

In their simulations, random errors of allothetic signals had only little influence, whereas those of idiothetic signals lead to noticeable misestimation. Benhamou and Séguinot (1995) conclude that the egocentric coding process is quite sensitive to idiothetic errors and organisms relying on allothetic cues for measuring directional changes by far outmatch those relying on idiothetic cues.

2 Cartesian model for egocentric path integration

2.1 System of linear differential equations for the global vector

The physiological sensing and locomotion apparatus of any arthropod is completely bound to its body architecture. Therefore, it is naturally related to its two symmetry axes, the posterior-anterior axis and the perpendicular right-left axis. Thus, when identifying these symmetry axes with the X and Y axes of a cartesian coordinate frame (X, Y) and taking the arthropod's body center as the origin $(0, 0)$, this constitutes a proper planar moving coordinate frame for representing the *relative position* of any object in the planar neighborhood of the arthropod, e.g. its nest, see Fig. II.2. In this *egocentric cartesian* model the global vector pointing from the arthropod's body to the nest, relative to the animal's actual body axis orientation, is just $G = (X, Y)$, corresponding to the same vector as in II.1.2, there only written in polar coordinates. Notice that the original ansatz by Benhamou et al. (1990) already mentioned this cartesian coordinate system, but then switched to polar coordinates for path integration (see II.1.2). Indeed, the continuous version of Eqs. (II.3) and (II.4), given the arthropod's *forward speed v* and *angular*

turning rate ω, yields the following model equations for a precise update of the global vector (X, Y) during motion

$$\frac{dX}{dt} = -v + \omega \cdot Y \qquad\qquad (\text{II.9})$$

$$\frac{dY}{dt} = -\omega \cdot X. \qquad\qquad (\text{II.10})$$

Compared to all other continuum equations or analogous discrete recursion algorithms developed previously (see II.1), this two–dimensional differential equation system is remarkably simple: It is linear in the two variable quantities X and Y, and it just uses the two speed input parameters as additive or multiplicative terms, v representing the rate of shifting the X coordinate backwards, ω the rate of rotating the (X, Y) frame clockwise. These operations can easily be performed by any suitable elementary analogue circuit network like the one shown in Fig. II.4.
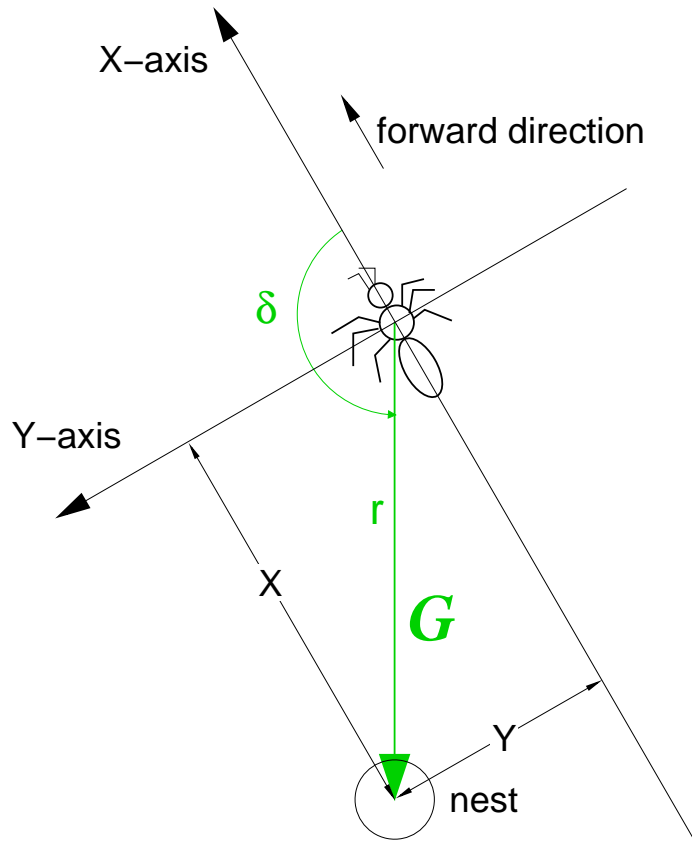
Figure II.2: Theoretical scheme of egocentric path integration by means of cartesian coordinates X, Y specifying the position of the nest relative to the arthropod's body axes and determining the global vector $G = (X, Y)$, here with $X < 0$, $Y > 0$. In contrast, the corresponding model in polar coordinates (II.1.2) uses the two variables r, distance to the nest, and δ, angle between head orientation and nest direction.

In conclusion, this *cartesian egocentric path integration model*, considered as a precise 'dead reckoning' system, offers the most simple computational

scheme to determine the global vector and, simultaneously, being related to a coordinate frame of the moving arthropod. For comparison with the other models see Table II.1.

Clearly, biological solutions of difficult problems can be complex, and the simplicity of this model does not make its realization more likely than that of other models. From a conceptional point of view the existence of a simple solution is nevertheless striking, and in the following I shall present its implementation and results.

2.2 Modelling foraging excursions, reorientation, and homing

This path integration model depends on the values of v and ω, cf. Table II.1. These can be regarded as the elementary physiological control variables which the arthropod uses to steer its locomotion, e.g. by changing speed or frequency of striking leg motion on both sides or, respectively, on one side relative to the other.

In order to model typical paths of directionally persistent random walks, as observed for desert arthropods, one has to account for mean values and standard deviations of speed v and turning rate ω as well as for their temporal auto-correlations which can be extracted from corresponding experimental time series (see Alt 1990). Discrete correlated random walk models sometimes used (e.g. Byers 2001) are not adequate as they assume piecewise constant walking directions ϕ_n and turning angles ω_n. The two speeds $v(t)$ and $\omega(t) = d\phi(t)/dt$, however, being related to the physiologically controlled, relatively fast leg movement on both sides of the arthropod, should better be modelled as fluctuating continuous processes on an adequate smoothness level. The simplest stochastic process of this kind is described by the following two independent Ornstein–Uhlenbeck equations for first order colored noise, which have previously been used also for modelling the systematic search of arthropods (Alt 1995),

$$dv \;=\; \frac{1}{T_v}\,(v_0 - v)\,dt + \beta_v\,dW_t \tag{II.11}$$

$$d\omega \;=\; \frac{1}{T_\omega}\,(\omega_0 - \omega)\,dt + \beta_\omega\,dW_t \tag{II.12}$$

Following the standard approach, random perturbations are expressed as additive Wiener increments dW_t (Itô and McKean 1965). In simulations one uses a sequence of values v and ω with *finite* time differences τ,

$$v_{t+\tau} \;=\; v_t + \frac{\tau}{T_v}\,(v_0 - v_t) + \beta_v\sqrt{\tau}\,\zeta \tag{II.13}$$

$$\omega_{t+\tau} \;=\; \omega_t + \frac{\tau}{T_\omega}\,(\omega_0 - \omega_t) + \beta_\omega\sqrt{\tau}\,\zeta \tag{II.14}$$

where ζ denotes a standard normally ($\mathcal{N}(0,1)$) distributed random variable, drawn independently at each step for each variable. Eqs. (II.11) and (II.12) are obtained in the limit $\tau \to 0$. v_0 and ω_0 are the preferred values of forward and turning speed, respectively, and the $T_{v|\omega}$ denote the corresponding mean persistence times of fluctuations with amplitudes $\beta_{v|\omega}$. In case of a stationary

time series they yield variances of size $\sigma_{v|\omega}^2 = \beta_{v|\omega}^2 T_{v|\omega}/2$ by an equilibrium of perturbations with strength $\beta_{v|\omega}$ and decay at rate $1/T_{v|\omega}$. In our presentation we assume, for simplicity, that T_v is negligibly small, such that during locomotion the forward moving speed has a constant value $v \equiv v_0$. The presented results also hold for the general case of fluctuating forward speed.
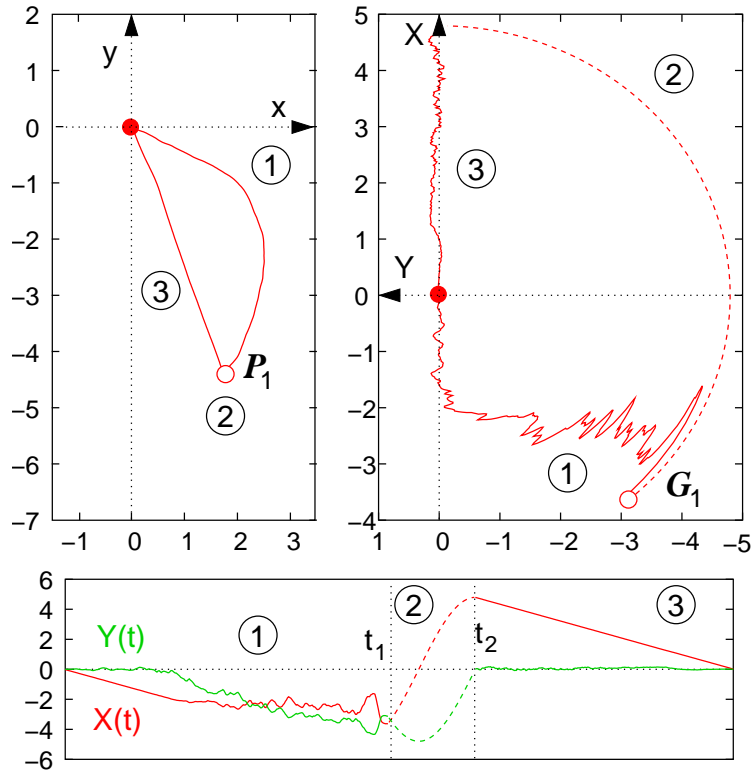
Figure II.3: Model simulation of a natural outbound path and the successful return path back to the nest due to precise path integration, according to the 3-Phase-model, see text. Parameters used for calculations are, (1) for the outbound path $T_\omega = 0.3$ s, $\beta_\omega = 1$ s$^{-3/2}$, and constant forward speed $v \equiv v_0 = 0.2$ m/s, (2) constant $\omega_{\mathrm{rot}} = 1$ s^{-1} during rotation and (3) for homing the same as in (1) but a feedback constant $c = 1/0.05$ m^{-1} s^{-1} for beacon steering. Top left: Plot of the actual path in cartesian (x, y)-coordinates of an observer. Position of the nest at $(0, 0)$ is marked by a filled circle. Top right: Corresponding plot of the nest position in the same scale in relative cartesian (X, Y)-coordinates, where the origin denoting the home position is marked by a filled circle. Note that the animal's head direction is the X–axis pointing upwards, while the lateral Y–axis points to the left. Bottom: Corresponding plots of X and Y over time. The Matlab routine used for this application is given on the CD that is enclosed (see appendix 5.1).

In the following, I will describe the three successive phases of an arthropod's typical excursion, using the egocentric path integration system Eqs. (II.9), (II.10) and the physiological motion control system Eqs. (II.11) and (II.12). I explain the corresponding dynamics of the global vector by means of a simulated example presented in Fig. II.3. Two more examples and their corresponding values are given in the appendix (appendix 2).

- Phase 1: **(Foraging)**
  The arthropod starts foraging at the nest site, e.g. $(x_0, y_0) = (0, 0)$,
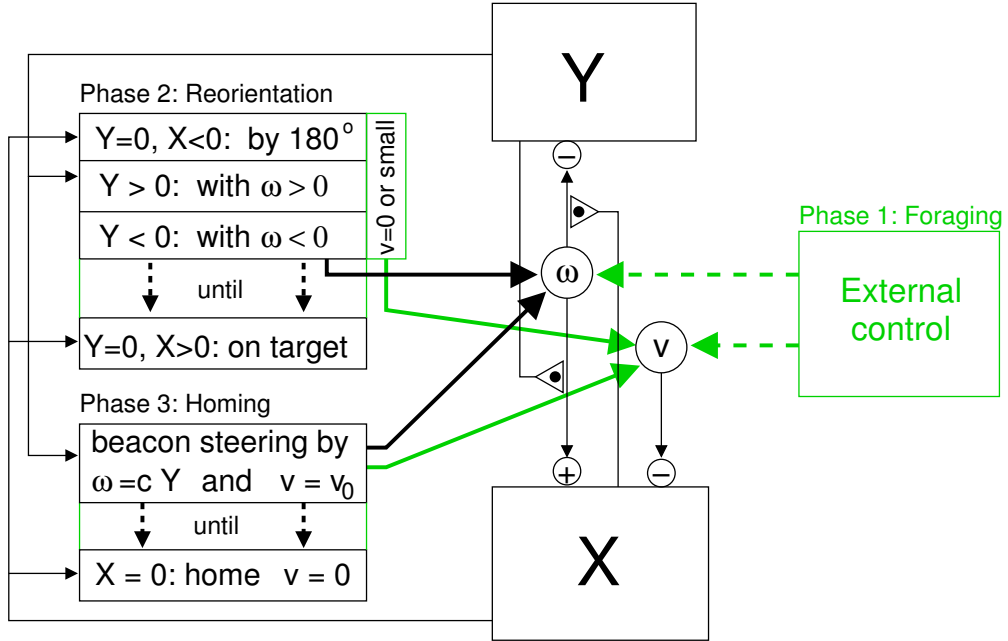
Figure II.4: Analogue circuit scheme of the egocentric cartesian path integration model: dynamics of the two variables X and Y according to the differential equations (II.9) and (II.10) and its coupling to the physiological control parameters represented by the two speed parameters for turning, ω, and forward locomotion, v. In *Phase 1*, ω and v are externally controlled (random search, trained path towards feeder, . . .). During *Phase 2* and *Phase 3* the X and Y values feed back into the speed control conditions such that, by counter–steering with respect to the 'internal beacon' $Y = 0$ in the latter case, equations (II.9), (II.10) and (II.12) constitute a coupled nonlinear control system along the homing path.

where the global vector is reset to zero $G = (X, Y) = 0$. Holding the mean turning rate $\omega_0 = 0$, the animal approximately keeps its chosen initial direction, $\phi = \phi_0$, for some time, leading it almost straight away from the nest, corresponding to increasingly negative X values of the internal global vector, while the Y component stay close to zero. This initial behavior is well expressed in the example of Fig. II.3, then followed by a random right-hand turn of the (x, y)-path, which corresponds to increasingly Y values meaning that now the nest lies to the right side the animal.

- Phase 2: **(Reorientation)**
  After finding food at some position $P_1 = (x_1, y_1)$, the arthropod stops there in its current angular orientation, $\phi = \phi_1$, keeping the actual global vector $G_1 = (X_1, Y_1)$ stored internally (even during handling the food). Then the arthropod starts its reorientation phase by turning on spot, say with constant rotation speed $\omega \equiv \pm\omega_{\rm rot}$, depending on whether the stored global vector G_1 has positive or negative Y_1 value. During rotation the global vector $G = (X, Y)$ also rotates according to path integration in Eqs. (II.9) and (II.10), since now we set $v \equiv v_0 = 0$. Finally, the arthropod is assumed to stop its rotation ($\omega = 0$) as

soon as the condition $Y = 0$ is fulfilled, meaning that now its head is oriented towards the nest and the actually positive X-value represents the arthropod's distance from the nest (cf. the scheme in Fig. II.4). For the example in Fig. II.3, see the counter-clockwise rotation circle ending on the positive X axis. Notice that the condition $Y = 0$ corresponds to $\delta = 0$ in egocentric polar coordinates (II.2.2 and Fig. II.2) because of the equivalences $Y = r \cdot \sin \delta$ ($\approx r\delta$ for small δ) and $X = r \cdot \cos \delta$ ($\approx r + r\delta^2/2$ for small δ).

- Phase 3: **(Homing)**
  The arthropod now returns back to the nest (as straightly as possible) according to the actually stored global vector $G = (X, 0)$. Since during walking the global vector will be constantly updated and, due to inevitable random perturbations, the Y component will eventually deviate from the zero value, the arthropod must tend to hold the internal *steering condition* $Y = 0$ as closely as possible. This can be modelled by implementing a *counter-steering* turning rate $\omega_0 = cY$ into the stochastic differential equation (II.12). See Fig. II.4 for an analogue circuit scheme describing this feedback control, which nonlinearly and cyclically couples the linear path integration system, Eq. (II.9) and (II.10), to the linear motor control equation (II.12).

  Finally, in this model the arthropod is assumed to stop its return phase as soon as the X value of its global vector becomes zero. The resulting home path in the simulated example of Fig. II.3 clearly shows how some random perturbations lead to small deviations in the homing direction of the (x, y) path and corresponding small Y deviations of the global vector, while the X component is almost linearly decreasing to zero.

Notice that, according to this modelling scheme, the path integration system in Eqs. (II.9) and (II.10) is supposed to work constantly in the arthropod's neural system during foraging, reorientating, and homing, except when the animal is seriously perturbed and not able to 'measure' and 'control' its forward motion and directional turning rate any more. If this happens, the animal is assumed to instantaneously halt the path integration system instantaneously and keep the actual value of the egocentric global vector and the orientational angle (with respect to an allothetic visual cue) stored until it can proceed in an unperturbed way.

Let us emphasise that the presented *internal* dynamics of the global vector $G = (X, Y)$, determined by the simple linear system differential equations (II.9) and (II.10), could equivalently be described in polar coordinates $G = r(\cos \delta, \sin \delta)$ using the more complicated nonlinear differential equations (II.7) and (II.8), including the 'rotation stop condition' $\delta = 0$ and the counter-steering term $\omega_0 = -cr\cos \delta$ or a stronger variant like $\omega_0 = -\tilde{c}\delta$. However, there is an important difference in modelling the 'nest stop condition': In polar coordinates, the obvious termination criterion would be chosen as $r = 0$ meaning that the global vector G becomes exactly zero. It remains to be proven which counter-steering rule could guarantee that this condition is attainable for stochastically perturbed random paths.

In contrast, the proposed termination criterion $X = 0$ in cartesian coordinates would, for randomly perturbed return paths, generically result in

a non-vanishing small Y value, then representing the lateral distance of the arthropod to the nest. Thus, depending on this value and on the current orientational angle of the animal, the realized 'stop position' can fluctuate around the true nest position, even in the so far considered case of *precise path integration*. The size of this random error increases with the length of the home vector, i.e. the distance between food and nest. This corresponds to experimental observations (e.g. for desert ants *C. fortis*, personal observations) which furthermore show that the lengths of outbound paths also contribute to such a positional error. Therefore, other errors in path integration, being accumulated along the path, have also to be considered, which is the topic of the following section.

3   Systematic errors

It has been shown that many arthropods (e.g. Bisetzky 1957; Görner 1958; Hoffmann 1985; Wehner and Wehner 1986; Müller and Wehner 1988) but also mammals (e.g. Séguinot et al. 1993; Etienne et al. 1996; Séguinot et al. 1998) exhibit errors in determining the exact homing direction. In general, we have to distinguish between random errors and systematic errors during path integration. There is evidence that random errors, in addition to the home vector steering error mentioned above, can originate from inaccurate measurements of angles or distances, whereas systematic errors probably arise at the neural level of the organism (Benhamou et al. 1990; Séguinot et al. 1998). Orientation is less error prone if allothetic reference frames are available, as polarised skylight for arthropods (e.g. Wehner 1998, 2003), but a more difficult task if not, as for mammals (Etienne and Jeffry 2004). Systematic errors play an important role, as the classical two–leg experiments (L-shaped angular turning tests) have shown in both mammals (e.g. Maurer and Séguinot 1995; Etienne et al. 1996) and arthropods (e.g. Müller and Wehner 1988; Bisch 1999). Apart from mistakes that concern directional aberrations, there occur also errors by underestimation of distances (Sommer and Wehner 2004).

From an evolutionary point of view the presence of systematic homing errors is interesting and has not been explained to date. It may have an advantage that a homing animal typically assumes a shorter path and ends up *in front of* its nest. It would then avoid an overshoot and find familiar features that it has just passed on the outgoing path which might help to reach the nest's entrance.

Here I implement two types of systematic errors into the new egocentric model. One concerns the estimation of nest distance following Sommer and Wehner (2004), the other exhibits different variations in processing the turns during path integration. All of them predict systematic deviations from correct homeward courses and are based on feasible neural assumptions, or reproduce behaviors that have been observed during experiments.

3.1   Underestimation of turning angles

Müller and Wehner (1988) trained desert ants to run through two channels

of 10 m and 5 m length and varied the connecting angle between them in several steps from 0 to 180°, see Figs. II.5 and II.6. The ants miscalculated their covered outbound route and, after leaving the second channel's end, turned about an angle which was *larger* than the correct one leading home. The authors reproduced this error very well by a simple formula, which accumulates systematic miscalculations in path integration whenever the animal walks different from the direct inbound and outbound directions (in the following, this error is called MW-error, see appendix 1, where all abbreviations are shown again). In Fig. II.6 the angular aberration function ε is shown, computed according to the approximative path integration model by Müller and Wehner (1988). In general, this function fits observations in other arthropods and mammals (Séguinot et al. 1993; Bisch 1999) quite well. Here it is shown that other error models can also reproduce these data. For evaluation and fitting of the corresponding error functions (see plots in Fig. II.6) I use the advantages of my egocentric path integration system.
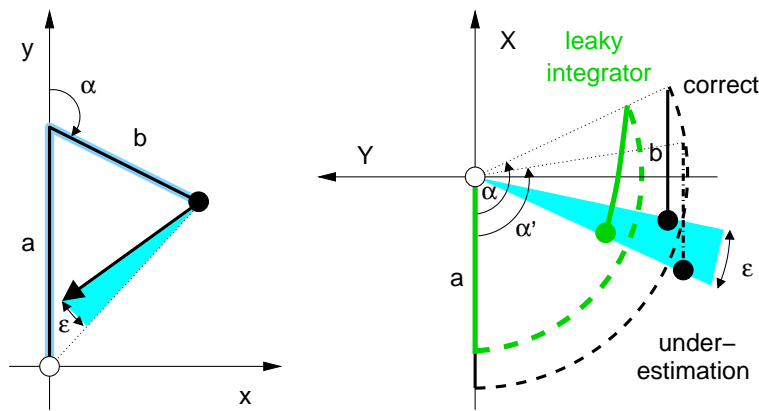
Figure II.5: Angular deviation ε in the two–leg experiment with channels of length a and b, respectively, and clockwise connecting angle α. Left side: Experimental situation as observed in geocentric (x, y)–coordinates. Right side: Representation of the global vector in internal (X, Y)–coordinates; correct representation indicated by thick black line, dashed during counterclockwise turn about angle α. *Angle underestimation* leads to turn by $\alpha' < \alpha$ and angular aberration ε after leaving the second channel (black dot–dashed line). *Leaky integrator* LI is shown in green, also leading to angular deviation. For more details see text.

As a first error mechanism I consider a *systematic underestimation* LU of body axis rotation. In principle, that error could occur during the estimation of ω, i.e. by simply perceiving a value lower than the actual value, or on the neural level. The high accuracy concerning the ability of desert arthropods measuring rotations makes it very likely that this error may be created on the neural level. Therefore, I assume the animal perceives the correct value ω_{real}, but uses a different value ω_{proc} for processing the path integration according to the differential equations (II.9) and (II.10).

In a first choice the underestimation is taken to be a linear function of the real value,

$$\omega_{\mathrm{proc}} = \lambda \, \omega_{\mathrm{real}} \qquad \qquad \text{(II.15)}$$

with a factor $\lambda < 1$ (error LU in Table II.2). In a second variant, the fully sat-
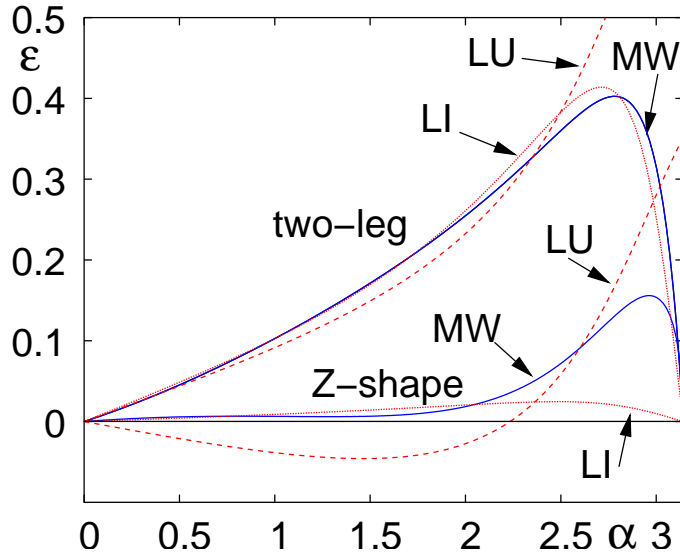
Figure II.6: Error angles ε as a function of the intermediate turning angle in the two–leg experiment (three upper curves) and a Z–shaped channel with three parts of 5 m length each (three lower curves) in radian units. Solid lines (MW): Deviation following Müller and Wehner (1988); dashed (LU): linear underestimation of turning rate with $\lambda = 0.87$; dotted (LI): leaky integrator with $\tau_L = 90$ s (resp. $\xi_L = 18$ m). Linear underestimation cannot account for correct path integration under full turns ($\alpha = \pi$) but does well for $0 \leq \alpha \leq (5/6)\pi$. In the Z–shaped channel errors are smaller than for single turn and experimentally visible (if at all) only for angles around $150°$ ($= 5\pi/6$) with errors MW and LU.

urated underestimation, ω_{real} is processed correctly for small values but saturates towards a certain maximal turning rate ω_c (error NLUs in Table II.2),

$$\omega_{proc} = \frac{\omega_c}{\omega_c + |\omega_{real}|}\,\omega_{real} \tag{II.16}$$

A linear combination of both is given by the error NLU in Table II.2,

$$\omega_{proc} = \left(\lambda + \frac{1-\lambda}{\omega_c + |\omega_{real}|}\,\omega_c\right)\omega_{real} \tag{II.17}$$

which again processes small values correctly.

For a related choice of errors I assume a temporal delay τ_{del} in processing the information of $\omega_{real}(t)$; the same underestimation could, in principle, be assumed also for $v_{real}(t)$, but here variation on natural outbound paths is rather low (personal observations on desert ants *Cataglyphis fortis*). Phenomenologically such a 'perception delay' PD is implemented by a linear ordinary differential equation representing a first order filtering process, namely

$$\frac{d\omega_{proc}}{dt} = \frac{\omega_{real} - \omega_{proc}}{\tau_{del}} \tag{II.18}$$

such that ω_{proc} is *smeared out* on a scale of τ_{del} as compared to ω_{real} (error PD in Table II.2).

Error	Differential Equations
Turning rate underestimation	
LU linear underestimation of ω $\qquad \omega_{\mathrm{proc}} = \lambda\,\omega_{\mathrm{real}}, \quad 0 < \lambda < 1$	
NLUs fully saturated underestimation $\qquad \omega_{\mathrm{proc}} = \dfrac{\omega_{\mathrm{c}}\omega_{\mathrm{real}}}{\omega_{\mathrm{c}} + \lvert\omega_{\mathrm{real}}\rvert}$ with $\omega_{\mathrm{c}} > 0$	
NLU partially saturated underest. $\qquad \omega_{\mathrm{proc}} = \omega_{\mathrm{real}}\left(\lambda + \dfrac{1-\lambda}{\omega_{\mathrm{c}} + \lvert\omega_{\mathrm{real}}\rvert}\,\omega_{\mathrm{c}}\right)$	$\begin{aligned}\dot{X} &= -v + \omega_{\mathrm{proc}}\,Y \\ \dot{Y} &= -\omega_{\mathrm{proc}}\,X\end{aligned}$
PD processing delay $\qquad \dot{\omega}_{\mathrm{proc}} = \dfrac{\omega_{\mathrm{real}} - \omega_{\mathrm{proc}}}{\tau_{\mathrm{del}}}$	
Nest distance underestimation	
LI Leaky integrator egocentric cartesian	$\begin{aligned}\dot{X} &= -v + \omega_{\mathrm{real}}\,Y - X/\tau_{\mathrm{L}} \\ \dot{Y} &= -\omega_{\mathrm{real}}\,X - Y/\tau_{\mathrm{L}}\end{aligned}$
egocentric polar	$\begin{aligned}\dot{r} &= -v\cos\delta - r/\tau_{\mathrm{L}} \\ \dot{\delta} &= v\sin\delta/r - \omega_{\mathrm{real}}\end{aligned}$

Table II.2: Error types in path integration and their respective formulae.

3.2   Underestimation of distance to the nest

The error due to distance underestimation, which will be considered here, has previously been referred to as *leaky integrator* — abbreviated as LI from now on — by Sommer and Wehner (2004). This idea can be implemented into the egocentric cartesian path integration model in a straightforward way: with a constant rate the integrated global vector 'leaks' or decays from the memory. Thus, the two–dimensional model Eqs. (II.9) and (II.10) are varied by simply adding a proportional decay term in each equation (error LI in Table II.2)

$$\dot{X} \;=\; -v + \omega_{\mathrm{real}}Y - \frac{X}{\tau_{\mathrm{L}}} \tag{II.19}$$

$$\dot{Y} \;=\; -\omega_{\mathrm{real}}X - \frac{Y}{\tau_{\mathrm{L}}} \tag{II.20}$$

with mean decay time τ_{L}. Also in egocentric polar coordinates, c.f. Eqs. (II.7) and (II.8), the leaky integrator is easily expressed by a proportional decay of radial distance r, see Table II.2.

In the case of a one–dimensional path, e.g. always walking along x without any turns ($\omega_{\mathrm{real}} \equiv 0$), Eqs. (II.19) and (II.20) lead to an exponential underestimation (x_{ue}) of the actual walking distances (x) as

$$x_{\mathrm{ue}} = \xi_{\mathrm{L}}\left(1 - \exp(-x/\xi_{\mathrm{L}})\right). \tag{II.21}$$

The estimated distance x_{ue} saturates at a length $\xi_{\mathrm{L}} = v\tau_{\mathrm{L}}$ in the limit of long walking distances x, but for short paths $x \ll \xi_{\mathrm{L}}$ the error is small and $x \approx x_{\mathrm{ue}}$.

This is precisely the best fit to the experiments performed by Sommer and Wehner (2004). The authors trained desert ants to walk through linear channels to a feeder. Afterwards the ants were captured at the feeder and released in a linear test channel. They headed off in homeward direction and performed a back and forth search around their assumed nest position. By extracting x_{ue} from the search behavior, Sommer and Wehner found the relation of Eq. (II.21).

In a truly two–dimensional path the leaky integrator of (II.19) and (II.20) may also lead to an *angular deviation* of the search path from the true homeward direction. Earlier sections of the outgoing path have decayed in the memory more than later ones. If the animal has turned in–between, this will result in a *different* misestimation of related directions and, consequently, in a homing angle misestimation. In Fig. II.5 this is explained for the classical two–leg experiment of Müller and Wehner (1988).

There is, however, a quantitative mismatch between the fit of the LI equations (II.19) and (II.20) to the experiments of Müller and Wehner (1988) and to those of Sommer and Wehner (2004). In the latter case one obtains $\xi_L \approx 90\text{m}$ which is substantially different from the value of 18m of the fit to Müller's and Wehner's two–leg experiments. At present we conclude that most likely some part of the error occurs during the turn. To fully answer this contradiction, one would have to take into account more details of the ants' walks, such as, e.g., walking speed or waiting times.

3.3   Resulting deviations

First, I document the outcome of a simulated experiment as in Müller and Wehner (1988). The left side of Fig. II.5 shows a sketch of the two–leg experimental setup which in Müller and Wehner (1988) had lengths $a = 10\text{m}$ and $b = 5\text{m}$. The ant starts at the nest (open circle), turns after distance a by an angle $0 \leq \alpha \leq \pi$ to the right, leaves the channel after another walked distance b (at the black circle), thereby overcompensating its turn to the correct home direction by an angular deviation ε.

The right side of Fig. II.5 represents this path in the internal (X, Y)–coordinates. First consider a correct processing without any systematic error: X decreases to $-a$ (thick black line) and $Y = 0$, then the animal turns by an angle α, such that now $X = -a \cos \alpha$ and $Y = -a \sin \alpha$ (black dashed line), finally X decreases further to $X = -a \cos \alpha - b$, whereas Y remains constant (black solid line with black circle). *Angle underestimation* would result in a turn by $\alpha' < \alpha$ such that in the end $X = -a \cos \alpha' - b$ (dot–dashed line with black circle) which lies off the true direction to the nest by an error angle ε. A similar result is obtained by the *LI* (fat grey lines): First X decreases from 0 to $-\xi_L \left(1 - \exp(-a/\xi_L)\right)$ and Y remains 0 (thick grey line), then X and Y are turned by an angle α (dashed grey line). The turn occurs so fast that "leakage" can be neglected ($\tau_{turn} \approx r_{turn}/v \ll \tau_L$, see also below). During the final decrease of X, both the values of X and Y "leak" such that finally

$$X_L = -\xi_L \left[e^{-b/\xi_L} \left(1 - e^{-a/\xi_L}\right) \cos \alpha + \left(1 - e^{-b/\xi_L}\right) \right] \qquad \text{(II.22)}$$

$$Y_L = -\xi_L \, e^{-b/\xi_L} \left(1 - e^{-a/\xi_L}\right) \sin \alpha \qquad \text{(II.23)}$$

which is indicated by the filled grey circle, again resulting in an angular deviation ε (in the sketch, for simplicity, the same as for angle underestimation).

The three upper curves of Fig. II.6 show theoretical predictions for the angle error ε in the two–leg experiment of Müller and Wehner: the error according to the formula of Müller and Wehner (1988) calculated numerically as a function of the angle $0 \leq \alpha \leq \pi$ between the outgoing channels in radian units (solid line); the best fit of turning underestimation (dashed line), i.e. $\lambda = 0.87$ in Eq. (II.15), and for the leaky integrator (dash–dotted line), $\tau_{\mathrm{L}} = 90$ s in Eqs. (II.19) and (II.20). The same model errors are applied to a Z–shaped channel and shown in the three lower curves with the same coding (solid, dashed, dotted). Note that errors are smaller, but deviations cancel only partially.

Nonlinear underestimation of the angular turning rate, Eqs. (II.16) and (II.17), does not show any different behavior from (II.15), because we can assume a *constant* turning rate $\omega_{\mathrm{turn}} = v/r_{\mathrm{turn}} = 4$ s^{-1} given by the ratio of the walking speed $v = 0.2$ m/s and radius of the turn in the channel $r_{\mathrm{turn}} = 0.05$ m, which is half the wall to wall distance, because in experiments deserts ants tend to keep equal distance to both channel walls (Heusser and Wehner 2002). However, nonlinear underestimation will lead to different results for arbitrarily curved paths as we will see next.

To investigate how well the different types of systematic errors fit random outbound paths I simulated runs, as they might be performed by an untrained ant searching for food without any knowledge on food sources (see Fig. II.9, upper panel). In particular, we considered a fluctuating turning rate $\omega(t)$ with a persistence time T_ω as in Eq. (II.12) of the model in II.2.2. For 1000 such runs we extracted correlations between characteristic indicators of the path, such as its integrated curvature $\phi_{\mathrm{end}} - \phi_0 = \int \omega(t)\, dt$, and the two most direct measures for homing deviation: the *angular misestimation ε* between calculated and correct homeward course, and the *euclidean distance* Δ between supposed and real nest positions.

The results are shown in Fig. II.7. There is a clear correlation between curvature $\int \omega$ and the directional mismatch of the homing vector, for all error mechanisms except for perception delay (see left panels in column). In particular, all mechanisms tend to *overcompensate* turns effectuated during the outbound path, as there is a *positive correlation* between $\int \omega$ and the deviation angle. Remind that all predict overcompensation for the two–leg experiment of Müller and Wehner as well.

There is a striking difference between the leaky path integrator and the approximative integration formula of Müller and Wehner on one side, and turning rate underestimation on the other side: The first two predict a larger euclidean distance from the nest for paths where left and right turns compensate ($\int \omega \approx 0$) and come closer to the nest when there is a substantial net turn, resulting in $\wedge$–shapes in the right hand panels of rows 1 and 2 in Fig. II.7. On the other hand, turning rate underestimation predicts smaller distance to the nest for compensated turns, and larger euclidean mismatch for paths with higher turns, leading to $\vee$–shapes of lines 3 and 4 in the right hand panels. Experiments which cover both the *full return path* and the *systematic search*, additionally to the initial direction analyzed by Müller and Wehner (1988) may be able to decide the type of homing error mechanism
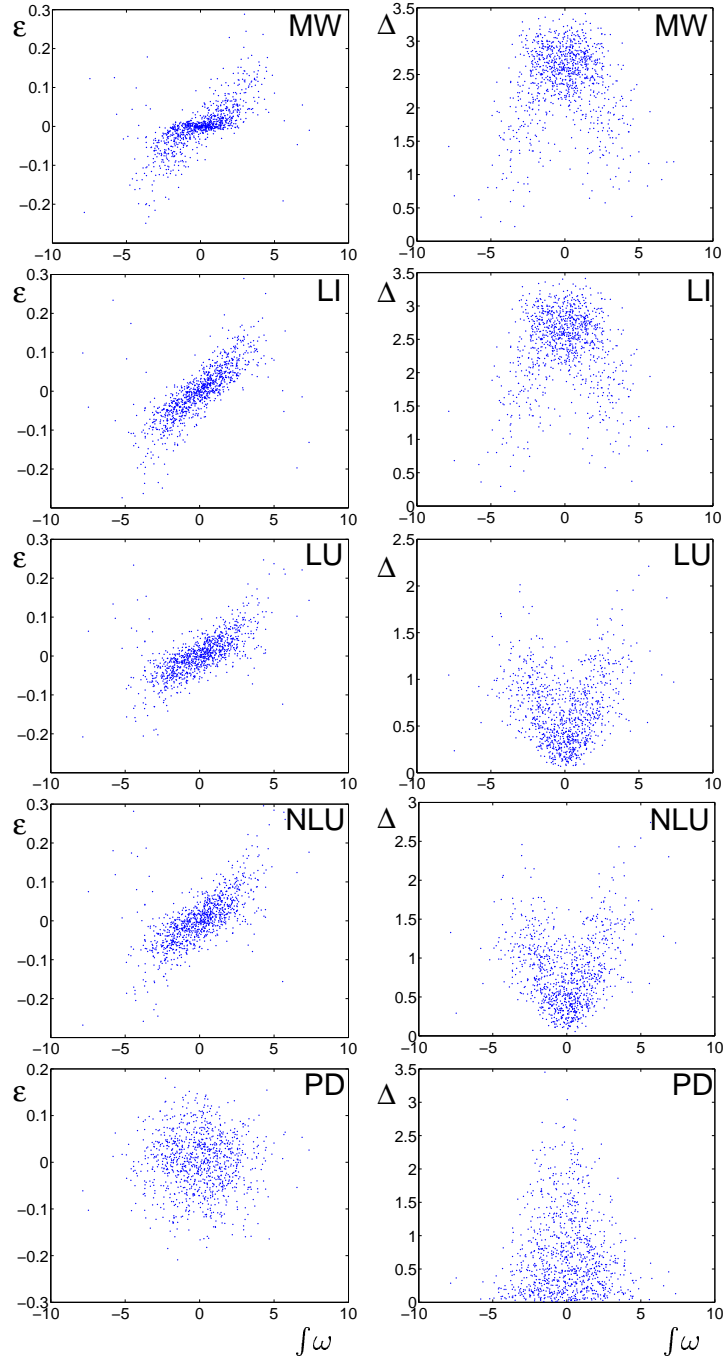
Figure II.7: Homing error for different path integration error types as function of integrated curvature $\int \omega(t)\,dt = \phi_{\text{end}} - \phi_0$ (in radians, 2π for full turn) of 1000 simulated random outbound runs of length 20 m each. Left columns: angular deviation ε in radians; right columns: euclidean distance Δ from nest in meters. Top row, MW: error of Müller and Wehner (1988); 2nd row, LI: leaky integrator with $\tau_{\text{L}} = 300$ s; 3rd row, LU: linear underestimation of $\omega(t)$ with $\lambda = 0.87$; 4th row, NLU: nonlinear underestimation; bottom row, PD: processing delay with $\tau_{\text{del}} = 0.3$ s exhibits no systematic dependence on curvature.

in desert ants (see experimental part of this work).

Fig. II.8 shows the homing errors produced by different error types as functions of the distances d between start and end points of foraging trips that had the same overall path lengths. Thus, the values of d indicate the
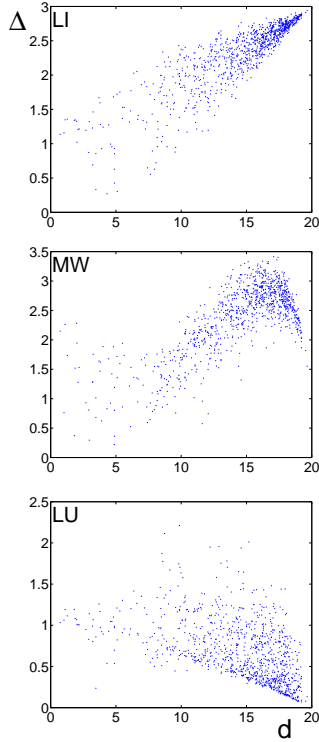
Figure II.8: Homing error in euclidean distance Δ between supposed and real nest position as function of distance between starting and end point of foraging path, i.e. distance of feeding site from nest, $0 \leq d \equiv |P(t_1) - Px(0)| \leq 20$. Simulated paths had arch length 20 m, so $d = 20$ m means a perfectly straight path. Top: The *leaky integrator* predicts increasing Δ with d, whereas according to Müller and Wehner (1988) Δ has a maximum for intermediate d (middle). Bottom: *Angle underestimation* leads to an opposite relation, Δ decreasing with d. Same parameters as in Fig. II.7.

sinuousity of the different paths: straight paths have large, winded paths small d. Roughly speaking the error of the *leaky integrator* increases with d and becomes maximal for perfectly straight paths. The error postulated by Müller and Wehner (1988) also increases with d over a wide range, but *decreases* for very large values for almost straight paths. *Angle underestimation* yields an opposite picture, the deviation decreases over the entire range of d, although large fluctuations may obfuscate measurements. Clearly these findings have to be further developed in comparison to real experiments, but they indicate how field work can enable an observer to differentiate between various error types.

The very same experiment was repeated, but this time the distances covered during the outbound runs were kept at the same value, irrespective of the overall lengths of the outbound run. The parameters had the same values as for the simulations with constant overall lengths of the outbound paths. As a result, it can be mentioned that there were no tendencies to be found, irrespective of the error mechanism that had been implemented to the path integration mechanism.

A difference is also visible in the predictions for the supposed nest positions, as presented in Fig. II.9. In its upper panel it shows the endpoints
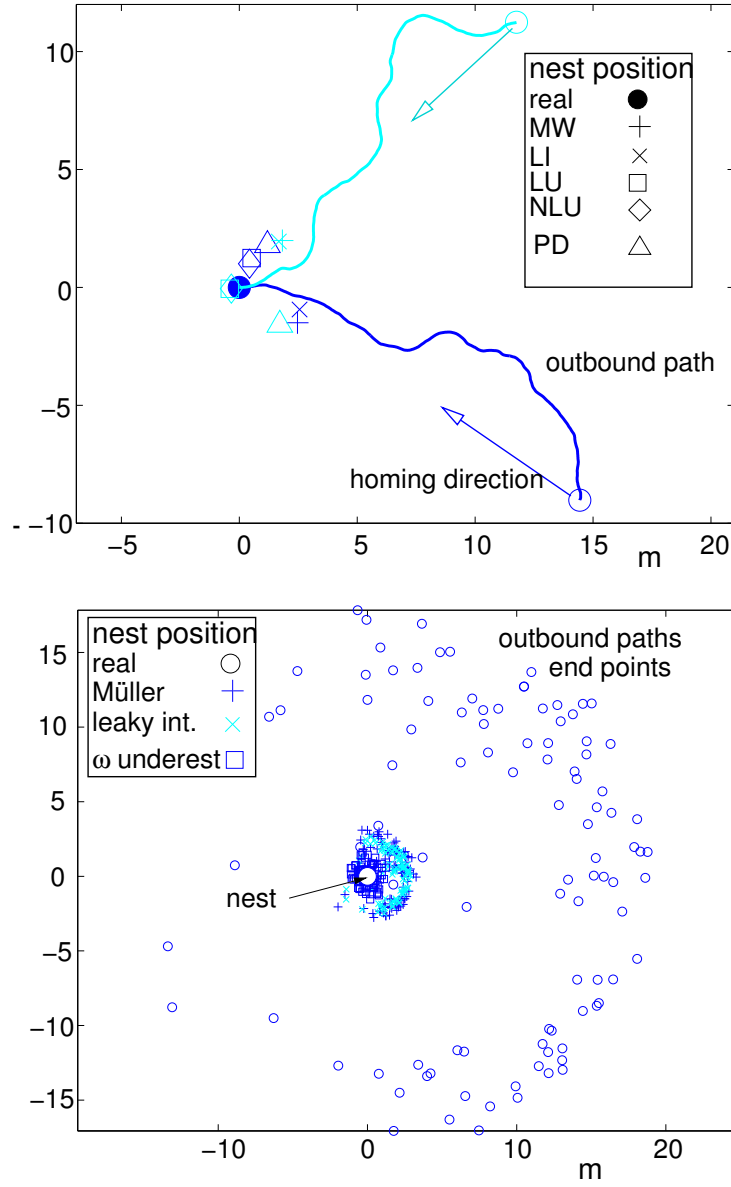
Figure II.9: Supposed nest locations for different error types. Upper panel: Two simulated random outbound paths both starting in direction $\phi_0 = 0$ and having arch length 20 m (blue and light blue) with supposed nest locations according to Müller and Wehner (+), leaky integrator with $\tau_L = 300$ s ($\times$), underestimation of ω with $\lambda = 0.87$ and $\omega_c = 0.2$ s^{-1} (linear: $\square$, nonlin.: $\diamond$) and processing delay of ω with $\tau_{del} = 0.3$ s ($\triangle$). Note that (+) and ($\times$) are relatively close. Lower panel: End points of 100 simulated outbound paths ($\circ$) with supposed nest positions after Müller and Wehner (+), leaky integrator (light blue $\times$), and ω–underestimation ($\square$). Real nest marked by filled white circle. Note that (+) and ($\times$) coincide well, in front of real nest. ($\square$) are grouped closely around the nest. Units are in meters.

of two random outbound runs of length 20 m (one in blue, the other one in light blue), together with the respective supposed nest locations under different error mechanisms: the formula of Müller and Wehner (MW, marked by +), linear (LU, $\square$) and nonlinear (NLU, $\diamond$) underestimation with $\lambda = 0.87$

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and $\omega_c = 0.2$ s^{-1} and turning perception delay with $\tau_{\mathrm{del}} = 0.3$ s (PD, $\triangle$). The time constant for the leaky integrator (LI, $\times$), $\tau_L = 300$ s, was chosen such that it best fitted the results of the phenomenological error formula of (Müller and Wehner 1988). In the lower panel of Fig. II.9 the same is shown for 100 paths (without the paths themselves), where all runs start in the same initial direction $\phi_0 = 0$, such that the end points ($\circ$) lie in a sickle shaped domain to the right. Again there is a striking coincidence between the leaky integrator and Müller's formula as opposed to the results of turning rate underestimation. Notice that only the two first error mechanisms lead to a home vector pointing to a location *in front of* the actual nest (see small sickle–shape domain to the right of nest position).

4 Discussion

In the modelling part I have presented a very simple model for path integration using egocentric cartesian coordinates. In contrast to all previous models, including the egocentric one using polar coordinates (see II.1.2), in this model the arthropod does not need to perform complicated calculations such as applying trigonometric or other non–linear functions, but rather can update two cartesian coordinate values of the relative global vector $G = (X, Y)$ by computing a simple system of linear differential equations. Moreover, although it is assumed that neither the actual relative angle δ nor the distance r to the nest have to be calculated or stored at any time, solely by using the internal G–vector information the arthropod has the ability to orient towards the nest position at any time along its path and to hold this orientation during the home run. Keeping $Y = 0$ serves as an 'internal beacon' for home orientation, where the simple counter–steering mechanism can be realized as an elementary negative feedback control of the turning rate by the internal variable Y, until the second internal variable X reaches the desired zero value. Thus, the path integration values (X, Y) do not only provide a record of the arthropod's positional movement, but can also be used as information input for orientation. Moreover, accumulated information on the whole internal (X, Y)-path, as depicted in Fig. II.3, for example, may be used by the arthropod to guide its observed systematic search for the 'true' nest position after failure.

Physiological realizations of the integration procedure itself and the underlying fundamental neural mechanisms are far from being clarified. On the other hand, there have been developed a series of neural network models related to sensory information flow, orientation and path integration in general (e.g. Wittmann and Schwegler 1995; Samsonovich and McNaughton 1997; Mittelstaedt 2000), and for desert ants in particular (Hartmann and Wehner 1995). In the latter case the authors even explicitly incorporate the systematic errors observed by Müller and Wehner (1988) on a neural level. Wehner (2003) postulates the existence of a fixed number of 'compass neurons', each with an accurately defined compass direction. All these models, so far based on polar coordinates, could be adapted to this cartesian path integration model. Moreover, it is also possible to formulate simple network models similar to the scheme presented in Fig. II.4.

A simple way would be to directly represent the internal cartesian coordinates (X, Y) by the deviations of two non–spiking interneuron activities N^X and N^Y from their basal activity values N_0^X and N_0^Y supposed to be attained when the animal is 'at home', i.e. $(X, Y) = (0, 0)$. Regulation of these interneurons as well as their mutual interactions could then be realized by suitably defined dendritic synapses of a neural net akin to the scheme presented in Fig. II.4. Again, the obvious simplicity of this 'linear' control network may favor the egocentric cartesian path integration model as candidate for a most elementary neural realization in the arthropod, compared to more complicated models. Though mathematical simplicity is not an ad–hoc argument to explain the evolution of biological control systems, it is tempting to let develop by evolutionary algorithms, neural networks for the task of orientation and analyze their mathematical structure post–hoc, as it has been done for robot motion control (e.g. Pasemann et al. 2001).

Though this work is focused on path integration in desert arthropods, the extensive work on neural 'head cell' and 'place cell' dynamics in mammals shall be mentioned, with the remarkable property that a change in angular information, represented by head cells, can induce a corresponding rotation of the two–dimensional activity pattern in the imaginary chart represented by the array of place cells (Samsonovich and McNaughton 1997; Mittelstaedt 2000). With regard to *desert ants*, Wehner (2003) postulates the existence of a certain number of 'compass neurons', each with an accurately defined compass direction resulting in a maximum firing rate of the respective neuron, whenever the arthropod is heading into that direction.

The ability to relocate successful feeding sites has been described before (I.1.3). It is therefore a natural question to ask, whether a similar simple rule as that of keeping $Y = 0$ may help to find a previously known feeding site. Consider all trajectories in geocentric coordinates that keep the egocentric $Y \equiv 0$ constant: they are the radii around the nest position. On the way home they all *converge*, and if by random fluctuations the animal switches over to a trajectory in its neighborhood it nevertheless is guided towards the nest by the beacon condition $Y = 0$. But for outbound routes they *diverge*, and random errors are not corrected on their own. It would even be better to follow a *fixed compass direction*, because trajectories of the same direction are parallel to each other, and randomly accumulated errors will not be enhanced during the course. In the light of my model it seems natural to suggest that the relative position of a feeding site is internally stored as another global vector $G_f = (X_f, Y_f)$ which is updated simultaneously with (X, Y). Depending on whether the animal steers towards the feeder or home, either $Y_f = 0$ with $X_f > 0$ is the beacon condition, or $Y = 0$ with $X > 0$. No experiments with obstacles on the way to a trained feeder have been performed corresponding to those described in Wehner (2003) (see fig. 2B therein) and Schmidt et al. (1992) for homing paths with obstacles. If the animals are able to compensate forced deviations on the path to the feeder in the same manner as on paths leading home, this would indicate a similar internal processing for both positions.

5 Model application to natural foraging and return runs of desert ants

Since several of my experiments investigated the natural outbound and inbound runs of *C. fortis* (III.2.3.1, 2.3.2, 2.3.3), the opportunity was given to apply the path integration model algorithms and error models discussed in II.2 and 3 to natural outbound runs and their return runs. The results are presented on the CD which is enclosed (appendix 5). For the model application only foraging excursions observed and recorded during experiment 1 (III.2.3.1) were used. In this experiment, the trajectories of desert ants were recorded during their outbound runs until the ants had reached a radial – short-cut – distance of 10 m from the nest. The homebound runs were also recorded (for more details on experimental paradigm and recording, see III.2.3.1). Due to the recording and analyzing procedure, the trajectories of the ants were available as geocentric cartesian coordinates. The distance between two following pairs of coordinates was about 0.05 m. These coordinates were then used to create the egocentric X and Y-coordinates of the path integration model by implementing them into the two differential equations (II.9), (II.10). The egocentric polar coordinates r and δ (see Fig. II.2) get transformed into cartesian coordinates via the two formulas $X = r\cos(\delta)$ and $Y = r\sin(\delta)$.

Fig. II.10 and applications 2 and 3 on the CD (appendix 5.2) show the natural outbound and corresponding inbound runs (terminated at the point where they start their systematic search behavior) of two ants in both geocentric (x and y) and egocentric coordinates (X and Y) upon which my model is based. Let us consider the ant is heading away from the nest on a straight path. Then, $X = -r$, since δ amounts to exactly 180°, whereas $Y = 0$, since $\sin(180°) = 0$. Accordingly to these considerations, an ant heading directly towards the nest would store values r for X and, again, 0 for Y.

With regard to Fig. II.10, it is striking that during the natural inbound run the X-value decreases continuously (red line in Fig. II.10) and the Y-value (blue line in Fig. II.10) gets closer and closer to zero and, finally, fluctuates around zero. As suggested by the model, the ant apparently tries to compensate for deviations from the correct homeward course, that is whenever $Y < 0$ or $Y > 0$, indicating at least the possibility that a 'countersteering turning rate' $\omega_0 = c\,Y$ (see also Fig. II.4) — a mechanism that has also been mentioned by Mittelstaedt (2000) — keeps the ant on course back to the nest. Thus, this implementation displays the result if a desert ant would perform exact path integration as described by the model. Indeed, it can also be detected easily that the ant does not reach the value 0 for X but engages in systematic search behavior before the home run — according to the model — is finished. As already mentioned, it will probably take a lot of time until we will definitely know how the ant or any other desert arthropod calculates its home or global vector and what kind of different errors come into play during the path integration process. So far, it cannot be decided which of the presented models, including the errors, comes closest to the actual path integrator.

Since the existence of systematic errors postulated by Müller and Wehner
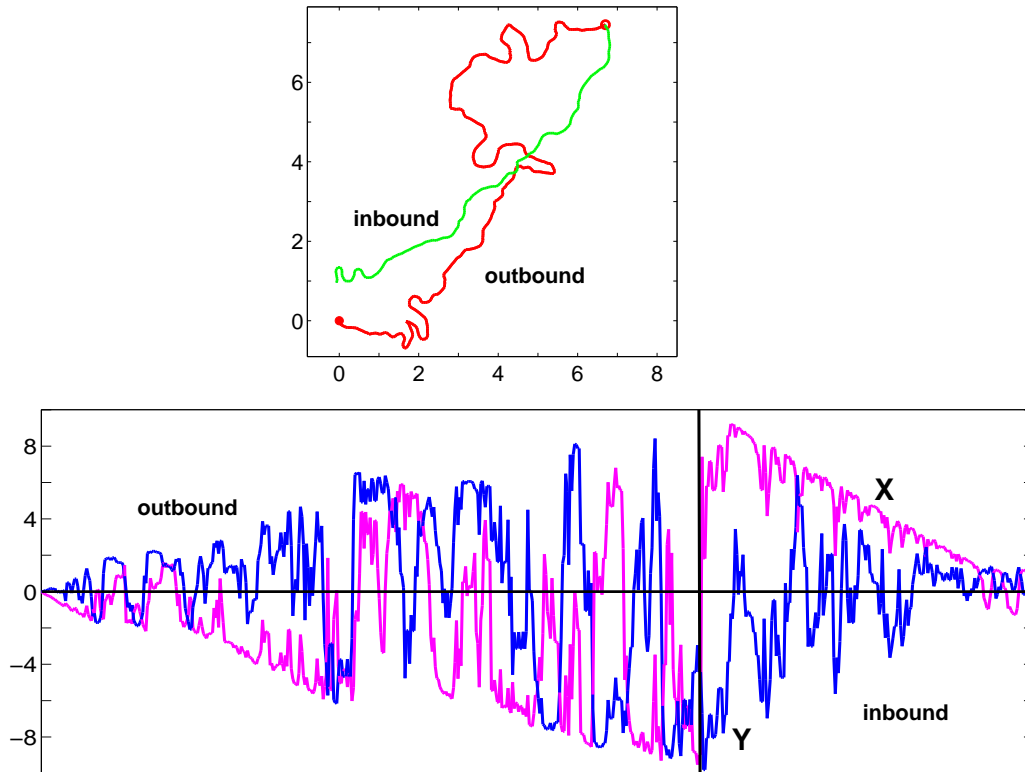
Figure II.10: Natural outbound and inbound run of a desert ant *Cataglyhphis fortis.* Top: Plot of the outbound (red) and inbound (green) run in *geocentric* cartesian (x, y) coordinates. Filled circle: nest position $(0/0)$; open circle: location at which the ant starts its home run. Bottom: Corresponding plots of *egocentric* cartesian coordinates X (magenta) and Y (blue) (see II.2) over time.

(1988) and Sommer and Wehner (2004) were proven during experiments, each model that demands to reproduce the natural path integration process must also be able to reproduce these errors. For my egocentric model, I have done this in II.3. For applications 4 to 7 on the CD (appendix 5.3 and 5.4) the error postulated by Müller and Wehner (1988), MW-error, and the Leaky Integrator (Sommer and Wehner 2004), LI, were implemented in the calculations during the outbound runs of the very same two ants (appl 4 & 5: *MW*; appl 6 & 7: *LI*). With regard to the MW-error, the same formulas by which X and Y were calculated were adapted by using changed values for r and δ according to the MW-error (for the exact values, see Müller and Wehner 1988). With respect to the LI, equations (II.19) and (II.20) were used. A mean decay time τ_L of 90 s was chosen in order to simulate the results found by Sommer and Wehner (2004).

The results for applications 4 and 6 are also shown in Figure II.11: The *correct* geocentric coordinates (x, y) are given, but the values of X and Y are adapted as described. In addition, the correct nest position and the nest position according to the respective error is given. As expected, the assumed nest positions now differ from the correct nest position. However, it is still striking that the position according to the *MW*-error or *LI* also differs from the end of the home run of the ants and that, again, not both values of X and Y reach 0. In addition, it is striking that the nest position according to
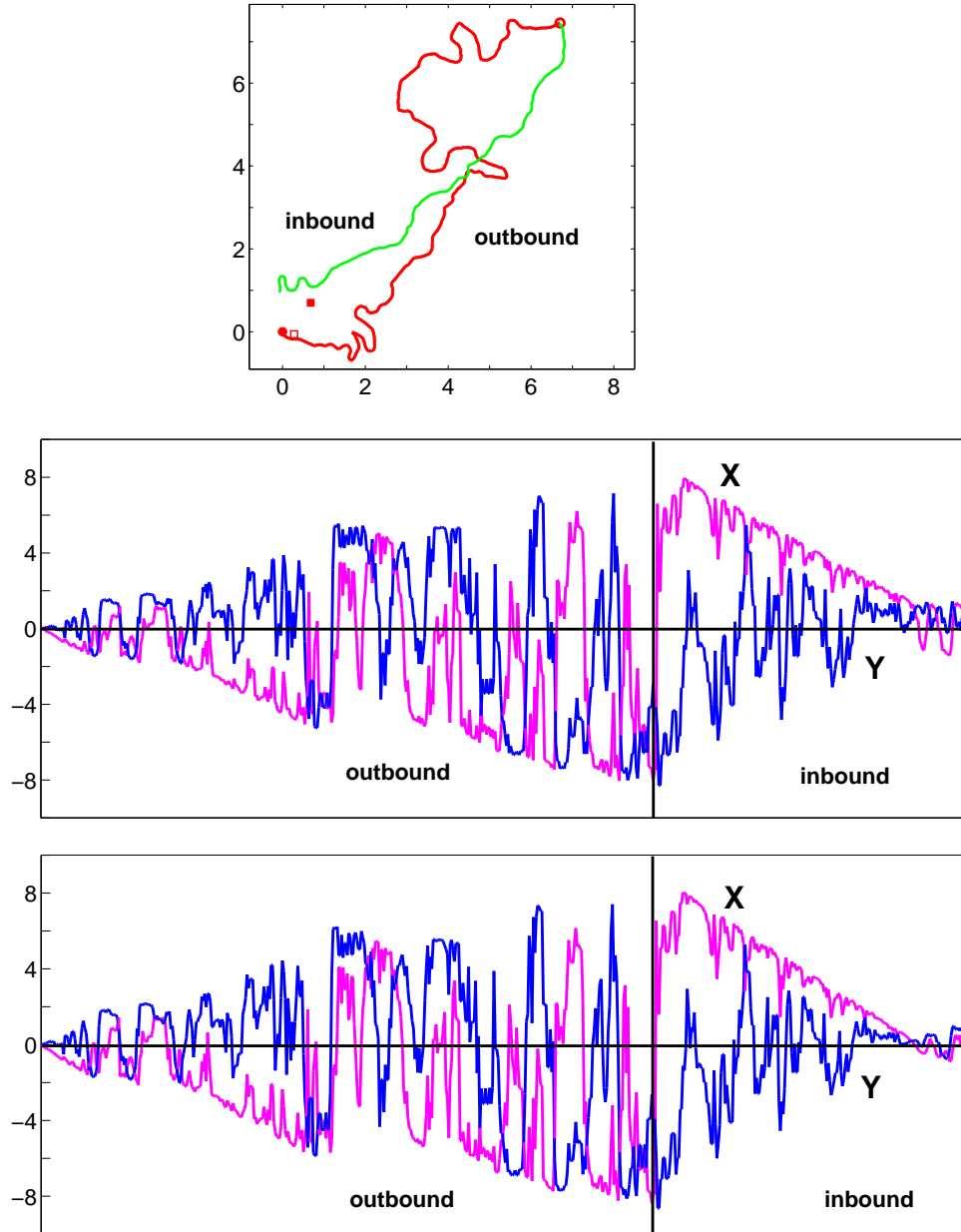
Figure II.11: Natural outbound and inbound run of the same desert ant as shown in Fig. II.10. Top: Plot of the outbound (red) and inbound (green) run in *geocentric* cartesian (x, y) coordinates. Filled circle: nest position; open circle: location at which the ant starts its home run; open square: location at which the ant suspects its nest position if the MW-error was implemented during the outbound run; filled square: location at which the the ant suspects its nest position if the leaky integrator was implemented during the inboun drun. Middle: Corresponding plots of the *egocentric* cartesian coordinates X (magenta) and Y (blue) that were adapted to the MW-error. Bottom: Corresponding plots of the *egocentric* cartesian coordinates X (magenta) and Y (blue) that were adapted to the leaky integrator.

the LI is closer to the end point of the home run than the position calculated while considering the MW-error. The impact of these two systematic errors on natural outbound runs has been investigated in the experimental part (III. 2.3.1).

Besides, again, it should be mentioned that also other models are able to reproduce these systematic errors, for example, the method by Müller and Wehner (1988) using geocentric coordinates. However, such an observer based representation would not allow direct interpretations in terms of possible neurophysiological path integration mechanisms, which can, in principle, better be formulated for egocentric models, see Hartmann and Wehner (1995) and II.4.

Thus, at the moment we cannot decide which path integration model is the most likely to be applied by desert ants or desert arthropods and which errors may influence the path integration process to an extent that becomes visible during the home run or systematic search. It might be helpful to know which shortcomings or error types dominate the path integration system. Then, one could at least get some hints within which model — and also within which neural implementation — this behavior can be reproduced most easily.

However, to approach this question in the proposed way, we would need a better knowledge of potential — critical — factors that may influence the accuracy of the global vector. Though two systematic errors have been shown to exist during specifically designed experiments (see above), many questions remain elusive up to now. Besides, the meaning of these errors under natural conditions has not been investigated yet. Therefore, my experiments aimed at investigating global vectors during inbound and outbound routes, during natural and trained experiments to confirm or falsify, respectively, the influence of the most important of these critical factor and to reveal which of them may play a role under natural circumstances. By including the systematic search behavior it could also be inquired whether the ants might have some knowledge concerning the inaccuracy of their path integrator and, if they do, in which way they might adapt to this knowledge. Finally, it was tested whether desert ants improve the straightness and accuracy of outbound and inbound runs; by answering this question it could be decided whether the path integrator is a simple path integrator per se which is only calculating or whether additional memory effects take part within the whole system of reckoning and orientating.

Part III
Experiments

Experiment 4 has been published in Journal of Experimental Biology (Merkle et al. 2006a).

1 Underlying questions

The path integration system of desert ants consisting of compass, odometer, and path integrator is error prone (II.3). This work aimed at (1) testing the most important factors that could affect the accuracy of this system and, if these postulated effects were confirmed, (2) investigating whether and how the ants cope with these errors. Specific experimental setups made it possible either to manipulate or to compare, respectively, the differences of the following — critical — factors:

- routes (outbound or inbound) that the ants were traveling

- spatial conformation of outbound runs

- training during outbound and inbound run

- length and distance of outbound or inbound runs

- part of the outbound- or inbound routes covered until 'capturing'

- presence of landmarks on outbound or inbound runs, respectively

- number of outbound and inbound runs performed

The results produced by the path integration system, the home vector as stored by the ant, cannot be directly measured. This has to be done via observation and analysis of home run and systematic search behavior, i.e. the results of the path integration process that are visible for an observer. Then, it is possible to test potential effects of different factors. Analyzes of both home run and systematic search center allow conclusions concerning the accuracy of the path integration by taking different values into account (see III.2.4.2 and 2.4.3). Especially by considering both home run *and* systematic search and comparing their visible results one can obtain a better understanding of the path integration process and potential factors that may influence the latter.

The pattern produced by the ants while performing their systematic search behavior can give an idea whether and, if so, in which way the systematic search is influenced by a potential 'knowledge' the ants might have about the accuracy of the path integration mechanism.

The particular intentions of the different experiments are presented when they are described (see III.2.3.1–2.3.8).

2 Materials and Methods

2.1 Study species, study area, and study period

The experiments were performed with desert ants *Cataglyphis fortis* (Forel 1902; Wehner 1983) within a salt-pan near Maharès, southern Tunisia (34.32° N, 10.32° E) from June to September in the years 2004 and 2005 (see Fig. III.1). For all experiments it was crucial that there were no landmarks around the nests of colonies under investigation. This prerequisite was given in the spacious areas free of vegetation. Therefore, the study area seemed to be the best choice for the experimental part of my work. Moreover, there are many active colonies of *C. fortis* to be found. The density of these colonies is rather high, showing distances between nests of different colonies of about 20 – 50 m. Thus, the range of foraging excursions in our study area is limited; in general, it does not exceed distances of 20 – 30 m, though in other areas workers of *C. fortis* have been observed conducting large foraging excursions with distances of 150 m and more (e.g. Wehner and Wehner 1986, 1990).

Figure III.1: The study site at Maharès.

Altogether, ants of 5 different colonies were tested. Usually, the colonies do not change their nest locations over several years (Dillier and Wehner 2004). For more details on the biology of *C. fortis* see Wehner (1983).

2.2 Experimental principles

All experiments differed with regard to their setup and execution. There are many procedures, though, that were the same for all of them. Therefore, these procedures will be described in detail here and, when the respective experiment is presented, I will refer to the corresponding description.

2.2.1 General remarks

The five colonies that took part in the experiments had no visible natural landmarks around the nest and within the further visual range of the foraging

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ants. Thus, the workers of these colonies had to rely exclusively upon their celestial compass information for determing directions and on their odometer for determing distances traveled, i.e. they had no natural landmarks nearby to reduce or avoid possible errors accumulating during path integration. For all experiments, each ant that had already been tested was excluded from further investigations.

2.2.2 Recording of the ants' trajectories

Runs recorded around the nest. During several experiments (experiments 1-3 and experiment 8, see below) the trajectories of ants were recorded in the neighborhood of their nests. Therefore, around those nests a white grid (mesh width: 1m; size variable, see different experiments) was painted on the flat desert ground with the nest entrance as center coordinate. The trajectories were drawn by hand on graph paper containing the same grid with scale 1:100. Time marks were set after each 10 seconds or each minute, respectively.

Runs recorded in a test area. Homing desert ants that are displaced, e.g. by an observer, continue their home runs after being released and, therafter, head exactly towards the same direction as prior to when they were removed (Wehner 1982, 1983; Müller 1989). This property of the path integration system of *Cataglyphis* ants allows an experimentator to capture ants and release them in an area to which they have never been before. Thus, the inbound runs and systematic search patterns of many ants were recorded in a specially designed test area. This test area consisted of a white grid (mesh width 1m, size 20×30 m). This size was sufficient for all experiments. Like the nest area, the test area did not contain any obvious landmarks, either. It was about $100 - 200$ m apart from the nests of all colonies that were tested. A sandy bank separated the areas around the colonies' nests and the test area. Thus, it was very unlikely that the ants had ever been to the test area before. In the test area ants could not find their actual nest. Therefore, it was possible to record their trajectories for deliberately long time periods. The recording procedure on graph paper was exactly the same as for the outbound runs (for more details on recording paradigms see Wehner, 1982).

2.2.3 Transfer to and release in the test field

Ants that had been captured at specific spots (e.g. feeders, during inbound or outbound runs, see below) were transfered to the test area within a small plastic flask. During the transport from the nest to the test area, which never took longer than 2 minutes, the flask was covered, so that the animals were prevented from seeing both the sun and the surrounding landscape. The release points of the ants were chosen in a way that made sure that all trajectories, which seemed possible to be performed by the ants during this specific test procedure took place within the test area and, therefore, could be recorded without any interruptions. Ants that were captured on their homebound runs, i.e. with food in their mandibles, or at the feeding site itself after grabbing some food, usually lost their food during the transfer.

Therefore, they were provided with food again (a biscuit crumb or a dead fly) to ensure that they continued their preceded or intended home run. Very rarely did an ant not accept the offered food; if that was the case, the respective ant was not tested.

2.2.4 Training procedures

It is possible to train the foraging behavior of workers of *C. fortis*. An ant that has encountered a feeder with food (here consisting of little biscuit crumbs) returns to this feeder over and over again (Müller 1989). As soon as an ant knows the position of the feeder, it approaches this feeder on a straight line similar to the home run. In experiments with trained ants they were color-marked at the feeder. This procedure took place at least 24 hours prior to the test to ensure the respective ant having performed a sufficient number of foraging and return trips before due to the test procedure (Åkesson and Wehner 2002).

2.3 Types of experiments

The experiments can be divided into three groups: experiments without manipulations ('natural outbound experiments', 1 and 2), training experiments (experiments 3, 4, 5, 6, and 7), and experiments concerning the ontogeny of the foraging behavior (8). Experiments 1 and 2 intended to get a deeper understanding of the potential effects of different factors and errors on the accuracy of the global vector, i.e. the path integration system. These are the first experiments based on large scale natural expeditions of *C. fortis* ever. Because of the high number of outbound runs that were recorded, these experiments made it possible to investigate the influence of (1) length, distance, or many other characteristic traits of the outbound run and (2) to test whether systematic errors, which have hitherto been demonstrated only during specific setups, do affect the accuracy of the path integrator under natural circumstances and, if this were the case, could explain some of the inaccuracies observed in the path integrator.

Whereas these experiments addressed the general question of the global vector produced by the path integration system, the other experiments turned towards more specific questions: They were performed to investigate some special effects that are believed to influence the path integration system of desert arthropods and, especially, of desert ants *C. fortis*. For these more specific setups, experimental paradigms were created that allowed to approach specific hypotheses exclusively.

In experiment 3 effects of training procedures on both home vector and systematic search pattern (by comparisons with the results of experiment 1) were scrutinized. Experiment 4 focused on testing whether the foraging distance of trained ants affects the same two parameters, whereas by conducting experiment 5 the effect of the portion an ant had already covered during outbound or inbound run was examined. Experiment 6 should reveal whether the route, i.e. the direction the ant is heading towards — inbound or outbound — affects the path integrator or the systematic search pattern (therefore, the results were compared to those of experiment 5). Since after

analyzing experiment 6 it became obvious that the majority of desert ants captured on their outbound run immediately sets out in direction to the nest instead of proceeding with the interrupted foraging run (see results), the interest arose to reveal whether the stability of the outbound run can be changed by adding landmarks during training and test procedure. That is why and how experiment 7 was conducted. The last question to be answered (in experiment 8) was to test whether desert ants are able to improve the accuracy of their out- and inbound runs by repetition, i.e. if their paths between nest and feeder and vice versa get shorter and more direct. Contrary to experiment 3, all outbound and inbound runs from the beginning were recorded and, therefore, even little changes could be discovered. By doing so, it was also possible to reveal if and after how many training runs changes occurred and if the consistence of the underground on the path integrating system showed effects regarding home run and systematic search behavior.

2.3.1 Experiment 1: Tortuosity of natural outbound runs

Setup. During this experiment, natural, i.e. untrained, outbound as well as inbound runs of a colony were recorded. A white grid around the nest with size of $24 \times 24 \text{m}^2$ as well as a circle (radius 10 m) were painted around the nest of this colony (Figs. III.2 and III.3). The area around the nest was kept free of food items as far as possible. In order to avoid representing a landmark myself during the waiting periods for foraging ants I moved all the time and kept a distance of 3 to 5 m to the nest entrance. This setup enabled me to observe most likely untrained desert ants on their natural outbound runs.

Test procedure. The outbound paths of foraging ants were recorded, beginning when the ants left the nest until they had reached a radial distance d of 10 m, i.e. until they crossed the painted circle (ants a and b in Fig. III.2). When an ant reached the circle it was captured, transferred to the test area, and released there with food (see Fig. III.2). Ants that returned to the nest without having reached the 10 m distance (with or without food) were not tested. In the test field, the ants ran off their home vectors, and then, since no nest was to be found, switched to their systematic search program. Altogether, the outbound, inbound and systematic search runs of 130 ants were tracked. The inbound and systematic search runs of the majority of this group was recorded for 10 min ($N = 100$) in the test field. For 30 ants, the recording times were between 5 and 10 min (for sample sizes: see Tab. III.1).

Purpose. Since all ants tested had reached the same radial distance d (10 m) when they were captured on the outbound run, this experiment allowed to compare the tortuosities — which corresponded to the overall path lengths L — and many other characteristics describing the conformation of the different outbound runs and to test for correlations between these and the results of inbound run and systematic search behavior, i.e. whether the spatial conformation of the outbound runs account for differences in the errors produced in the path integrator and, if this was the case, whether *Cataglyphis* ants adjust their systematic search behavior accordingly.

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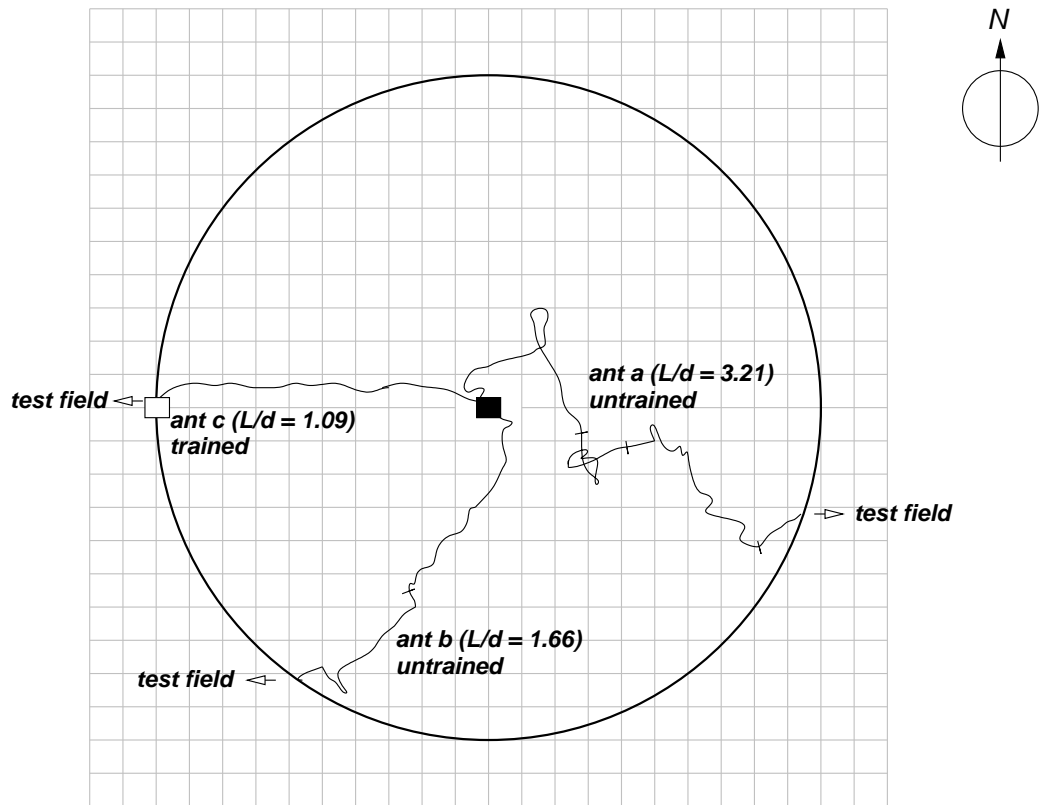
Figure III.2: Setup of experiments 1 and 3. The outbound runs of either untrained or trained ants were recorded. Examples of real outbound runs of untrained ants: ants a and b; example of real outbound run of trained ant: ant c; L/d =length/distance (for explanation: see data analysis III.2.5.1). After having reached a radial distance of 10 m the ants were captured and transfered to the test field. Time marks were set each minute. Filled square: nest; open square: feeder; open arrows: spots where the ants were captured and transfered to the test field. Mesh width of grid was 1 m.
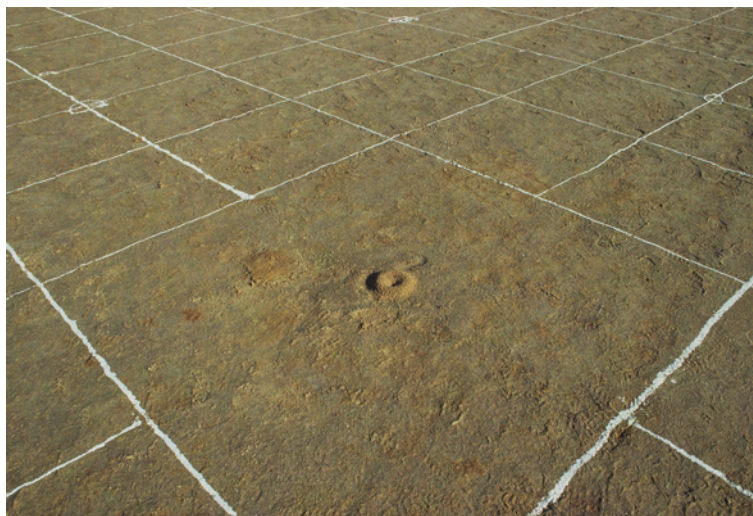
Figure III.3: Grid painted around the nest of a colony.

2.3.2 Experiment 2: Distance of natural outbound runs

Setup. Again, natural outbound runs as well as inbound runs were recorded. However, in contrast to experiment 1, the distances after which the ants were captured, varied. Therefore, the graph paper on which the outbound trajectories were drawn, contained 7 circles of with radius ranging from 6 to 12 meters. The size of the white grid was the same as in experiment 1 ($24{\times}24\text{m}^2$, see Fig. III.4); all other circumstances of this experiment were equivalent to experiment 1.
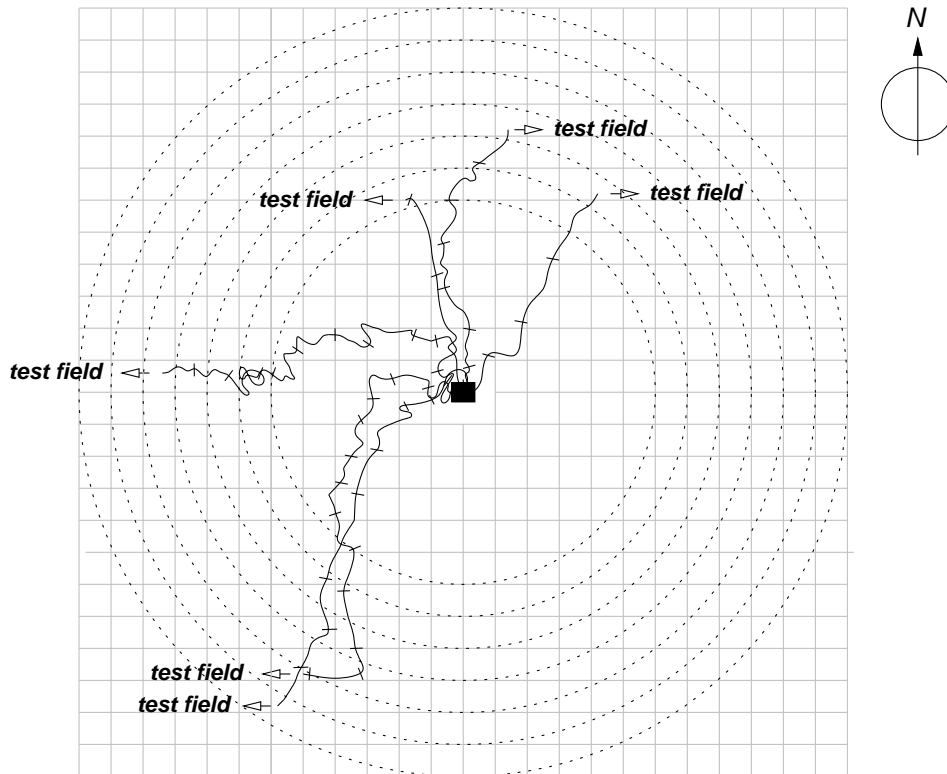
Figure III.4: Experiment 2. The outbound runs of untrained ants were recorded until the ants had reached radial distances of 6 – 7, 7 – 8, 8 – 9, 9 – 10, 10 – 11, 11 – 12 m from the nest (real, i.e. recorded, example for each range is given, time marks every 10 sec). After having covered the respective distance the ants were captured and transferred to the test field. Filled square: nest; open arrows: spots where the ants were captured; dotted circles: circles drawn on the graph paper.

Test procedure. The trajectories of foraging ants were recorded during their outbound runs until the ants had reached a radial distance d between 6 and 7, 7 and 8, 8 and 9, 9 and 10, 10 and 11, and 11 and 12 m ($N = 10$ for each group, i.e. total number $N = 60$, see Fig. III.4, Tab. III.1). After that, the procedure was the same as in experiment 1. All trajectories of these groups during inbound and systematic search program were recorded for 10 min.

Purpose. This experiment made it possible to investigate whether differences with regard to the distances d from the nest reached during natural outbound runs may influence the accuracy of the path integrator, visible by the errors performed through home runs and systematic search behaviors. Moreover, since due to the experimental procedure the lengths of the different outbound runs varied to a greater extent than during experiment 1, potential correlations of the length of natural outbound runs with the accuracy or inaccuracy of the inbound runs and systematic search patterns could be scrutinized. As in experiment 1, if differences were detected, one could test whether the ants adjust their systematic search pattern.

2.3.3 Experiment 3: Training effects

Setup and training. The setup of experiment 1 was used again. However, ants were trained to feeders located either 10 m north, east, south, or west of the nest (i.e. they were on the 10 m circle).

Test procedure. Due to the training for 24 hours, the outbound runs of this group of ants were straighter than those of the untrained ants of experiment 1. However, the test procedure resembled that of experiment 1: outbound runs were recorded and the ants captured at the 10 m circle (in this case the location where the feeder was situated, see Fig. III.2). Then, they were transferred to the test field where their trajectories (total $N = 40$, 10 ants for each compass direction, see Tab. III.1) were recorded for 10 min each in the test field.

Purpose. The results were compared with the results of experiment 1. Thus, the effects of repeated training on home run and systematic search behavior (accuracy and extension) could be investigated.

2.3.4 Experiment 4: Distance between nest and feeder

Training procedure. Desert ants were trained to feeders south of their nest (Fig. III.5a). The distances between nest and feeder were varied systematically (5m, 10m, 20m, Fig. III.5a).

Test procedure. Animals that were trained to a feeder 5 m (in the following called 5-m ants, $N = 51$), 10 m (10-m ants, $N = 53$), or 20 m (20-m ants, $N = 50$, Fig. III.5a, Tab. III.2) south of the nest were captured at the feeder, transferred to the test field and released with food. Recording time in the test field was 5 min for 5-m and 10-m ants and 10 min for 20-m ants in order to record the larger loops and longer home runs of this group.

Purpose. This experiment was intended to reveal whether different lengths of the foraging paths account for differences in the errors produced by the path integrator, and, if this were the case, whether the ants may be able to adjust their systematic search patterns.
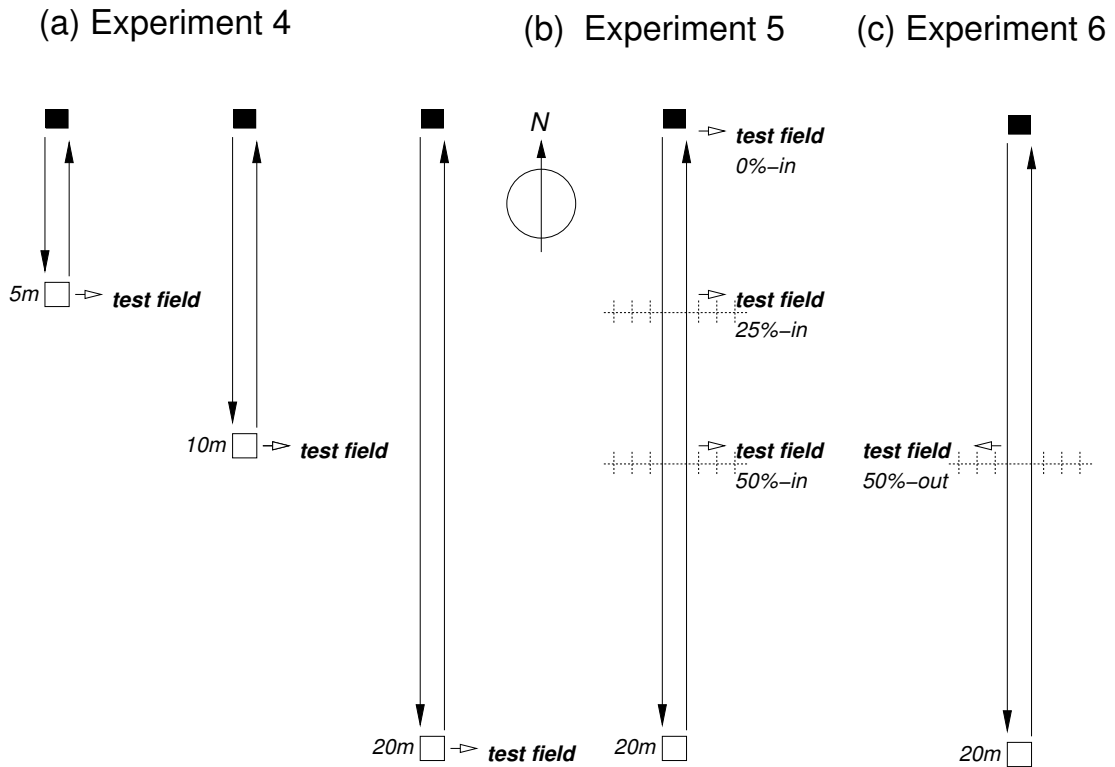
Figure III.5: Experimental paradigm of experiments 4, 5, and 6. (a) Experiment 4: Ants trained to a feeder located either 5 m, 10 m, or 20 m south of the nest entrance were captured at the feeder and transferred to the test field. (b) Experiment 5: Ants trained to a feeder located 20 m south of the nest were captured on their inbound runs after 10 m (50%-in), 15m (25%-in), or shortly before entering the nest (0%-in). (c) Experiment 6: Ants were captured on their outbound runs after 10 m. The transect lines with deviation marks (dotted, for explanation: see text) made it possible to record the deviation from the beeline the ants displayed when captured. Filled squares: nests; open squares: feeders, where the ants were captured in experiment 4; open arrows: locations where the ants were captured and then transfered to the test field.

2.3.5 Experiment 5: Inbound route

Training procedure.   In this experiment, as in experiment 4, all ants were trained to a feeder 20 m south of the nest (Fig. III.5b).

Test procedure.   Contrary to experiment 4, the ants were allowed to take a food crumb at the feeder and head for the nest, before they were captured — with food in their mandibles — at three different locations: either after having covered a distance of 10 m, i.e. they still had to run off 50 % of their 20m-homevector (in the following called 50%-in ants, $N = 50$), after a distance of 15 m, i.e. they still had to run off only 25 % of the homevector (25%-in ants, $N = 50$) or shortly before entering the nest (0%-in ants, $N = 50$, Fig. III.5b, Tab. III.2). Whenever 50%-in and 25%-in ants were captured, they were not on the beeline between feeder and nest, but deviated to the east or west, respectively. This distance was measured with the help of a transect line painted on the ground of the training area perpendicular to the beeline at distances of 10 m and 5 m from the nest (Fig. III.5b). It was

recorded in order to calculate the actual distance and direction the ants had to take into account for the remaining part of their home run during data analysis (see III.2.5.4). In the test area, the ants' trajectories were recorded for 5 min each. The 50%-in ants ran off their homevectors and switched to the systematic search program afterwards. The 0%-in ants, as expected, immediately started their systematic search program. 15 of the 25%-in ants (30%) also started with the systematic search, thereby skipping the running off of the homevector (see Tab. III.2). The criterion for deciding which ants did start their systematic search program immediately was that these ants did not reel off at least 50%, i.e. 2.5 m, of their home run before the first change of direction (see III.2.4.1 for definition of end point of home run) occurred.

Purpose. Since for all groups the distance between nest and feeder was the same during training and test, this experimental paradigm could reveal potential effects of the portion of the inbound run that still had to be traveled on the accuracy of the path integrator. Besides, the groups could be compared to the groups tested in experiment 4. By doing so, for instance, 50%-in ants could be compared against 10-m ants and 25%-in ants to 5-m ants in order to see if the nest-to-feeder distance or the distance still to cover on the inbound run or both influence the path integration system. Also, all groups could be compared to the 20-m ants of experiment 4, since they all had been trained to that distance. Thus, it should be tested if the ants develop some kind of route- or even nest-specific cues (0%-in ants) that guide them home to the nest.

As for all experiments, potential differences were tested in view of the errors produced by the path integrator, visible via home run and systematic search pattern. Again, as for all experiments, the question whether *Cataglyphis* adjust its systematic search pattern was scrutinized.

2.3.6 Experiment 6: Outbound route

Training procedure. Again, all ants were trained to a feeder 20 m south of the nest (Fig. III.5c).

Test procedure. During this test, the ants were captured during their outbound run after 10 m (50%-out ants, $N = 50$, see Fig. III.5c). Again, as in experiment 5, distance and direction deviating from the beeline were recorded by means of transect lines. Since the ants had no food in their mandibles, they were released in the test area without food. Then, their trajectories were recorded for 5 min each (sample sizes: Tab. III.2)

Purpose. Contrary to homing ants that continue their inbound runs when replaced (as long as they keep their food or get food again, see 2.2.2) it was not known if ants would continue their preceding run when captured during the outbound run. Thus, the first aim of this experiment was to answer this question by comparing the numbers of ants that returned to the nest, i.e. interrupted their outbound runs, and those that continued the foraging run. Besides, both groups were compared with the 50%-in ants (experiment 5,

same location of capture but different route when captured) and the 20-m ants (same training distance) in view of home run and systematic search.

2.3.7 Experiment 7: Landmarks on outbound route

Training procedure. This experiment represented a supplement to experiment 6. The training procedure was mostly the same, but in contrast to experiment 6, the outbound and inbound route of the ants was flanked by six round, black cylinders (diameter 20 cm, height 30 cm). Their arrangement is shown in Fig. III.6a: three pairs were located at distances of 12 m, 14 m, and 16 m from the nest. They were placed with a lateral distance of 1 m from the beeline between nest and feeder.
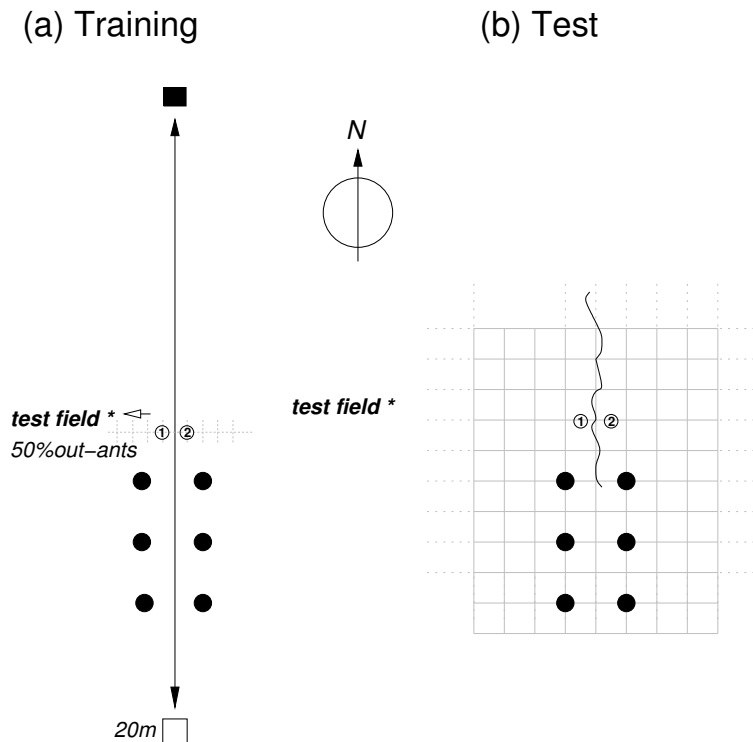
Figure III.6: Experiment 7. (a) Training procedure. Ants were trained to a feeder 20 m south of their nest and captured on their outbound runs after 10 m. Filled square: nest; open square: feeder; filled circles: black cylinders (diameter 20 cm, height 30 cm); open arrow: location where the ants were captured and transferred to the test area. Dotted line: auxiliary line for measuring the deviation from the beeline. 1, 2: examples of places were ants were captured. (b) Test situation. The center of the test area and the arrangement of the landmarks (filled circles) in relation to the two release points (1,2 for the respective ant) are shown. The correct nest position would be 10 m north, the correct position of the feeder 10 m south, i.e. ants heading for the feeder had the same landmark corridor as during training.

Test procedure. Again, the ants were captured during their outbound run after 10 m (50%-out-LM ants, $N = 50$, see Fig. III.6a and Tab. III.3), transferred to the test field and released there without providing food. As in experiment 6, the distance between point of capture and the beeline between

nest and feeder was recorded. Within the test area, 3 pairs of landmarks (same size as during training) were placed 2 m, 4 m, and 6 m south of the test field center (Fig. III.6b). The ants were released in the test field at spots that exactly resembled those at which they had been captured before the transport, i.e. the ants had exactly the same view at the beginning of the test that they had had when they were captured: three pairs of landmarks heading to the feeder and flat area without any obvious landmarks leading to the nest (Fig. III.6b). Recording time in the test field again was 5 min.

Purpose.   This experiment should reveal whether the percentage of ants captured after 50% of the outbound run changes if landmarks are presented. Furthermore, it aimed at investigating if landmarks can influence the accuracy of the path integration system. Therefore, the data obtained by the conduction of experiment 5 could be used as a reference in order to compare errors of the path integration system via both home run and systematic search pattern and the extension of the systematic search behavior.

2.3.8   Experiment 8: Ontogeny of foraging behavior

Setup.   A feeder was placed 15 m away from the nest of this colony. The exact position of the feeder was varied in a way that the ants had to approach the feeder all the time against the blowing wind and the nest with the wind blowing from behind. Thus, the position of the feeder varied, but was always in east or east-south-east direction. A white grid was painted on the ground, covering the area between nest and feeder around the possible outbound and inbound paths of the ants (Fig. III.7).

Test procedure.   As soon as the first ant had encountered the feeder, it was marked with a two-digit color code. Then, the inbound run (inbound 1) as well as the next four outbound (outbound 2 - 5) and inbound runs (inbound 2-5) were recorded. After recording outbound run 6 the ant was captured at the feeder and transferred to the test area. There, it was released with food. Then, the home run was recorded. As soon as the ant engaged in systematic search behavior, it was captured and put back to the nest entrance, where it entered the nest immediately. The following outbound and inbound runs (no.s 7) as well as outbound run no 8 were recorded in the nest area until the ant was captured again and performed its home run 8 in the test field. This procedure was repeated until an ant had performed a total of 20 outbound and inbound runs: out of the outbound runs 19 (no.s 2 - 20) were recorded (all in the nest area). All 20 inbound runs could be recorded, 12 of them in the nest area (nos. 1,2,3,4,5,7,9,11,13,15,17,19) and 8 in the test area (no.s 6,8,10,12,14,16,18,20). Whenever an ant was released in the test area it was released at a different spot than during the release before to avoid the possibility that this ant had ever been in this specific area before. The feeder was closed all the time and only opened when the test procedure of one ant was finished until the next ant encountered the feeder. Also, during the test of one specific ant, the feeder was closed and only opened when this ant was approaching the feeder and shortly before it was entering it. By doing so, it was ensured that none of the other ants could

encounter the feeder and that each ant due to be tested had never seen the feeder before. Of course, a major change regarding the wind direction within the test procedure of one specific ant would have caused a termination of this test trial. But only short periods were necessary to record all 20 outbound and inbound runs of one specific ant. Therefore, it was sufficient to change the position of the feeder only once or twice per day (mainly in the early afternoon when the direction of the blowing wind changed from east to east - south - east). Altogether, 15 ants were tested in this experiment, resulting in a total record of 285 outbound and 300 inbound runs.

Purpose. This experiment should reveal whether desert ants are able to increase the accuracy and straightness of their outbound respective inbound runs during repeated training and if the transfer to the test area has any influence on the accuracy of the inbound or outbound runs.
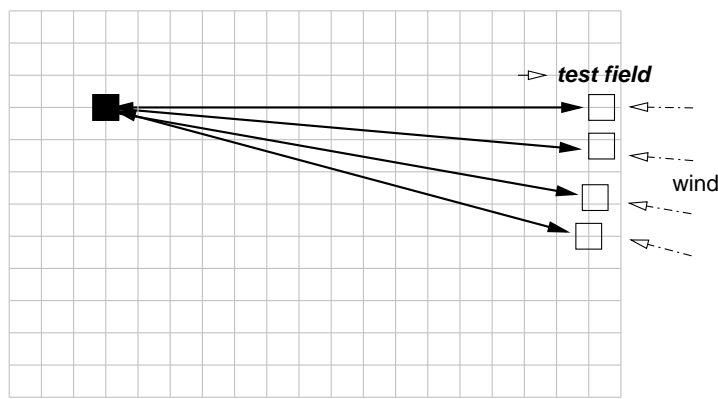
Figure III.7: Experiment 8. A feeder was placed 15 m away from the nest. If an ant had encountered the feeder, its outbound and inbound runs were recorded. For 8 out of 20 inbound runs the respective ant was captured at the feeder and released in the test field with food, where the inbound run was recorded, before the ant was brought back to the nest (for more details on the procedure: see text). Filled square: nest; open squares: different positions were the feeders were placed.

2.4   Principles of data analysis

2.4.1   General

Digitization process. All recorded trajectories were digitized using a graphics tablet and GEDIT Graphics Editor and Run Analyzer (Antonsen 1985). By means of this procedure, the overall path was discretized by creating cartesian coordinates $x(s), y(s)$ with $ds = s_{i+1} - s_i$, where s denotes the arc length along the path that amounted to roughly 0.05 m and displayed only very small variations. These cartesian coordinates $x(s), y(s)$ could then be imported, using Excel for Windows.

In general, foraging and homing speeds of desert ants are rather constant (personal observation, see also Müller 1989). On the other hand, speeds of home runs are influenced by size and weight of the food item an ant is carrying in its mandibles (personal observation). Due to the hand-based recording,

the changes of the speed could only be recorded via the time marks that were set. Since, in contrast, the exact path coordinates were known, the data analysis is based upon them.

All outbound runs, inbound runs, and systematic search patterns were digitized separately. Since no visible interruptions between home run and systematic search behavior occurred, these had to be recorded together and separated during the digitizing process. The switch from playing out the home vector to systematic search was defined as the point at which the overall direction of the path changed by at least 30°. An additional condition was that the animal did not revert to the direction it was heading towards before for the next 3 m (again, 30° was the reference value). In most cases, one could discover this point unambiguously as sharp turn performed by the animal (see open in Figs. III.8, III.9). This 'turning point' immediately shows up in the model developed during the theoretical part of this work (see section II.2). Then, the Y-value of the animal's own egocentric reference system that was close to 0 during the home run suddenly increased in its absolute value for a longer period.
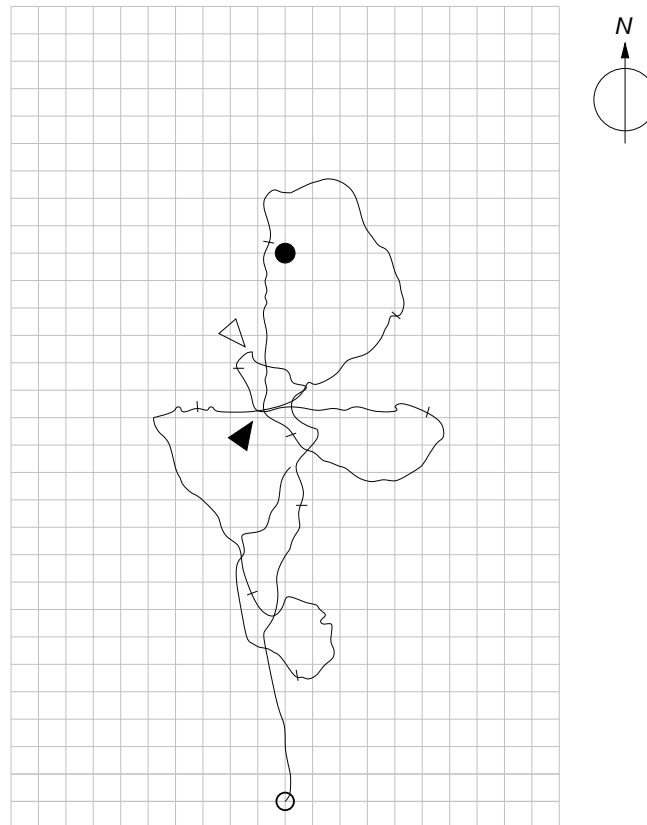
Figure III.8: Example of a trajectory of a 20-m ant (experiment 3) that was captured at the feeder, transferred to the test field, released there with a little biscuit crumb, and then recorded for 10 minutes. Time marks are set at intervals of 1 min each. Open circle: point of release; filled circle: correct position of the nest; open triangle: end point of home run; filled triangle: center of systematic search (for definition of end of home vector and center of systematic search see data analysis).
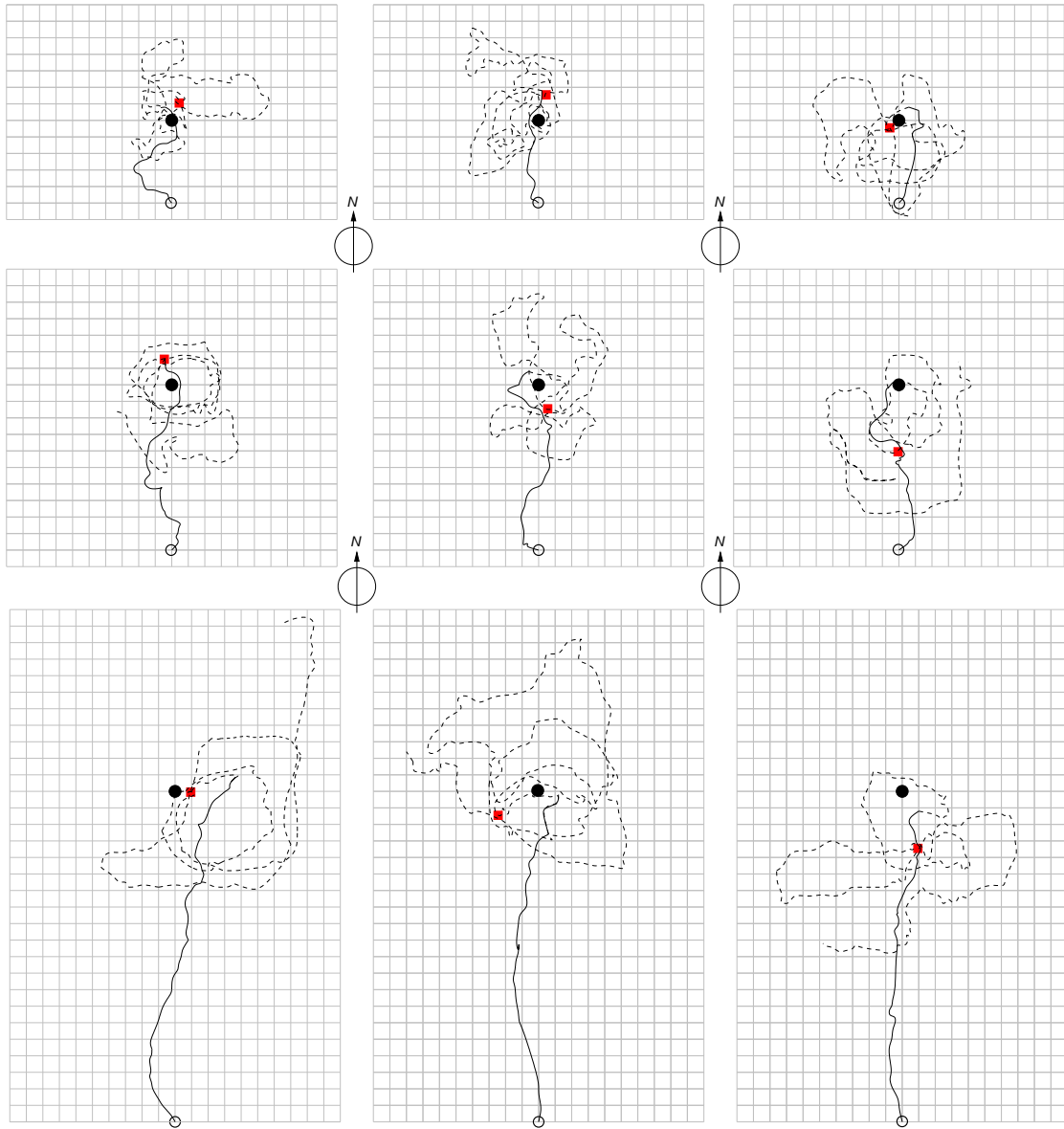
Figure III.9: Examples of home runs and systematic search patterns of 5-m ants (top row), 10-m ants (middle row), and 20-m ants (bottom row). Shown are home run (solid line), systematic search (dashed line) and the center of the systematic search (red square). Note the different locations of end of home run (end of solid line) and systematic search center. Open circle: point of release; filled circle: correct position of the nest.

Analysis of runs. The powerful programming tool MATLAB language for technical computing (version 4.0.7, Beucher 2005) was used for further analysis and numerical processing of the data in order to automatize most analyses of the recorded trajectories.

Statistic analysis were performed by SPSS 12.0 statistic package for Windows (Brosius 2004), MATLAB statistics tool box, and Oriana 2.02c for circular statistics (Kovach 2004).

For experiments 1 to 7, density plots (two-dimensional and three-dimensional diagrams) were created, which showed the spatial distribution (total path lengths in squares of $0.5m \times 0.5m^2$) of the different test groups during home run, systematic search, or both together, respectively. These plots are helpful to get a first overview of the different groups.

Experiments 1 to 7 relied upon the same principle: potential differences were to be detected via the outcome of both home run (or run to the feeder, see experiments 6 resp. 7) and systematic search behavior around the nest or feeder. Thus, the first step within the data analysis was the development of suitable values describing and analyzing these two behaviors. These values were the same for all different experiments and will be presented at the beginning of this paragraph.

The factors that were manipulated or compared, respectively, as well as the procedures for analysis including statistical tests will be given for each experiment in detail.

Experiment 8 differed most from all the other experiments and, therefore, will be described in detail at the end of this section.

2.4.2 Analysis of the home run

Euclidean distance between end point of home run and correct nest position (ED). The Euclidean distance between the end point of the home run as defined above and the correct position of the nest P_c was calculated (ED in Fig. III.10). Surely, this value is the most relevant for the ant's homing success.

Directional deviation ($DIR8$ and $DIRM$). The overall direction of the home run was determined in two different ways: the first intersection of the homing path with a circle that had its center at the starting point of the run determined the direction of the ant's home vector (Fig. III.10). This procedure was used for all experiments with a circle of a diameter that resembled 80% of the theoretically correct homing distance, e.g. 8 m for the ants of experiment 1, that were captured at a distance of 10 m from the nest. The direction obtained by means of the ants' crossing points with the 80% circle can represent the general direction an ant is heading towards after 'leveling off' during the first few metres of the home run (the difference to the correct homing direction is shown as $DIR8$ in Fig. III.10). No angle at the circle with a diameter of 80% distance could be determined for ants that switched over to the systematic search program before reaching this distance, i.e. ants that underestimated the distance between point of release and nest heavily. These ants were excluded from this part of the analysis. The remaining sample sizes in all experiments are given in Tables III.1, III.2, and III.3.
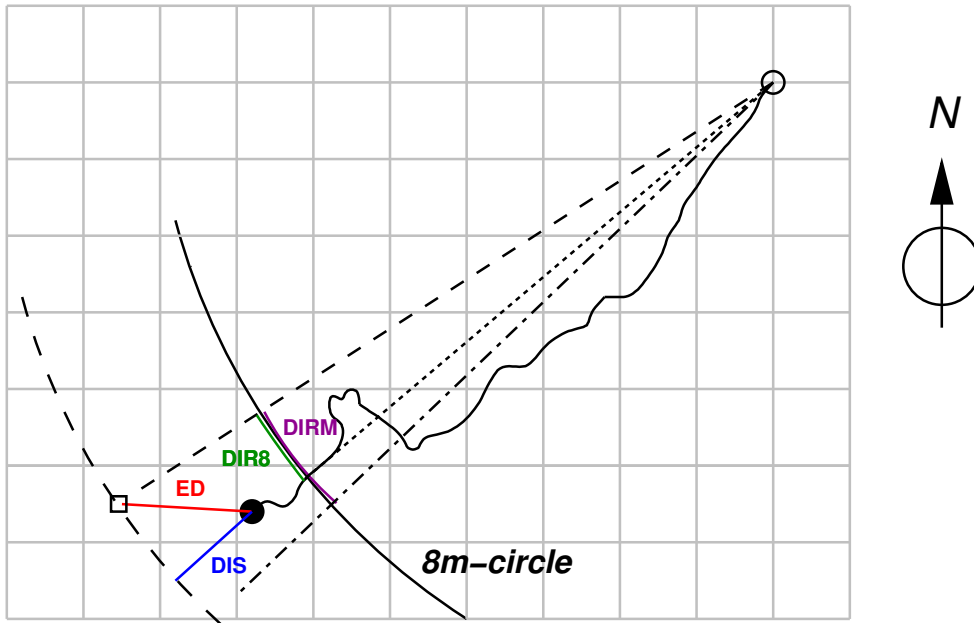
Figure III.10: Example of a home run of an ant that was captured after 10 m of its natural outbound run (experiment 1), transferred to the test field and released there with food. Open circle: point of release; filled circle: end of the home run; open square: correct position of the nest P_c; dashed line: correct homing direction; dotted line: direction determined via 8m circle; dashed-dotted line: direction of the home vector according to the minimization method; ED: Euclidean distance between end of home run and position of the nest; $DIR8$: deviation between correct homing direction and direction of the home vector according to 80%circle; $DIRM$: deviation between correct homing direction and homing direction according to minimization method; DIS: difference between correct distance and distance covered by the ant during the home run. For more details see text.

In addition, circles with different diameters — e.g. 1 m ($DIR1$)— were used for some of the analyses (see different descriptions of the experiments). The circle method, described in detail by Batschelet (1981), has been the most used method to determine desert ants' directions (e.g. Wehner and Menzel 1990; Wehner et al. 2002; Bisch-Knaden and Wehner 2003b).

Besides, a new method for defining the overall direction of the home runs was developed: this was done with the aim to fit a straight line that — similar to a linear regression — is as close as possible to the path, but is fixed at the point of origin (the starting point of the home run). Let us assume, the path is directed towards north, i.e. the y–values in a geocentric coordinate system increase, whereas the x–values fluctuate around a straight line $x = b\,y$, with a value b substantially smaller than unity. In this case b is found by means of the standard regression procedure of a linear model.

Thereby, the integrals can be well approximated by the sums over the path segments of almost constant length supplied by GEDIT (see III.2.4.1). Clearly, the slope b is related to the angular deviation θ from the north by $b = \tan\theta$, (see $DIRM$ in Fig. III.10).

This method for determing directions (the *minimization method*) is more

general than the method of locating intersection points with certain circles around the origin. As its main advantage, it is applicable for all paths, irrespective of their lengths. Statistical tests were performed for some of the samples when the method using the 80%-circle could also be used. These tests yielded no remarkable differences between both methods (see III.3.1.1).

The directions obtained by these two methods were compared with the theoretically correct homing directions and the deviations were taken into account for successive statistical analysis. Depending on the experiment, these values were used either as absolute numbers ($|DIR8|, |DIRM|$), or considering the sign ($DIR8, DIRM$) for further analysis.

Distance deviation (DIS). The distance an ant had covered was defined as the beeline between release point and end of home run (Fig. III.10). This value was compared to the theoretically correct distance and the deviations were used for the analysis (e.g. in experiment 1: DIS = distance - 10 m, see Fig. III.10).

Tortuosity (TOR). The tortuosity during the inbound run was calculated as the length of the home run divided by the distance covered during the home run, i.e. Length/distance. More details about this parameter are given below (see Experiment 1, III.2.5.1).

2.4.3 Analysis of the systematic search behavior

Center of systematic search. As described above, by means of GEDIT and MATLAB, density plots were created. Thereby, an ant's search area was divided into squares (side length 0.5m) and for each square the path length of the ant within this square divided by the total path length of the systematic search of this ant was calculated (in %, see Fig. III.11, III.12).

The center of the systematic search behavior was defined as the square that contained the 'highest density', i.e. the square in which the ant spent the highest amount of 'time' — though measured by means of arc length — during its systematic search. Since the ants return to the center of their search over and over again (Wehner and Srinivasan 1981), this seemed to be a suitable method for defining the search center. If the density in two squares was the same, the respective ant was excluded from the systematic search analysis (see Tabs. III.1, III.2, and III.3 for the different experiments).

With regard to experiment 1, only ants that had been recorded for 10 minutes in the test field were taken into consideration for the analysis of the systematic search behavior. Out of this sample, runs with two or more squares with the same density also were excluded from further analysis (for exact numbers: see Tab. III.1).

The 0%-in ants of experiment 4 had reached their nest entrance before being tested. Since they were captured at the nest entrance, they started their systematic search around the point of release, knowing that the nest was supposed to be at this spot. Therefore, no center of the systematic search pattern was determined for this group. For these systematic search runs, only the extension of the systematic search pattern was calculated (see below and Table III.2).
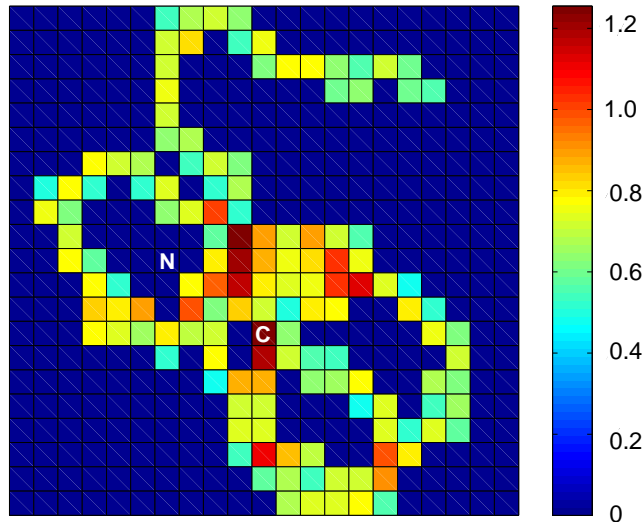
Figure III.11: Density plot of the systematic search behavior of the ant of Fig III.10. For each square (size $0.5 \times 0.5\text{m}^2$) the path length divided by the total path length of this particular systematic search run was calculated. Density (%) is represented by the color of the respective squares (see colorbar on the right); N: correct nest position P_c; C:center of systematic search. The square with the highest density can be detected easily and represents the center of the systematic search as defined here.
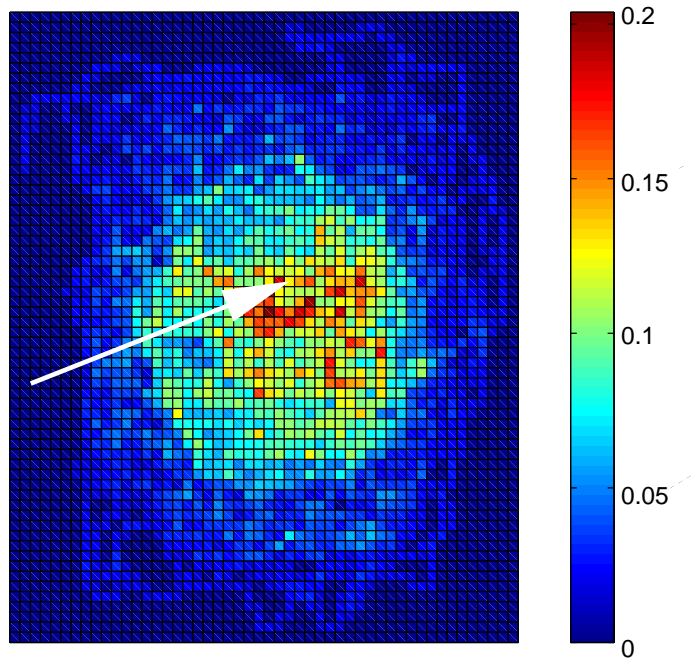
Figure III.12: Density plot of the systematic search behavior of all 20-m ants tested in experiment 4 ($N = 50$). For each square (size $0.5 \times 0.5\text{m}^2$) the path length divided by the total path lengths of all systematic search runs was calculated. Density (%) is represented by the color of the respective squares (see colorbar on the right); correct nest position P_c is shown by white arrow.
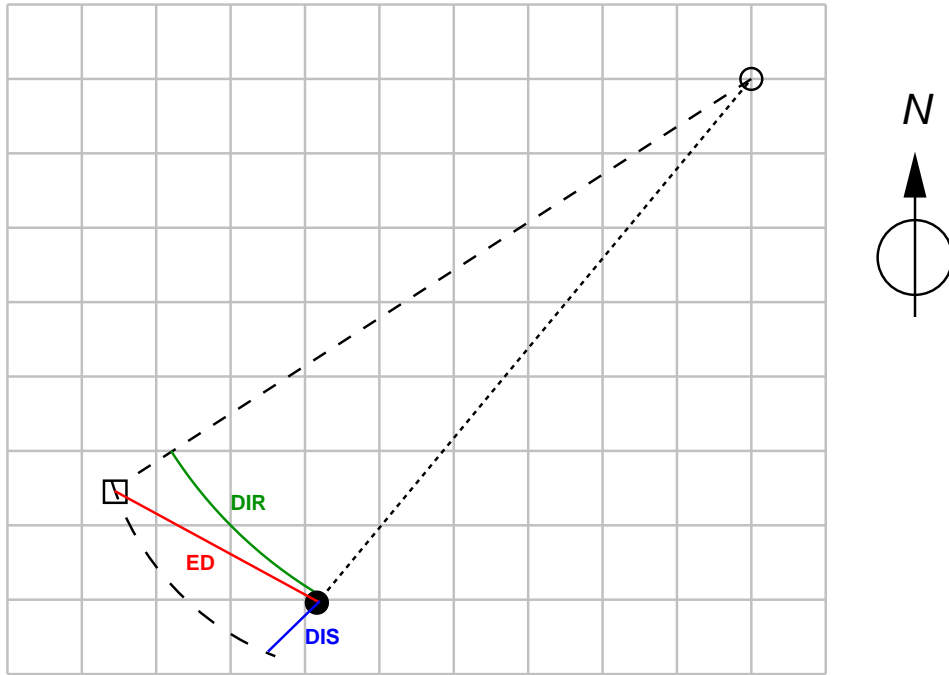
Figure III.13: Analysis of the systematic search behavior of the ant shown in Fig III.10. Open circle: point of release; filled circle: center of systematic search; open square: correct nest position P_c; dashed line: correct homing direction; dotted line: direction of the home vector that leads to the square with the highest density, i.e. the systematic search center; ED: Euclidean distance between systematic search center and correct position of the nest; DIR: deviation between correct homing direction and direction according to the systematic search center; DIS: distance covered according to systematic search center.

By means of the center of the systematic search behavior (Fig. III.11) I determined the following values:

Euclidean distance between systematic search center and correct nest position (ED). This value was obtained by measuring the Euclidean distance between the center of the systematic search and the correct position of the nest P_c (ED in Fig. III.13) .

Directional deviation (DIR). The center of the systematic search program was connected with the ants' point of release to determine the direction of the systematic search center. As for the directions determined for the home run, this direction was compared with the theoretically correct direction (DIR in Fig. III.13). Again, depending on the experiment either the absolute number ($|DIR|$) or the number considering the sign (DIR) was applied for analysis.

Distance deviation (DIS). The same connection line was used to calculate the distance and tested for deviations from the correct homing distance (DIS in Fig. III.13).

Extension of the systematic search behavior (EXT). In addition to these values that describe the accuracy of the global vector via the assumed nest position the systematic search patterns were compared among different groups or ants. In order to do this, the systematic search runs were cut at a path length (not the radial distance!) of 100 m (experiments 1, 2, 3, $EXT100$) or 40 m (experiments 4, 5, 6, 7 due to shorter recording times, $EXT40$), respectively. After an ant's overall path had reached this length the ant had completed at least two search loops. Animals with systematic search runs shorter than the respective criterion were excluded from this analysis (again, the exact numbers are given in Tables III.1, III.2, and III.3). The area obtained as product of the path extents in x- and y-direction characterizes the spatial extension of the systematic search.

One might argue that using the path path extents in x- and y-direction could falsify the results, since there might be large areas within the search loops that are not covered by the ants' systematic search program. Therefore, the systematic search patterns of 25 randomly chosen ants were also analyzed by counting and summing up the squares covered during the systematic search. The comparison with the extension as obtained via the determination of the path extents in x- and y-direction yielded no significant differences; thus, the method applied is appropriate for characterizing the extension of the ants' systematic search pattern.

	N total	N home run 80% circle crossed	N sys search with unique maximum of density	N sys search extended over at least 100 m
Experiment 1	130	102	98	73
Experiment 2	60	44	58	57
Experiment 3	40	39	38	37

Table III.1: Sample sizes for experiments 1-3. Col 1: Total number of runs. Col 2: Number of home runs that crossed the 80%-circle. Col 3: Number of search runs which had a unique maximum of search density (see Fig. III.11). Col 4: Number of search runs which extended over 100 m or more to allow for determination of their extension.

	N total	N home run performed	N home run 80% circle crossed	N sys search with unique maximum of density	N sys search extended over at least 40 m
5-m ants	51	51	50	49	45
10-m ants	53	53	50	41	35
20-m ants	50	50	43	49	50
50%-in ants	50	50	31	48	48
25%-in ants	50	35	30	49	49
0%-in ants	50	0	0	0	50

Table III.2: Sample sizes for experiments 4 and 5. Additional or different columns as compared to Table 1: Col 2: Number of ants that performed a home run and did not immediately start the systematic search, as some of the 25%-in and all 0%-in ants. Col 5: Systematic search behavior was cut at a path length of 40 m for determination of extension. Cols 1, 3, 4: Conventions as in Table 1. With regard to the 0%-in ants, only the extension of the systematic search center was determined.

	N total	N direction determined	N home run or run to feeder 80% circle crossed	N sys search with unique maximum of density	N sys search extended over at least 40 m
50%-out ants	50	41	25	38	39
50%-out-LM ants	38	34	32	33	34

Table III.3: Sample sizes for experiments 6 and 7. Different columns as compared to Tables 1 and 2: Col 2: Number of ants for which a direction (home or to feeder) could be determined (see III.2.5.4). Col 3: direction at the crossing of the 80% circle was also tested for outbound runs to the feeder.

2.4.4 Statistical analysis

For all sets of linear data, non-parametric statistical tests were used (Zar 1974; Conover 1980; Zöfel 1988; Lamprecht 1992). Significance (p-level) was set at 0.05. Some data sets did not differ from a normal distribution (tested via the Kolmogorov-Smirnov test for one sample, see Figs. III.14, III.15). When the non-parametrical tests yielded results with p within 0.05 and 0.1 and the distribution did not differ from a normal distribution, the statistical procedure was repeated by means of the equivalent parametric procedure. Since these additional statistic procedures did not show any relevant discrepancies with regard to the non-parametric tests, only the relevant non-parametric tests shall be described here and only the results by performing those tests will be given in the section results. In particular, the following tests were applied:

- Spearman rank-order correlation coefficient as test for correlations between groups

- One-sample Wilcoxon signed rank test to check whether data deviated from expected values

- Wilcoxon signed rank test for pairwise comparisons to test for differences between 2 related groups

- Mann-Whitney U-test for independent samples to compare 2 independent samples (Mann and Whitney 1947)

- Fisher's exact test to examine the significance of the association between two variables in a 2×2 contingency table

- Kruskal-Wallis one-way analysis of variance to determine whether more than two samples have come from different populations (Kruskal and Wallis 1952)

- Tukey's test (with Bonferoni correction if required) as post-hoc test to identify the deviating subgroups when Kruskal-Wallis gave significant results

- Friedman's test to determine if more than two related groups come from different populations

Whenever the Friedman test gave significant results, the Nemenyi-test — described by Hollander and Wolfe (1960) — was applied.

The Mardia-Watson-Wheeler (Batschelet 1981) test came into play, whenever directions were compared. Since this test is not based upon the assumption of normal distribution, it was the appropriate tool for circular statistics.

To check for equality of variances of different groups, the Ansari-Bradley test (Ansari and Bradley 1960) for two groups and Levene's test for more than two groups (Brown and Forsythe 1974) were employed.

The p-values given are two-tailed, if not indicated otherwise. For most of the experiments (exception: experiment 8) medians (M) and interquartile ranges (IR) are given. For circular statistics mean angles (MA) and r-values are presented.
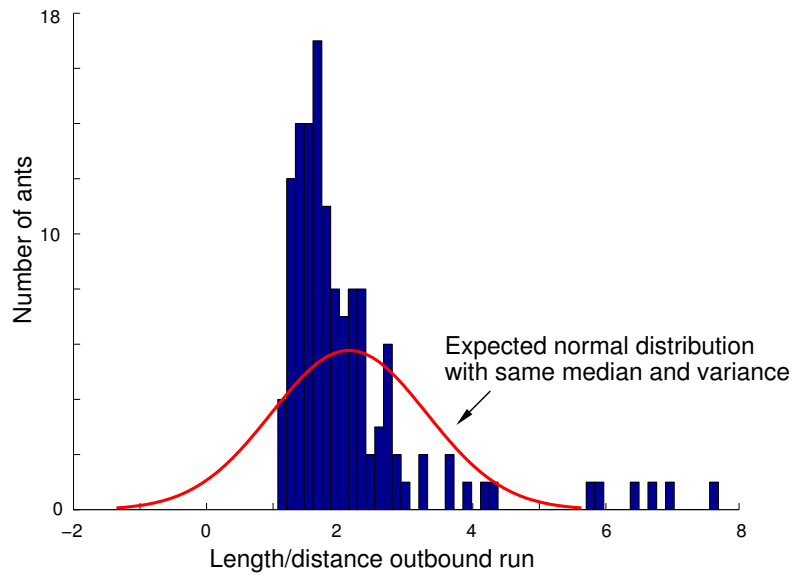
Figure III.14: The tortuosities of the 130 natural outbound runs (for definition of tortuosity: see data analysis) of experiment 1 differ from a normal distribution (Komogorov-Smirnov-Test, p<0.001, N = 130). The normal distribution with same median and variance is also shown.
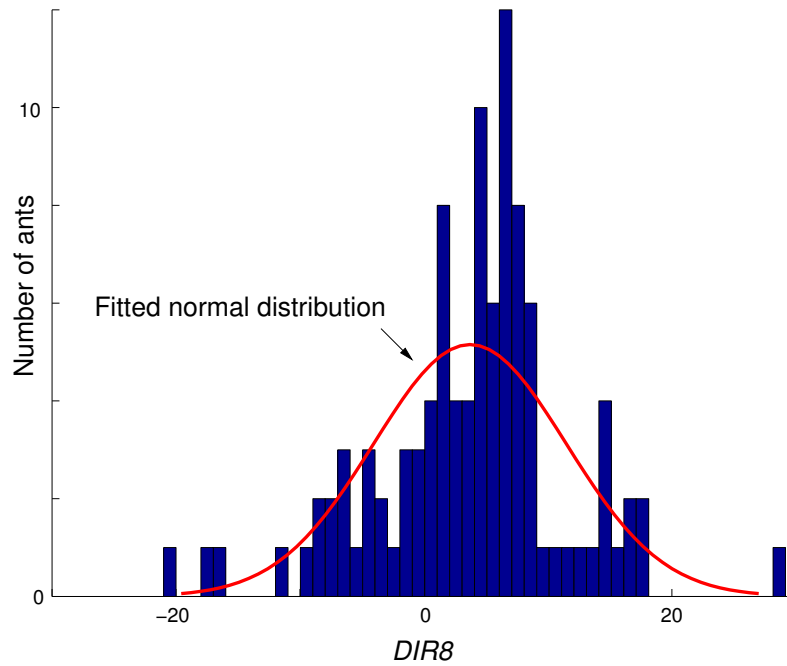
Figure III.15: Example of a data set that does not differ significantly from a normal distribution: deviations of the homing directions of 130 ants measured as $DIR8$ (experiment 1, see data analysis). Also shown: Gaussian distribution fitted to the empirical one.

2.5 Analysis of experiments

2.5.1 Experiment 1

Values describing the characteristics of the outbound runs. To quantify the structure of the free outbound runs simple indicators describing their mean direction and their curvedness or tortuosity are needed. The basic quantity in all these definitions is the tangential vector $\vec{\tau}(s)$, a vector of unit length, $|\vec{\tau}(s)| = 1$, pointing in the actual running direction at each point s of the path, where s parameterizes the path by its arc length.

GEDIT gives the path coordinates in a discrete set of subsequent, equidistant points $\vec{x}_i = (x_i, y_i)$ with $i = 1, \ldots, N$. The tangential vector is then easily calculated to be

$$\vec{\tau}_i = \frac{\vec{x}_{i+1} - \vec{x}_i}{|\vec{x}_{i+1} - \vec{x}_i|}. \tag{III.1}$$

Integrating $\vec{\tau}(s)$ along the path yields a vector pointing from the start $\vec{x}(s{=}0)$ to the end of the path $\vec{x}(s{=}L)$, or

$$\int_0^L ds\, \vec{\tau}(s) = \vec{x}(L) - \vec{x}(0), \tag{III.2}$$

and integrating $\vec{\tau}(s)^2$ gives the path length

$$\int_0^L ds\, \vec{\tau}(s)^2 = \int_0^L 1\, ds = L. \tag{III.3}$$

The following values were used as characteristics of the outbound runs:

- **Tortuosity of outbound path (TOR).**

  Along a very tortuous path $\vec{\tau}(s)$ varies a lot, along a perfectly straight path not at all, so it is natural to define the variance of $\vec{\tau}(s)$ as a measure of tortuosity. By simple algebra this is related to the ratio of path length L and end–to–end distance $d = |\vec{x}(L) - \vec{x}(0)|$ of the path

$$\mathrm{var}(\vec{\tau}(s)) = \frac{1}{L} \int_0^L \vec{\tau}(s)^2\, ds - \left(\frac{1}{L} \int_0^L \vec{\tau}(s)\, ds \right)^2 = 1 - \left(\frac{d}{L} \right)^2. \tag{III.4}$$

  Based upon these considerations, the tortuosities of the 130 outbound runs recorded during this experiment were calculated by means of the length of the outbound path L divided by its end–to–end distance d (in the following called TOR). Thus, the relation between $\mathrm{var}(\vec{\tau}(s))$ and TOR is $1 - \frac{1}{TOR^2}$.

  Another simple mathematical tool allows to evaluate both tortuosity and mean direction of a path. Assuming, for simplicity of notation, a path starting at $\vec{x}(0) = 0$ one searches for a straight line going through this point which is as close as possible to the path. The direction of this line is given by the eigenvector of the larger eigenvalue of the matrix

$$M = \begin{pmatrix} \int_0^L ds\, x(s)^2 & \int_0^L ds\, x(s)\, y(s) \\ \int_0^L ds\, x(s)\, y(s) & \int_0^L ds\, y(s)^2 \end{pmatrix} \tag{III.5}$$

whereas the other eigenvector points into the perpendicular direction. The ratio of the smaller vs. the larger eigenvalues gives the square of the lateral extent of path fluctuations divided by the square of its longitudinal extent — which is another measure for the path's tortuosity.

Since the points $\vec{x}_i$ supplied by GEDIT are equidistant, the integrals in Eq. (III.5) can be replaced by sums, i.e. $\int ds\, x(s)^2$ by $\sum_i x_i^2$ and the same for $x(s)\, y(s)$ and $y(s)^2$.

By applying this method, the tortuosities of the 130 outbound runs were determined again.

The results of these two simple evaluations, TOR and ratio of eigenvalues, of all 130 natural outbound runs were compared to each other (see appendix, 3). This comparison revealed no remarkable differences for both methods.

Therefore, the L/d-index (TOR) was chosen as standard index for the determining tortuosities of outbound runs. TOR was also used for determining the tortuosity of inbound runs (see III.2.4.2). Two natural outbound runs and their corresponding tortuosities are shown in Fig. III.2.

- **Autocorrelation function (ACF)**

  Other than the *global* measures of tortuosity defined above, the auto-correlation function (ACF) of the directions also reflects information about the *local* structure of a tortuous path (Alt 1990). More precisely, the ACF

  $$C(s) = \langle \vec{\tau}(s') \cdot \vec{\tau}(s' + s) \rangle \qquad \text{(III.6)}$$

  indicates how much the ant's walking directions at two points differ from each other, where it has walked a path length s between them (velocity is assumed to be constant with v = 0.05 m / arc length). If ϕ is the direction an ant is heading towards, then the ACF corresponds with the mean cosine of angular changes within correlation length s:

  $$C(s) = \langle \cos(\phi(s' + s) - \phi(s')) \rangle. \qquad \text{(III.7)}$$

  Clearly $C(0) = \langle \vec{\tau}(s') \cdot \vec{\tau}(s') \rangle = 1$, and $C(s)$ decreases with increasing path length s between correlated point pairs, indicating decreasing alignment with greater distance. For great values of s $\vec{\tau}(s' + s)$ gets 'independent' of $\vec{\tau}(s')$, and then $C(s) \approx |\langle \vec{\tau}(s') \rangle|^2$.

  How fast $C(s)$ decays, and whether it does so via an intermediate 'plateau' value or with oscillatory structure may give important general information about the path structure.

  Thus, the ACF was used as a tool determining the structure of outbound run and, especially, to address the question whether the natural outbound runs somehow show a preferential direction or whether their changes of directions occur randomly.

  The 130 runs were divided into subgroups that differed with respect to their path lengths (defined by the numbers of arc lengths that one path

contained, since those amounted to about 0.05 m, see III.2.4). Thus, 10 subgroups were created, ranging from overall path lengths of 10 m to more than 30 m, and their ACFs will be presented. In addition, the runs were divided into 2 groups (overall path length $<$ or $>$ 17.5 m) and again their ACFs were calculated.

Since the tortuosity as defined above does not reveal whether the overall direction of an outbound path is biased, I calculated the directional changes ω of all ants' outbound paths for each arc length (thereby, the first arc length got the value 0 and was used as a reference). Then, the following values were determined for all runs:

- **Integrated curvature of outbound path:** $\int \omega(t)\, dt = \phi_{\text{end}} - \phi_0$ (*OM*).

  This value seems to be an interesting value regarding the overall curvature especially with regard to errors that may cancel each other out as the error postulated by (Müller and Wehner 1988; Müller 1989). However, it does not show how many, especially big, changes of ω occurred during a path. Therefore, another value was calculated:

- **Integral of cubed curvature of outbound path:** $\int \omega^3(t)\, dt$ (*OM3*).

  This value that considers large values of ω more than small ones, takes also into account the number and signed values of ω during the run.

Grouping of outbound runs. Considering their tortuosities, the 130 outbound runs were divided into two subgroups: one containing the ants that had displayed high tortuosities (N = 65) and the other one containing those ants that performed straighter outbound runs (N = 65). These groups were compared in terms of all the values determined for their of home runs (ED, $DIR8$, $DIRM$, DIS, TOR and systematic search behavior (ED, DIR, DIS, $EXT100$). In addition, they were compared with regard to the equality of variances of the directional deviations of their inbound runs (measured as $DIR1$, $DIR8$, and $DIRM$).

Values describing the inbound runs. The values described in 2.4.2 were used as characteristics for the inbound run. Additional values that were calculated for the inbound run were the directional deviation after 1 m ($|DIR1|$) and the tortuosity during the first 2 m ($TOR02$) and 5-7 m ($TOR57$) of the inbound runs.

Since it became obvious that many home runs show a conspicuous deviation from the correct homeward course at the beginning but then seem to approach the correct homing direction more and more, the interest arose to test if this deviation accounts for most of the errors observed during the experiments. Therefore the direction of each inbound run was determined after 1m, 2m, 4m, and 6m by means of the intersection point with the corresponding circle. Then, it was checked for each ant if the deviations keep the same sign, that is, if the respective ant stays on the same side of the

straight correct homing path. Then, the distances in meters from the bee-line between nest and feeder at each of the circles were determined. These values were used to calculate a linear regression curve for each ant, thereby considering the distances from the correct homing direction at 1, 2, 4, and 6 m (Fig. III.16). Thus, for each ant the starting point, i.e. the intersection point of this ant's regression curve x with the y-axis (a in the equation $y = a + bx$) and the slope of this curve (b in the same equation) could be calculated. The last step of this procedure was to test whether there exist negative correlations between a and b showing that errors get smaller with increasing distance covered during the inbound run.
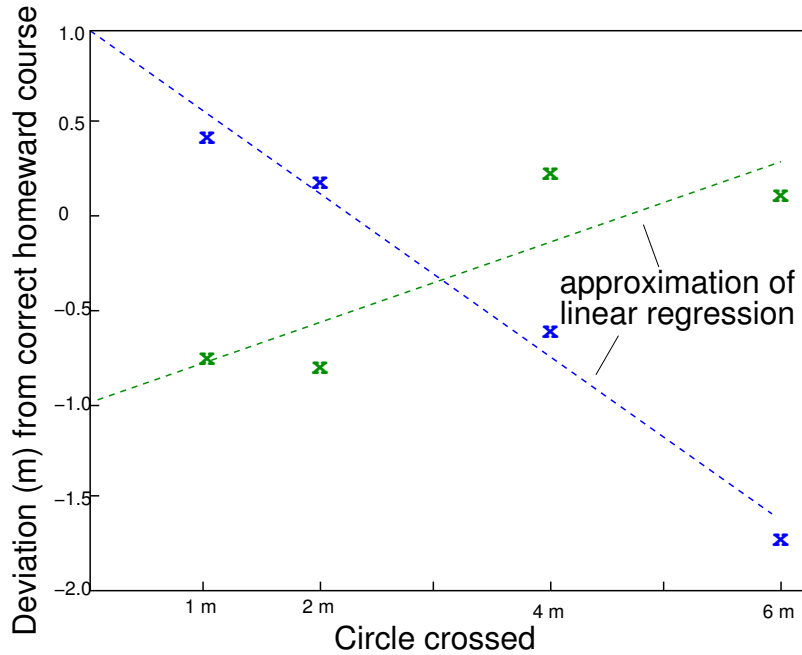
Figure III.16: Home runs of two ants for which the linear regressions based upon the distances from the beeline between point of release and correct nest position in metres after 1 m, 2 m, 4 m, and 6 m were calculated.

Values describing the systematic search runs. As for the inbound runs, the values described in 2.4.3 were used as characteristic values describing the systematic search patterns. As mentioned above, the extension of the systematic search runs was determined at path lengths of 100 m ($EXT100$). In addition, the extension during the first 20 m of systematic search ($EXT20$) was calculated.

Correlation between outbound and inbound run. The tortuosities TOR of the 130 outbound runs were tested for correlations with all characteristic values of their corresponding inbound runs (ED, $|DIR8|$, $|DIRM|$, DIS, TOR) and the additional values mentioned above ($|DIR1|$, $TOR02$, $TOR57$).

Integrated curvature (OM) and integral of cubed curvature ($OM3$) of the outbound runs were tested for positive correlations with regard to the Euclidean distance (ED) and directional deviations ($DIR8$ and $DIRM$) of the

inbound runs. In this case one-tailed p-values were calculated, since the integration of curvature considers the sign of the respective angular movement. Since ED all the time yielded positive values, for the tests for correlations between OM and $OM3$, respectively, and ED the absolute values $|OM|$ and $|OM3|$ were used instead.

Test for correlation between outbound run and systematic search behavior. Again, TOR of the 130 outbound runs were tested for correlations with all values describing the systematic search. (ED, $|DIR|$, DIS, $EXT100$ & $EXT20$). In addition, it was checked if there exist positive correlations between $|OM|$ and $|OM3|$, respectively, of the outbound runs and ED measured via systematic search as well as between OM and $OM3$ (outbound) and DIR (inbound); again, this test was performed as a one-tailed test, since a one-tailed hypothesis of a potential positive correlation was tested.

Systematic errors. With regard to errors that have been discovered earlier during specific experimental setups (Müller and Wehner 1988; Müller 1989; Sommer and Wehner 2004) it was scrutinized if some of the inaccuracies displayed by the ants during their home runs and systematic search behaviors could be based, at least partially, on these errors.

Therefore, both the homing direction and the adapted position of the nest according to the MW-error were calculated (for details: see II.3).

Then it was investigated whether the homing direction predicted by the model of Müller and Wehner (MW-model) — in the following called MW-direction — differs substantially from the theoretically correct homing direction by comparing both directions for each run (see Fig. III.17) and, if this were the case, whether the deviations of the ants' homing directions can be explained by the MW-error.

Therefore, the deviations of the ants' actual homing directions were determined at the intersection points of several concentric circles (0.5 m, 1 m, 2 m, 8 m) as well as by means of the minimization method and the systematic search center. The deviations from the correct homing directions (home run: $DIR0.5$, $DIR1$, $DIR2$, $DIR8$, $DIRM$, systematic search: DIR see also Fig. III.17) and the deviations from the MW-directions (home run: $DIR0.5_{MW}$, $DIR1_{MW}$, $DIR2_{MW}$, $DIR8_{MW}$, $DIRM_{MW}$, systematic search: DIR_{MW}, see also Fig. III.17) were calculated during the next step. Then, the absolute values of these deviations ($|DIR0.5|...$) were used to answer the question whether the ants' homing directions were closer to the correct homing direction or the MW-direction (Fig. III.17).

Whenever ants are deviating from the correct homing direction during the inbound run, this deviation can either get them closer to the MW-direction or further away. This is illustrated in Figure III.17: both ants are deviating during their home runs, but the home run of ant a is closer to the direction predicted by the MW-model, whereas for the ant b this does not hold true. For each method (intersection circles at different distances, minimization method, systematic search center) the number of ants deviating more to the direction predicted by the MW-model (ant a in Fig. III.17) and the
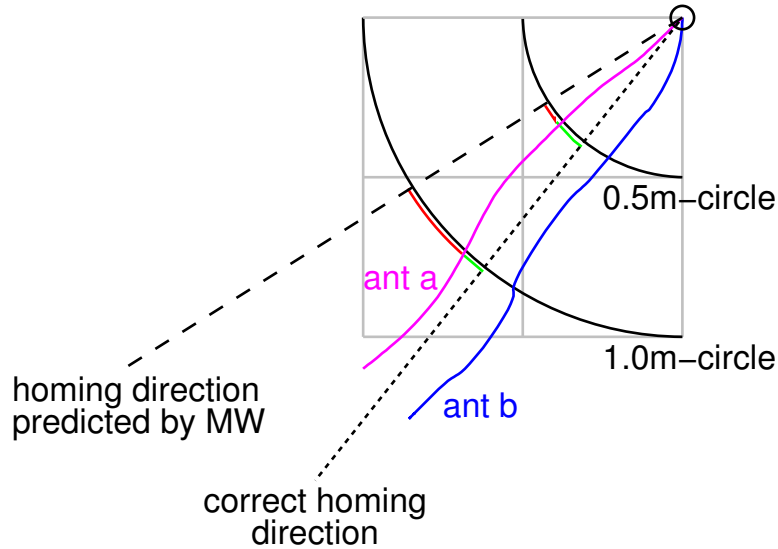
Figure III.17: MW-error. The beginnings of the (fictive) home runs of two ants (a and b) are shown. Dotted line: correct homing direction, dashed line: MW-direction. Ant a: $|DIR0.5| > |DIR0.5_{MW}|$, $|DIR1| < |DIR1_{MW}|$, green: $DIR0.5$, $DIR1$; red: $DIR0.5_{MW}$, $DIR0.5_{MW}$, i.e. after 0.5 m the homing path of ant a is closer to the MW-direction than to the correct homing direction and after 1.0 the opposite holds true. Ant b: $|DIR0.5| < |DIR0.5_{MW}|$, $|DIR1.0| < |DIR1_{MW}|$. Ant a is deviating from the correct homing direction towards the direction predicted by the MW-model, whereas ant b is deviating further away from the latter direction. For more details: see text.

corresponding number of ants whose homing directions deviated even more from the direction predicted by the MW-model (ant b in Fig. III.17) were calculated. Then, it was tested whether the relation between both numbers revealed a significant tendency.

Since for many ants correct homing direction and MW-direction differed only slightly (see 3.2.3), the whole test procedure was repeated for all ants for whose home runs the difference of the correct direction and the MW-direction amounted to at least 5° and, finally, for all ants for which the respective directions differed by at least 10°.

Finally, the Euclidean distances between end point of home run and correct position of the (assumed) nest P_c (ED) and the nest position adapted to the MW-error P_{MW} (ED_{MW}) were calculated. The procedure was repeated by taking the systematic search center into account.

A similar procedure was applied considering the leaky integrator LI (Sommer and Wehner 2004): the homing distance predicted by the LI was calculated (for details see II.3.2 and II.5) and then the question was addressed whether the deviations from the correct homing distance (DIS) and from the homing distance according to the LI (DIS_{LI}) differed. This was done via the formulas by which the LI was implemented into the theoretical model. This test was performed taking both end point of home run and systematic search center into account. In addition, ED and ED_{LI} were compared. This was done — as for the MW-error — via both end point of home run and

systematic search center.

2.5.2 Experiment 2

The 6 groups that had covered different distances during their outbound runs were compared to each other with regard to the accuracy of their home run (ED, $|DIR8|$, $|DIRM|$, DIS, TOR) and systematic search (ED, $|DIR|$, DIS, $EXT20$, $EXT100$). In addition, the two most extreme groups, i.e. those with the shortest and longest distances covered, were compared in view of all these values of inbound run and systematic search. As for experiment 1, the groups were also compared with regard to the equality of variances of directional deviations of their inbound runs (measured as $DIR8$ and $DIRM$).

There exists a problem whenever directional deviations are to be compared of ants that have to cover different distances back to the nest. Comparing the directional deviations as they are might falsify the results. Let us assume that two ants suspect the nest position to be at the same spot (Fig. III.18) that does not correspond to the correct nest position. Depending on the distance these ants still have to cover the angular deviations differ remarkably. Thus, in this experiment one should keep in mind that the lateral deviation might cause different directional deviations, depending on the distance from the nest, i.e. smaller angular deviations do not necessarily lead to smaller overall errors.
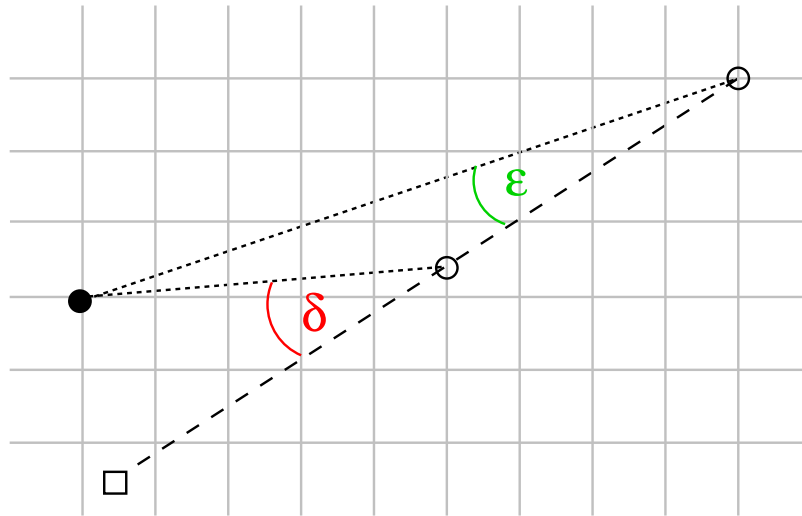
Figure III.18: Two ants that suspect the nest at the same location, but whose distances to this assumed nest position differ by factor 2. Open circles: locations of the ants; filled circle: suspected nest position; open square: correct position of the nest. Though they suspect the nest at the same location the directional deviations of both ants (δ and ϵ) differ remarkably.

Besides, it was checked whether the overall lengths L of the outbound paths may influence the accuracy of the home run and the systematic search center (same values as used for comparisons of groups). This test can be seen as kind of an additional test to the question of tortuosity TOR investigated during experiment 1, but, in contrast to experiment 1, the distances varied. Thus, of course, the differences in terms of overall lengths were greater

than those of experiment 1. The procedure resembled exactly the one of experiment 1: all 60 runs were put together and were tested for potential correlations between lengths of the outbound runs and characteristics of inbound runs or systematic search behaviors, respectively.

As in experiment 1, both OM and $OM3$ as well as $|OM|$ and $|OM3|$ were calculated for all runs. The values obtained by this calculation were checked for correlations with some of the values of the inbound runs (ED, $DIR8$, $DIRM$) and systematic search behavior (ED, DIR) in the same fashion as described above (III.2.5.1).

2.5.3 Experiment 3

In a first step, it was scrutinized whether the group of trained desert ants differs with regard to TOR of its outbound runs as compared to the ants whose natural outbound runs were recorded (experiment 1). Then, both groups were compared in view of the accuracy of their path integration system via the accuracy of home run (ED, $|DIR8|$, $|DIRM|$, DIS, TOR) and systematic search behavior (ED, $|DIR|$, DIS, $EXT100$, $EXT20$) and in terms of equality of variances of the directional deviations ($DIR8$ and $DIRM$) of their inbound runs.

Finally, for the 40 trained ants TOR during outbound and inbound run was compared.

In the case where both groups differed in view of the tortuosity of the outbound run a difference between home runs or systematic search patterns could be caused by either an improved accuracy of the path integrator due to the training effect or the lower tortuosity of the outbound runs. Therefore, for this case an additional analysis was conducted. 12 pairs of ants (each pair consisting of one untrained and one trained ant) that had displayed the same value for TOR during their outbound runs were chosen randomly and their home runs and systematic search behaviors were compared to each other. Thus, it was tested whether the observed differences still existed for the two subgroups with same values of TOR. So, it should become obvious if training effects or the lower tortuosity did account for differences in the accuracy of the path integrator. Since in this specific case a one-sided hypothesis, i.e. if a potential difference between the whole groups also occurs when comparing the subgroups, one-tailed p-values are given.

2.5.4 Experiments 4, 5, 6, and 7

General The results of these four experiments were analyzed together in order to make it possible to conduct cross-comparisons between different groups. This statistical procedure was necessary in order to compare the results between different experiments (Lamprecht 1992).

The accuracy in terms of the home run or run to the feeder was investigated by the aid of the Euclidean distance (ED) between correct nest position and end of the homevector. For ants heading towards the feeder, the Euclidean distance (ED) was defined as the distance between the end of the run to the feeder and the correct position of the feeder (for more details, see descriptions of experiments 6 and 7)

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With regard to the systematic search, the very same 7 groups were compared to each other. As for the home runs, only the Euclidean distance (ED) between systematic search center and correct position of the nest (or feeder, 50%-out and 50%-LM-out ants heading for the feeder, see above) was evaluated. The extension of the systematic search behavior was determined for all groups for the first 40 m of systematic search ($EXT40$); with regard to this value, also the 0-in ants were included in the analysis.

For both home runs and systematic search of experiments 4 and 5 (5-m, 10-m, 20-m, 50%-in, 25%-in) it was tested whether there exist any systematic tendencies within the groups. Therefore, by examining ED of these 5 groups they could be divided into subgroups that were overshooting or undershooting, respectively, or in groups that suspected the nest either to the left or to the right of the correct position of the nest.

For the ants captured during their outbound or inbound runs (experiment 5: 50%-in and 25%-in ants; experiment 6: 50%-out ants, and experiment 7: 50%-out-LM ants), the distance between the point of capture and the beeline between nest and feeder was measured via the transect lines. By taking this distance into account, a new 'correct' homing direction (deviating from, say, a strictly northern direction for homing ants) was determined. This correct homing direction was used for determing $DIR8$ and $DIRM$ of the home run and DIR of the systematic search center. In the same way, a new 'correct' nest position had to be calculated, and, again, this position was considered when calculating ED via home run or systematic search. The correct homing distance, in contrast, did only slightly change due to this deviation (0.01-0.1 m) and, therefore, could be neglected. For ants heading to the feeder, the equivalent procedure to determing correct foraging direction and position of the feeder was applied. In addition, directions and nest or feeder positions were also calculated without considering these deviations for 50%-in ants and 25%-in ants.

For some groups three-dimensional density plots containing both home runs and systematic search patterns of the different groups were created; these plots give a first overview of the different groups.

Additional values for the home runs ($|DIR8|$, $|DIRM|$, DIS, and TOR) and systematic search ($|DIR|$, DIS) were calculated. Though they will not be discussed, they are presented in the appendix (appendix, 4.4, 4.5.1, 4.6, 4.7).

Experiment 4   The three groups (5-m ants, 10-m ants, and 20-m ants) were compared against each other with regard to their ED of home run and systematic search center and in view of potential systematic tendencies, i.e. overshooting or undershooting the distance or biases towards the right or left side of the nest. It was also tested if they differ in view of $EXT40$ of the systematic search behavior.

Experiment 5   The values for Euclidean distance (ED) and directional deviations (home run: $DIR8$, $DIRM$; systematic search: DIR) obtained by the two different procedures were compared to each other for both the 50%-in and the 25%-in ants.

Then the hypothesis was tested whether the deviation at the point of capture is somehow correlated with the direction the ants were heading towards after the release, e.g. if ants that had deviated to the east head to the west during the remaining part of the home run and vice versa. This was done by testing for (negative) correlations between the direction headed towards until the time of capturing and the direction headed towards after being released in the test field. For this analysis both 50%-in and 25%-in ants were used.

50%-in ants and 25%-in ants were compared to each other in terms of ED (home run and systematic search center) as well as $EXT40$ and systematic tendencies. With regard to the end of the home run, only that fraction of the 25%-in ants that started a home run, were included in the analysis (see III.2.3.5). Both groups were also compared to 5-m, 10-m and 20-m ants with respect to ED and to 5-m, 10-m, 20-m, and 0%-in ants with respect to $EXT40$. Furthermore, they were compared in view of systematic tendencies.

Experiments 6 and 7: outbound runs with and without landmarks
The ratio of ants proceeding their foraging trip against those heading back to the nest was determined. This was done for both the group that was trained and tested without landmarks and the group trained and tested with landmarks for comparison. Therefore, concentric circles were laid around the point of release with diameters 1 m and 5 m. The point at which the ants crossed that circle was the criterion whether they were heading to the feeder (180-360°) or to the nest (0-180°). Ants that did not cover at least 50% of the theoretical distance to nest or feeder, respectively, i.e. 5 m, before they changed their general direction for at least 3m, were excluded from this analysis (see also Table III.3). Then, it was tested wether the ratios differed essentially between the 50%-out and the 50%-out-LM ants. However, since the 5-m circle appeared as the more meaningful values (a number of ants headed for the nest or feeder, respectively, for 1 to 3 metres, but then changed the direction by 180° to run of the vector to the feeder or the nest, respectively) the values obtained via using the 5-m circle were used to define if an ant was heading towards nest or feeder.

Due to the separation of both groups into ants proceeding with their foraging runs and those returning to the position of the nest, altogether 4 new subgroups were created: 50%-out ants heading for the feeder, 50%-out-ants heading for the nest, 50%-LM-out ants heading for the feeder, and 50%-LM-out ants heading for the nest. These four groups were compared with respect to the Euclidean distances ED between home runs and systematic search centers, respectively, and correct position of nest (or feeder) and extension of the systematic search during the first 40 m, $EXT40$. In addition, they were compared against 20-m ants (same training distance), 10-m ants (same distance to cover for reaching the nest) and 50%-in ants (again, same distance to cover for reaching the nest) in view of ED of home run and systematic search and in terms of $EXT40$ with the same groups as well as the 0%-in ants. Finally, it was investigated if there exist any systematic tendencies for some of the groups (over- or undershooting, preferred side with regard to the correct nest position).

2.5.5 Experiment 8

Outbound runs. For the 19 recorded outbound runs of the 15 tested ants (no.s 2-20) tortuosities (L/d, TOR), deviations from the correct direction to the feeder at the beginning (intersection with fictive 1m-circle, $|DIR1|$) and overall deviations (12m-circle, i.e. 80% of distance nest-feeder, $|DIR12|$; minimization method, $|DIRM|$) from the correct foraging direction were determined.

Outbound runs 7, 9, 11, 13, 15, 17, and 19 (recorded after transfer and test in the test field) were compared to the successive outbound runs 8, 10, 12, 14, 16, 18, 20 (that took place without replacement to the test field) in view of these four values.

Then, all 15 ants were checked for (suspected negative) correlations between the number of run and the 4 values characterizing the outbound runs. Since a correlation could be hidden by natural fluctuations occurring during the large number of outbound runs, runs 2, 6, 10, and 20 were analyzed during an additional test. Especially by comparing runs 2 and 6 possible effects of the manipulations during the experiments could be excluded, since until outbound run 6 had been performed no manipulations had taken place. For this additional test, runs 2, 6, 10, and 20 of all 15 ants were pooled and compared against each other.

Inbound runs. For all inbound runs the same characteristic values as for the outbound runs were calculated. With regard to TOR and the directional deviations determined by the minimization method ($|DIRM|$) only runs with the same distance can be compared against each other. Since the ants in the test field could not reach the nest and, therefore, the runs were interrupted by the observer (as soon as it was obvious that they had started the first loop of the systematic search), the runs were cut at a distance of 12 m and tortuosities and directional deviations via the minimization method were calculated. The same procedure was used for the inbound runs performed in the training area in order to compare both groups of inbound runs.

The characteristic values of inbound runs 5, 7, 9, 11, 13, 15, 17, and 19 (training area) then were compared to inbound runs 6, 8, 10, 12, 14, 16, 18, 20 (test area).

For all 15 ants potential correlations between number of the inbound run and one of the 4 values were investigated. As for the outbound runs (and the very same reasons given above) inbound runs 1, 5, 9, and 19 were pooled for all 15 ants and checked for potential differences in terms of the very same 4 values.

Inbound runs — outbound runs. This part of the study aimed at testing whether the outbound or inbound runs, respectively, differ with regard to TOR or $|DIR1|$, $|DIR12|$, or $|DIRM|$. Thus, the corresponding out- and inbound runs 2, 3, 4, and 5, that is only runs, that took place before any manipulations occurred, were compared with regard to the 4 values mentioned above.

Are there specific paths used during inbound or outbound runs?
To answer this question, plots were created which show all inbound or outbound runs, respectively, of specific ants. Besides, two-dimensional density profiles were drawn that indicate the spatial extension of a specific ant during several successive out- or inbound runs.

In order to define the spatial layout of outbound or inbound paths, the procedure developed by Kohler and Wehner (2005) was applied: the beeline between nest and feeder (length: 15 m) was divided into 30 segments of 0.5 m length and at the end of each segment the distance between the actual (inbound or outbound) path and the beeline was measured perpendicular to the beeline (see Fig. III.19). This was done for all 29 segments inside the path, resulting in a set of 29 numbers representing each path's spatial layout. Depending on which side the path was located as compared to the beeline, it got a positive (left side) or a negative sign (right side). By adding up and comparing the numbers of each outbound or inbound run of one ant, one can decide whether one run is biased towards one side. If this were the case, most of the runs would show the same sign and amount to similar values. The runs of an ant without preferred side, in contrast, would differ in view of their signs and their overall sums, thereby probably not differing from an equal distribution of 0 or at least significantly less differing than runs with a preferred side.

Figure III.19: Method used for defining the specific layout of each run (outbound and inbound) of each ant. The beeline between nest (N) and feeder (F) was divided into segments of 0.5 m length and at the end of each segment the distance between the actual (outbound or inbound) path and the beeline was measured perpendicular to the beeline.

For ants that had no preferred side the question for specific paths could be denied. For ants displaying preferred sides on which they performed their outbound or inbound runs, respectively, the mean of the distance after segment 15, i.e. after covering half the path, where the deviations from the beeline are rather high, between beeline and actual path was calculated for all outbound and inbound runs. Then, the absolute deviation from this mean during each of the (outbound or inbound) runs was calculated: by doing so, it could be seen whether ants have preferred 'paths' which they use (very low values for the deviations) or not (rather high values for the deviations from the mean distance between beeline and actual path). For this specific case, the means and standard deviations instead of medians and interquartile ranges were used, since the distributions did not differ from normal distributions (Wilcoxon-test: $p > 0.9$).

3 Results

The results presented in this section allow a better understanding of the path integration process by testing which factors influence the path integrator's accuracy and how *Cataglyphis* deals with problems or inaccuracies resulting from the path integration system. The specific purposes of the particular experiment were presented in III.2. The results are presented in the same order, i.e. starting with the experiments relying on natural outbound runs (III.3.2, 3.3, 3.4), followed by the training experiments (III.3.5), and finally the ontogeny experiment (III.3.6).

3.1 General remarks

At the beginning, two methodical issues have to be clarified: (1) whether the two methods determining homing directions differ (see III.2.4.2) and (2) whether the two locations indicating the ant's assumed nest position, i.e. end point of home run and center of systematic search (see III.2.4.2 and III.2.4.3) are correlated with each other.

3.1.1 Determination of homing directions

Directional deviations of the home runs in experiments 1, 2 and 3 were determined via the crossing point of the 80%-circle ($DIR8$) and the minimization method ($DIRM$, see III.2.4.2). In order to allow comparisons, for the ants of experiment 4, i.e. 5-m ants, 10-m ants, and 20-m ants, the homing directions were calculated using both methods. Then, for the 5-m ants the deviations from the correct homing direction, i.e. $DIR4$ (crossing point after 4 m = 80%-circle) and $DIRM$, for 10-m ants $DIR8$ and $DIRM$, and for 20-m ants $DIR16$ and $DIRM$ were compared. The deviations of the 5-m ants did not differ significantly ($DIR4$: mean directional deviation $MD = +2.47°$, $r = 0.964$, $N = 50$; $DIRM$: $MD = +1.86°$, $r = 0.981$, $N = 51$; Mardia-Watson-Wheeler: $p = 0.186$). This was confirmed when comparing the directional deviations for 10-m ants ($DIR8$: $MD = +2.20°$, $r = 0.980$, $N = 50$; $DIRM$: $MD = +2.03°$, $r = 0.983$, $N = 53$; Mardia-Watson-Wheeler: $p = 0.19$) and 20-m ants ($DIR16$: $MD = -2.06°$, $r = 0.996$, $N = 43$; $DIRM$: $MD = -1.05°$, $r = 0.997$, $N = 50$; Mardia-Watson-Wheeler: $p = 0.202$). Since the Mardia-Watson-Wheeler test compares whole groups against each other, a Wilcoxon matched pairs signed ranks test for pairwise comparison was conducted, too: the results were confirmed (5-m ants: $p = 0.257$, $N = 50$; 10-m ants: $p = 0.981$, $N = 50$; 20-m ants: $p = 0.569$, $N = 43$). Though both methods yield similar results, the directional deviations obtained by means of both methods were used for the data analysis of experiments 1,2, and 3 in order to reconfirm the results obtained by either method.

3.1.2 Nest position, as suspected by the ant

It is not known at which exact spot the ant suspect its nest to be. Thus, I used two different methods to measure the accuracy of the ant's path integration system, i.e. the end point of the ant's home run as well as the center of the
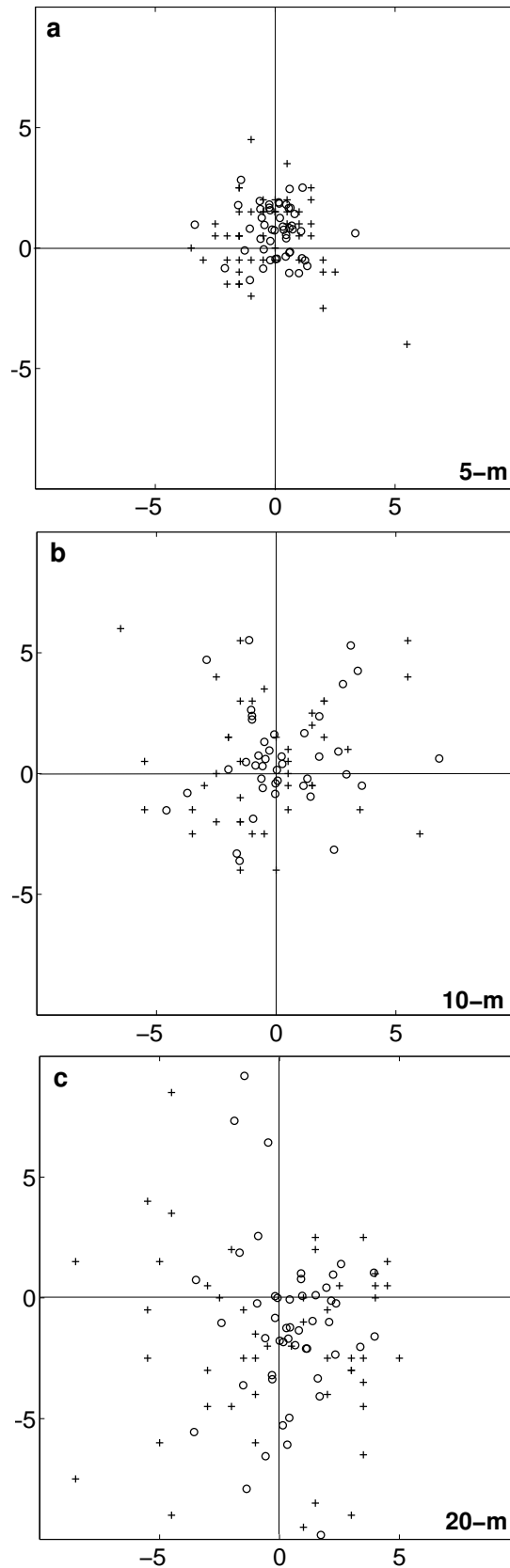
Figure III.20: End points of home runs (○) and systematic search centers (+) of (a) 5-m, (b) 10-m, and (c) 20-m ants of experiment 4. The trajectories were recorded for five respective 10 min searches (see III.2.3.4). The correct position of the nest P_c is the origin (0/0).

ant's systematic search behavior. Various procedures have been applied to determine the 'end point' of an ant's home run, i.e. the point at which the ant assumes its nest position (e.g. Wehner and Srinivasan 1981; Collett et al. 1998; Bisch-Knaden and Wehner 2003b).

In this work, this point was defined as a substantial directional change for a remarkable distance (for details: see III.2.4.1). However, one cannot be sure whether this point really reflects the ant's guess of its nest position, or whether at this point the ant has already started its first search loop. As an ant should focus its search at that position, at which it assumes its nest to be, the position of the ant's search density peak (see III.2.4.3) might yield clearer results about the ant's perspective of the nest.

Fig. III.20 correlates the ends of the home runs and the centers of the systematic search with the correct position of the nest P_c for the three groups tested in experiment 4. By using these data sets I compared the distances between the end of each home run and its corresponding center of search with the average distance to the centers of search of all ants. As a result, the end of the home run of a particular ant is closer to the systematic search center of this particular ant (5-m ants: median $M = 2.08m$, $N = 49$, 10-m ants: $M = 3.12m$, $N = 41$, 20-m ants: $M = 3.78$, $N = 49$) than to the centers of the systematic search of all other ants (5-m ants: $M = 2.24m$, $N = 49$, Wilcoxon signed-rank-test: $p = 0.395$; 10-m ants: $M = 3.76m$, $N = 41$, $p = 0.012$; 20-m ants: $M = 5.05m$, $N = 49$, $p = 0.001$, Fig. III.21). Obviously, there exists a correlation between the end of the home run and the systematic search center. Nevertheless, since the median distance between the end of the home run and the center of the ant's search is rather large (Figs. III.21, III.9), for further analyses I decided to take both parameters into account.
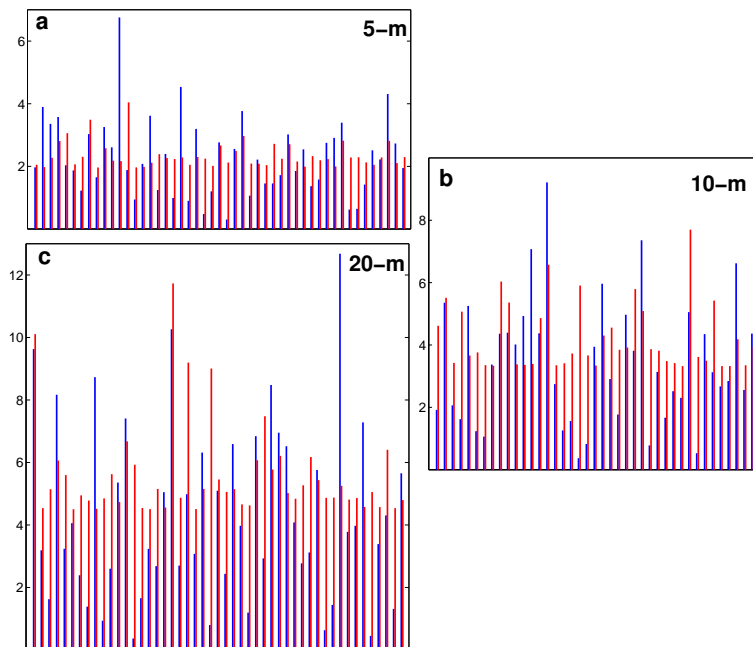

Figure III.21: Distances between the end of each home run and its corresponding center of search (blue) and the average distance to the centers of search of all ants (red) are shown for all 5-m ants (a), 10-m ants (b) and 20-m ants (c).

3.2 Experiment 1: Natural outbound runs with fixed distance

3.2.1 Structure of outbound runs

Although natural outbound runs of untrained ants are tortuous, they show a preferential direction the ants are heading towards. This can be seen in Fig. III.22 where the directional autocorrelation functions ACF for all outbound runs are shown. Since all outbound runs amount to the same distance (10 m), the length of the path, in Fig. III.22 shown as number of segments of arc length (0.05 m), is a value representing the tortuosity of outbound runs.
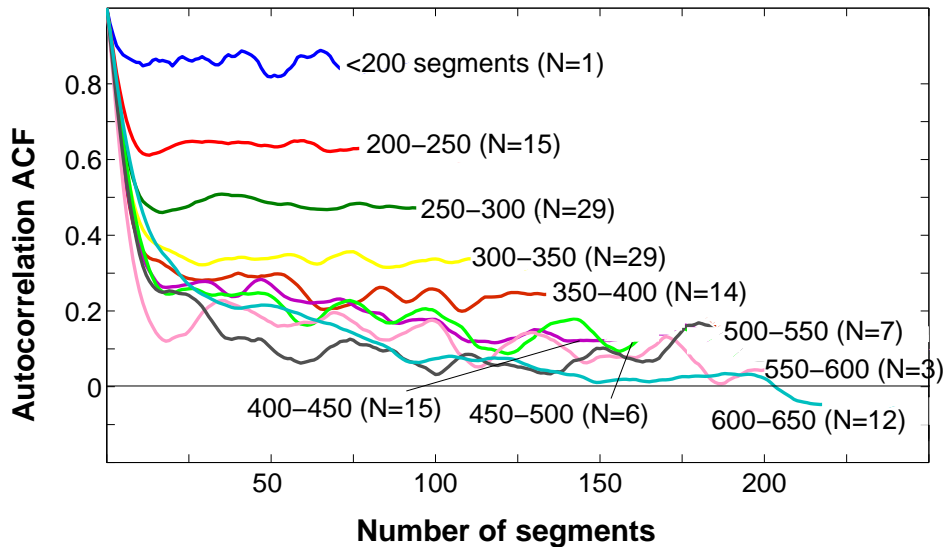
Figure III.22: Directional autocorrelation of moving directions of 130 outbound runs, subdivided by path lengths, thus indicating their tortuosities. For each group the autocorrelation function is shown for one third of their segments, i.e. for an overall path length of 0.05 m × the respective number of segments. Straighter runs display and keep higher degree of correlation than the more tortuous ones. Notice two scales of decay, initial fast to a shoulder value and subsequent slow decay. See text for explanation.

Nevertheless, all groups shown in Fig. III.22 — even the very tortuous ones consisting of 300 segments or more — reach an asymptotic plateau value or a regime of much slower decay, indicating that even those runs have a 'directional persistence' or mean orientation, and that these runs are not completely random. The mean orientation of the more tortuous runs is not as striking — and not as easily provable — as for less tortuous runs whose plateaus are remarkably higher.

In order to measure the mean decay time ('directional persistence length') the outbound runs were divided into only 2 groups according to their path lengths (path length either < or > 17.5 m, Fig. III.23). The mean time constant of 'exponential decay' can be fitted by exponential functions, with a characteristic scale of 5.9 segments (more tortuous runs) and 4.8 segments, corresponding to 0.30 m and 0.24 m, respectively. However, this values should be taken with care, since they might be due to unavoidable inaccuracies of the recording procedure in the field. A second decrease happens for both

groups, that can be seen in Fig. III.23: for the less tortuous runs this decay is rarely visible, whereas for the more tortuous runs it can be detected easily. This second slow decay has characteristic scales of 430 m (straighter runs) and 9.0 m (more tortuous runs, see also Fig. III.22). This value shows clearly the remarkable difference with respect to the directional persistence length that is much greater for straighter runs.

The average 'time' an ant keeps a direction it is heading towards is shorter for more tortuous runs, i.e. runs that consist of more segments (see Figs. III.22, III.23).
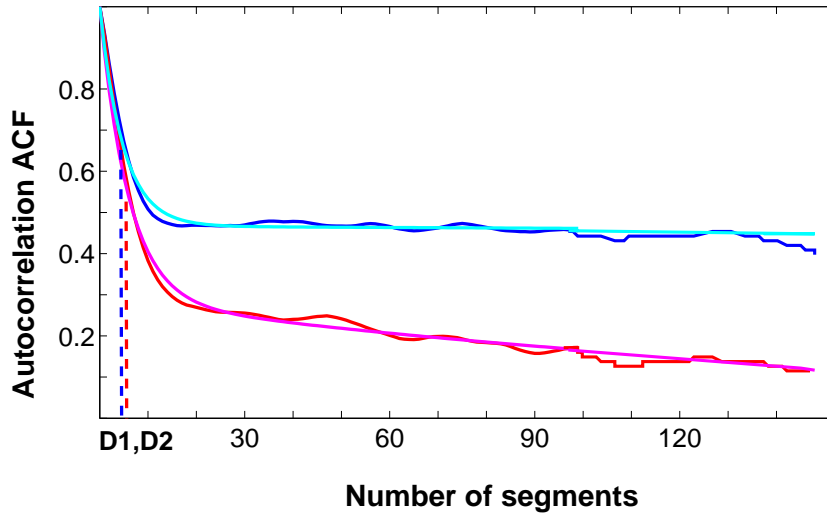
Figure III.23: Autocorrelation for correlation lengths less than 150 segments (arc lengths). Blue line: straighter paths (< 17.5 m path length); red line: tortuous paths (> 17.5 m path length). D1, D2: Directional persistence length = mean time constant of the initial fast decay (0.24 and 0.30 m, respectively). For more explanation: see text.

3.2.2 Does the conformation of the outbound run influence the accuracy of the ant's path integrator?

Since the results of the two methods to determine the tortuosity (L/d and ratio of eigenvectors) of the ants' outbound paths were highly correlated (see appendix, 3) only the L/d index was used for determining the tortuosity TOR.

In Fig. III.24 both the end points of the home runs and the systematic search centers relative to P_c are presented. It can easily be seen that they differ from each other; thus, it seems reasonable to take both points into account for further analyses.
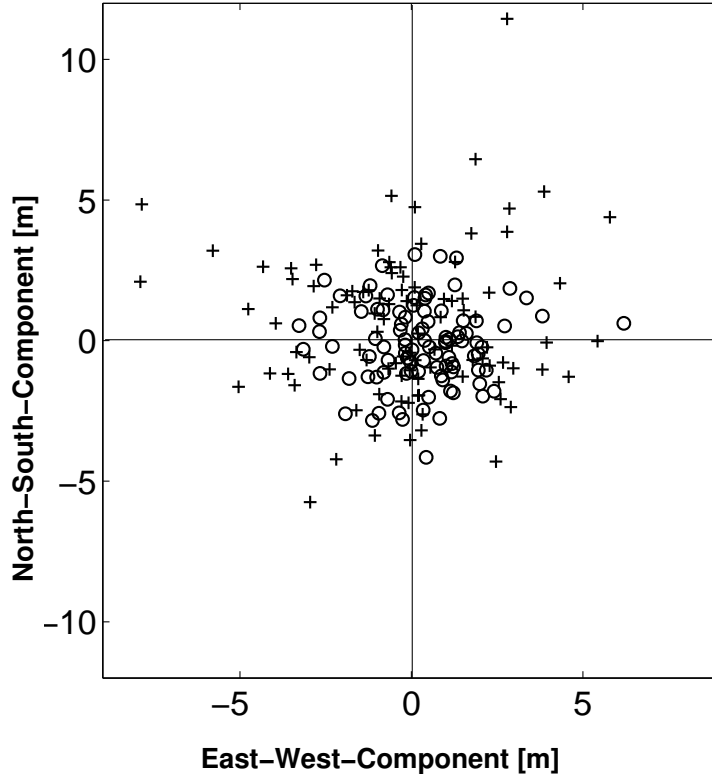
Figure III.24: End points of home runs ($\circ$) and systematic search centers ($+$) in relation to the correct position of the nest P_c (fixed at 0,0) of ants that were captured after having reached a distance of 10 m during their natural outbound runs (experiment 1). Only those ants whose systematic search runs were recorded for 10 min and for which a unique systematic search center could be calculated were included in the analysis ($N = 98$).

What influence has the conformation of the outbound run on the accuracy of the path integrator?

Tortuosity TOR measured as Length/distance. The tortuosity TOR of the outbound run is not correlated with the accuracy displayed during the inbound run (Fig. III.25): neither did it affect the Euclidean distance ED between end of inbound run and P_c (Spearman $r_s = -0.005$, $N = 130$, $p = 0.958$), nor the deviation from the correct homing direction of the inbound run ($|DIR8|$: $r_s = 0.038$, $N = 102$, $p = 0.704$; $|DIRM|$: $r_s = 0.040$, $N = 130$, $p = 0.648$), the deviation from the correct distance

$(DIS : r_s = -0.028, N = 130, p = 0.753)$, or the tortuosity TOR of the inbound run (TOR: $r_s = 0.124$, $N = 130$, $p = 0.160$).
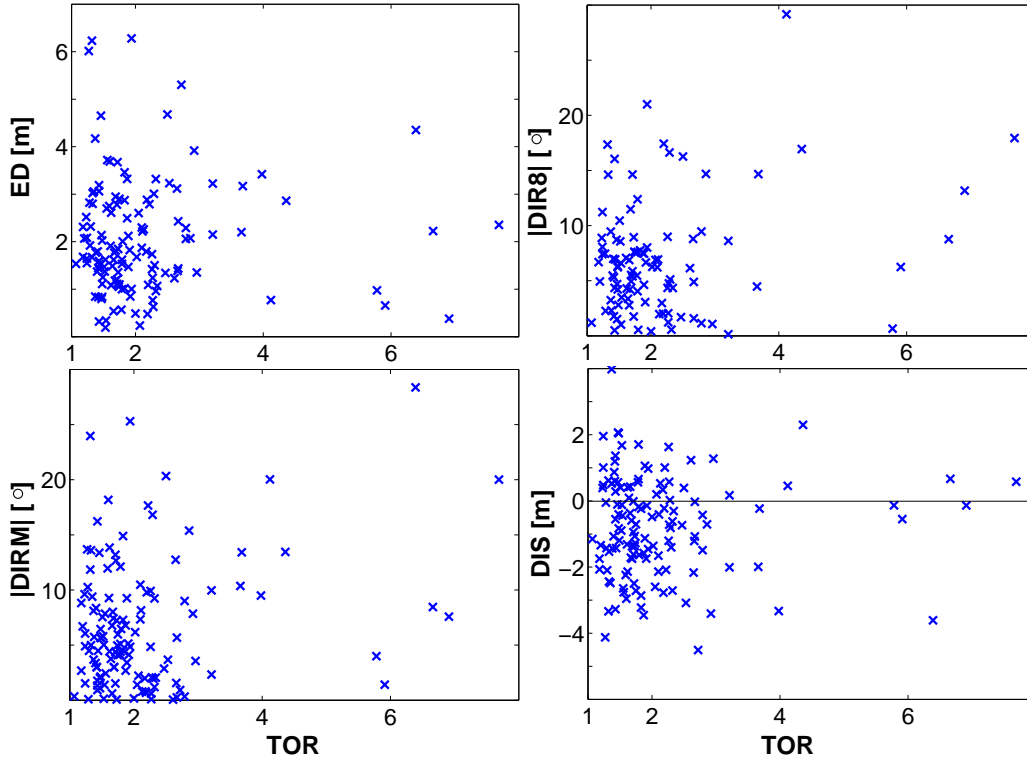
Figure III.25: Accuracy of the inbound runs of 130 ants captured after their natural outbound runs at a distance of 10 m as function of tortuosity TOR (L/d) during outbound run. Abbreviations from top to bottom: Euclidean distance between end of home run and P_c (ED), directional deviation measured at crossing of 8m-circle ($|DIR8|$), directional deviation measured via minimization method ($|DIRM|$), and over- oder underestimating of distance (DIS).

The tortuosity of the outbound run also did not influence the accuracy at the beginning of the home runs, measured as the deviation from the correct homing direction after 1 m ($|DIR1|$: $r_s = 0.023$, $N = 130$, $p = 0.795$). Similar results were found for the tortuosity during the first 2 meters of the inbound run ($TOR02$: $r_s = 0.0255$, $N = 130$, $p = 0.781$) and between 5 and 7 m of the inbound run ($TOR57$: $r_s = -0.018$, $N = 130$, $p = 0.842$).

With regard to the systematic search behavior, these results were confirmed (ED: $r_s = 0.077$, $N = 98$, $p = 0.450$; $|DIR|$: $r_s = 0.042$, $N = 98$, $p = 0.683$; DIS: $r_s = -0.004$, $N = 98$, $p = 0.970$, Fig. III.26).

Ants that had displayed more tortuous outbound runs also showed no change with regard to the extension of their systematic search behavior: for the first 100 m as well as the first 20 m of the systematic search, the extensions were not correlated with the tortuosity of the outbound run ($EXT100$: $r_s = -0.005$, $N = 73$, $p = 0.967$, see Fig. III.26; $EXT20$: $r_s = 0.05$, $N = 130$, $p = 0.570$).

Ants caught after more tortuous outbound runs, i.e. the half of the test group whose TOR-index was higher than 1.75 (consiting of > 350 segments, see Fig.III.23) showed a slightly higher variance with regard to the directional deviations of their home runs, when measured at the intersection point with
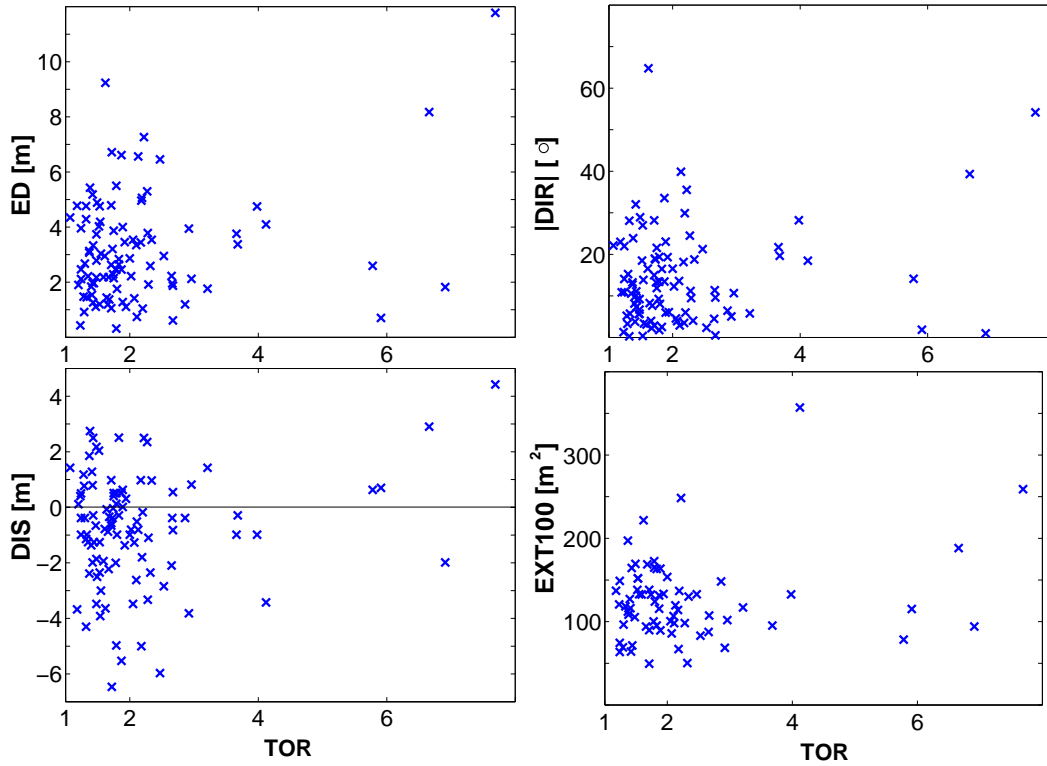
Figure III.26: Systematic search behavior of ants captured after their natural outbound runs at a distance of 10 m as function of tortuosity TOR during outbound run: Euclidean distance between systematic search center and P_c (ED), directional deviation measured by means of systematic search center ($|DIR|$), misestimation of distance (DIS), extension of the first 100 m systematic search ($EXT100$).

the 8-m circle (Ansari-Bradley-Test: $DIR8$: $N = 102$, $p = 0.056$). This result was not confirmed when applying the minimization method ($DIRM$: $N = 130$, $p = 0.31$) or $DIR1$ ($N = 130$, $p = 0.53$). With regard to the other values of inbound run and systematic search, there were no remarkable differences found (Wilcoxon-test: all p-values> 0.5).

Integrated curvature of the outbound paths. The absolute value of the integrated curvature of the outbound paths $|\int \omega(t)\,dt| = |\phi_{\text{end}} - \phi_0|$ is not positively correlated with ED of the inbound run ($r_s = -0.041$, $N = 130$, $p = 1$). The same holds true for the results obtained by testing for correlations between $\int \omega(t)\,dt$ of outbound run and $DIR8$ ($r_s = -0.116$, $N = 102$, $p = 1$) and $DIRM$ ($r_s = -0.106$, $N = 130$, $p = 1$) of inbound run (Fig. III.27).
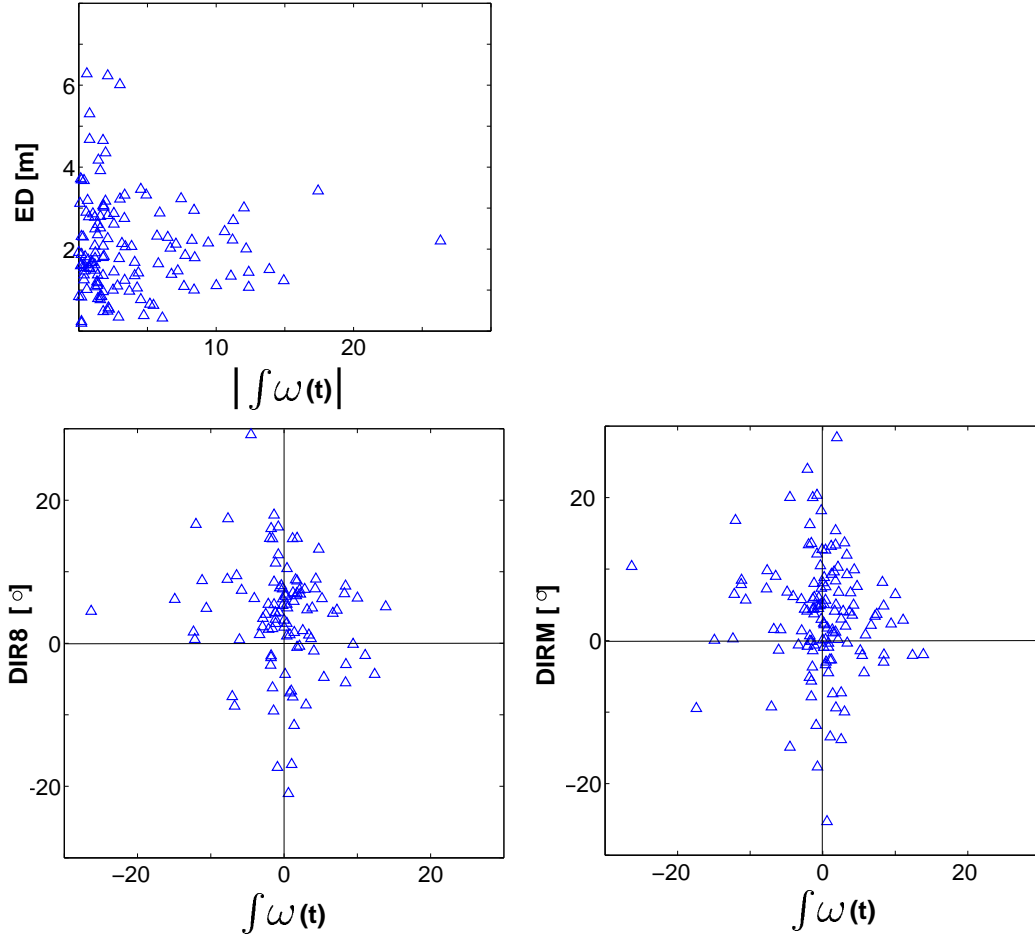
Figure III.27: Accuracy of the inbound runs of 130 ants as function of the integrated curvature during their natural outbound runs until a radial distance of 10 m has been reached. ED of the inbound runs was checked for correlations with $|\int \omega(t)\,dt|$ of outbound run [in radians, 2π for full turn], $DIR8$ and $DIRM$ were checked for correlations with $\int \omega(t)\,dt$ of outbound run.

By applying the same procedure for the accuracy determined by the systematic search behavior it became obvious that the results are in accordance with those obtained by analyzing the home runs. ED and DIR determined by means of the systematic search are not positively correlated with $|\int \omega(t)\, dt|$ and $\int \omega(t)\, dt$, respectively (ED: $r_s = -0.017$, $N = 98$, $p = 1$; DIR: $r_s = -0.190$, $N = 98$, $p = 1$, Fig. III.28).
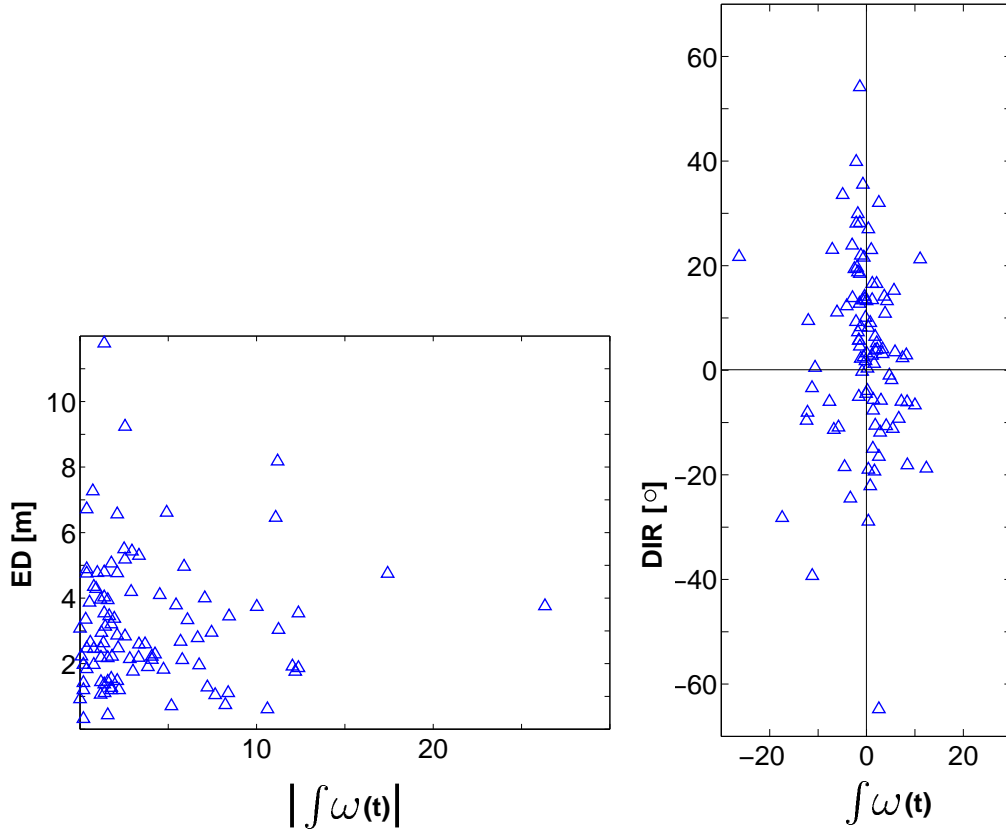
Figure III.28: ED and DIR measured via systematic search center as function of the integrated curvature ($|\int \omega(t)\, dt|$ or $\int \omega(t)\, dt$) of the natural outbound runs of 98 ants.

Integral of cubed curvature of outbound paths. $|\int \omega^3(t) \; dt|$ and $\int \omega^3(t) \, dt$ of the outbound runs are not correlated positively with ED, $DIR8$, and $DIRM$ of the inbound runs (ED: $r_s = -0.019$, $N = 130$, $p = 1$; $DIR8$: $r_s = -0.096$, $N = 102$, $p = 1$; $DIRM$: $r_s = -0.070$, $N = 130$, $p = 1$, Fig. III.29).
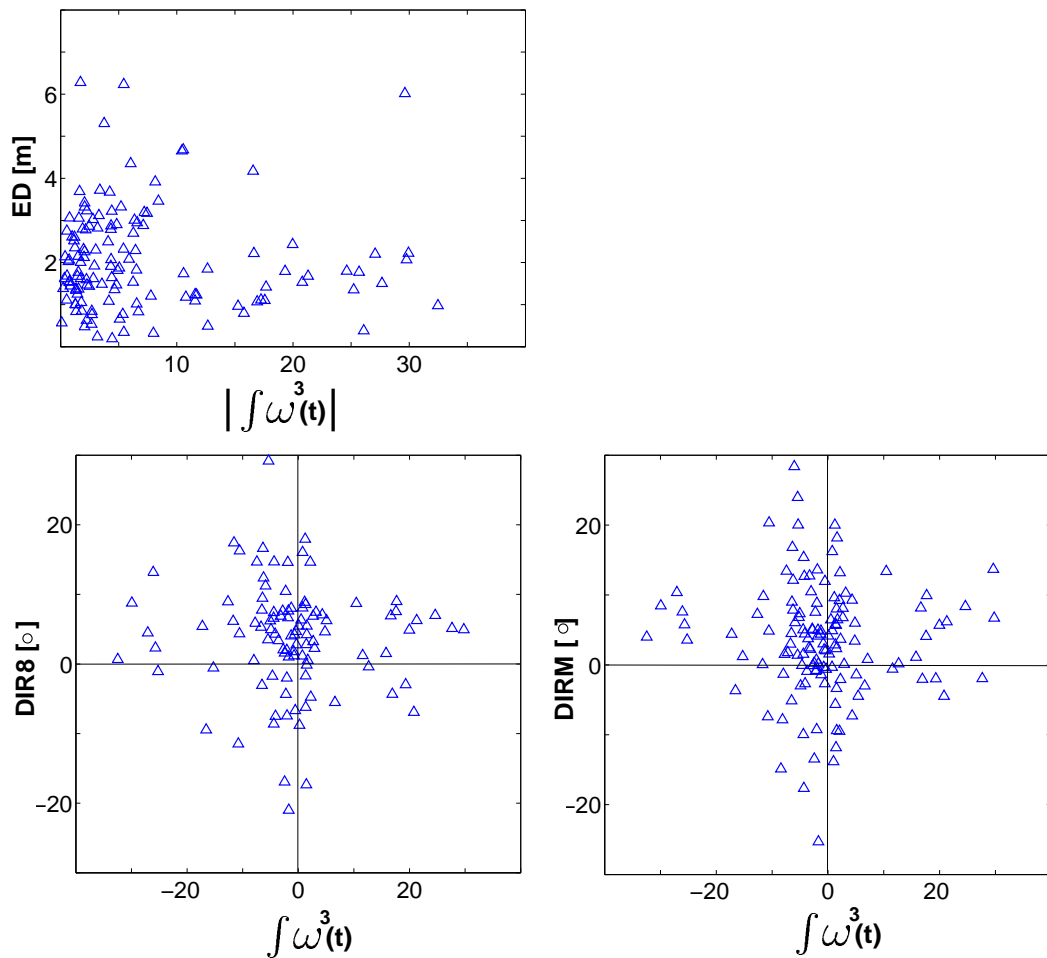
Figure III.29: Errors of inbound runs as function of $|\int \omega^3(t) \, dt|$ and $\int \omega^3(t) \, dt$ of outbound runs. For conventions see Fig. III.27.

Again, the results were confirmed when taking the systematic search center into account: no positive correlations between $|\int \omega^3(t)\, dt|$ of outbound run and ED (systematic search) ($r_s = -0.099$, $N = 98$, $p = 1$, Fig. III.30) and $\int \omega^3(t)\, dt$ of outbound run and DIR (systematic search) ($r_s = -0.264$, $N = 98$, $p = 1$) were detected.
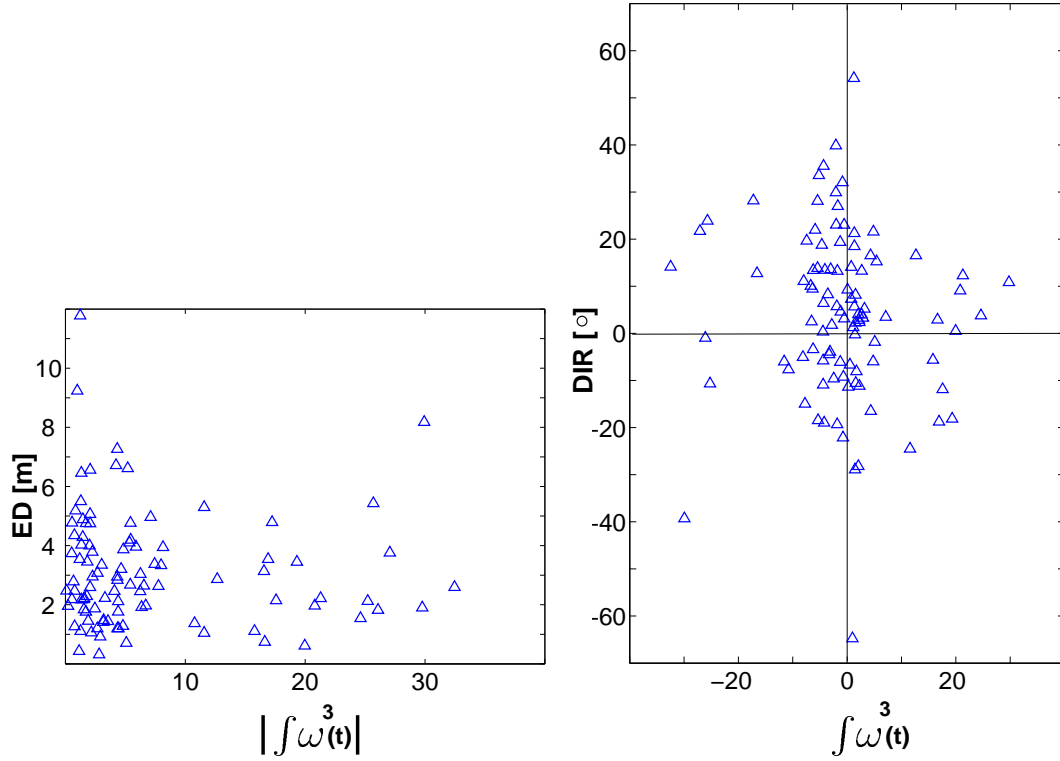
Figure III.30: Errors measured via the systematic search runs as function of $|\int \omega^3(t)\, dt|$ and $\int \omega^3(t)\, dt$ of outbound runs. For conventions see Fig. III.28.

3.2.3 Systematic errors

Both systematic errors, MW-error and leaky integrator LI (see II.3) were investigated. With respect to the MW-error, Euclidean distances (ED, ED_{MW}) and directional deviations (DIR, DIR_{MW}) were compared in order to see if the errors displayed by the ants can be explained by adapting homing direction and nest position according to the MW-error.

The LI, in contrast, is supposed to influence mainly the distance estimation of the ants. Therefore, ED and ED_{LI} as well as DIS and DIS_{LI} were compared to each other.

Error postulated by Müller and Wehner (MW-error). For the outbound runs of all 130 ants tested in experiment 1, the homing directions as predicted by the model of Müller and Wehner (Müller and Wehner 1988; Müller 1989) — MW-directions — were calculated. Although for the majority of runs the MW-directions did not differ essentially from the correct homing directions (median of angle differences $M = 0.18°$, interquartile range $IR = ((-4.83°) - 5.00°)$ there were some runs for which these directions differed from each other to a greater extent (Figs. III.31, III.32).
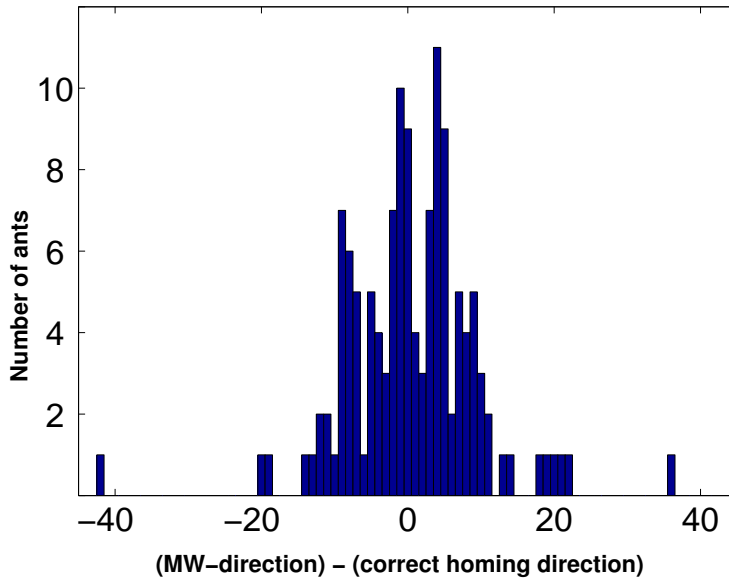
Figure III.31: Frequency distributions of the differences between correct homing directions and MW-directions of all ants of experiment 1, i.e. ants that were captured after having reached a distance of 10 m during their natural outbound runs. Values were obtained by subtracting the MW-directions from the respective correct homing directions.

At the crossing of the 0.5m circle there was no significant difference between the angular deviation from the correct homing direction $|DIR0.5|$ and the angular deviation from the MW-direction $|DIR0.5_{MW}|$ (see Tab. III.4); similar results were found for the comparisons between $|DIR1|$ and $|DIR1_{MW}|$ as well as between $|DIR2|$ and $|DIR2_{MW}|$ (Tab. III.4).

However, after having covered larger parts of the home vector the ants were much closer to the correct homing direction than to the MW-direction (see $|DIR8| < |DIR8_{MW}|$ and $|DIRM| < |DIRM_{MW}|$ in Tab. III.4).
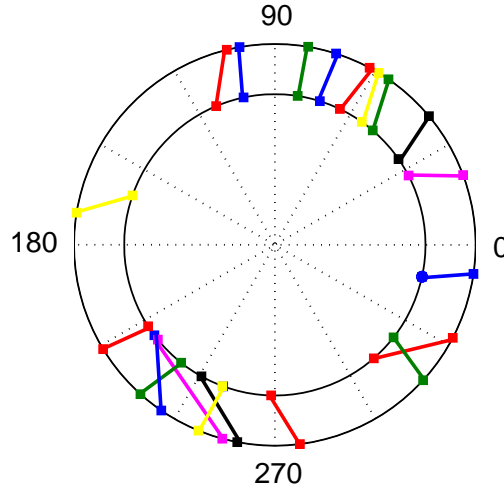
Figure III.32: Correct homing directions (outer circle) and MW-directions (inner circle) of 20 randomly chosen ants of experiment 1. Corresponding symbols show the respective directions for each ant.

With respect to the systematic search center, the directional deviations again did not differ significantly (see $|DIR|$ and $|DIR_{MW}|$ (SS) in Tab. III.4).

	N	deviation from correct homing direction	deviation from MW-direction	Wilcoxon signed-ranked test
$|DIR0.5|, |DIR_{MW}0.5|$	130	29.1°(13.19-48.22°)	26.95°(11.04-46.44°)	0.0895
$|DIR1|, |DIR_{MW}1|$	130	19.35°(9.81-39.22°)	19.32°(8.25-37.68°)	0.412
$|DIR2|, |DIR_{MW}2|$	130	14.13°(4.77-23.12°)	15.9°(7.21-24.28°)	0.531
$|DIR8|, |DIR_{MW}8|$	102	6.22°(3.18-8.73°)	8.28°(4.63-14.64°)	**0.007**
$|DIRM|, |DIR_{MW}M|$	130	5.12°(2.21-9.42°)	7.23°(4.65-12.97°)	**<0.0001**
$|DIR|, |DIR_{MW}|$ (SS)	98	10.9°(5.46-18.77°)	12.46°(5.70-19.23°)	0.315

Table III.4: The deviations (median M and interquartile range IR, in parentheses) from the correct homeward direction and the MW-direction are given for the directions determined by the crossing of the concentric circles with diameters 0.5 m, 1 m, 2 m, 8 m, and the via the minimization method for the home run as well as for the center of systematic search. P-values that are significant on a 5%-level are printed in bold types.

For the intersections with circles with short diameters the majority of ants deviated in the MW-direction (numbers of ants with tendency to MW-

direction given first: $DIR0.5$: 80 vs 50, one-sample Wilcoxon signed-rank-test: **p = 0.0086**, $N = 130$; $DIR1$: 80 vs 50, Wilcoxon: **p = 0.0086**, $N = 130$; $DIR2$: 75 vs 55, Wilcoxon: $p = 0.080$, $N = 130$), whereas for the crossing of the 8-m circle and the direction determined via the minimization method no significant tendencies were found ($DIR8$: 43 vs 59, Wilcoxon: $p = 0.1136$, $N = 102$; $DIRM$: 68 vs 62, Wilcoxon: $p = 0.5997$, $N = 130$). The direction to the center of the systematic search, indeed, displayed a significant tendency towards the Müller-Wehner-homing-direction (71 vs 27, Wilcoxon: **p < 0.001**, $N = 98$).

The corresponding tests for all ants whose correct homing direction and MW-direction differed by at least 5° confirmed the results obtained before by including all runs, though there was no significant tendency for the systematic search center detectable (see appendix, 4.1).

Finally, the whole procedure was repeated for all ants for which the respective directions differed by at least 10°. Though the sample sizes were quite small ($N = 19$ for $DIR0.5$, $DIR1$, $DIR2$, and $DIRM$, $N = 17$ for $DIR8$, and $N = 15$ for DIR systematic search), these tests also confirmed the results of the other procedures (with the only exception of the crossings of the 2 m circles). They are also given in the appendix (4.2).

The correct position of the nest P_c and the position adapted to the MW-error (P_{MW}) differed substantially (median M of distances between correct nest position and position according to MW-error $= 1.72m$, $IR = 1.52 - 2.05m$). The end point of each home run was closer to P_c (ED: $M = 1.78m$, $IR = 1.19 - 2.74m$) than to P_{MW} (ED_{MW}: $M = 2.16m$, $IR = 1.41 - 3.11m$, Wilcoxon signed-rank-test: $p = 0.0046$, $N = 130$, see Figs. III.33a, III.34a). Again, the results were confirmed if only ants were tested whose directions differed more than 5° or 10°, respectively (see appendix, 4.1 and 4.2).

Figure III.33: Positions of end point of home run and systematic search center relative to P_c and P_{MW}. P_c (○) and P_{MW} (+) are shown in relation to the end points of the home runs (a) or the systematic search centers (b), respectively, that are fixed at the origin (0/0).

The Euclidean distances of the systematic search centers to P_c (ED: $M = 2.62m$, $IR = 1.90m - 4.07m$) were not significantly smaller than those to

P_{MW} (ED_{MW}: $M = 2.72m$, $IR = 1.79m - 4.15m$, Wilcoxon: $p = 0.706$, $N = 98$, Figs. III.33b, III.34b). However, the tests for the two groups for which the directions differed by at least 5° or 10°, respectively, showed significant differences: in both cases, the systematic search centers were farther away from P_{MW} than from P_c (see appendix, 4.1 and 4.2).
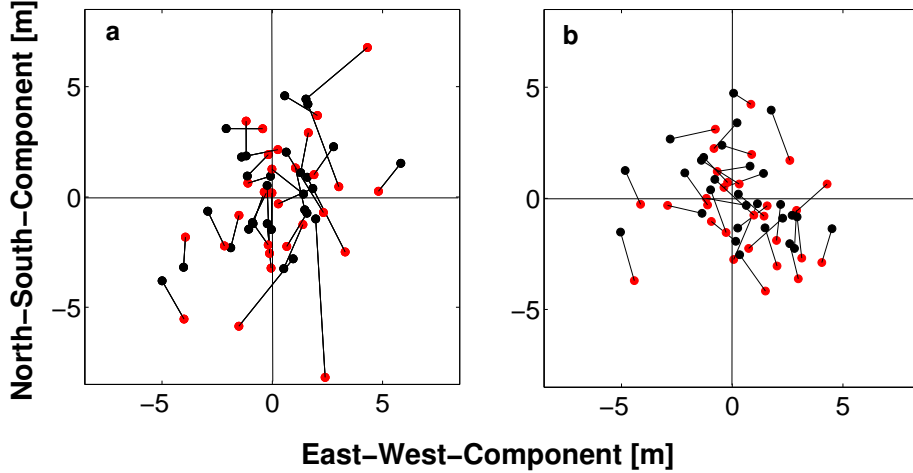
Figure III.34: Relative positions of end points of home runs and systematic search centers for 30 randomly chosen ants of experiment 1. As in Fig. III.33, the end of each home run (a) or the systematic search center (b) is fixed at the origin (0/0). P_c (black ∘) and P_{MW} (red ∘) for each ant are shown in relation to the end point of the home run or systematic search center, respectively, and connected via the respective line.

Leaky integrator. The distance predicted, if the Leaky Integrator (Sommer and Wehner 2004) was included ($\xi_L = 90m$, for details, see II.3) in the calculation of the home vector during the outbound run, was shorter than the correct distance of 10 m for most of the 130 ants ($M = 9.3m$, $IR = 9.14 - 9.48m$). The absolute value of the distance deviation DIS, i.e. $|DIS|$ — with respect to the correct distance of 10 m — measured via the end point of the home run ($M = 1.19m$, $IR = 0.52m - 2.02m$) was greater than $|DIS_{LI}|$ ($M = 0.99m$, $IR = 0.56m - 1.87m$, Wilcoxon: $p = 0.0586$, $N = 130$, Fig. III.35a), though this difference turned out not to be significant. With regard to the distance determined via the systematic search center there were no substantial differences to be found ($|DIS|$: $M = 1.16m$, $IR = 0.57 - 2.38m$; $|DIS_{LI}|$: $M = 1.13m$, $IR = 0.58m - 2.40m$, Wilcoxon: $p = 0.240$, $N = 98$, Fig. III.35b).

The comparison with regard to the Euclidean distances ED between end point of home run and P_c and nest position according to the Leaky Integrator (P_{LI}), respectively, revealed that the latter distance is shorter (ED: $M = 1.78m$, $IR = 1.19m - 2.74m$; ED_{LI}: $M = 1.81m$, $IR = 1.13m - 2.52m$; Wilcoxon: $p = 0.005$, $N = 130$, Fig. III.36a). The same holds true for the systematic search center: again, $ED > ED_{LI}$ (ED: $M = 2.62m$, $IR = 1.90m - 4.07m$; ED_{LI}: $M = 2.57m$, $IR = 1.57m - 3.79m$; Wilcoxon: $p < 0.001$, $N = 98$, Fig. III.36b).
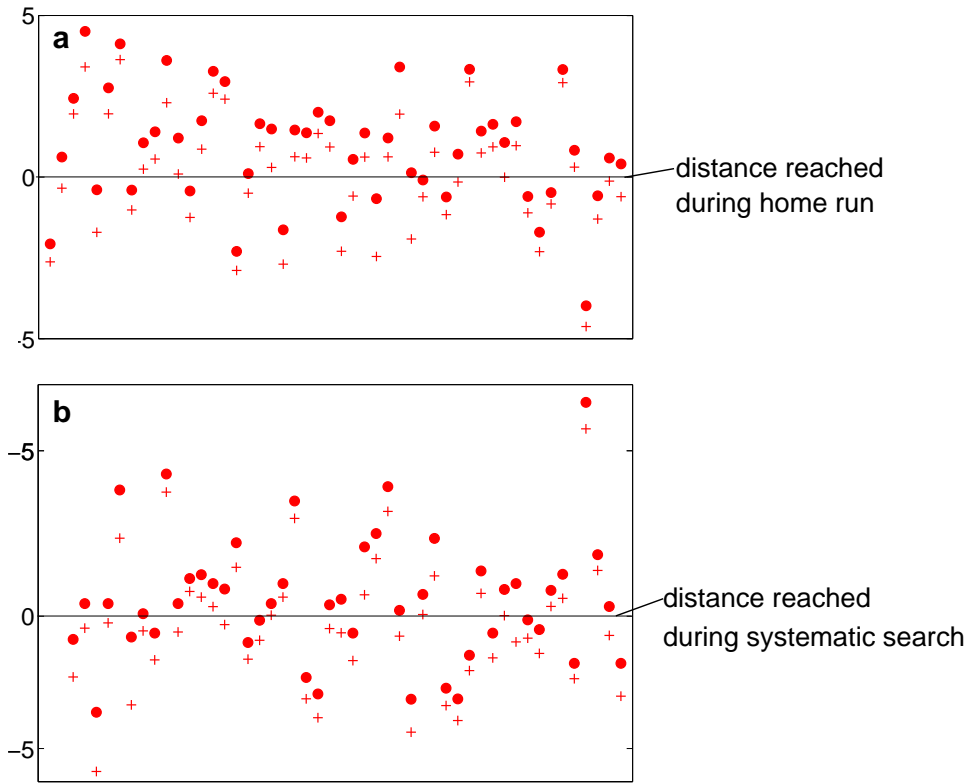
Figure III.35: Distance deviations with respect to correct homing distance (DIS) and homing distance according to LI (DIS_{LI}) of the home runs or systematic search centers of 50 randomly chosen ants. The distance reached by the ants, determined either via the end of the home run (a) or via systematic search center (b) is represented by the abscissa. The correct homing distance ($\circ$) and the homing distance predicted by LI ($+$) are shown in relation to the distance reached by each ant.
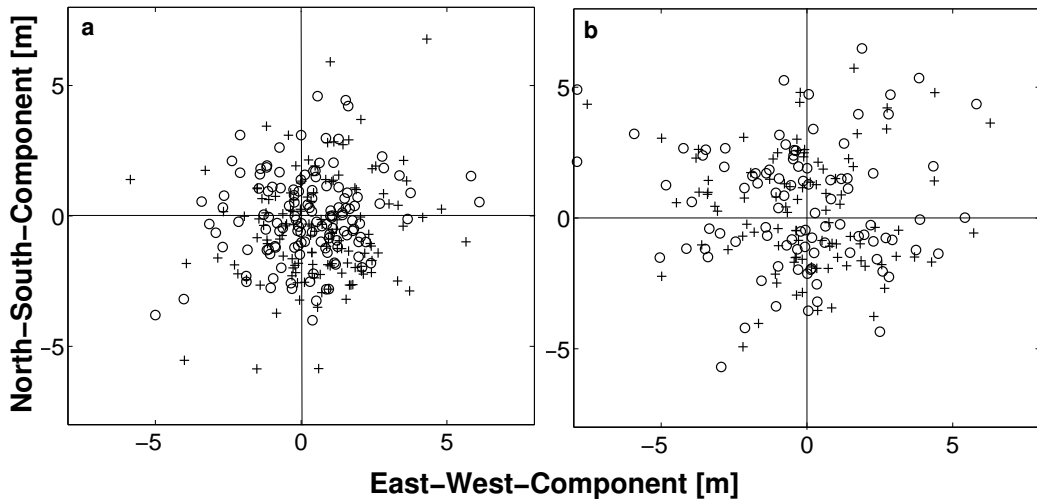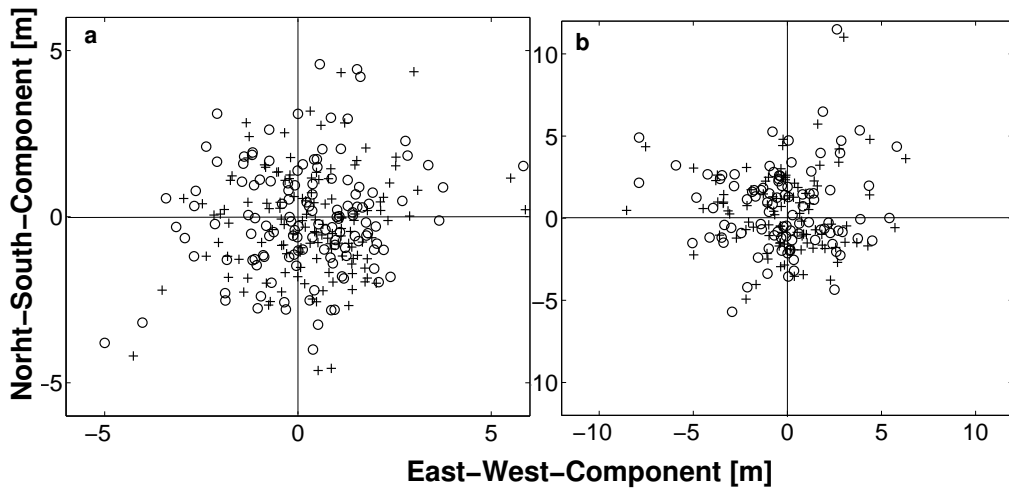

Figure III.36: Positions of end point of home run and systematic search center relative to P_c and P_{LI}. P_c ($\circ$) and P_{LI} ($+$) are shown in relation to the end points of the home runs (a) or the systematic search centers (b), respectively, that are fixed at the origin (0/0). Notice the different scale of a and b.

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3.2.4 Are there specific parts of the home runs accounting for the errors performed during the inbound run?

As described above (III.2.5.1), for each home run the deviation (in meters) from the beeline between point of release and correct nest position was calculated at the intersection point of the 1-m, 2-m, 4-m, and 6-m circles (Fig. III.37a). The signs of these deviations depended on the side from the beeline the ant was at the respective spot. As a result, 89 out of 130 ants stayed on the same side (Wilcoxon signed rank test: $N = 130$, $p < 0.0001$), i.e. the signs of the deviations did not change between 1-m and 6-m circle. Considering Fig. III.38, it becomes obvious that the home runs of the ants have a tendency to the left, i.e. the majority of the ants performs its home run on the left side of the beeline between point of release and correct position of the nest P_c.

With regard to the regression curves that were calculated for all ants (see also 2.5.1), striking negative correlations were found between the crossing point of the regression curve with the y-axis (a in Fig. III.37a) and its inclination curve (b in Fig. III.37a, Spearman correlation coefficient: $r_s = -0.546$, $p < 0.001$, $N = 130$, Fig. III.37b). That is, the hypothesis that if $a > 0$, then $b < 0$ and vice versa was confirmed.
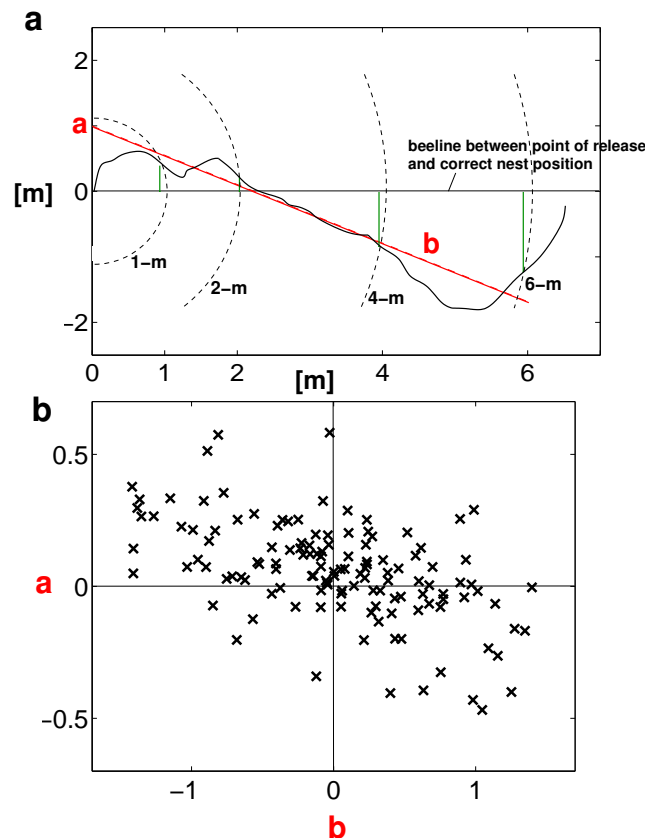
Figure III.37: (a) Deviations in meters from the beeline between point of release and correct nest position, i.e. from the correct home vector at intersection points with circles of 1 m, 2 m, 4 m, and 6 m radius (green), are shown for one specific home run. Also shown is the regression curve (red, a = crossing point with y-axis, b = inclination). (b) Correlations between the two variables of the regression curve, a and b, of all 130 ants of experiment 1. For more details: see text.
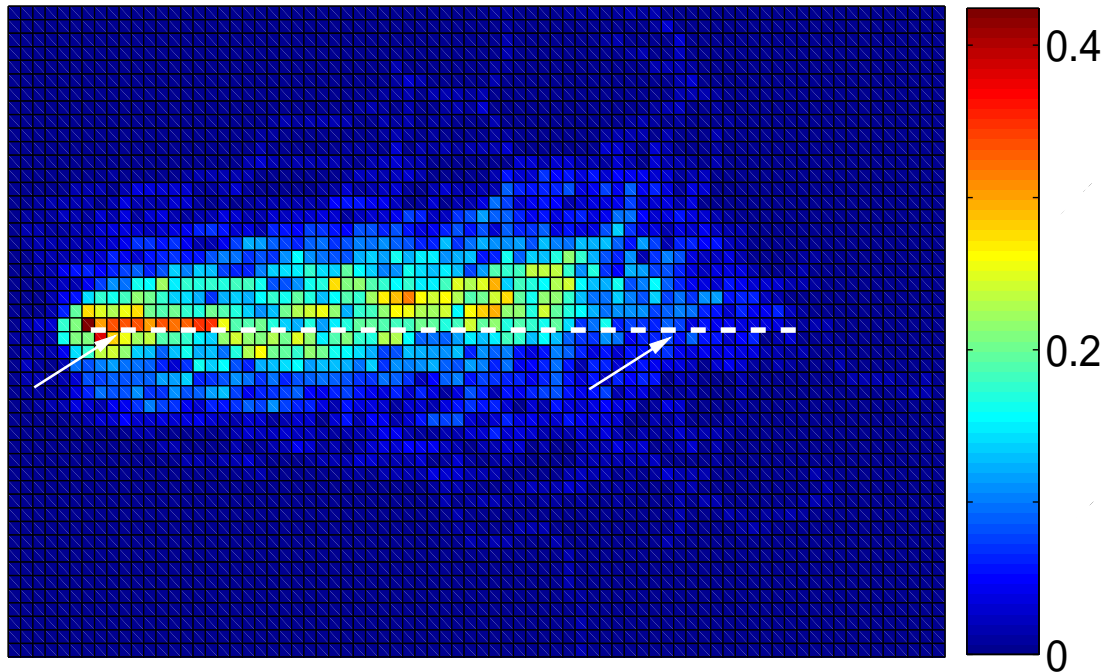
Figure III.38: Density plot of the home runs of 130 ants that were captured after 10 m on their natural outbound runs. For each square (size $0.2 \times 0.2\text{m}^2$) the path length divided by the total path length of all home runs was calculated. Density (%) is represented by the color of the respective squares (see colorbar on the right); left arrow indicates position of release, right arrow indicates correct nest position; white dashed line: beeline between nest and feeder.

3.2.5 Summary of experiment 1

The results obtained by observing and analyzing natural outbound runs with fixed distance and their home runs and systematic search patterns revealed that

- desert ants perform outbound runs generally showing a certain directional persistence

- the spatial conformation, i.e. tortuosity of their outbound runs varies from ant to ant, though these variations are limited

- the tortuosities of outbound runs of ants having covered the same distance during their outbound runs apparently does not account for inaccuracies during home run and systematic search behavior or for changes in the systematic search behavior's extension

- the number and values of the directional changes, measured as integrated curvature or integral of the cubed curvature, respectively, is neither correlated with any of the inaccuracies of home run and systematic search nor with the systematic search pattern

- in many cases the potential influence of the MW-error on homing direction and suspected nest position is very limited; if remarkable differences between correct homing direction and MW-direction were found, the ants were closer to the correct homing direction; in addition, the nest position assumed by the ants is closer to the correct nest position than to the nest position according to MW

- the Leaky Integrator LI predicts shorter distances for home runs; the distances covered by the ants during their home runs lay somewhere between the distance predicted by LI and correct distance; with respect to the nest position, the systematic search centers are closer to the nest positions calculated via the LI

3.3 Experiment 2: Natural outbound runs with varying distance

3.3.1 Comparison between six groups

Home run. There were no significant differences between the groups in terms of the accuracy of their inbound runs (Fig. III.39, III.40). The medians and interquartile ranges or mean angles of the errors displayed by the six groups during their inbound runs are given in Tab. III.5.
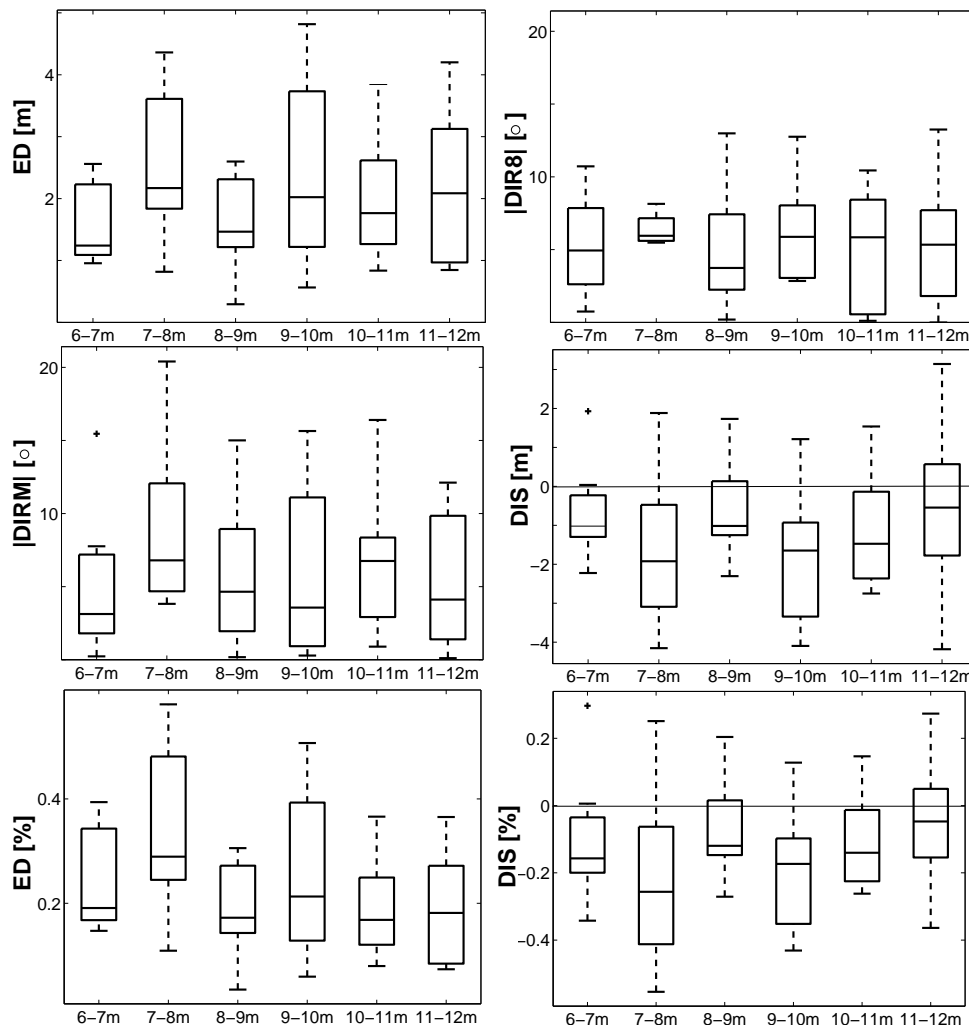
Figure III.39: ED, $|DIR8|$, $|DIRM|$, and DIS for the inbound runs of six groups of ants captured after having reached different radial distances during outbound run. Shown are medians, interquartile ranges, outliers and whiskers. FOR ED and DIS the values relative to the distance covered during the outbound run are also shown (in %). For abbreviations: see text.

In addition, the p-values yielded by conducting the Kruskal-Wallis-test are presented. With regard to the equality of variances of directional deviations no significant differences were found ($DIR8$: Levene's test = 0.896, $N = 44$, $p = 0.494$; $DIRM$: = 1.599, $N = 60$, $p = 0.176$).

The two most extreme groups (6-7 m and 11-12 m) did not differ noteworthy (TOR: Mann-Whitney: $p = 0.174$; ED, $|DIR8|$, $|DIRM|$, DIS: $p > 0.4$).
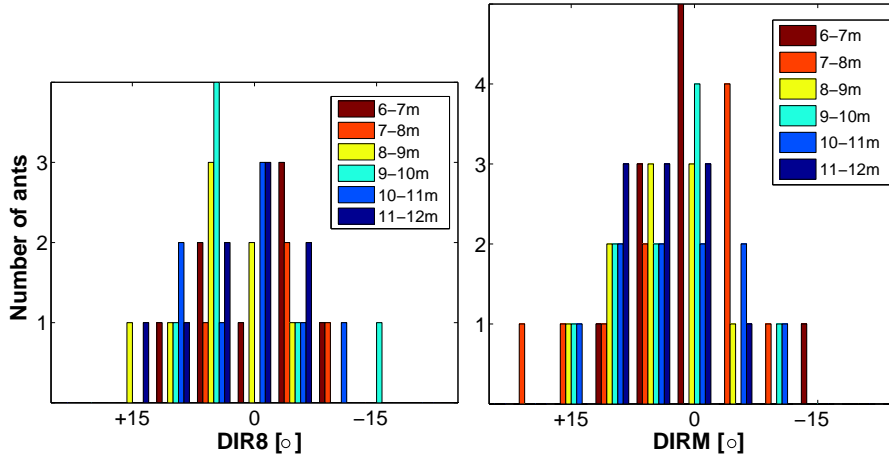
Figure III.40: Angular deviations from the correct homeward course for the same six groups as in Fig.III.39, measured as $DIR8$ (a) or $DIRM$ (b). X-axis: angular deviation; Y-axis: respective number of ants.

Systematic search behavior. With regard to ED and $|DIR|$ no remarkable differences could be found between the groups (Table III.5, Fig. III.41). However, there were striking differences in view of distance estimation DIS: the only group that overestimated the distance, i.e. the group whose outbound runs ranged from 8 to 9m, differed on a a 5%-level (Tukey's test) from two other groups: the ants that had covered 7-8m or 9-10m, respectively, during their outbound runs until capturing. These groups underestimated the distance covered heavily.

Though the extension of the systematic search runs differed among the groups, these differences turned out to be not significant, irrespective whether they were measured for the first 20 ($EXT20$) or 100 m ($EXT100$) (Table III.5, Fig. III.41).

With regard to the most two extreme groups (6-7 and 11-12 m), the latter group was less accurate with regard to the systematic search; however, the differences were not significant (ED: $p = 0.102$; DIR: $p = 0.086$; DIS: $p = 0.053$). The systematic searches of groups captured after longer distances were more spacious, but, again, they did not differ significantly ($EXT20$: $p = 0.059$; $EXT100$: $p = 0.171$).
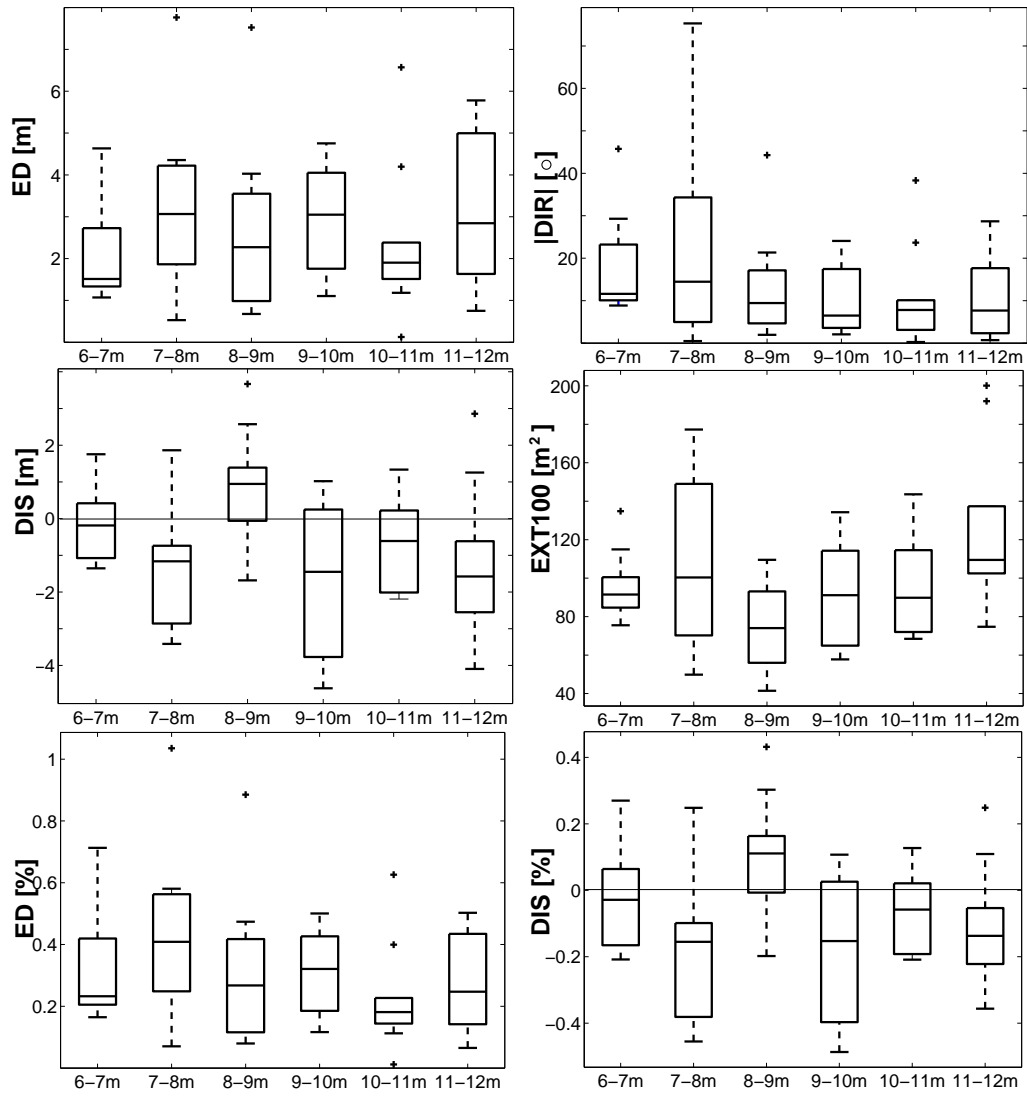
Figure III.41: Errors (ED, $|DIR|$, DIS) and extension $EXT100$ of the systematic search behavior of six groups of ants that had covered different distances before capturing during outbound run. ED and DIS are also shown as relative values (in %).

	6-7 m	7-8 m	8-9 m	9-10 m	10-11 m	11-12 m	p-value Kruskal-Wallis
ED HR	1.24m (1.09-2.23m)	2.17m (1.84-3.61m)	1.47m (1.22-2.31m)	2.02m (1.22-3.73m)	1.76m (1.26-2.62m)	2.09m (0.97-3.13m)	0.450
$|DIR8|$	5.29° (0.996)	6.38° (0.997)	5.00° (0.998)	6.17° (0.996)	5.03° (0.995)	5.49° (0.991)	***
$|DIRM|$	4.77° (0.997)	9.14° (0.996)	5.44° (0.997)	5.74° (0.996)	6.75° (0.997)	5.15° (0.997)	0.795
DIS	-1.02m (-1.29- -0.23m)	-1.92m (-3.09- -0.47m)	-1.02m (-1.25-0.13m)	-1.65m (-3.34- -0.09m)	-1.47m (-2.36- -0.14m)	-0.76m (-1.78-0.57m)	0.413
TOR	1.32m (1.24-1.34m)	1.24m (1.17-1.29m)	1.34m (1.24-1.42m)	1.33m (1.27-1.48m)	1.31m (1.29-1.33m)	1.24m (1.22-1.30m)	0.097
ED	1.51m (1.33-2.73m)	3.07m (1.86-4.22m)	2.27m (0.98-3.55m)	3.05m (1.76-4.05m)	1.90m (1.51-2.38m)	2.84m (1.63-5.00m)	0.469
$|DIR|$	18.28° (0.98)	20.73° (0.934)	13.29° (0.978)	10.22° (0.991)	10.54° (0.981)	10.34° (0.987)	0.332
DIS	-0.19m (-1.08-0.42m)	-1.16m (-2.86- -0.74m)	0.94m (-0.06-1.39m)	-1.45m (-3.77-0.25m)	-0.61m (-2.01-0.22m)	-1.58m (-2.55- -0.61m)	**0.029**
$EXT20$	14.79m² (11.87-18.27m²)	16.15m² (14.85-18.32m²)	14.86m² (13.18-18.85m²)	17.84m² (12.00-23.72²)	17.24m² (12.56-24.69²)	21.88m² (16.22-25.58²)	0.337
$EXT100$	91.49m² (84.69-100.51m²)	100.35m² (70.25-149.00m²)	74.04m² (55.97-93.12m²)	91.13m² (64.93-114.27m²)	76.60m² (72.02-114.54m²)	109.47m² (102.5-137.37m²)	0.092

Table III.5: Inbound run (rows 1-5) and systematic search behavior (6-10) of six groups of ants that were captured after having reached different distances during their outbound runs (6-7 m, ..., 11-12 m). Shown are medians M and interquartile ranges IR (in parentheses) for values measured in meters and mean angles MA and r-values (in parentheses) for deviations from directions. Sample sizes for inbound runs were 60 for each value, i.e. N=10 for each group; exception: $|DIR8|$ (N=44). Sample sizes for systematic search were 58 for each value; exceptions: $EXT20$: $N = 60$; $EXT100$: $N = 57$. ***: Due to the lower sample size, the Kruskal-Wallis-test could not be conducted.

3.3.2 Path lengths of all ants

All runs were pooled and their outbound path lengths determined. Then, it was checked for correlations between the length of the outbound runs and the accuracy of the path integrator. Their were no notable correlations found in view of the inbound run (ED: $r_s = 0.056$, $p = 0.673$, $N = 60$; $|DIR8|$: $r_s = 0.011$, $p = 0.941$, $N = 44$; $|DIRM|$: $r_s = -0.055$, $p = 0.678$, $N = 60$; DIS: $r_s = 0.011$, $p = 0.941$, $N = 60$; TOR: $r_s = 0.011$, $p = 0.941$, $N = 60$, Fig. III.42).

By analyzing the systematic search behavior a negative correlation between the overall length of the paths and the deviation from the correct homing direction — determined via the systematic search center ($|DIR|$) — was found, i.e. ants that had performed longer outbound runs showed smaller deviations from the correct homeward course (Spearman: $r_s = -0.350$, $p = 0.007$, $N = 58$). For all other values no notable correlations were found (ED: $r_s = -0.070$, $p = 0.602$, $N = 58$; DIS: $r_s = -0.069$, $p = 0.605$, $N = 58$; $EXT20m$: $r_s = 0.169$, $p = 0.197$, $N = 60$; $EXT100$: $r_s = 0.061$, $p = 0.653$, $N = 57$, Fig. III.43).

OVERALL LENGTH OF OUTBOUND RUN
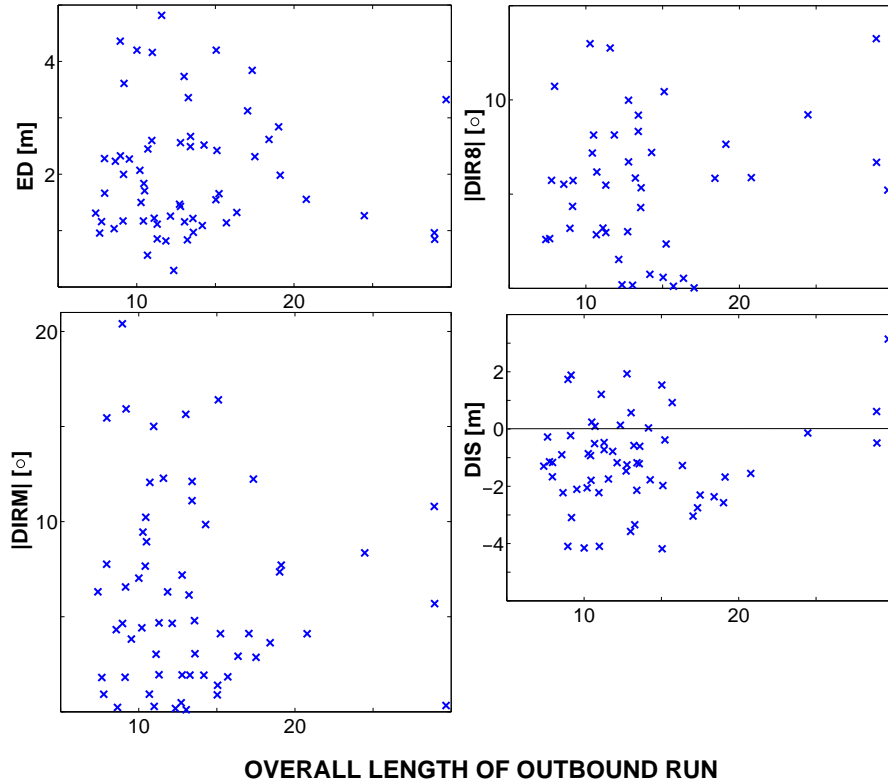
Figure III.42: Accuracy of inbound runs, measured via ED, $|DIR8|$, $|DIRM|$, DIS of ants that had covered different distances during their outbound runs as function of the overall length of the outbound runs.
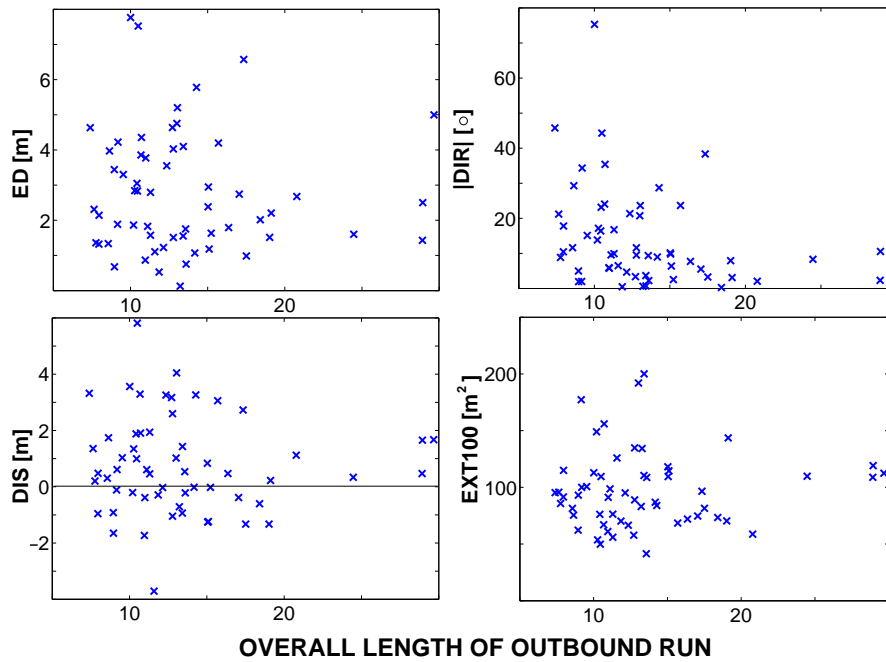
Figure III.43: Accuracy of systematic search behavior, determined by means of ED, $|DIR|$, DIS, $EXT100$, of ants that had covered different distances during outbound run as function of the overall lengths of their outbound runs.

3.3.3 Integrated curvature

For all runs the integrated curvature and the integral of the cubed curvature were calculated and tested for correlations with the accuracy of inbound run and systematic search behavior. Since all results were far away from being remarkable (all p-values for Spearman-correlation coefficients > 0.15, most of them > 0.5) they are not presented here (they can be seen in the appendix, 4.3).

3.3.4 Summary of experiment 2

The conclusions from experiment 2 are the following:

- different distances covered during natural outbound runs (ranging from 6 to 12 m) are not correlated with the errors displayed during home run and systematic search behavior

- with respect to the systematic search, there exists a (though not significant) tendency that ants which have reached a greater distance when captured are less accurate and extend their systematic search patterns

- the results of experiment 1 are confirmed: the path length of natural outbound runs does not account for errors in the path integration system

- as in experiment 1, both integrated curvature and integral of cubed curvature of natural outbound runs are not correlated with the errors displayed during home run and systematic search

3.4 Experiment 3: Differences between untrained and trained ants

3.4.1 Comparison between the groups

Outbound run. The outbound runs of trained ants were, when recorded, much straighter than those of the untrained ants, as measured via the L/d-index (TOR trained: $M = 1.12$, $IR = 1.07 - 1.20$, $N = 40$; TOR untrained: $M = 1.79$, $IR = 1.48 - 2.28$, $N = 130$; Mann-Whitney U-Test for independent samples: $p < 0.001$; see Fig. III.44). Furthermore, outbound runs of trained ants were also straighter than their inbound runs (Wilcoxon paired-sample-test: $p = 0.002$, $N = 40$).
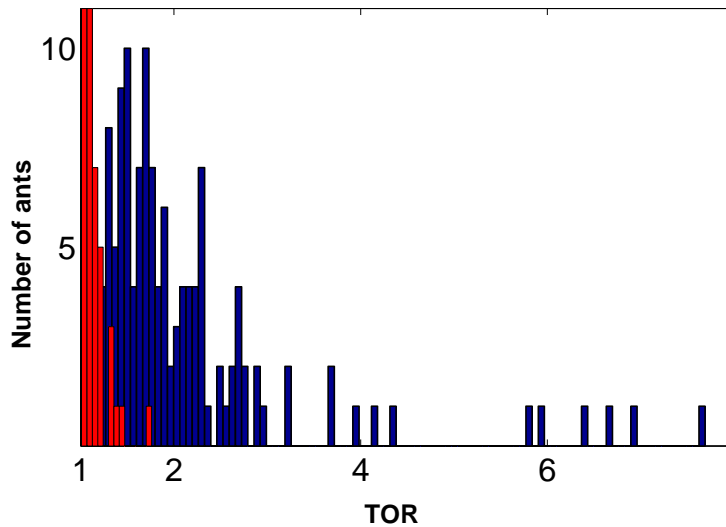
Figure III.44: Histogram of tortuosity values TOR - measured as L/d - of the outbound runs of 130 untrained (blue) and 40 trained (red) ants.

Inbound run. The ants that had been trained before performed substantially fewer errors as compared to the untrained ants: There is a striking difference with regard to ED (untrained: $M = 1.81m$, $N = 130$; trained: $M = 1.40m$, $N = 40$, Mann-Whitney-U-test: $p = 0.0052$, Figs. III.45, III.46). The deviations from the correct homing direction, irrespective whether determined after 8 m ($|DIR8|$) or via the minimization method ($|DIRM|$) differed on a significant level, too ($|DIR8|$: untrained: mean angle MA $=6.86°$, $r = 0.996$, $N = 102$, trained: $MA = 4.34°$, $r = 0.998$, $N = 39$, Mardia-Watson-Wheeler: $p = 0.05$, Fig. III.47a; $|DIRM|$: untrained: $MA = 6.71°$, $r = 0.995$, $N = 130$, trained: $MA = 4.33°$, $r = 0.998$, $N = 40$, Mardia-Watson-Wheeler: $p = 0.002$, Fig. III.47b). Whereas the trained ants estimated the homing distance correctly, the untrained ants underestimated it, resulting in a significant difference between both groups (DIS untrained: $M = -0.72m$, $N = 130$; trained: $M = -0.02m$, $N = 40$; Mann-Whitney: $p = 0.0019$, Fig. III.45). The inbound paths of trained ants were straighter than those of the untrained ants (TOR untrained: $M = 1.33$, $N = 130$; trained: $M = 1.21$, $N = 40$, Mann-Whitney: $p < 0.001$, Fig. III.45).

The variance with regard to the directional deviations when measured via $DIRM$ was higher for untrained ants (Ansari-Bradley-Test: $DIRM$:
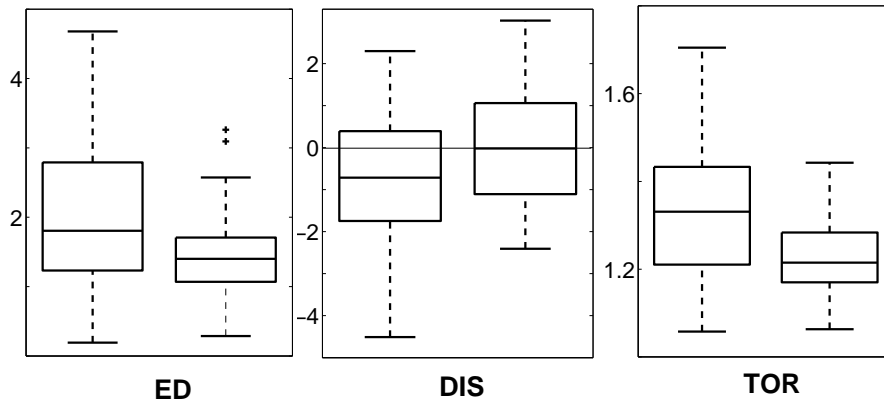
Figure III.45: *ED, DIS, TOR* of inbound runs of untrained (left) and trained (right) ants. Boxplots give the median, 25% and 75% quartiles, whiskers and outliers (+).
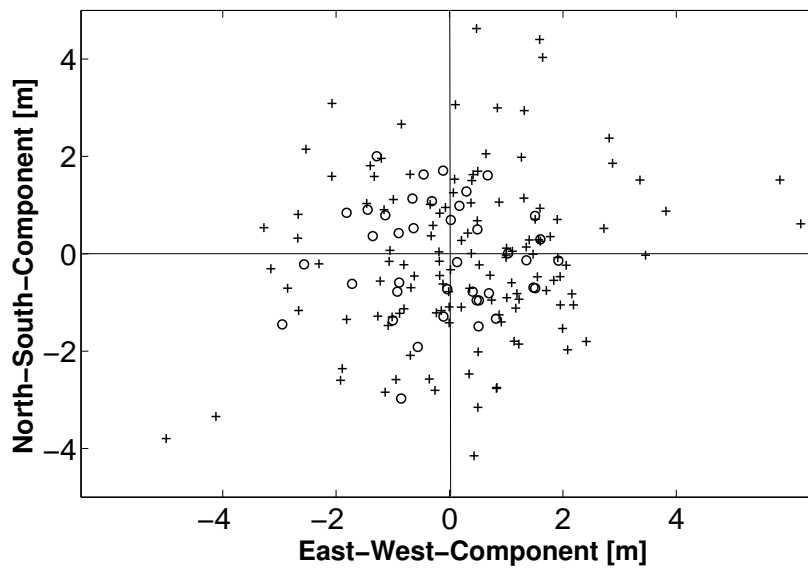
Figure III.46: End points of the home runs of untrained (+) and trained (∘) ants. The correct position of the nest is at the origin (0,0).
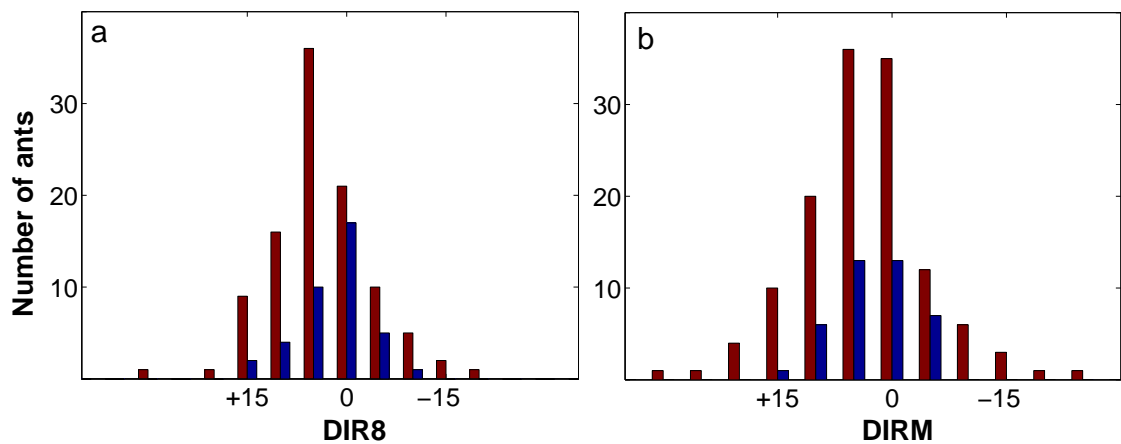
Figure III.47: Deviations of untrained or trained ants from the correct homeward direction. Directions measured at the intersection of the 8-m circle (a, *DIR8*) or via the minimization method (b, *DIRM*).

$N = 130, 40$, $p = 0.042$); when measured via $DIR8$ the variances of both groups did not differ on a significant level ($DIR8$: $N = 130, 40$, $p = 0.251$).

Systematic search behavior. With regard to the systematic search behavior, no significant differences between both groups were found (ED: untrained: $M = 2.66m$, $N = 98$; trained: $M = 2.92m$, $N = 38$; Mann-Whitney: $p = 0.803$; $|DIR|$ untrained: $MA = 13.55°$, $N = 98$, trained: $MA = 10.73°$, $N = 38$; Mardia-Watson-Wheeler: $p = 0.31$, Figs. III.48, III.49, III.50). Untrained ants underestimated the distance between release point and correct nest position, whereas the trained ants overestimated slightly; again, the difference was not significant (DIS untrained: $M = -0.66m$, $N = 98$; trained: $M = 0.13m$, $N = 38$, Fig. III.48).
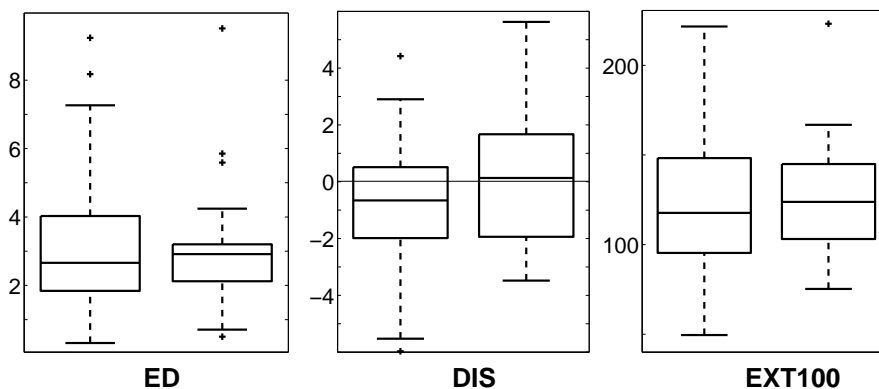
Figure III.48: ED, DIS, and $EXT100$ of the systematic search of untrained (left) and trained (right) ants.
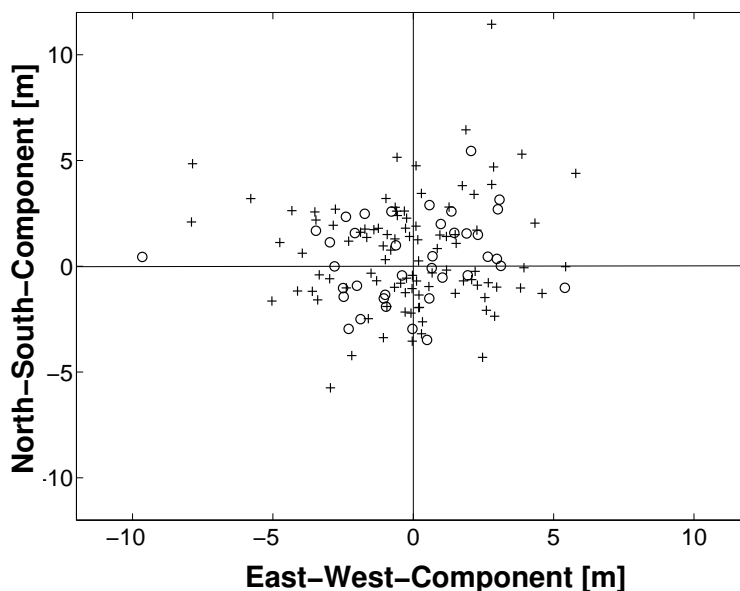
Figure III.49: Systematic search centers of untrained (+) and trained (○) ants. The correct position of the nest is at (0,0).

$EXT20$ and $EXT100$ did not differ remarkably ($EXT20$ untrained: $M = 20.65m^2$, $N = 130$; trained: $M = 21.29m^2$, $N = 40$; Mann-Whitney: $p = 0.734$; $EXT100$ untrained: $M = 119.49m^2$, $N = 73$; trained: $M = 124.83m^2$, $N = 37$; Mann-Whitney: $p = 0.463$, Fig. III.48).
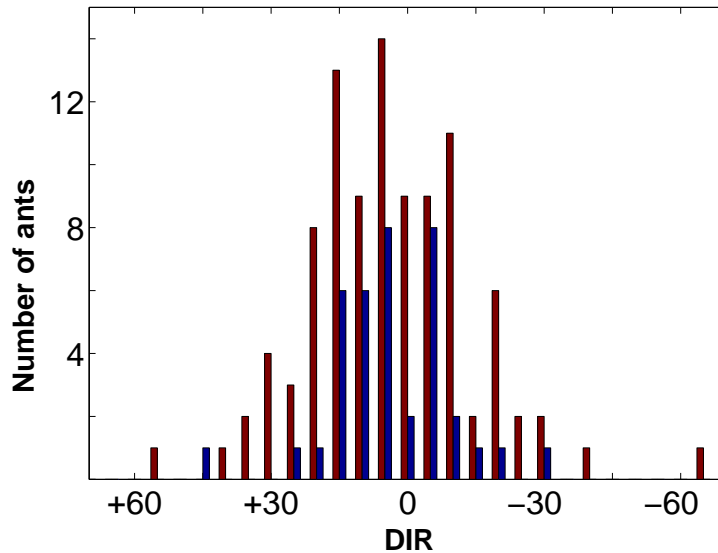
Figure III.50: Deviations of untrained or trained ants from the correct homeward direction. Directions measured by means of the systematic search center.

3.4.2 Comparing ants which have performed outbound runs of equal tortuosity

12 trained and 12 untrained ants whose outbound runs displayed the same tortuosity were compared against each other with regard to the accuracy of their path integrator, measured by means of inbound run and systematic search. The p-values given here are *one-tailed* (see III.2.5.3).

Inbound run. The 12 trained ants performed smaller errors during the inbound runs than the untrained ones (Fig. III.51). The Euclidean distances ED amounted to smaller values (untrained: $M = 1.87m$; trained: $M = 1.38m$, $N = 12$; Wilcoxon signed-rank-test for pairwise comparisons: $p = 0.017$, Fig. III.51), they deviated less from the correct homing direction ($|DIR8|$ untrained: $M = 7.54°$, $N = 9$; trained: $M = 3.27°$, $N = 12$; Wilcoxon: $p = 0.043$, $N = 9$; : $|DIRM|$ untrained: $M = 4.69°$; trained: $M = 3.71°$, $N = 12$; Wilcoxon: $p = 0.154$). Untrained ants underestimated the distance (DIS: $M = -0.93m$, $N = 12$), whereas trained ants overestimated it ($M = 0.81$, $N = 12$; Wilcoxon: $p = 0.017$).

Finally, the home runs of trained ants were less tortuous than those of the untrained ants (TOR untrained: $M = 1.28m$, $N = 12$; trained: $M = 1.23m$, $N = 12$; Wilcoxon: p=0.026).
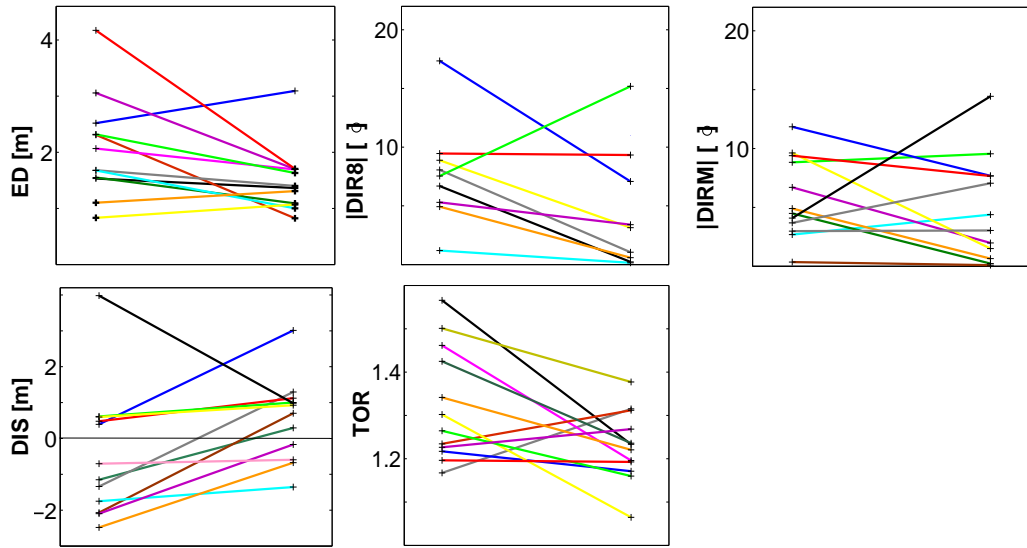
Figure III.51: ED, $|DIR8|$, $|DIRM|$, DIS, and TOR of inbound runs of 12 untrained (left) and trained (right) ants that had displayed equal values for tortuosity during their outbound runs.

Systematic search. The characteristic values of the systematic search behavior did only differ marginally (see Table III.6).

	untrained ants	trained ants	Wilcoxon-test
ED	2.41m (2.01m-4.0m)	3.0m (2.55m-3.54m)	p=0.107
$|DIR|$	12.01° (10.18-14.95°)	11.31° (4.76-14.74°)	p=0.395
DIS	-0.14m (-1.23m-0.70m)	-1.94m (-2.98m-2.04m)	p=0.289
$EXT20$	19.92m^2 (16.66-23.56m^2)	26.27m^2 (14.46-30.35m^2)	p=1.0
$EXT100$	120.68m^2 (85.48-167.17m^2)	122.27m^2 (102.26-136.81m^2)	p=0.96

Table III.6: Differences between the values obtained for the systematic search of 12 untrained and 12 trained ants. Shown are medians M and interquartile ranges IR (in parentheses). Sample size for the untrained ants were 12 (exception: $EXT100$, N=5), for the trained ants 11, since for one ant no systematic search center could be determined. Thus, sample sizes for all Wilcoxon tests for pairwise comparisons were 11 (with exception of $EXT100$).

3.4.3 Summary of experiment 3

The comparison between untrained and trained ants revealed that

- the outbound runs of trained ants are much less tortuous than those of untrained ants

- trained ants perform smaller errors during their home runs than untrained ants

- with regard to the systematic search center, no remarkable differences between both groups are found, but untrained ants extend the ranges of their systematic search less than trained ants

- the comparison of ants which had performed outbound runs with equal tortuosity indicates that the differences concerning the home runs are due to the training procedure rather than to the lower tortuosity of the trained ants' outbound runs

3.5 Experiments 4,5,6, and 7

The training experiments investigated whether the lengths of outbound path or the 'portions' that have been covered by the ants before being captured had effects on the accuracy of the home runs and the systematic search as well as on the extension of the systematic search. Additional experiments should reveal what happens if ants are captured during their outbound runs with and without landmarks.

3.5.1 General

The Euclidean distances (ED) between end of home run or systematic search center, respectively, and correct position of the nest are the most relevant quantities describing the accuracy of the ants' path integrator. Therefore, for experiments 4,5,6, and 7 the Euclidean distances obtained by the end point of the home run and the systematic search center as well as the extensions of the systematic search patterns during the first 40 m shall be presented here. Though neither given nor discussed here, the remaining values defined and calculated for the analysis of experiments 1, 2, and 3 ($|DIR8|$, $|DIRM|$, DIS etc.) have been calculated for experiments 4, 5, 6, and 7, too (see appendix, 4.4, 4.5.1, 4.6, 4.7).

Euclidean distances (ED) and directional deviations ($DIR8$, $DIRM$, DIR) of 50%-in ants and 25%-in ants were calculated via two different methods (see III.2.5.4) and the results were compared. There were no significant differences for the values of the inbound runs that were investigated (ED, $|DIR8|$, $|DIRM|$, Wilcoxon tests for pairwise comparisons: p 0.3, for data see appendix, 4.5.2). With regard to the systematic search center, ED and $|DIR|$ differed on a 5%-level (50%-in ants) or $5-10$%-level (25%-in ants). Thus, the differences caused by the deviations from the beeline displayed by ants captured during inbound or outbound run, would have been negligible (e.g. 'correct' homing direction for 50%-inbound ants either 90° or 88.71°, depending on the method). Nevertheless, the directions and nest or feeder positions were calculated with consideration of the deviations from the beeline.

3.5.2 Comparison of all groups

All 7 groups (5-m ants, 10-m ants, 20-m ants, 50%-in ants, 25%-in ants, 50%-out ants, 50%-out-LM-ants) were compared with respect to ED, measured either via end point of home run or systematic search center, respectively. The very same groups were also compared with regard to the extension of the systematic search pattern for a path length of 40m ($EXT40$); for this analysis the 0%-in ants were also included.

The 50%-out and 50%-out-LM ants were divided into two groups before the Kruskal-Wallis test was performed. For each group the subgroup that continued the preceding outward journey and the subgroup returning to the nest were analyzed separately. The exact numbers for the partitioning as well as the numbers of ants that were excluded from further analyses are given below (see III.3.5.7).

ED home run (and run to the feeder). The Kruskal-Wallis-variance analysis for ED between the end points of the home runs and the correct positions of the nest (or between end of runs to feeder and correct position of the feeder, respectively, for 50%-out and 50%-out-LM ants) were highly significant (Kruskal-Wallis-one-way-analysis of variance= 59.67; $p < 0.001$, number of groups= 9, total sample size= 315). Thus, there were significant differences with regard to the different groups, making it worthwhile to compare them against each other.

ED systematic search for the nest (or the feeder). Again, a Kruskal-Wallis-variance analysis for ED between the center of the systematic search and the correct position of the nest (or the feeder in case of 50%-out and 50%-out-ELM ants) was performed. With regard to the 50%-out ants, which continued their outbound run to the feeder, a systematic search center could be determined only for four ants. Due to this small sample size, this group was excluded from Kruskal-Wallis and further analysis. Again, this test revealed highly significant differences between all groups (Kruskal-Wallis= 59.03, $p < 0.001$, number of groups= 8, total sample size= 302) and, therefore, it was also worthwhile and necessary to compare the EDs between the groups.

Extension of the systematic search behavior over the first 40 m EXT40. Since the extension measurements for ants captured shortly before entering the nest (0%-in ants) were included, the Kruskal-Wallis analysis was conducted for 9 groups (the sample size for the 50%-out ants heading for the feeder again was only N=4 and, therefore, this groups was excluded again). As before, the differences among the groups were highly significant (Kruskal-Wallis= 146.78, $p < 0.001$, number of groups= 9, total sample size= 345); as were the differences in mean variation (Kruskal-Wallis= 30.147, $p < 0.001$).

3.5.3 Experiment 4: Different distances of outbound runs

In Fig. III.52 three-dimensional density profiles for 5-m, 10-m, and 20-m that include both home run and systematic search behavior are shown. For each square (size 0.5×0.5 m^2) the path lengths of all ants divided by the total path lengths of all ants have been calculated.
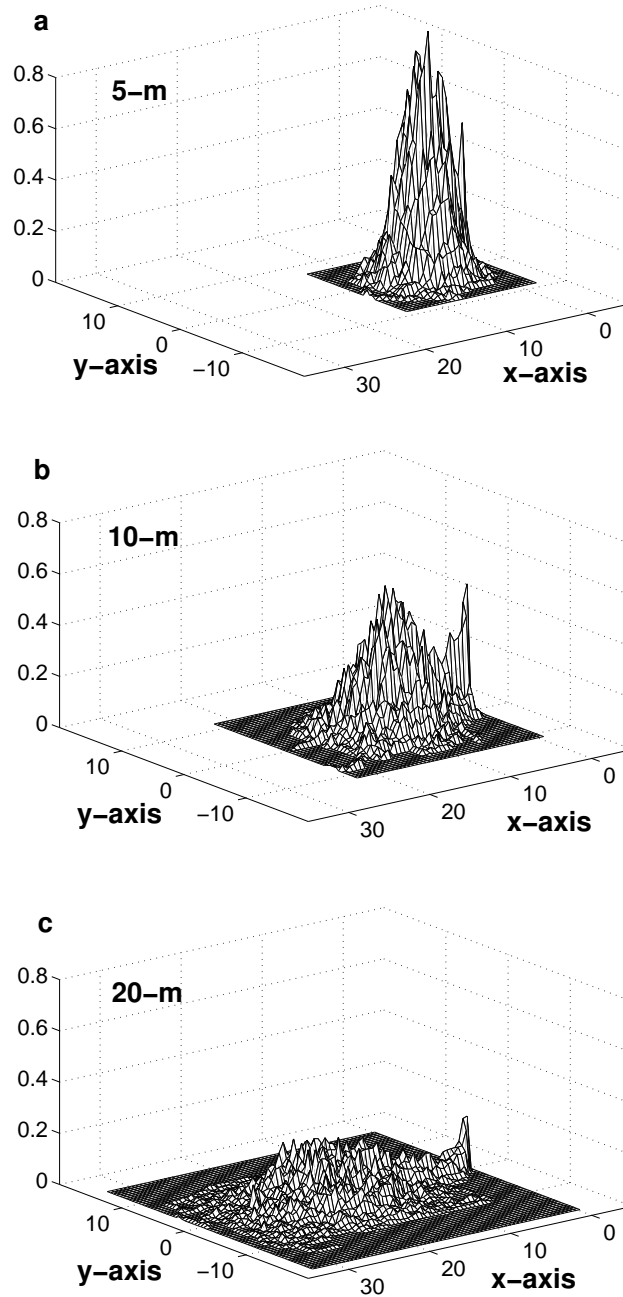
Figure III.52: Density profiles of home runs and systematic search behaviors of (a) 5-m, (b) 10-m, and (c) 20-m ants. Start point of the home run at (0/0), correct position of nest at (5/0) for 5-m ants, (10/0) for 10-m ants, and (20/0) for 20-m ants. The z-axis displays the percentage of the path lengths within the respective square (size 0.5×0.5m^2) divided by the total path lengths of all ants.

Home run. After longer foraging trips the ant's accuracy in pointing to the nest position is reduced, i.e. the accuracy is affected by the length of the preceding foraging trip. Ants that returned from a feeder 10 m and 20 m away from the nest started their systematic search behavior farther away from the correct nest position than ants that returned from a distance of only 5m (ED: 5-m ants: $M = 1.27m$, $IR = 0.79 - 1.78m$, $N = 51$; 10-m ants: $M = 2.45m$, $IR = 1.04 - 3.87m$, $N = 53$; 20-m ants: $M = 2.47m$, $IR = 1.68 - 4.07m$, $N = 50$; Tukey's posthoc test: 5-m vs 10-m $p = 0.002$, 5-m vs 20-m $p < 0.001$, 10-m vs 20-m $p = 0.631$, Figs. III.53a, III.20). The test for systematic tendencies revealed that 5-m and 10-m ants overshoot heavily, whereas 20-m ants underestimate the distance to cover to the nest (p-values for all three groups < 0.01, Wilcoxon test). 5-m and 10-m ants showed no striking preferences for one side of the nest (Wilcoxon: $p > 0.4$), whereas 20-m ants start their systematic search mainly east of the correct nest position (Wilcoxon: $p = 0.034$).

Figure III.53: Accuracy of the path integrator. (a) Euclidean distances (ED) between the end of the home run and the correct position of the nest for three groups of ants (5-m, 10-m, 20-m) captured at the feeder. (b) Euclidean distances (ED) between the center of the systematic search and the correct position of the nest for the same groups of ants captrued at the feeder. Boxplots give the median, 25% and 75% quartiles, whiskers and outliers (+).

Systematic search behavior. The Euclidean distance ED between the center of the systematic search and the correct position of the nest increased with increasing foraging distance (ED 5-m ants: $M = 2.0m$, $IR = 1.56 - 2.51m$, $N = 49$; 10-m ants: $M = 3.04m$, $IR = 2.33 - 4.07m$, $N = 41$; 20-m ants: $M = 4.30m$, $IR = 2.89 - 5.79m$, $N = 49$; Tukey's posthoc test: 5-m vs 10-m $p = 0.045$, 5-m vs 20-m $p < 0.001$, 10-m vs 20-m $p = 0.007$, Fig. III.53b, III.20). As for the end points of the home runs, 5-m and 10-m ants overshoot, whereas 20-m ants underestimated the distance to the nest (5-m and 20-m ants significant on a 5%-level, 10-m ants: $p = 0.08$). Preferences for the eastern or western side of the correct nest position were not significant for any of the groups.

Range of systematic search. The systematic search patterns, measured as extension during the first 40 m ($EXT40$) were compared for the same

three groups. As for ED, the ants that had returned from a distance of only 5 m differed dramatically from those that that had foraged over longer distances. The difference between 10-m ants and 20-m ants is also striking (5-m ants: $M = 37.77m^2$, $IR = 32.04 - 43.23m^2$, $N = 45$; 10-m ants: $M = 66.28m^2$, $IR = 54.08 - 76.28m^2$, $N = 35$; 20-m ants: $M = 77.81m^2$, $IR = 62.72 - 91.20m^2$, $N = 50$; Tukey's posthoc test: 5-m vs 10-m $p = 0.045$, 5-m vs 20-m $p < 0.001$, 10-m vs 20-m $p = 0.003$, Fig. III.54). Hence, the ants seem to be aware of the correlation that obviously exists between the errors accumulated during path integration and the foraging distance (Fig. III.53), and respond accordingly by broadening their search pattern with increasing foraging distance. Fig. III.54 does not only show the values for the range of the first 40 m of systematic search, but also three-dimensional search density profiles that are obtained by measuring the path lengths all ants displayed within certain squares (0.5m×0.5m) and dividing them by the total path length of the systematic search of all ants. Again, 5-m ants showed the smallest and 20-m ants the highest variation, though only the difference between 5-m ants and each group of 10-m and 20-m ants turned out to be significant.
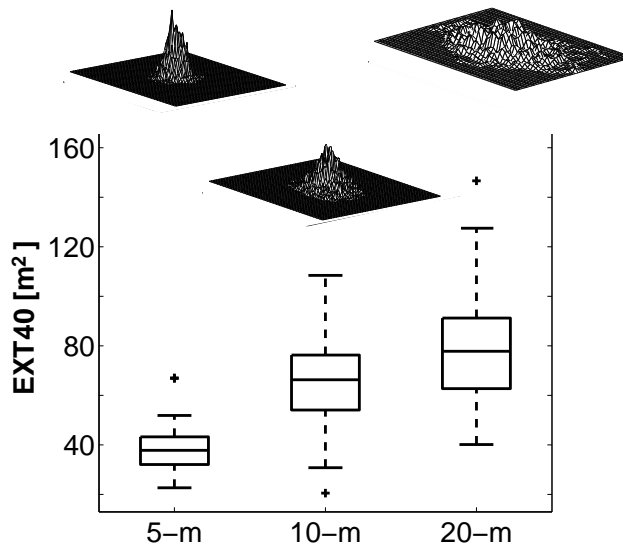
Figure III.54: Areas covered during the first 40m of systematic search of 5-m, 10-m, and 20-m ants. Conventions as in Figure III.53. Corresponding three-dimensional search-density profiles are shown above.

3.5.4 Summary of experiment 4

The results can be summarized as follows:

- the longer the distances of foraging excursions, the larger the errors occurring during path integration

- the ants adapt their systematic search strategy by extending their search patterns with increasing foraging distance

3.5.5 Experiment 5: Ants captured during their inbound runs

Do the ants respond to the deviation from the correct homeward course at the point of capture? With regard to the 50%-in ants, the deviation angle from the correct homeward direction (straight to north) at the point of capture, calculated via the distance measured between beeline feeder-nest and point of capture (see III.2.5.4) had no influence on the direction the ants were heading towards during the second half of their trip ($DIR8$: Spearman: $r_s = -0.145$, $p = 0.435$, $N = 31$; $DIRM$: $r_s = 0.077$, $p = 0.597$, $N = 50$, Fig. III.55a). That means, the ants do not compensate errors accumulated during the first half of their return trip during the second half (if this had been the case, there should have been a negative correlation).
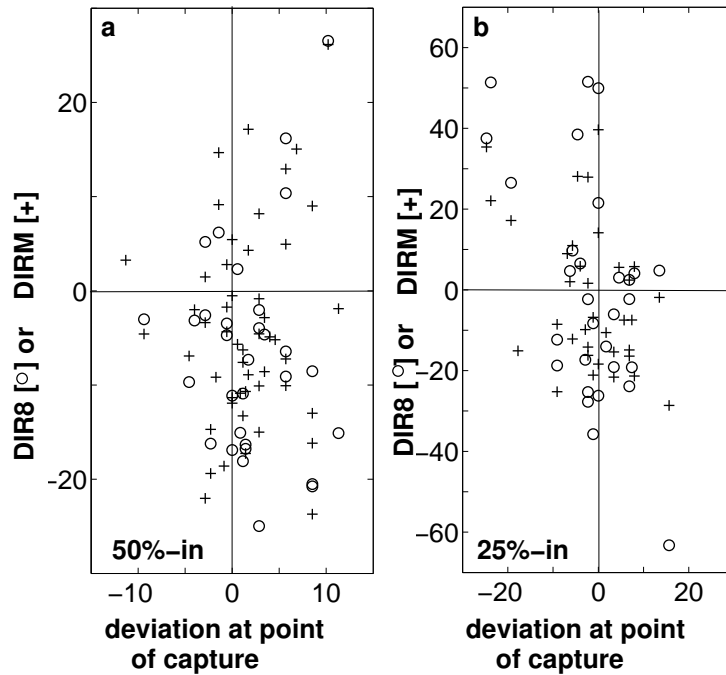
Figure III.55: a) Feasible interrelations between angular deviation from correct homeward course measured at the point of capture (x-axis) and angular deviation from course to north during the second half of the home run (y-axis) of 50%-in ants, measured via $DIR8$ ($\circ$) and $DIRM$ (+). b) Feasible interrelations between deviation from correct homeward course at the point of capture (x-axis) and deviation from northern course during the third quarter of the home run (y-axis) of 25%-in ants, measured by the aid of $DIR8$ ($\circ$) and $DIRM$ (+).

25%-in ants were tested in the same way. But, for these ants negative correlations between the direction headed towards until captured and the direction during the last quarter of the inbound run could be found ($DIR8$: Spearman: $r_s = -0.363$, $p = 0.049$, $N = 30$; $DIRM$: $r_s = -0.348$, $p = 0.04$, $N = 35$, Fig. III.55b). Thus, the ants seem to compensate their errors during the home run mainly within the 'final approach to the nest'.

Home run. Although 50%-in and 25%-in ants were trained to the same distance of 20m, and therefore had the same home vector stored at the feeder, the 25%-in ants were more accurate in terms of pointing at the correct nest

position (ED: $M = 1.79m$, $IR = 0.93 - 2.37m$, $N = 35$) than the 50%-in ants (ED: $M = 2.78m$, $IR = 1.85m - 3.64m$, $N = 50$; Tukey's post-hoc test: $p = 0.039$, see Fig. III.56a).

The errors displayed by 50%-in ants were quite similar to those of the 20-m and 10-m ants (Tukey's test for both comparisons: $p > 0.8$), but differed from those of the 5-m ants ($p < 0.001$, Fig. III.56a).

The 25%in-ants, in contrast, differed dramatically from the 20-m ants ($p < 0.001$), whereas the differences to 10-m ants were not significant ($p = 0.104$), and those to the 5-m ants were not worth mentioning ($p = 0.996$, Fig. III.56a).

50%-in ants undershot the distance and preferably deviated to the east (Wilcoxon: both p-values < 0.01); for 25%-in ants no significant tendencies could be found.
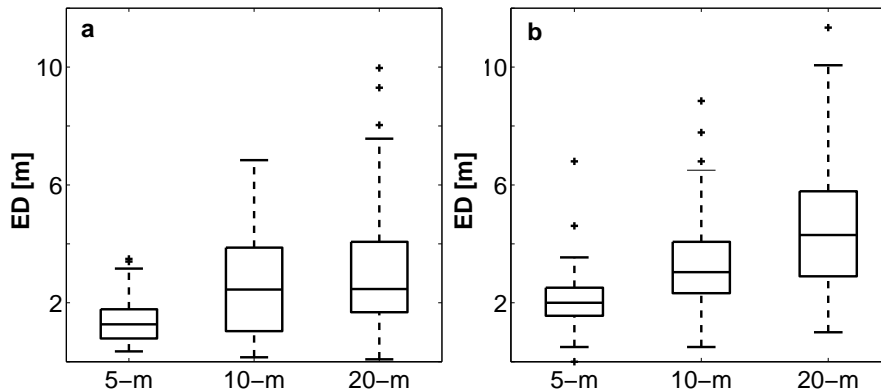

Figure III.56: Accuracy of the path integrator. (a) Euclidean distances ED between the end of the home run and the correct position of the nest for 50%-in and 25%-in ants; 5-m, 10-m, and 20-m are also shown for comparison. (b) Euclidean distances ED between the center of the systematic search and the correct position of the nest for the same two groups and the groups for comparisons.

Systematic search behavior   The accuracy of the path integrator measured by means of systematic search center showed no relevant discrepancies between 50%-in and 25%-in ants (ED 50%-in ants: $M = 3.82m$, $IR = 2.89 - 5.92m$, $N = 48$; 25%-in ants: $M = 3.64m$, $IR = 2.48 - 4.60m$, $N = 49$; Tukey's test: $p = 0.394$, see Fig. III.56b). 50%-in ants did not differ from 20-m ants ($p = 0.981$) and only slightly from 10-m ants ($p = 0.111$), but

significantly from 5-m ants ($p < 0.1001$, Fig. III.56b). 25%-in ants, however, were less accurate than 5-m ants ($p = 0.002$) but more accurate than 20-m ants ($p = 0.044$) and did not differ from 10-m ants ($p = 0.996$, Fig. III.56b).

50%-in as well as 25%-in ants underestimated the distance to the nest, but both groups showed no substantial preferences for one side of the nest where they were starting their systematic search behavior.

Range of systematic search.   For the comparison of the systematic search patterns of the first 40 m $EXT40$ of the systematic search runs the 0%-in ants were included. The range of this group's search patterns ($EXT40$: $M = 39.18m^2$, $IR = 30.91 - 46.58m^2$, $N = 50$) was much smaller than those of 50%-in ants ($M = 62.15m^2$, $IR = 48.71 - 72.80m^2$, $N = 48$) and 25%-in ants ($M = 57.13m^2$, $IR = 45.18 - 68.13m^2$, $N = 49$;Tukey's test for all comparisons: $p < 0.001$, see Fig. III.57); the latter groups did not differ significantly ($p = 0.927$). 50%-in ants did not differ from the 10-m ants ($p = 0.966$), but from the 5-m and 20-m ants ($p < 0.001$, Fig. III.57) in view of $EXT40$. The ranges of the 25%-in ants, indeed, were greater than those of 5-m ants ($p < 0.001$) but smaller than the ranges of the 20-m ants ($p = 0.001$). They resembled the systematic search ranges of the 10-m ants ($p = 0.519$, Fig. III.57). 0%-in ants showed smaller ranges than all other groups ($p < 0.001$) with the exception of 5-m ants ($p = 0.999$, Fig. III.57).
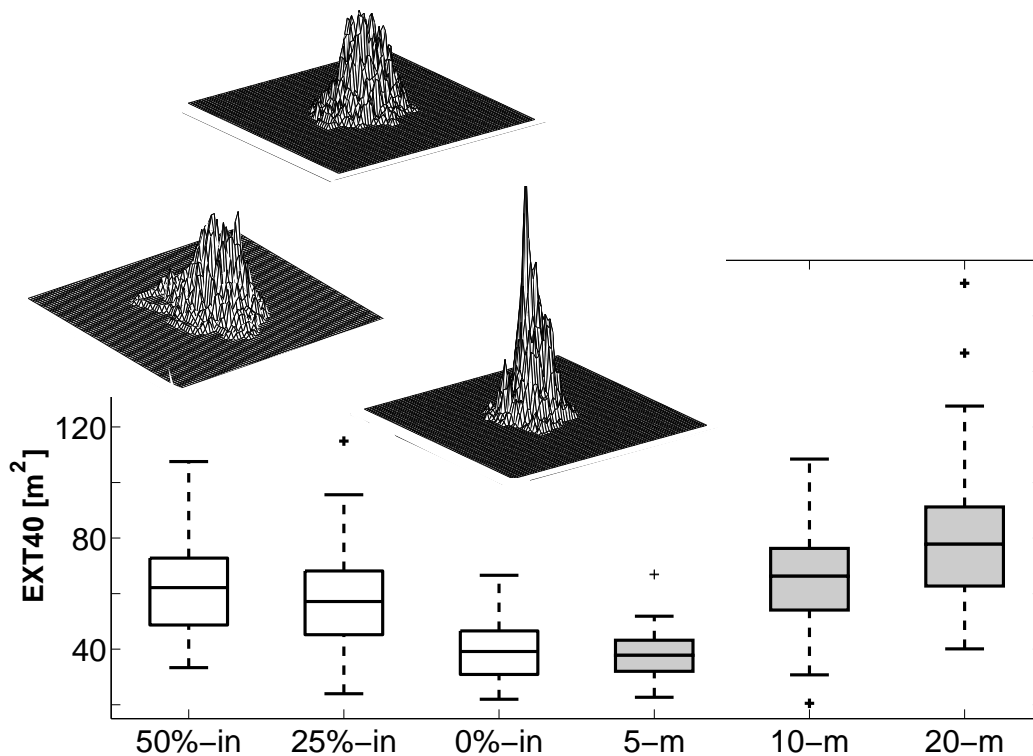
Figure III.57: Areas covered by the first 40 m of systematic search ($EXT40$) of 50%-in, 25%-in, and 0%-in ants. The three groups' extensions of experiment 4 are given for comparison. Corresponding search-density profiles are shown above.

3.5.6   Summary of experiment 5

To sum up, the results of experiment 5 brought evidence that

- homing desert ants start their compensation for directional errors during the inbound run during the last part of the run

- though trained to the same distance, the errors of 50%-in and 25%-in ants differ (measured via the end point of home run): 25%-in ants display small errors that are comparable to 5-m ants and smaller than those of 50%-in ants whose errors differ only marginally from 20-m and 10-m ants

- when determined by means of the systematic search center, no differences between 50%-in and 25%-in ants can be observed; 50%-in ants are similar to 20-m and 10-m ants, 25%-in ants to 10-m ants

- 0%-in ants show smaller systematic search patterns than 25%-in ants and 50%-in ants whose patterns do not differ remarkably and are similar to those of 10-m ants

3.5.7 Experiments 6 and 7: Ants captured during their outbound runs (with or without landmarks).

Do the ants continue their foraging path or return to the nest?
Based upon the 5-m circle, 35 out of 50, i.e. 70% of the 50%-out ants aborted their foraging run and returned to the nest. 6 ants continued their preceding foraging run, whereas 9 ants did not cover at least 50% of one of the possible routes (outbound- or inbound) and, therefore, were excluded from this analysis. Thus, a significant majority of 50%-out ants rather returned to the nest instead of carrying on the foraging run (Wilcoxon test for one sample: $p < 0.001$, $N = 41$, see Figs. III.58, III.59).

The ants trained and tested with the presence of landmarks (50%-out-LM ants) gave a different impression: only 21 out of 38 ants returned to the nest, 13 reeled off their vector to the feeder (Wilcoxon test: $p = 0.174$, $N = 34$, Figs. III.58, III.59) and 4 stayed more or less around the point of release.
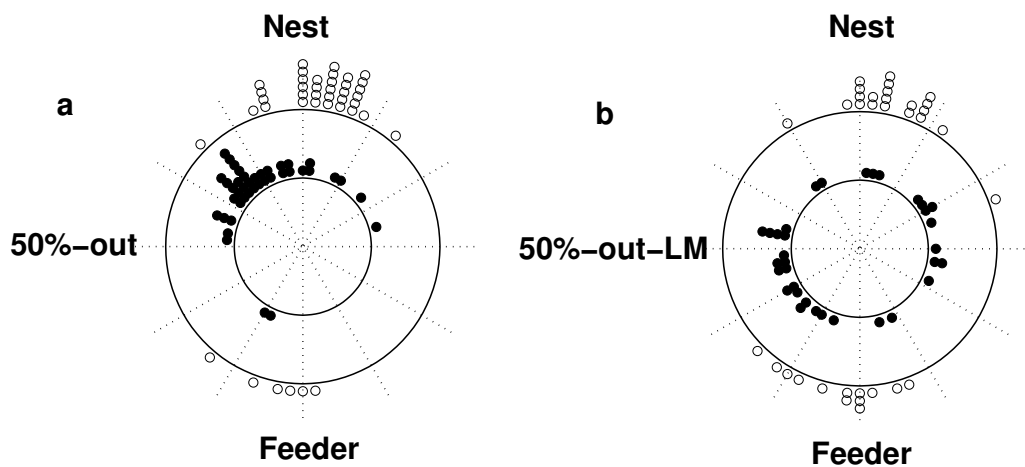
Figure III.58: Directions towards which 50%-out ants (a) or 50%-out-LM ants (b) were heading towards after 1m (inner circle) or 5m (outer circle), respectively.

Thus, the ratios between ants trained and tested without (35:6) and with landmarks (21:13) were different (Fisher's exact test: $p = 0.032$, $N = 75$).

If the 1-m circle was used as a benchmark, the difference between these two groups was even more striking (without LM: 39 ants heading for the nest and 2 heading for the feeder; with LM: 16 ants heading for the nest and 18 for the feeder, Fisher's exact test: $p < 0.0001$, Figs. III.58, III.59). However, since the 5-m circle appeared to be the more meaningful parameter (a number of ants headed for the nest or feeder, respectively, for 1 to 3 metres, but then changed the direction by 180° to run of the vector to the feeder or the nest, respectively) the values obtained using the 5-m circle were used for further analysis and for comparison with other groups.
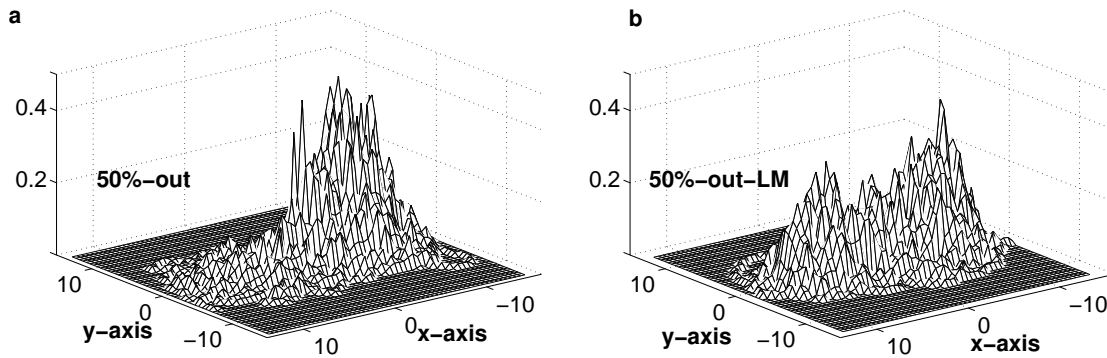
Figure III.59: Density profiles of home runs and systematic search behaviors of (a) 50%-out, and (b) 50%-out-LM ants. Point of release at (0/0), position of nest at (-10/0), position of feeder at (10/0).

Home run or run to the feeder. Figure III.60a shows ED between end of home run or run to feeder and the correct position of nest or feeder, respectively, for all four groups. The four groups, i.e. 50%-out ants heading for the nest (ED: $M = 2.39m$, $IR = 1.55 - 3.28m$, $N = 35$), heading for the feeder ($M = 3.49m$, $IR = 2.33 - 4.78m$, $N = 6$), 50%-out-LM ants heading for the nest ($M = 4.00m$, $IR = 2.95 - 4.67m$, $N = 21$), and 50%-out-LM ants heading towards the feeder ($M = 1.80m$, $IR = 0.71m - 2.94m$, $N = 13$) did not differ on a significant level (all p-values > 0.08).

All four groups did not substantially differ from the 10-m ants and 50%-in ants (the groups that had the same distance to cover, at least if compared with the ants heading for the nest) and the 20-m ants, which had been trained to the same distance (Tukey's test: all p-values>0.2, see also Fig. III.60a).

Also, all groups heavily underestimated the distance to the nest or feeder, respectively (Wilcoxon: all p-values < 0.01), but only the 50%-out ants showed a directional preference, with the majority of the ants starting the systematic search pattern on the right side of the nest (Wilcoxon: $p < 0.001$, all other p-values > 0.2).

Systematic search behavior All ants that returned to the nest - irrespective whether landmarks were present or not - searched for the nest entrance. On the other hand, some of the ants that continued their foraging run did not start a systematic search for the feeder but, after not finding the feeder immediately, also returned to the nest and searched for it. In particular, only 4 ants out of the 50%-out ants heading for the feeder started a systematic search at the suspected position of the feeder; the remaining ants did not. Therefore, only for 4 ants of this group a systematic search center as well as the extension of the systematic search could be determined. That is why this group was excluded from this part of the analysis. With regard to the 50%-out-LM ants heading for the feeder, one ant did not search for it. Again, this ant was excluded from the analysis of the systematic search behavior.

As for the home runs and runs to the feeder, the values for ED obtained by taking the center of the systematic search into account revealed no significant differences between the groups, as can be seen in Fig. III.60b. The p-values
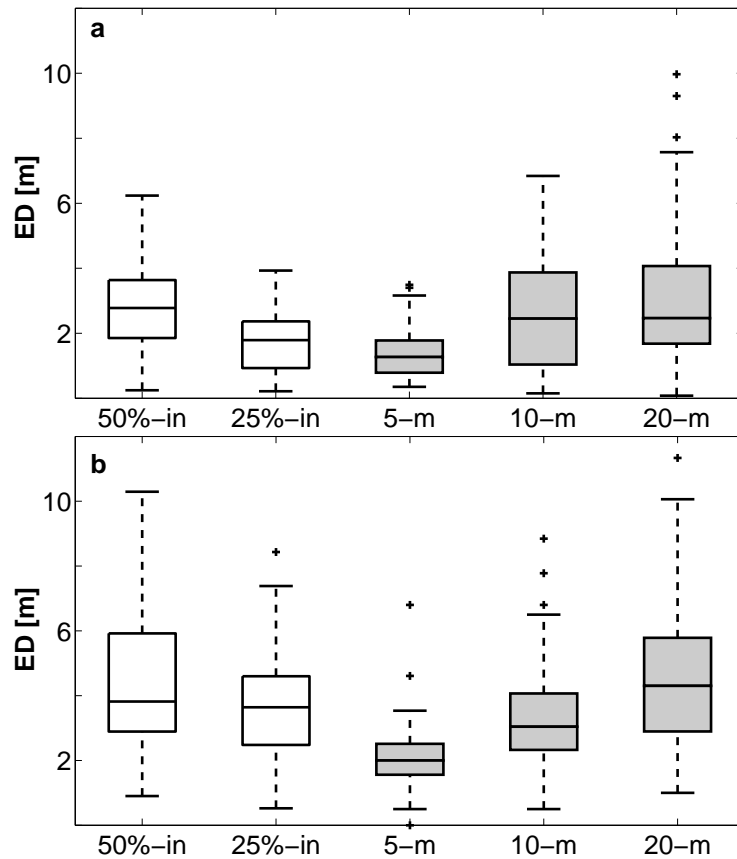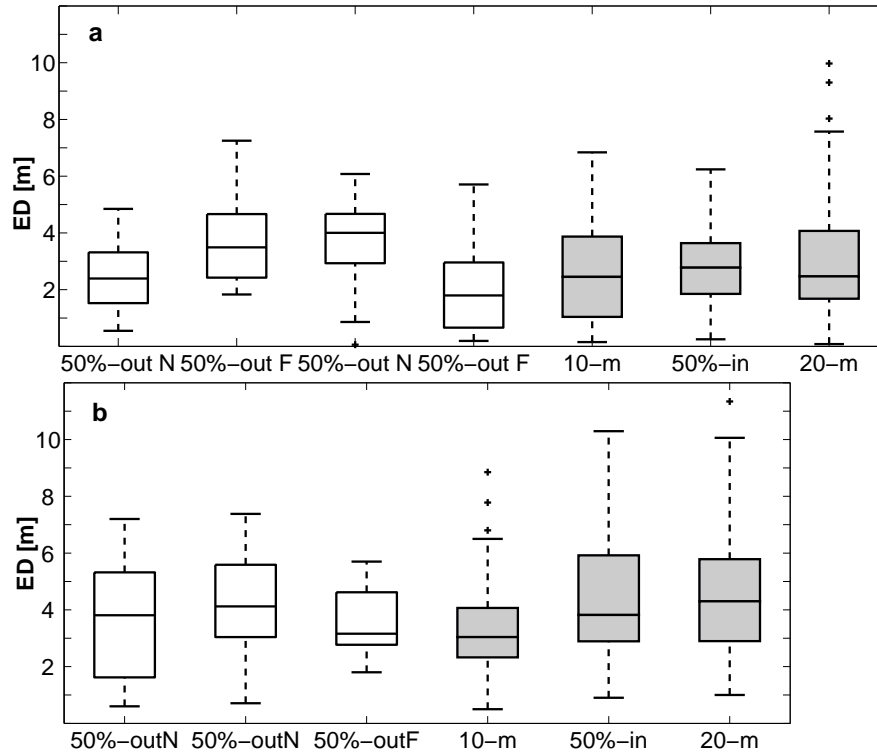
Figure III.60: Accuracy of the path integrator. (a) Euclidean distances ED between the end of the home run and the correct position of the nest are given for 50%-out and 50%-out-LM ants returning to the nest. For 50%-out and 50%-out-LM ants proceeding with their interrupted foraging runs ED between the end of the foraging run and the correct position of are presented. P-values of comparisons between groups and ED of 10-m, 20-m, and 50%-in ants for comparison are shown, too. (b) Euclidean distances ED between the center of the systematic search and the correct position of the nest or feeder, respectively, for the same groups. Since for only 4 out of the 6 50%-out ants a unique systematic search center could be determined, this group is not shown here. ED of 10-m, 20-m, and 50%-in ants are shown for comparison.

for all comparisons between 50%-out ants heading for the nest (ED: $M = 3.81m$, $IR = 1.62 - 5.32m$, $N = 34$), 50%-out-LM ants heading for the nest ($M = 4.12m$, $IR = 3.04 - 5.59m$, $N = 21$), and 50%-out-LM ants heading for the feeder ($M = 3.16m$, $IR = 2.77 - 4.62m$, $N = 12$) were between 0.9 and 1.0.

The comparison with 10-m, 20-m and, 50%-in ants yielded a similar result as the one found for the home runs or runs to the feeder, respectively: the differences were not worth mentioning (Tukey's test: all p-values>0.2, Fig. III.60b).

Again, all groups underestimated the distance to nest or feeder, respectively (Wilcoxon: all p-values< 0.001) and the 50%out-ants heading for the nest did not only start their systematic search on the right side of the correct position of the nest, but also their center of systematic search could be located there, whereas for the latter groups no significant tendencies in this regard were encountered (50%out- ants: Wilcoxon: $p = 0.017$, other groups: p> 0.15).

Range of systematic search The extensions of the first 40 m of systematic search $EXT40$ (50%-in ants heading towards nest: $EXT40$: $M = 52.02m^2$, $IR = 42.95 - 66.04m^2$, $N = 35$, 50%-in-LM ants heading towards nest: $M = 49.84m^2$, $IR = 37.69 - 60.64m^2$, $N = 21$, 50%-in-LM ants heading towards feeder: $M = 57.01m^2$, $IR = 49.47 - 66.43m^2$, $N = 13$) did not vary at all (Tukey's test: 50%-in vs 50%-in-LM for nest: $p = 0.999$; 50%-in vs 50%-in-LM for feeder: $p = 0.962$; 50%-in-LM for nest vs 50%-in-LM for feeder: $p = 0.801$, see Fig. III.61).

The groups showed no remarkable differences to the 10-m and 50%-in ants (all p-values> 0.05), but their ranges were smaller than those of the 20-m ants (all p-values< 0.001, Fig. III.61). If compared to the 0%-in ants, the ranges of the 50%-out ants heading for the nest and the 50%-out-LM ants heading for the feeder were larger (p-values$= 0.011$ and 0.005, respectively, Fig. III.61), whereas the 50%-out ants heading for the nest showed no significant differences if compared to the 0%-in ants.
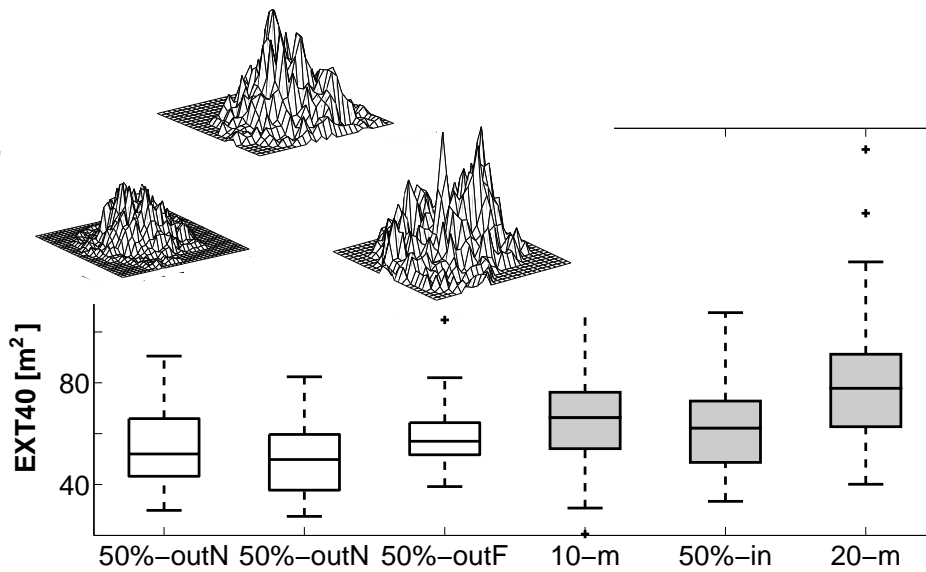
Figure III.61: Areas covered by the first 40m of systematic search (EXT 40m) of 50%-out ants heading back to the nest, 50%-out-LM ants heading for the nest, and 50%-out-LM ants proceeding with the foraging runs and the 10-m, 20-m and 50%-in ants for comparison. Corresponding search profiles are shown above.

3.5.8 Summary of experiments 6 and 7

The outbound experiments 6 and 7 can be summarized:

- the majority of ants captured during their outbound runs return to the nest; when landmarks are presented, a considerably higher number of ants proceed with their foraging run

- with regard to the Euclidean distance for the end point of home run or run to the feeder, respectively, no remarkable differences between the 50%-out and 50%-LM-out ants exist; irrespective whether heading towards nest or feeder

- the above mentioned result is confirmed if determined via the systematic search center

- the systematic search ranges of the groups do not vary notably

3.6 Experiment 8: Ontogeny of outbound and inbound runs

This experiment took on the problem that has been touched in experiment 3: I investigated whether desert ants are able to improve both accuracy and straightness of their outbound and inbound runs by recording and analyzing the first 20 foraging excursions of an ant to a known feeding site. In addition, this experiment provided the possibility to test whether transferring ants to a different area might influence the orientation and whether desert ants develop specific paths.

3.6.1 Outbound runs

Does the transfer effect the structure and accuracy of the outbound runs? The successive outbound runs recorded after transfer to and test in the test field, i.e. runs 7, 9, 11, 13, 15, 17, and 19, were more tortuous than the successive outbound runs that took place without previous disturbance (runs 8, 10, 12, 14, 16, 18, 20) (Tab. III.7, Fig. III.62). With regard to the accuracy in terms of directional deviation, there were no remarkable differences to be found; irrespective whether the initial direction at the intersection point of the 1-m circle $|DIR1|$ (Wilcoxon test: all p-values > 0.2, $N = 7$) or the overall direction was investigated ($|DIR12|$: Wilcoxon test: outbound run 14 less tortuous than 15, $p = 0.013$; outbound run 18 more tortuous than 19, $p = 0.044$; all other p-values > 0.15, $N = 7$; $|DIRM|$: again outbound run 14 less tortuous than 15, $p = 0.027$; but outbound run 18 more tortuous than 19, $p = 0.049$; all other p-values > 0.2, $N = 7$).

no. outbound run after manipulation	successive outbound run	Wilcoxon-test
7	**8**	Z = -2,726, p = 0.006
9	**10**	Z = -2,953, p = 0.003
11	**12**	Z = -2,272, p = 0.023
13	**14**	Z = -2,329, p = 0.020
15	**16**	Z = -2,158, p = 0.031
17	**18**	Z = -1,590, p = 0.112
19	**20**	Z = -2,783, p = 0.005

Table III.7: Results for comparison of tortuosities of different outbound runs. Runs 7, 9, 11, 13, 15, 17, and 19 were performed after transfer and test in the test field, the corresponding runs 8, 10, 12, 14, 16, 18, 20 faced no manipulation by the experimentator. Sample size was 15 ants for each run. Column 1: total number of ants whose runs were recorded. Col 2: outbound run recorded after manipulation Col 3: corresponding outbound run recorded without manipulation. Col 4: result of Wilcoxon pairwise comparison test. Apart from two exceptions, all runs differed remarkably. The respective runs with lower tortuosities are printed in bold types.
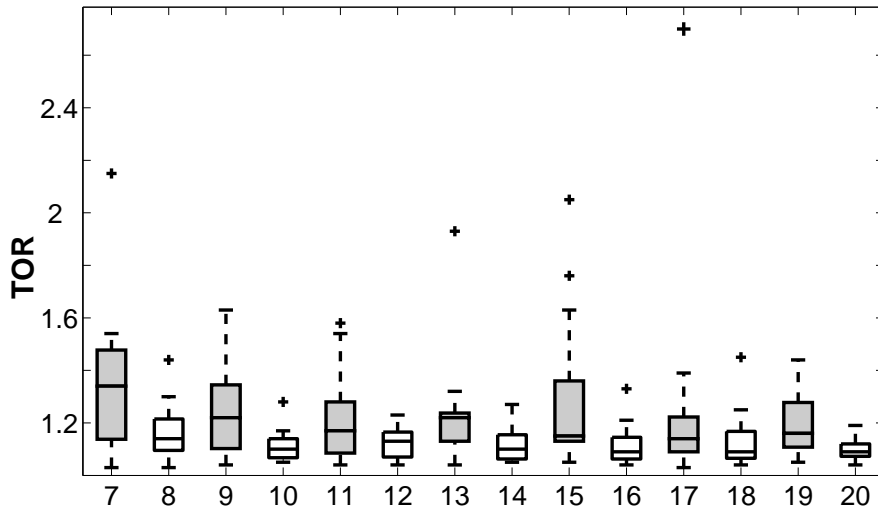
Figure III.62: Tortuosities TOR of 15 ants during their outbound runs 7-20 in the training area. One half of the runs were recorded after the ants were transfered to and back from the test field (filled), whereas open boxes show runs without manipulation immediately before. For each run the medians and interquartile ranges of all 15 ants are shown.

Do the ants improve the accuracy of their outbound runs? I addressed this question by testing whether the ants' runs get straighter and more accurate with increasing number of the outbound runs (negative correlation between number of run and TOR, $|DIR1|$, $|DIR12|$, or $|DIRM|$). This test was performed for each of the 15 ants. In addition, runs 2, 6, 10, and 20 of all ants were compared with respect to the same characteristics (see III.2.5.5).

Since the transfer to the test field did indeed influence the ants' tortuosities during their outbound runs, runs 7,9,11,13,15,17,19 were excluded from further analysis in view of tortuosity. For the remaining outbound runs it was tested whether they get straighter, i.e. less tortuous, with increasing number (negative correlation between number of run and TOR). This question can be answered in the affirmative for all but two ants, though in only three cases this negative correlation happened to be significant (Spearman correlation coefficient: $r_s > 0.5$, $p < 0.05$, $N = 12$, Figs. III.63a, III.64a). The tortuosities of outbound runs 2, 6, 10, 20 differed remarkably (tortuosity run 2: median M of 15 ants = 1.21, run 6: $M = 1.10$, run 10: $M = 1.10$, run 20: $M = 1.09$; Friedman test for more than two dependent samples $= 13.295$, $p = 0.004$, $N = 15$, Fig. III.64a). Run 2 is more tortuous than run 10 ($p < 0.05$) and runs 6 and 20 ($p < 0.1$, Nemenyi - Test). All other runs do not differ remarkably (Nemenyi-test: all p-values > 0.2). That is, at least in the long term, the outbound runs get straighter.

With regard to the directional accuracies of the outbound runs, the runs performed after the transfer and test in the test field were not excluded from further analyses because the transfer obviously had no influence on the directional accuracy (see effect of transfer, previous paragraph).

$|DIR1|$ did not decrease with increasing number of runs (Figs. III.63b, III.64b); for 14 ants no remarkable correlations were found, whereas one ant's
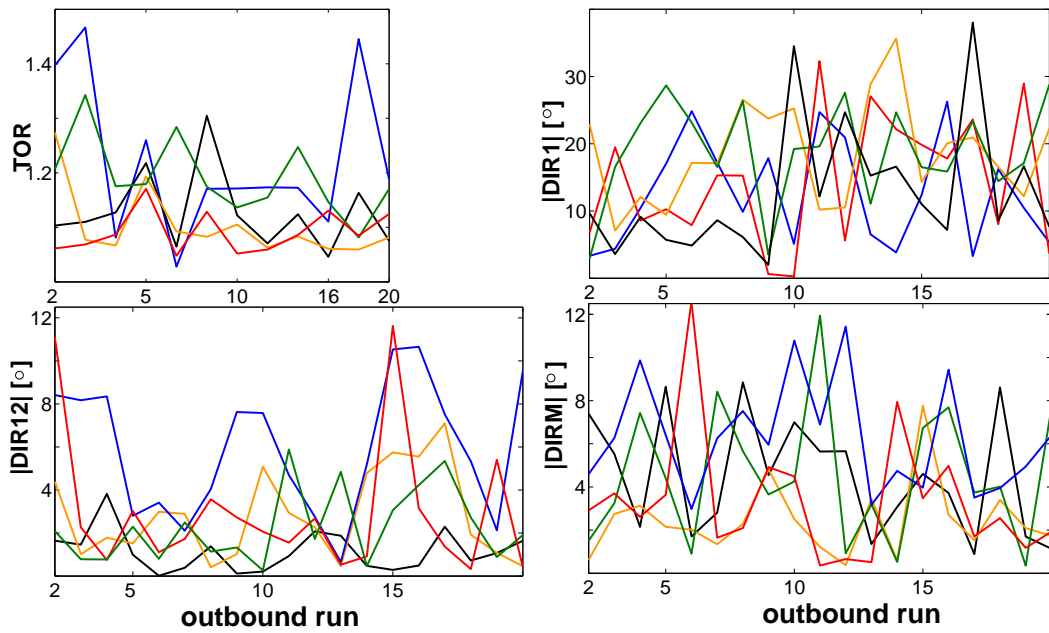
Figure III.63: *TOR* (runs after manipulations excluded from this analysis), |*DIR*1|, |*DIR*12|, and |*DIR M*| for outbound runs 2-20 of five randomly chosen ants.
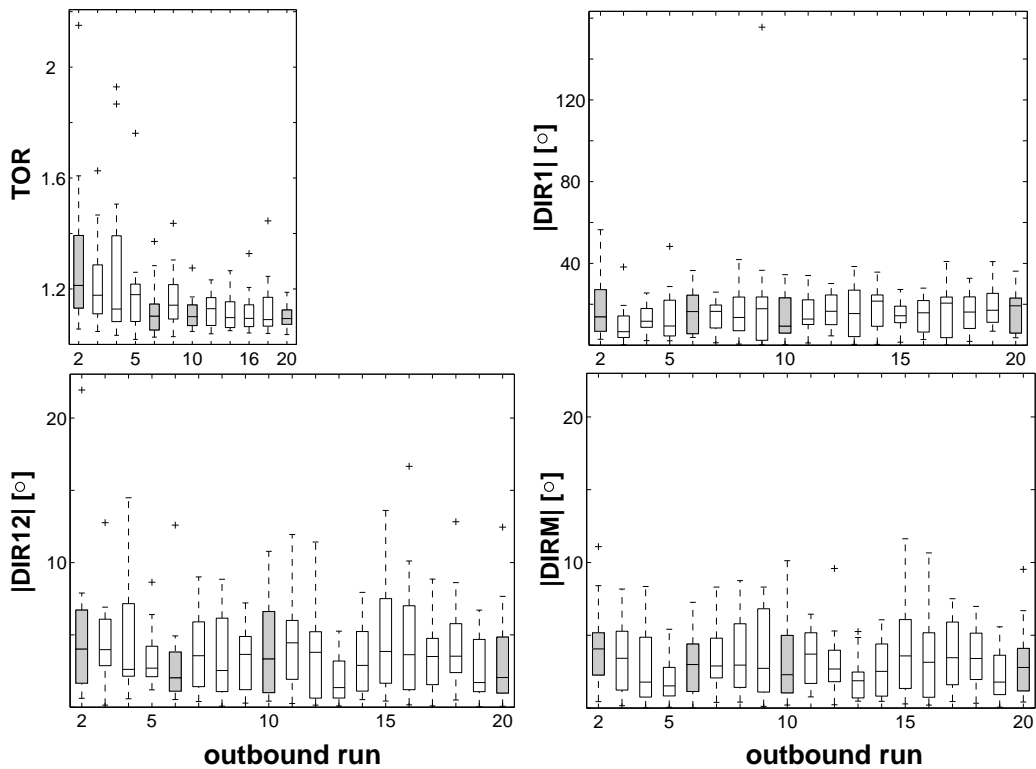
Figure III.64: Median *M* and interquartile ranges *IR* of all 15 ants for *TOR* (runs after manipulations excluded from this analysis), |*DIR*1|, |*DIR*12|, and |*DIR M*| of their outbound runs. Given are all outbound runs 2 - 20. Plots of runs selected for further analyses (2, 6, 10, and 20) are filled.

accuracy deteriorated with increasing number of runs ($r_s = 0.489$, $p = 0.033$, $N = 19$). When outbound runs 2,6,10, and 20 were compared, no significant

differences were detected (Friedman-test $= 0.987$; $p = 0.804$, $N = 15$; M of 15 ants for run 2: 13.78°, run 6: 16.43°, run 10: 9.28°, run 20: 19.28°, Fig. III.64b).

9 out of 15 ants displayed decreasing errors at the intersection point with the 12-m circle ($|DIR12|$), though no significant negative correlation coefficients were found (Figs. III.63c, III.64c). Deviations for outbound runs 2 ($M = 4.01°$), 6 ($M = 2.02°$), 10 ($M = 3.33°$), and 20 ($M = 2.05°$) did not differ to a remarkable extent (Friedman-test $= 1.080$; p $= 0.782$, N $= 15$, Fig. III.64c).

The overall directional deviation measured as $|DIRM|$ revealed a similar result: 7 ants improved their accuracy, 8 did not. One of the other 8 ants even deteriorated on a significant level (Spearman $r_s = 0.508$, $p = 0.026$, Figs. III.63d, III.64d). The outbound runs 2, 6, 10, and 20 did only differ marginally (M of 15 ants for run 2: 4.06°; run 6: 2.99°; run 10: 2.29°; run 20: 2.79°, Friedman-test $= 3.926$; $p = 0.270$, $N = 15$, Fig. III.64d).

3.6.2 Inbound runs.

Do inbound runs in the training and test area differ with regard to tortuosity and accuracy? The inbound runs in the training area (5,7,9,11,13,15,17,19) were compared to those performed in the test area (6,8,10,12,14,16,18,20). Therefore, the total number of tested ants were pooled (see III.2.5.5).

In 6 out of 8 cases the inbound runs in the training area were more tortuous than those performed in the test area, though none of these comparisons showed significant results (Wilcoxon-test: comparison inbound run 9 and 10: $Z = -3.124$, $p = 0.061$, p-values for all other values > 0.1).

In view of $|DIR1|$, inbound run 11 showed higher deviations than the corresponding run 12 (Wilcoxon-test: $Z = -1.817$, $p = 0.069$, $N = 15$) and during outbound run 17 higher errors were performed than during the following run 18 ($Z = -1.761$, $p = 0.078$, $N = 15$). For all other comparisons no remarkable discrepancies were found (Wilcoxon-test: all p-values > 0.3). Thus, the ants tend to perform larger errors in their familiar training area, though none of these differences turned out to be significant on a 5%-level.

With regard to $|DIR12|$, inbound runs 5 and 13 were less error prone than 6 and 14, respectively (Wilcoxon-test: $Z = -1.704$, $p = 0.088$; $Z = -1.817$, $p = 0.069$, $N = 15$). However, the ants performed remarkable larger errors during inbound run 9 as compared to the following run in the test field, run 10 (Wilcoxon-test: $Z = -2.385$, $p = 0.017$, $N = 15$), whereas all other comparisons yielded no remarkable results (all p-values > 0.65, $N = 15$).

When the overall directional deviation was determined as $|DIRM|$, the results obtained by the use of the 12-m intersection points were mainly confirmed: all tendencies were exactly the same, though no difference turned out to be significant on a 5%-level.

Do the ants improve the accuracy of their inbound runs? As for the outbound runs (III.3.6.1), it was tested for each ant whether its inbound runs get more accurate and straighter with increasing number (see also III.2.5.5)

and — for the total sample of 15 ants — whether runs 1, 5, 9, and 19 differ with regard to $|TOR|$, $|DIR1|$, $|DIR12|$, or $|DIRM|$.

If all 20 inbound runs were compared in view of their tortuosities, the following result was found: for two ants the inbound runs became even more tortuous with increasing number of runs (Spearman: $r_s = 0.627$ and 0.5, corresponding p-values = 0.003 and 0.025, $N = 20$, respectively). For the other ants no striking trends were found (Spearman: all p-values > 0.1). Inbound runs 1, 5, 9 and 19 were compared as groups of all 15 ants in order to test whether the inbound runs get straighter over longer periods. They differed remarkably in terms of their tortuosities (Friedman-test = 19.027, p = 0.0002, N = 15, Figs. III.65a, III.66a). Inbound run no. 5 was less tortuous than inbound runs 1, 9, and 19, though only the difference with regard to runs 1 and 9 turned out to be significant on a 1%-level (Nemenyi-test). The medians of all 15 ants were 1.09 for inbound run 1, 1.05 for inbound run 5, 1.1 for inbound run 9, and 1.06 for inbound run 19 (see also Fig. III.66a). Thus, the inbound runs did not get straighter over longer periods.

For 13 out of 15 ants no visible changes for their directional deviations at the beginning $|DIR1|$ were found (Spearman correlation coefficient: p-values > 0.2, $N = 20$). Only one ant showed a remarkable improvement during its 20 inbound runs (Spearman: $r_s = -0.484, p = 0.031$, N = 20), whereas the errors of one ant obviously became bigger during the 20 inbound runs ($r_s = 0.576, p = 0.008$, N = 20, Figs. III.65b, III.66b). Inbound runs 1, 5, 9, and 19, if compared as entire groups, did not differ remarkably (Friedman-test = 2.440, p = 0.486, N = 15 inbound run 1: median of all 15 ants: 12.4°, inbound run 5: 20.52°, inbound run 9: 32.51°, inbound run 19: 14.25°, Fig. III.66b).

$|DIR12|$ revealed no significant correlations, neither positive nor negative. Two ants showed some, though not significant, tendencies: for one of them the errors decreased with increasing number of runs, for the other one the opposite was the case (Figs. III.65c, III.66c). Inbound runs 1,5,9, and 19 differed, when compared as entire groups consisting of the runs of 15 ants (Friedman-test= 2.440, $p = 0.049$, $N = 15$). The posthoc procedure by Nemenyi displayed that only this difference was significant only for runs 1 and 5 (p < 0.05, median of all 15 ants for inbound run 1: 4.27°, run 5: 2.33°, run 9: 3.99°, 3.34°, Fig. III.66c), i.e. there is first a decrease in directional deviation, followed by anew increase.

Finally, the direction measured via the minimization method was determined (Figs. III.65d, III.66d). Two ants displayed smaller errors with increasing numbers of inbound runs, for one of them this improvement turned out to be significant (Spearman: $r_s = -0.462, p = 0.040, N = 20$) and during one ant's inbound runs the accuracy decreased (Spearman: $r_s = -0.462, p = 0.040, N = 20$). For all other ants no visible tendencies were found (all p-values > 0.13). If only runs 1, 5, 9, and 19 of all 15 ants were compared, it became obvious that there were striking differences (Friedman-test = 13.16, p = 0.0043, N = 15, Fig. III.66d). During run 5 the error (median = 1.3°) was smaller than during the other three runs (run 1: 2.47°, run 9: 4.79°, and run 19: 1.88°). This difference was significant on a level of 5% if run 5 was compared with runs 1 and 9. Again, there was no significant tendency, since the decrease of the deviation at the beginning

changed to an increase during the nest inbound runs.
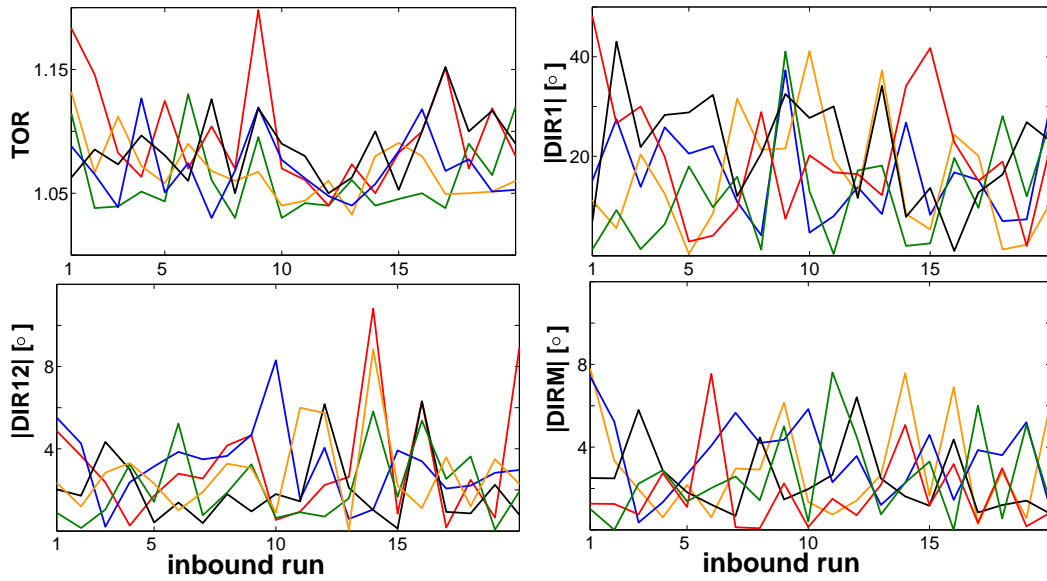
Figure III.65: *TOR*, $|DIR1|$, $|DIR12|$, and $|DIRM|$ for inbound runs 1-20 of five randomly chosen ants.
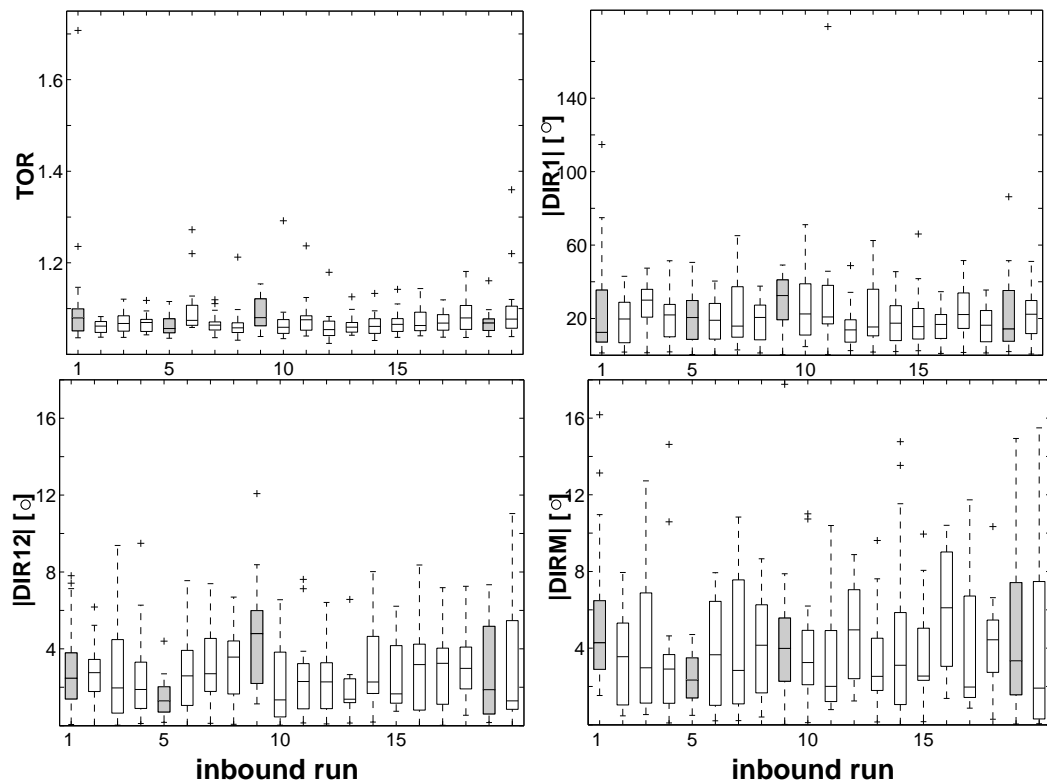
Figure III.66: *M* and *IR* of all 15 ants for *TOR*, $|DIR1|$, $|DIR12|$, and $|DIRM|$. All inbound runs 1 - 20 are shown. Inbound runs 1, 5, 9, and 19 were analyzed again and are shown as filled boxes. All runs were cut to 12 m in order to compare runs in the training and test field, see III.2.5.5.

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3.6.3 Comparison of outbound- and inbound runs.

Outbound runs 2,3,4,5 were more tortuous than the corresponding inbound runs (Wilcoxon test: run 2: $Z = -3.237$, $p = 0.001$, $N = 15$; run 3: $Z = -2,272$, $p = 0.023$, $N = 15$; run 4: $Z = -2,271$, $p = 0.023$, $N = 15$; run 5: $Z = -3.01$, $p = 0.003$, Fig. III.67a). $|DIR1|$ of inbound runs 3 and 4 was smaller as compared to the respective outbound runs (run 3: Wilcoxon test: $Z = -3.067$, $p = 0.002$, run 4: $Z = -2.329$, $p = 0.020$, $N = 15$, Fig. III.67b). For $|DIR12|$ and $|DIRM|$ no significant differences between outbound and inbound runs were found (exception: inbound run 5 more accurate than outbound run 5, if measured via $|DIR12|$: $Z = -2.726$, $p = 0.006$, Fig. III.67c and d).
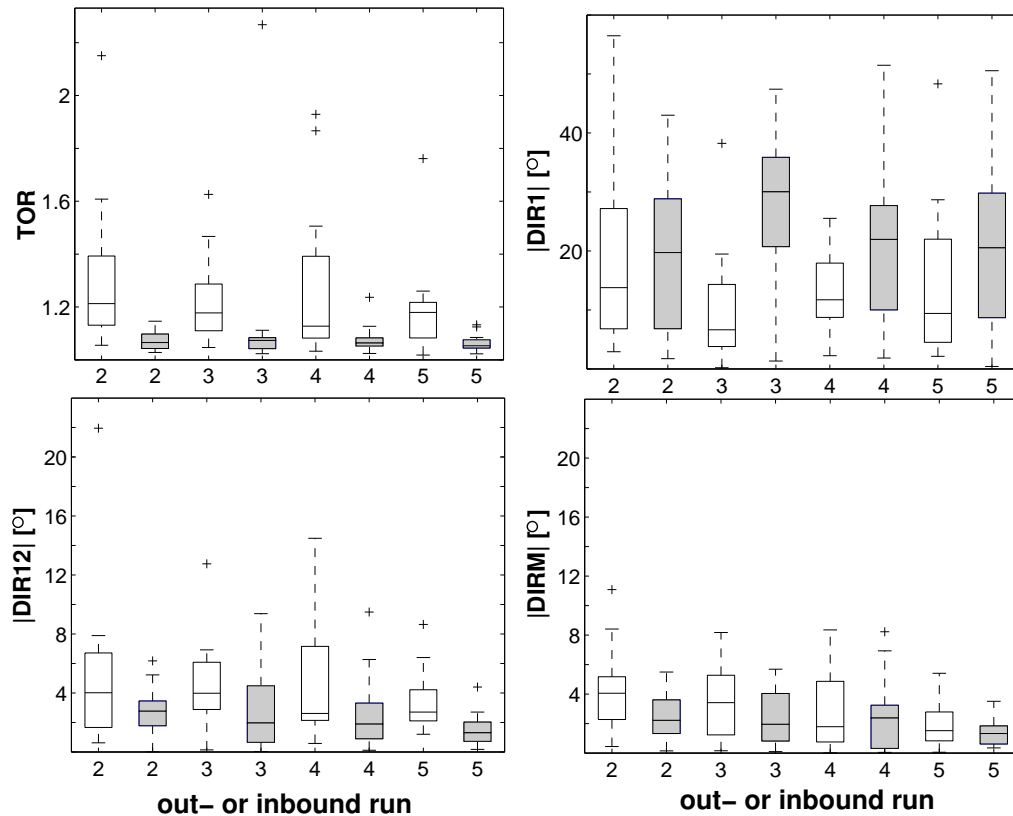
Figure III.67: M and IR of all 15 ants for TOR, $DIR1$, $DIR12$, and $DIRM$ of their outbound and inbound runs (filled) 2, 3, 4, and 5.

3.6.4 Do desert ants choose specific paths to the feeder or back to the nest?

Figures III.68 and III.69 show the paths and density plots of all segments of all outbound and inbound paths of one ant that were performed in the training area. In this representation, in each square the ratio of the lengths of all segments of each ant's 19 outbound or 20 inbound, respectively, paths covering that square to the total lengths of all the ants' 19 outbound or 20 inbound runs were computed (Åkesson and Wehner 2002; Kohler and Wehner 2005).
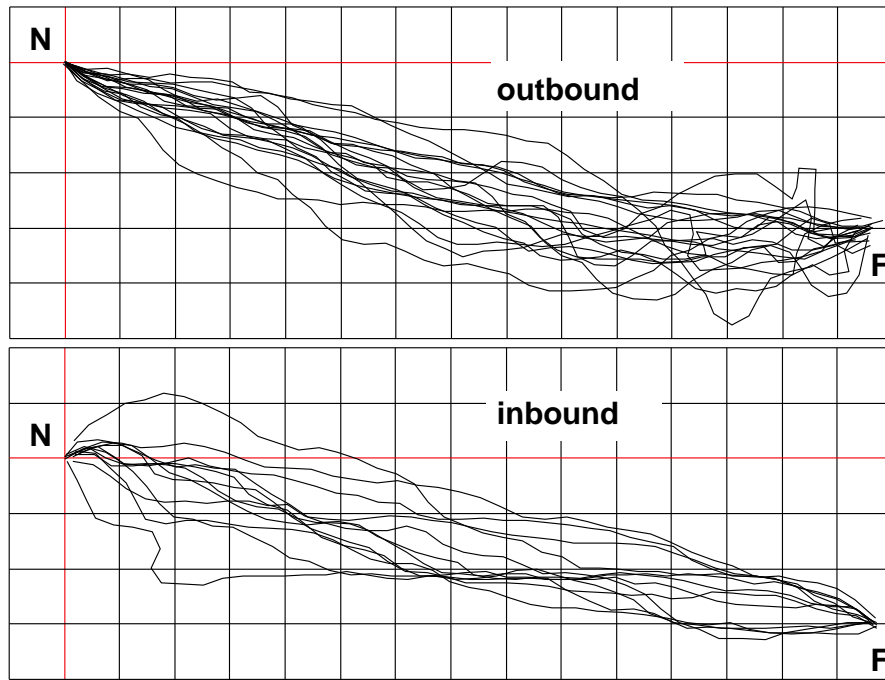
Figure III.68: 19 successive outbound (a) and 12 successive inbound runs (b) of ant 06 shown as individual trajectories. N = position of nest, F = position of feeder.
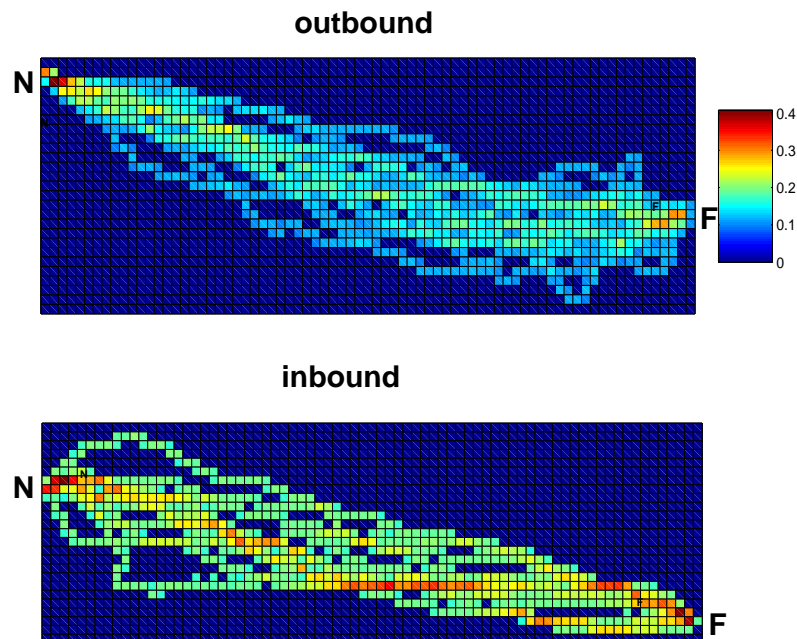
Figure III.69: The outbound (a) and inbound runs (b) of ant 06 are shown again, but this time as density plots. The area around the beeline between nest and feeder was divided into squares of 0.2×0.2 m and the path lengths of all runs within each square divided by the total path lengths of this ant are plotted. N: position of nest; F: position of feeder.

Outbound runs. The first step in addressing the question whether desert ants develop specific paths during their outbound runs was to test if they

forage preferably on one side of the beeline between nest and artificial feeder. For 8 out of 15 ants this question can be answered affirmatively (Wilcoxon-test: p-values < 0.05, $N = 19$ for each ant). 5 out of these 8 ants foraged preferably on the left, the remainder on the right side. Thus, there was obviously no path to the feeder that was used by all or at least most of the ants. Also, the ants obviously had no 'side' which they prefered during foraging. Following the approach described in III.2.5.5, for the seven ants that did not prefer one side of the course a specific path on the outbound runs could be excluded.

For each of the 8 ants that preferred to forage on one specific side the mean of the distance between beeline between nest and feeder and the location of the ant after segment no. 15, i.e. after covering half the way, was calculated for each outbound run. The deviations from this mean value (mean and standard deviations, see III.2.5.5) for these 8 ants are shown in Fig. III.70. They confirm the impression obtained by a first inspection of Figs. III.68 and III.69: the deviations are rather high (most of the means being higher than 0.5m), suggesting that the runs of each ant differ from each other. Apart from that, the rather high standard deviations (see also Fig. III.70) show to which extent the ants variate with regard to their outbound paths. Therefore, further analyses of the spatial layout of these runs are not helpful, since the prerequisite that each ant has a specific path was not given.

Inbound runs. With regard to the inbound runs in the training area, only 5 of 15 ants stayed more on one side of the track than the other one (for procedure: see above, Wilcoxon-test: p-values < 0.05, $N = 12$ for each ant). As for the outbound runs, these 5 runs to the nest were tested by the aid of the means of the deviations from the mean direction after section 15 of each path. And, again, all the means were rather large (at least 0.3m), indicating that the ants do not develop specific paths for their inbound runs, either. Again, no specific 'sidedness' could be detected.
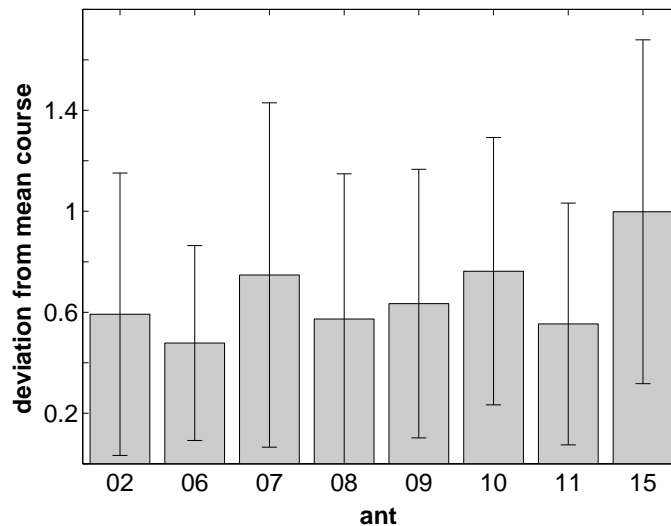
Figure III.70: Means and standard deviations of the absolute deviations from the mean course after segment 15 of 8 ants that showed a preferred side where they performed their foraging runs. For explanation: see text and III.2.5.5.

3.6.5   Summary of experiment 8

The ontogeny experiment revealed the following:

- the transfer to the test field causes higher tortuosities of the successive outbound runs, though it has no remarkable influence on their accuracy

- the ants do not improve the accuracy of their outbound runs with increasing number of runs, although the outbound runs get straighter with increasing number

- inbound runs in the test field do not differ remarkably from those performed in the training area with regard to their straightness or accuracy

- there is no consistent improvement of the inbound runs, but the directional deviations — measured for the whole runs — decrease during the first 5 inbound runs and increase thereafter again

- in general, outbound runs are more tortuous than inbound runs, whereas inbound runs are slightly more accurate with regard to their directions

- no evidence was found for desert ants developing specific inbound or outbound paths during repeated training; besides they do not preferebly forage or return to the nest on one specific side of the beeline between nest and feeder

4 Discussion

In this last section of the work, the results of the experiments are discussed in the same order as in III.2 and 3. Though they will be discussed separately, particular results will be related to results of other experiments and to the theoretical part (II) whenever it seems useful and appropriate.

4.1 Experiment 1: Natural outbound runs

4.1.1 Directional persistence of outbound runs

Many ant species develop specific routes to specific sites during lifetime (e.g. Wehner et al. 1983; Wehner 1992; Wehner et al. 1996; Hölldobler and Möglich 1980; Hölldobler and Wilson 1990). The study of Wehner et al. (2004) for the first time revealed that foragers of the species *Cataglyphis bicolor*, whose nutritional resources (mainly dead corps of arthropods) are distributed homogeneously rather than heterogeneously, exhibit a strong 'sector fidelity' during their outbound runs.

This sector fidelity as well as duration and distance of the outbound run increase over lifetime at a rate that depends mainly on the feeding success. The authors offer a number of plausible explanations for this behavior. Similar results were found for *Melophorus bagoti* (Muser et al. 2005) and *C. fortis* (Wehner, personal communication). Thus, even ants that do not rely on external cues such as landmarks, do develop a high directional fidelity.

Here, I show that the ants' moving directions (i.e. the directions of each segment, or arc length, see III.2.4.1) on their outbound runs are not randomly distributed, i.e. a directional persistence of the ants' outbound runs can be observed. This directional persistence was measured as *directional persistence length* (III.3.2.1); converted into a directional persistence time while considering foraging speeds of 0.5 to 0.6 m (Müller 1989) it would result in a approximate 'directional persistence time' of about 0.5 sec.

The arguments for increasing section fidelity (outlined by Wehner et al. 2004) also hold true for the development of mean directions. This ability may be one useful tool to shorten the time of foraging excursions and, thereby, to reduce 'travel risks' (Wehner et al. 2004).

However, this behavior varies at a high rate between different individuals, indicated by the differences of the plateau values obtained for different groups of ants via the autocorrelation function. What could be a reason for these findings, i.e. why are the outbound runs of some foragers more directed than those of others? Since the ants were not marked individually and, therefore, their 'foraging histories' until they were tested were not known, the answer for this question remains somewhat speculative. A very high number of ants was tested in this experiment. Thus, almost certainly the ages of these ants varied to a greater extent. It is likely that the outbound runs of more experienced ants were more directed than those of 'younger' ants (see also Wehner et al. 2004). This hypothesis has been investigated in detail in experiment 8 and will be discussed later. If it held true, it would expand the findings that desert ants increase their direction fidelity by the fact that they also increase their directional performance during outbound runs.

4.1.2 Does the tortuosity of the outbound run influence the accuracy of home run and systematic search ?

The path integration system of desert ants is error prone. Two types of error come into consideration that could occur during path integration (see also I.1.4 and II.3), namely systematic errors (with respect to desert ants, MW-error and Leaky Integrator, see Müller and Wehner 1988; Sommer and Wehner 2004) and random errors (Benhamou et al. 1990). It is more difficult to provide evidence for random errors than for systematic errors.

In this study, natural outbound runs of untrained ants of *C. fortis* were recorded for the first time. They were tested for correlations with the accuracy of the path integrator. Therefore, the first step was to take a closer look at the geometrical properties of the outbound runs. The simplest value describing the natural outbound runs is their tortuosity TOR, measured as ratio of path length and distance covered L/d. This index is particularly interesting with regard to random errors and the distance underestimation shown by Sommer and Wehner (2004).

For this reason the distance was fixed to 10 m in this experiment, to be able to compare ants that have covered the same distance during their outbound runs, while their path lengths could vary. No correlations between the tortuosities of the outbound runs and the accuracy of the home runs and the systematic search behavior were found, regardless which value of inbound run or systematic search, respectively, was analyzed (III.3.2.2). This result is very astonishing: as described in I.1.4, random as well as systematic errors should accumulate during the outbound runs, suggesting that longer paths (i.e. a higher TOR in this case) account for larger errors in the path integrator.

Now, why did the postulated hypothesis not come true?

First, the variations of tortuosity between the ants are low. For 117 out of 130 ants (90%) values for TOR below 3 were measured, and more than 60% of them displayed values below 2. (III.3.2.2). This is consistent with the result shown above, that the outbound paths of foraging *C. fortis* are quite straight. Therefore, it is rather difficult to obtain subgroups for which TOR varies to a remarkable extent. This could also explain that not even for the two groups (high and low tortuosity) any significant differences were found.

Second, in contrast to the low variations of TOR, the values of ED, $|DIR8|$, $|DIRM|$, and DIS (home run) as well as ED, $|DIR|$ DIS (systematic search) vary substantially (Fig. III.71). Therefore, (1) a potential influence of the tortuosity on the accuracy of the path integrator — if existing at all — could just be invisible or covered by the high variance of the values characterizing accuracy of home run and systematic search. It is difficult to find a correlation between two variables whenever the independent one (in this case the TOR) varies much less than the dependent one (ED, $|DIR8|$...). Furthermore, the high variance is also a hint that there may be other factors than the tortuosity that have an impact on the accuracy of the ants' path integrator. The limited precision during the recording and the digitization of the data may also be one factor that has covered potential correlations.

Third, although conspicuous landmarks were not present in this experi-
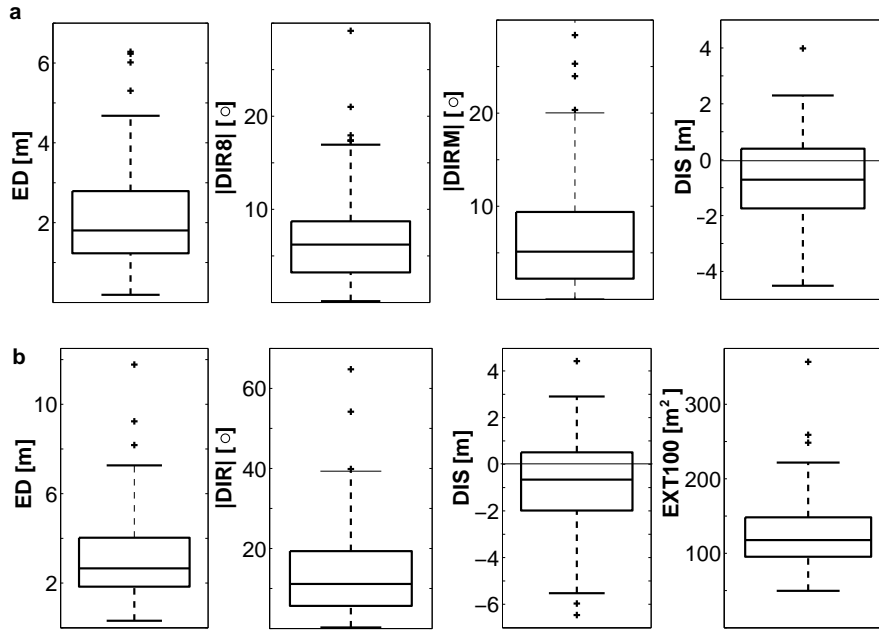
Figure III.71: Boxplots of *ED*, *DIR*8, *DIRM*, *DIS* of home runs (a) and *ED*, *DIRM*, *DIS*, and *EXT*100 of systematic search patterns (b) of the 130 ants of experiment 1 whose outbound, inbound and systematic search runs were recorded. Given are medians, interquartile ranges, outliers and whiskers.

mental setup in order to avoid that ants make use of them to adjust their bearings (e.g. Wehner and Räber 1979; Wehner 1996; Collett et al. 1998, 2001; Collett and Collett 2002; Bisch-Knaden and Wehner 2003a; Collett et al. 2003a), the soil was not totally even. Therefore, it cannot be ruled out that ants had learned some route - or nest-specific features that guided them back to the nest entrance (Santschi 1913; Seidl and Wehner 2006). The same argumentation applies for other cues like the presence of nest mates (Bisch-Knaden and Wehner 2001) or landmarks at the horizon (Zeil 1993; Southwick and Buchmann 1995; Wehner et al. 1996). In the distant test area, in contrast, these cues were missing completely. Carrying on these considerations, all ants were deprived of such cues and therefore their inaccuracies could have generally increased. However, such considerations remain speculative at this stage.

It is tempting to argue, that the ants just forage in a way that keeps their errors in the path integrator at a minimum. On the other hand, the errors were quite large, though no significant differences between the animals were found. Thus, it can hardly be a successful development that results in errors of that size.

Also, the extension of the systematic search again is not correlated with the tortuosity of the outbound runs (III.3.2.2). This result allows two interpretations: (1) the systematic search pattern is a fixed program that just gets 'reeled off' after the nest is not found at the tip of the homevector; (2) it is adaptive rather than a fixed program, but is influenced by factors experienced during outbound or inbound run that give the ants some knowledge concerning the accuracy of their path integrator. This knowledge then could determine the ants' 'confidence' in their path integrator and a possible adap-

tion of the systematic search behavior. Then, again, the systematic search patterns should not differ due to the fact that the errors displayed by the ants search did not differ remarkably, i.e. even if the ants got some hints concerning the accuracy of their path integrator, these would lead to similar systematic search patterns, since the errors did not differ remarkably. According to previous studies on the systematic search program (Wehner and Srinivasan 1981; Wehner 1992) the latter interpretation is the more likely one.

There do not exist any correlations between the tortuosity of the outbound run and that of the inbound run (III.3.2.2). This also holds true if only the first 2 m of the inbound run or the range between meters 5 and 7 was investigated. As for the systematic search, two interpretations are possible at this stage: (1) the home runs of ants captured at the same distance from the nest never differ at all, i.e. they are not influenced by other factors or (2) the tortuosities are a factor that might display the ants' confidence in their path integrator. This would imply that not only the errors are mostly the same for all ants, but also that the ants' confidence in their path integration system does not differ, expressed by similar tortuosities of the home runs.

With regard to the variance of the directional deviations from the correct homeward courses the minimization method $DIRM$ seems to provide the more meaningful results, since the probability that the deviation at the 80%-circle is based upon a random deviation at this specific distance (8m) is rather high. No remarkable differences between more and less tortuous runs were found (III.3.2.2). Thus, it is not only that the error *per se* is not influenced by the tortuosity but also the ants' variation in terms of accuracy is not influenced by the tortuosity of the outbound runs. This finding corroborates the hypothesis that the errors are just randomly distributed and do not depend on small differences of the outbound runs' tortuosities.

Some of the questions raised here (the presence of random errors, the meaning of nest- or route-specific cues, the systematic search behavior, the tortuosity during the inbound run) could not be answered finally, but left 2 or more possible explanations that were outlined. These questions will be taken up again during the discussion of the training and ontogeny experiments (see III.4.4, 4.5, 4.6, 4.7).

4.1.3 Are integrated curvature of the outbound run and accuracy of the path integrator correlated?

To answer this question all rotations performed during the ants' outbound runs were integrated. This integration OM produced a value representing the number and amounts of these rotations.

Let us assume, for instance, an ant underestimates each rotation during its outbound run in a linear fashion (see the linear underestimation in the theoretical part II.3.1). Let us further assume, no additional error plays a major role within the path integration system of the ant. Then, errors during leftward and rightward movements would compensate each other, if the number and amount of these errors was the same, indicated by an integrated curvature of zero (see also Müller and Wehner 1988; Müller 1989).

For both the Euclidean distances and the directional deviations no cor-

relations were found. This was the case for the evaluation of the home runs as well as for the systematic search centers (III.3.2.2).

Since the systematic errors that have been shown hitherto are anything but linear (MW-error, see Müller and Wehner 1988), the procedure was applied for the cubed curvature, i.e. strong rotations were weighted more than slight ones. Besides, due to the predominant straightness of outbound runs, it might be more important for desert ants to be as accurate as possible with respect to the measurements of small rotations, whereas the effect of inaccuracies during measurements of large rotations seems limited. This supposition is backed up by the types of systematic angular errors that have been discovered for *C. fortis* (Müller and Wehner 1988) as well as other arthropods (Görner 1958; Bisch 1999) or mammals (Benhamou et al. 1990; Séguinot et al. 1998).

The results obtained via the integral of the cubed curvature $OM3$ corresponded well with the results of the analysis of the integrated curvature: no correlations between the integral of the cubed curvature and the accuracy of home run and systematic search center could be detected (III.3.2.2).

Thus, the errors displayed by path integrating desert ants might not simply be explained by linear or non linear errors during the measurements of directions or their integration. Such errors — if existing at all — seem to be of minor importance. Since OM and $OM3$ are close to zero for many paths, i.e. quite often there is a balance in amount of turns to the right and left, these errors might not be detectable for an observer, but again covered by other, say, random errors.

As outlined for the tortuosities, nest- and route-specific cues may play a role within the path integration system, and their absence in the test field also may have covered potential systematic errors concerning the measurement of rotations.

As a result, it can be resumed that errors concerning the measurement or integration of directions do not seem to be the 'problem' mainly responsible for shortcomings of the path integration system.

In the theoretical part I have shown that if systematic errors play a dominant role within the path integration system, they can be revealed by integrating the curvature of the outbound runs (II.3.3). However, this holds only true if the outbound runs have the same overall length, and not, if, the ants covered the same distance, as it was the case in this experiment.

Having natural outbound runs at hand gives the unique opportunity to check the meaning of systematic errors that have been shown to be displayed by *C. fortis* in specific experimental paradigms. Thus, it was possible to figure out once and for all, whether these errors play a role during the natural foraging process. Furthermore, their meaning as compared to random errors could be investigated.

One systematic error to be investigated was the

4.1.4 Error postulated by Müller and Wehner (MW-error and MW-direction)

In general, after natural outbound runs the difference between MW-direction and the correct homing direction is rather small. For one half (N=66) of

the ants the correct homing direction and the MW-direction did differ only marginally (III.3.2.3). So the conclusion drawn by Müller and Wehner (1988), i.e. that *C. fortis* only rarely develops overall directional biases during foraging and, therefore, the potential effect of the MW-error of the homing direction is rather low, seems justified.

The directions towards which all ants were heading were determined after 0.5m, 1m, 2m, 8m, via the minimization method, and the systematic search center (the crossing point of the 2m-circle and a method similar to the minimization method were used by Müller and Wehner). After 0.5 m, the ants' deviations displayed no tendencies towards the correct homing direction nor to the MW-direction, i.e. $|DIR0.5|$ and $|DIR0.5_{MW}|$ did not differ remarkably; similar results were obtained for $|DIR1|$ and $|DIR1_{MW}|$, $|DIR2|$ and $|DIR2_{MW}|$ and the deviations determined via the systematic search center ($|DIR|$ and $|DIR_{MW}|$), whereas when $|DIR8|$ and $|DIR8_{MW}|$ or $|DIRM|$ and $|DIRM_{MW}|$ were compared to each other, the ants were significantly closer to the correct homing direction (Table III.4). The results obtained when only the ants for which the homing direction and the MW-direction deviated by more than 5% or 10%, respectively, were considered, confirmed these results (the only difference was that for these groups already after 2 m there was a significant bias towards the correct homing direction, see appendix 4.1 and 4.2).

The results presented here clearly show that the directions displayed by ants after having covered most of their home runs are closer to the correct homing directions. Thus, the relevance of the MW-error seems very limited.

The results for the Euclidean distances ED ($ED < ED_{MW}$, see III.3.2.3) were expected: since the MW-error's relevance for distances is small and another key factor for the determination of distances comes into play here (the Leaky Integrator, Sommer and Wehner 2004), the ED cannot be regarded as the most important value for the investigation of the MW-error. Though in the modelling part I have shown that the angular deviation caused by the MW-error can be revealed by integrating the curvature of outbound paths, this did not hold true for ED (II.3.3).

Nevertheless, when approaching the problem in a more qualitative than quantitative fashion, there is some evidence for an influence by the MW-error, since if there was a trend concerning the deviations from the correct homing direction after short distances, this trend was biased into the direction predicted via the MW-error (III.3.2.3).

Müller (1989) argues that desert ants might only integrate their mean directions during their outbound paths, thereby neglecting, short, but heavy rotations. To test this hypothesis he did not take the outbound runs into account as they were but calculated frequency polygons that approximated these runs by only incorporating rotations that resulted in enduring changes of the general outbound direction. From the present viewpoint, this interpretation raises some doubts, as many studies have suggested that the path integrator is running all the time during outbound and inbound run (e.g. Collett et al. 1999; Collett and Collett 2000; Wehner et al. 2004).

Nevertheless, I checked Müller's assumption for my data sets. Therefore, I tested whether this approximation could explain the results obtained for ants for which correct homing direction and MW-direction did only differ

marginally, but the ants' homing directions deviated remarkably from both. Of the 22 ants for which the correct and the MW-homing-direction did only differ less than 2° (N=22), 10 ants nevertheless deviated more than 5° from the correct homing direction. Could the approximation of the outbound path explain this result? I approximated the outbound paths by only taking rotations into account that lead to overall directional changes of more than 2 meters. The directions predicted by Müller and Wehner still differ significantly from the actual homing directions of the ants (measured via the minimization method, Mardia-Watson-Wheeler: $p < 0.001$, N = 10). Thus, this conclusion could not be confirmed taking my results into consideration.

Which influence has the leaky integrator on the ants' path integrator?

4.1.5   Leaky Integrator (LI)

The Leaky Integrator LI (Sommer and Wehner 2004) predicts shorter homing distances for the ants than the correct distance of 10 m. The distances covered by the ants were shorter than 10 m, irrespective whether they were determined via the end of the home run or the systematic search center, respectively. They were somehow 'in between' the correct distance and the distance predicted by the Leaky Integrator. Therefore, and since the majority of the ants underestimated the distance, the Leaky Integrator could be one mechanism that influences the accuracy of the ants' path integration system.

Considering the shortcoming of the definition of the end of the home run (see III.2.4.2) and therefore assuming a slightly shorter home run than actually determined, the Leaky Integrator could explain my data in terms of the end of the home run at least partially (the distance covered by the home run was closer to the LI-distance than to the correct distance, see III.3.2.3).

The results conflict with the observation by Sommer and Wehner (2004) in one respect: they found significant deviations from the correct distance not only for the end of the home run (in channel experiments), but also for the center of systematic search. With regard to the systematic search, my results suggest that the ants are able to compensate the underestimation error throughout the systematic search by shifting its center more to the correct nest position. This could be achieved by a mechanism that the ant, though having completed the home run and starting to perform larger directional changes, still keeps a certain directional persistence with respect to its homing direction.

In an ecological sense, to start the systematic search in front of the nest has one advantage: the ants can perform their final approach to the nest or commence their systematic search program in an area that they know very well, since they tend to head out into the same directions during their lifetime (Wehner 1987; Wehner et al. 2004). Sommer and Wehner (2004) argue that, following these arguments, the Leaky Integrator could be an adaptation connecting the path integrator with the backup systems of desert ants, i.e. the use of landmarks or the systematic search, respectively. This conclusion is supported by the results presented in this work; if the LI were an adaptation to connect path integrator and systematic search, a shift of the systematic search center could be another helpful tool to make the orientation

process as accurate as possible.

Sommer and Wehner (2004) forced the ants to search in channels, i.e. their systematic search behavior was restricted to one dimension. The search behavior presented here, in contrast, corresponds to the natural search an ant performs after not finding its nest entrance exactly; this might explain the discrepancies between both experiments in view of systematic search.

Having two-dimensional outbound and inbound runs at hand allowed me to compare ED and ED_{LI} for both end point of home run and systematic search center. This was done by means of the model introduced during the theoretical part of this work (III.2.5.1). As a result, the ants are closer to the LI-positions than the correct position of the nest (III.3.2.3). A theoretical relation between the ED and the distance between nest and feeder — while the overall outbound length was fixed — has been shown in the theoretical part (see Fig. II.8).

Therefore, it seems very likely that the Leaky Integrator is indeed one systematic error that has a strong influence on the path integration system, even under natural conditions. Furthermore, the results suggest that LI outravels the MW-error by far. This conclusion is supported when taking a closer look at the origin of both errors: the MW error can be canceled out by keeping turns to the right and to the left at balance, whereas the LI can only be 'deactivated' by extremely short foraging distances (Sommer and Wehner 2004). At this stage it should be mentioned again that the experimental MW-error can also be explained by applying the LI-equations, although the lengths at which the estimated distances saturate differ dramatically between LI and MW.

The LI was also calculated in the way proposed by Vickerstaff and Paolo (2005), i.e. including the home runs. Due to the short outbound and inbound distances in this experiment, the results did not differ substantially from the results presented hitherto.

Finally, it should be mentioned that the Leaky Integrator causes high inaccuracies only for very long foraging distances (Sommer and Wehner 2004). Therefore, it would be interesting to expand these experiments to longer distances, say 20 to 50 m. Then, the distance and the nest position as calculated theoretically and predicted by the LI would vary substantially and the influence of the LI might be measured in a quantitative way. But such experiments are difficult to conduct in our study area due to the high density of nests (Dillier and Wehner 2004) and the resulting short foraging distances that normally do not exceed 20 to 30 m.

4.1.6 The adjustment to the homing direction as calculated by the path integrator could take time

The negative correlations between the crossing point of the regression curve with the y-axis on the one hand and its inclination on the other hand (III.3.2.4) suggest that the ants perform notable errors especially at the beginning of their inbound runs, and afterwards try to compensate. External cues that might be helpful to reduce errors during the inbound runs shall be discussed later (see III.4.5).

Another explanation is that at the beginning from the home run the ants

do not exactly head for the nest. That is, during the first part of the home run, the ants do not keep the correct homeward course that they get from their path integrator, but rather deviate to a remarkable extent. At this point, let us recall the theoretical model: whenever the ant is approaching the nest directly according to the model, it keeps the Y-value, i.e. the lateral deviation from the correct homing course, at a value very close to 0. It might be possible that this 'adjustment' takes some time during the initial phase of the inbound route. Only after this time they set out in the correct direction — or rather what they 'believe' is the correct direction — towards the nest. However, until now there is no evidence in other arthropods or mammals that support this conclusion. The results shown here also suggest that — if this interpretation is correct — the ants even have one side they prefer to deviate to at the beginning of the home run.

4.1.7 Conclusions

If desert ants cover the same distance but different overall lengths during their outbound runs, this does not lead to significant differences of the path integrator's accuracy, regardless whether measured via the home run or the systematic search center. In addition, the extension of the systematic search does also not vary to a remarkable extent. The results obtained by the integration of overall curvature and cubed curvature during the outbound run strongly suggest that the relevance of errors concerning the measurement or integration of directions generally is limited. However, the variations of all the considered parameters of the outbound runs were relatively small; this fact might explain that no clearly visible differences were found; the high variations of the values obtained for home runs and systematic search patterns, in contrast, indicate that many different factors contribute to the overall errors in the path integration system. So far, two errors, Müller-Wehner-error and Leaky Integrator, have been shown to exist; the results obtained here reveal that during natural outbound runs of *C. fortis* the relevance of the former is rather low, whereas the latter can explain some of the errors observed.

Simulated outbound and inbound runs, into which systematic errors had been implemented, show that the directional accuracy of the path integrator decreases with increasing values of integrated curvature only for outbound runs with fixed overall length, whereas whenever the distance was fixed (i.e. the same situation as during experiment 1) no correlations between integrated curvature and amount of errors was found for any systematic error tested. Since it is not possible to keep the overall path lengths of desert ants fixed, the next step was to vary the distances during the foraging runs.

4.2 Experiment 2: Distance of natural outbound runs

4.2.1 Comparisons between 6 groups that had covered different distances during their outbound runs

This experiment addressed the question whether different distances covered during outbound runs cause differences with regard to the accuracy of the path integrator. Thus, this experiment is, as experiment 1, based on the assumption that an ongoing accumulation of errors does occur during the

outbound run. Since the majority of the outbound runs are rather straight (see III.4.1.1), I again investigated this hypothesis by comparing different distances of the outbound runs.

Besides, there might be shortcomings of the path integration system that are more distance- than length-related. Take the MW-error as an example: following this model, the ants are assumed to change the distance stored at a maximum whenever the ant is heading towards the exact direction (or the opposite) of the stored homing direction. Whenever an ant is moving towards a direction perpendicular to that homing direction, the distance stored does not change at all. Finally, during the most recent experiments in literature (e.g. Sommer and Wehner 2004, 2005; Seidl and Wehner 2006; Knaden et al. 2006) the ants were made to forage and head back in one-dimensional channels. In these experiments, the covered lengths during out- or inbound runs resemble exactly the distances covered. So, it cannot be distinguished between length and distance. Now, with natural outbound runs at hand, it became possible to test the influence of the distance covered.

No differences between the six different groups were found with regard to the accuracy measured via the end of the home run. Furthermore, the scatter between the groups in terms of directional deviations did not differ remarkably. Finally, if the group that had covered the shortest distance (6-7m) was compared against that one with the longest distance covered (11-12m) no differences were found (III.3.3.1). As in experiment 1, the systematic search behavior confirmed the results obtained by the analysis of the end of the home run for most values. However, one exception (distance deviation) was found. This exception will be discussed at the end of this section.

Why did the groups with different outbound distances again not display remarkably larger errors of the path integrator, with differences even larger than during experiment 1, up to a factor 2 between the two most extreme groups?

First, the distances as well as the overall lengths were still quite short, although they corresponded to the distances covered by workers of this nest in an area with high density of nests (Dillier and Wehner 2004). This personal observation is supported by the rather high number of ants (N = 27, 17%) that, during experiment 1, did not reach the 10-m circle, and therefore were not captured. Most of these ants returned to the nest without food, since the area was cleaned of food ever and ever again. Thus, the ants rather returned to the nest without food instead of extending the foraging distance. Observations of ants from the same nest that were not captured during their foraging trips showed that they very rarely exceeded distances of 15 m during their foraging excursions (personal observation in 2004).

Ants of the species *Cataglyphis bicolor* increase their sector fidelity as well as their foraging distances over their lifetime (Schmid-Hempel and Schmid-Hempel 1984; Wehner et al. 2004). This also holds true for *Cataglyphis fortis*. Therefore, one reason for the nonexisting differences with respect to the home runs could be that the portion of older and, therefore, more experienced ants could have been higher after longer distances and therefore, these ants were able to compensate the originally larger errors. The question whether desert ants improve their accuracy during training of their outbound and inbound runs has been investigated in experiments 3 and 8 (see discussion below in

III.4.3 and 4.7). Nevertheless, this explanation can be ruled out for several reasons: if they had been able to establish route- or nest-specific features, they should even be more 'lost' in the remote test field, where these cues were missing. Additionally, this explanation can be rejected keeping in mind the results of experiment 1, where the more experienced ants would have been the ants with lower tortuosities during their outbound runs. The fact that these ants' home runs and systematic search patterns were not more accurate is contradictory to this idea.

Thus, the most likely reason for the obtained result is that again the differences between runs were too low for causing significant error changes or, that relatively large errors might be induced by other factors than the outbound distance. The last explanation would support the general hypothesis that was postulated, also considering the results of experiment 1, that the relatively large error-variation (see also Fig. II.8) is caused by several factors including systematic and maybe also random errors.

If experiment 1 had revealed a correlation between the tortuosity of the outbound run and the accuracy of the path integrator, this correlation could have been caused either by an accumulation of random errors or by the numerous changes of directions of ants with high tortuosities. Then, the data of experiment 2 might have made it possible to rule out or corroborate, respectively, these error types. Let us assume, as an example, we could compare runs with a long distance, say 11-12m, that were very straight (imagine a tortuosity of 1), and were as accurate or inaccurate as runs with a very short distance, e.g. 6-7m, but a high tortuosity index of, say, approximately 2. These runs had the same overall length, but the shorter ones incorporated a high number of rotations. If these groups of runs were equally with respect to their accuracy, the systematic errors concerning the angular component could be ruled out, whereas an accumulation of ongoing errors would be very likely. Unfortunately, due to the shapes of the runs, such comparisons could not be conducted.

The animals that had ventured out for 8-9 m were the only group that overestimated the distance from the point of capture to the nest, if the systematic search center was considered (III.3.3.1). This result is surprising, since with regard to the home run this tendency could not be confirmed. Up to now, the values obtained by analyzing the end of the home run were confirmed when the systematic search center was taken into account. Here I encountered a conflict between values obtained by the two different methods for the first time. At this stage, no explanation for this result is at hand. Since the result is striking in such an unexpected way and is in no way confirmed by all other groups, it might be due to a sampling error, since the sample sizes with only 10 ants per group are quite small.

No differences with respect to the extension of the systematic search were found, regardless whether the first 100 or 20 m were considered. The two interpretations outlined above for experiment 1 again hold true and, which interpretation is the more likely one, will be revealed during the training experiments (see III.4.4). The discussion of the nonexisting differences in view of tortuosities during the inbound runs of the groups — again, the two interpretations as described for experiment 1 are possible — has also to be postponed to the discussion of experiment 8 (see III.4.7).

4.2.2 Comparisons of overall path lengths

The results of experiment 1 suggest that the tortuositiy, i.e. the overall path length, during natural untrained outbound runs of lengths that corresponded to the lengths of normal foraging excursions did not influence the accuracy of the path integrator. However, this result might have been due to the very low differences with regard to the tortuosities. Since, using the data set of experiment 2, it was possible to test different outbound runs that varied to a larger extent in terms of their overall lengths (7.39 -29.67 m) it seemed worthwhile to check these data for correlations with the accuracy of the path integrator.

No correlations were found between the overall path lengths and the accuracy of the path integrator for all but one value determined by using the end of the home run (Fig. III.42) or the systematic search center (Fig. III.43, III.3.3.2). Ants that had performed longer foraging excursions showed significantly smaller deviations from the correct homing direction, when the systematic search center was considered. This result is due to a shortcoming of the methods applied here and will be described in detail below.

How could it be that longer foraging excursions again do not account for larger errors of the path integrator?

First, only 5 ants performed foraging paths longer than 20 m. Most of them lay within the range of 7.5 and 15, i.e. their foraging paths differed by a maximum factor of 2. Thus, again it is very likely that the differences were too low to cause significant error changes or, that the overall length is only one factor that might influence the ants' path integrator's accuracy.

At this stage, I cannot exclude an accumulation of errors; I can sum up that systematic errors seem to be of minor importance for the ants' path integration system and that ants that are not manipulated forage in such a manner that there errors do not differ significantly amongst them.

Ants that had performed longer foraging excursions — measured via the overall path length — showed significantly smaller deviations from the correct direction, when the systematic search center was evaluated. How can this result be explained? Because the systematic search program was recorded for 10 min, one can be sure that the center of the systematic search represented the spot where the ant assumed its nest to be. As mentioned in Materials and Methods, if the error — which is probably best represented by the Euclidean Distance ED — does not increase to a greater extent, in a theoretically sense, the directional deviation should become smaller (see Fig. III.18 and III.2.5.2). This might be the reason for this result. However, why was a similar result not found in the comparison of groups with different distances? It might be due to the fact that there the two most extreme groups did only vary by factor 2. The directional deviation seems to decrease with increasing foraging distance measured via the six groups. Thus, the tendency is the same but obviously can only be quantified with higher differences between the different ants.

The conflict could be solved using the formula of intersecting lines: the lateral deviation LD (that corresponds to the maximum of $|ED|$ (see also Fig. III.18) can be formulated as $LD = \tan(\alpha)\, d$, where d is the distance between ant and nest and α the angular deviation. Using this formula, α can

be calculated. Now I took the shortest distance to cover in this experiment (6.15 m) as a reference, i.e. instead of distance d I used d/6.15. Then, there was no correlation at all between path length and angular deviation for the 60 runs ($p = 0.328$).

This result shows that the angular deviation as used here and in experiments with fixed distances (e.g. experiment 1) is not a suitable reference value for experiments with varying distances. Furthermore, it suggests that for future analyses it might be important, not only to consider apparent outcome values of home run and systematic search as seen by the observer, but also to analyze the home run as viewed by the animal itself, i.e. in terms of the hypothetically reconstructed home vector in egocentric coordinates, as exemplified by applying my path integration model (see II.2).

4.2.3 Integrated curvature

The results in view of integrated curvature confirmed the results of experiment 1 (see appendix, 4.3). Thus, simple linear errors during the measurement of angles or during their integration cannot explain the number and the final amount of errors. The test was an extension of experiment 1, since in experiment 2, due to the experimental setup, the differences between the groups varied to a greater extent.

4.2.4 Conclusions

Different distances of natural outbound runs are not correlated with the accuracy of the path integrator measured via home run or systematic search center, and they also do not influence the systematic search pattern. As in experiment 1, the variations with regard to the values determing the accuracy of home run and systematic search were rather high, whereas the distance variation was rather low; this fact may again be able to explain that no significant differences between groups with different outbound distances were found. In addition, the overall path lengths of the outbound runs — that, as in experiment 1, only varied to a low extent — were not correlated with the accuracy of the path integration system. Thus, as for experiment 1, it can be concluded that due to the low variations during natural outbound runs path length *and* distance of outbound runs seem to be of minor importance for the path integrator's accuracy, and that obviously a number of other factors may contribute to the errors observed.

The limited amount of variations in natural outbound runs made it necessary to conduct experiments, during which the factors that most likely might influence the path integrator, could be manipulated and, therefore, the variations during the foraging runs could be increased. Thus, it should be possible to get a better understanding of the most essential errors and their interactions.

4.3 Experiment 3: Training effects

4.3.1 Outbound runs

The outbound runs of trained ants were less tortuous than those of untrained ants (III.3.4.1). When desert ants have encountered a feeder, they return to this feeder over and over again. This effect applies to artificial feeders (Wehner 1982) as well as natural feeding sites (Wehner et al. 1983; Harkness and Maroudas 1985). It is the basis for many experiments, be it channel experiments (e.g. Müller and Wehner 1988; Collett et al. 1998, 1999) or experiments in the open landscape (see experiments 4,5,6,7,8). By doing so, the ants just perform path integration to approach a known feeding site, that is they recall a previous state of the path integrator and this way (by a simple vector subtraction) return to the feeder over and over again (Collett et al. 1999; Collett and Collett 2004). This ability has also been shown for other ant species (e.g. wood ants Nicholson et al. 1999), other arthropods (e.g. honey bees or desert beetles, see Frisch 1965; Bisch 1999) as well as mammals (e.g. hamsters, see Etienne et al. 1998, 2004). Thus, it was expected that trained ants were much straighter during their outbound runs than untrained ants.

Schmid-Hempel (1984) and Wehner et al. (2004) have shown that foragers of *Cataglyphis* develop an astonishing section fidelity over their lifetime; an ability that has also been observed for other arthropods (e.g. bumblebees, Heinrich 1976). The natural outbound runs of experiment 1 displayed low values for tortuosity, but a directional persistence. Trained ants do not only stay in a successful foraging sector but even forage in an almost straight path to the feeder. Ants venturing out for food have to be successful in terms of bringing as much food as possible to the nest. This success has to be measured in a quantitative way during the entire lifetime (Wehner et al. 1983), i.e. the ants have to be as efficient as possible to avoid predatory risk (at our study site mainly spiders, genus *Zodarium*, and robber flies (Asilidae, Diptera), see Harkness and Wehner 1977; Schmid-Hempel and Schmid-Hempel 1984) and desiccation (Wehner et al. 1992, 2004), whereas they can tolerate temperatures of more than 50° (Gehring and Wehner 1992; Wehner et al. 1992). Thus, from an ecological point of view it seems an adaptive strategy to approach a known feeding site as directly as possible without wasting time by larger slopes and this is what could be observed in this experiment.

4.3.2 Outbound- and inbound runs

Since a difference between the two groups during their outbound paths may have been expected, it is surprising that the outbound paths of trained ants were even straighter than their inbound paths in the test field (III.3.4.1). This result cannot be easily explained, since surely the motivation to get back to the nest with a biscuit crumb is at least as high as finding a feeder again (e.g. Wehner et al. 1996; Loch and Wehner 1997). Two reasons might explain this result: (1) the capturing and the transfer to the test field confuses the ants and, therefore, their inbound paths are less straight than expected.

However, this argument should hold for trained as well as untrained ants. Therefore I reject it, since the manipulation of the observer should result in inbound runs of both groups that do not differ. Furthermore, in experiment 8, I got clear evidence that such an transfer did not influence the tortuosity of inbound runs remarkably. (2) The more plausible explanation is that trained ants had the chance to develop route-specific cues. These cues may be very small landmarks acquired during the foraging and return runs, very distant landmarks or the presence of nestmates; such cues were missing in the test field, where the ants performed their home runs, whereas they performed their outbound runs in the familiar training area. Therefore, this explanation for the difference is the most likely. However, the result is still striking, and, therefore, this topic will be taken up and scrutinized in more detail in experiment 8.

4.3.3 Accuracy of inbound runs and systematic search

Different studies (Collett et al. 1999; Wehner et al. 2002) have shown that *Cataglyphis* is able to recalibrate the home vector as well as the systematic search behavior. Now, are they also able to improve their accuracy during repeated training? With respect to the home vector, the differences between both groups are striking: trained ants perform smaller errors (in view of ED, $DIR8$, $DIRM$), and their home runs are straighter than those of untrained ones (III.3.4.1). Before trying to explain that surprising result, let us take a look at the reasons *why* it is so surprising:

First, it seems reasonable that the path integrator mostly and above all takes into account the most recent foraging trip, since the memory costs might be high and it can hardly be an optimization to keep more foraging runs stored in some higher memory (Dukas 1999; Cheng et al. 2006), and the food is more randomly distributed than clustered (Wehner et al. 1983). Therefore, the situation with a feeder that offers food abundantly and all the time, is a very unnatural one for *C. fortis*. Second, recent studies have shown that desert ants do not integrate the length of their preceding outward journeys, if they had differed to a larger extent (Cheng and Wehner 2002; Cheng et al. 2006; Narendra et al. 2007). Third, the authors of these surveys could indeed show that an integration only occurs when the ants were prevented from foraging for a longer time (Cheng et al. 2006). This was not the case in my experiment. The ants were travelling to and fro between nest and feeder and, though they were not marked individually, it is very unlikely that many of them had spent a lot of time in the nest and then were captured during their next outbound trip.

Thus, how can the difference in accuracy of home run between trained and untrained ants be explained?

Trained ants were captured at the feeder, that is at a point, where their path integrator had reached a certain reference value (Collett et al. 1999; Knaden and Wehner 2005a) and they were going to head homewards, whereas the ants captured on their outbound runs had the path integrator still running into the other direction. Knaden and Wehner (2005a) have shown that for setting the path integrator to zero, the ants must actually enter the nest actively. It might be possible that a similar process occurs when ants grab

food at a known feeder. The untrained ants, in contrast, are forced to take the point of capture as a reference value and to calculate the home vector immediately. This interpretation is backed by the systematic search center, that failed in revealing significant differences between the groups. Thus, both groups probably did not differ with the accuracy of the stored nest position. So, in a first hypothesis I interpret the difference between the groups not in an inaccuracy of the path integration itself, but rather suspect that the untrained ants were not able to head for the nest position as accurately as the trained ants. This hypothesis is backed up by the deviations from the correct nest position as measured via the systematic search centers that did not differ significantly.

In the theoretical part I have proposed a 'counter-steering' turning rate for the egocentric path integration model (II.2.2). Transferring this idea to the modelling part, the untrained ants were 'worse' in counter-steering, that is in keeping the egocentric Y-value close to zero, at least at the beginning of the run.

This interpretation is backed by the differences in terms of variance of the directional deviations between untrained and trained ants (III.3.4.1). The higher variations of the untrained ants might also be a hint that they are not able to head towards the nest as accurately as trained ants.

The lower tortuosity of home runs of trained ants and their lower variance of directional deviations may also be a hint that these ants are more confident with respect to the results produced by their path integration system than untrained ants; this question will be investigated in more detail later.

Let us approach this question from a different point of view: trained ants displayed straighter outbound paths than untrained ones. The training procedure was conducted for at least 24 hours. In general, differences could be due to training or low tortuousness of the outbound runs. Though the latter explanation is quite unlikely, I took the chance and compared 12 ants of each group with the same tortuosity during their outbound runs (III.3.4.2). With respect to the home runs, at least for most of the characteristics, including the most important Euclidean distance ED, there were significant differences. Thus, obviously there do occur training effects, since the lower tortuosity of trained ants' outbound runs could be ruled out as explanation for the observed discrepancy by conducting this additional analysis. Again, with regard to the systematic search center, no substantial differences between the groups were found. Thus, the hypothesis mentioned above seems substantiated.

As we shall see later, the systematic search is an indicator for the ants' confidence in their path integration system. Therefore, the non-existing differences between the groups (130 vs. 40 or 12 vs. 12) might be due to the fact that the ants know that the differences amongst them are rather low.

Untrained ants underestimate the distance more than trained ones (with respect to the homevector). This result is confirmed if 12 ants were tested against 12 ants (III.3.4.1 and 3.4.2). As mentioned in III.4.1.5, it might be helpful for ants to search in an area they might know for some nest-specific cues. Thus, this result may be a hint that trained ants have more confidence in the path integrator and, therefore, do not underestimate the distance to the nest as much as untrained ants.

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4.3.4 Conclusions

Repeated training increases the straightness of outbound runs. After ongoing repetition of the procedure, the straightness of outbound runs can even outperform that of the inbound runs. This increase in straightness allows the ants to approach known feeding sites as efficiently as possible. The training procedure in this experiment obviously increased the accuracy and the straightness of the ants' inbound runs. Since this result is unexpected, only some speculations were drawn, but the result made it worthwhile to conduct experiment 8 (see III.4.7), in which all the remaining questions were again addressed and investigated in more detail.

4.4 Experiment 4: Different distances of outbound runs

4.4.1 Do different distances of foraging runs cause larger errors of the path integrator?

I tested whether longer distances of foraging trips account for larger errors in the path integrator. Both the accuracy of the home vector and the systematic search behavior were more accurate for ants heading back after shorter foraging excursions (III.3.5.3). Therefore, longer distances do indeed lead to a decreasing accuracy of the path integrator.

Many theoretical approaches dealing with path integration (e.g. Mittelstaedt and Mittelstaedt 1973, 1982) claim that an ongoing accumulation of errors — systematic or random errors — during the egocentric path integration process should happen most certainly. Whereas in other species of arthropods (e.g. honeybees, see Srinivasan et al. 1997; Cheng et al. 1999) such an accumulation has been shown before, for desert ants such data were missing. The data presented here provide clear evidence that indeed an accumulation of errors over the entire froraging trip of *C. fortis* does occur.

Errors concerning the determination of the correct homing direction (Wehner and Wehner 1986; Müller and Wehner 1988) as well as errors due to misestimation of distances (Sommer and Wehner 2004) have been shown to exist for desert ants and also for other invertebrates such as honey bees (e.g. Srinivasan et al. 1997). The relevance of such systematic errors has been investigated intensively in the former three experiments. Benhamou et al. (1990) and Séguinot et al. (1998) claim that systematic errors probably arise at the neural level of the organism, whereas random errors can originate from inaccurate measurements of angles or distances. This is in concordance with the MW-error (Müller and Wehner 1988) and the leaky integrator LI (Sommer and Wehner 2004): the MW-error is based upon a incorrect integration of angles that have been measured properly, and due to the LI, the ants in their memory 'shorten' the distance to the nest with a constant decay rate during their journey.

However, considering the specific setup of experiment 4 and keeping in mind the results obtained in experiments 1, 2, and 3, systematic errors due to misestimation of angles or distances do not account for the results of experiment 4: since inbound and outbound runs of trained ants are almost straight (Wehner 1982; Wehner et al. 1983, 2002), the MW-error should not influence

the accuracy of the path integrator. Such is not the case for the leaky integrator (see II.3.2 and Sommer and Wehner 2004) which could account for some of the inaccuracies of the home run. On the other hand, the LI has, if at all, only very limited effects during short distances (Sommer and Wehner 2004). Furthermore, both groups of 5-m ants and 10-m ants overestimated the distance between feeder and nest (by the end point of the home run or the systematic search center, see III.3.5.3). Therefore, at least the striking difference between ED of these two groups must be caused by something else. Keeping in mind the results presented in experiments 1, 2, and 3, random errors are the likely reason for the differences between 5-m, 10-m, and 20-m ants result. Such errors — wherever they emerge — cancel partially and, therefore, accumulate sublinearly. More precisely, uncorrelated random errors, by the central limit theorem, cause the total error to grow as the square root of time or path length. To test for such a relation quantitatively, however, distances varying by a factor 10 or more would be required.

With regard to the leaky integrator, one more point should be mentioned: all three groups differ significantly from the predicted distance, i.e. 5m, 10m, or 20m, the 5-m and 10-m ants overestimating and the remaining group underestimating the distance. If only random errors accounted for this error, one would expect a normal distribution around the nest, i.e. no preference for the groups in terms of over- or underestimating the correct distance. Since this is not the case, a combination of random and systematic errors seems likely.

The result of this experiment conflicts with the result of experiment 1 (III.4.1.2): there, the the distance was fixed (10m). Therefore, the tortuosity TOR was directly correlated with the length of the outbound runs. In experiment 4, the distance of an outbound run corresponded to its overall path length. That is, distance of the outbound runs of experiment 4 and TOR of the outbound runs of experiment 1 can be compared to each other. Whereas in experiment 4 a striking influence of the distance on the accuracy of the path integrator was found, the same does not hold for experiment 1.

So, why did the ants of experiment 1 after longer outbound runs not show greater inaccuracies regarding their path integration system? This question might be answered by comparing the differences regarding the lengths of the outbound runs: they were rather low in experiment 1 (see III.3.2.2). In this experiment, in contrast, they varied by factor 2 (5-m vs 10-m and 10-m vs 20-m) or even 4 (5-m vs 20-m).

Somehow the results also conflict with those obtained via experiment 2 (III.3.3.1), since there no significant correlation between outbound distance and accuracy of the path integrator was detected. This is a surprise, since the differences in outbound distance of the two most extreme groups of experiment 2 varied by factor 2, i.e. the same factor by which 5-m ants and 10-m ants or 10-m ants and 20-m ants varied in experiment 4. Assuming the existence of a random error that is responsible for some of the inaccuracies, it is very likely that a higher sample size — as it was the case in this experiment — is necessary to find remarkable differences that are not covered by the large spreading of the results as in experiment 2.

Benhamou (1997) showed that errors displayed by swimming rats performing path integration are mainly random errors; surprisingly, they do not

increase with the length of the outbound path. In general, one must admit that — keeping in mind our current knowledge of the neuronal basis of path integration — such considerations remain rather speculative.

The first part of the results of experiment 4 supports the conclusion that (1) random errors play an essential role within the path integration system of desert ants and (2) that under natural circumstances desert ants cope quite well with the shortcomings of their path integrator, since a specific experimental setup was necessary to increase the performed errors considerably.

The increase of the path integration error with the covered distance leads me to the nest question:

4.4.2   Is this increasing error also reflected in the ants' confidence in their path integrator?

Several models describe the search behavior of desert arthropods as mathematical functions (Wehner and Srinivasan 1981; Hoffmann 1983b,c,a; Alt 1995). Whereas Alt (1995), in a mainly theoretical approach, proposed a model of temporal locomotion control of search behavior, Wehner and Srinivasan (1981) presented a mathematical model based upon a Gaussian probability density for the radial component of the systematic search behavior.

The systematic search program of desert ants is not an equidistant spiral, but rather concentrated around the area in which the nest is most likely to be found (Müller and Wehner 1994). Hence, the systematic search density profile gets adapted to the probability density function of the target. Now, does the search pattern also get adapted to path integration errors, which, as shown above, increase with larger foraging distances?

Cataglyphis indeed adapts its search behavior to the larger errors by widening its search loops (III.3.5.3, see also Hoffmann 1983c). Obviously, its confidence in its path integrator seems to be lower the larger the foraging distance it had covered before finding a food item. Ecologically speaking, it is essential for the ants to reach the nest in the shortest possible time. If the errors to be expected are small, the ants should concentrate their search around the end of the home vector, and this is exactly what they do. On the other hand, the bigger the uncertainty of the ants gets the wider is the spread of the loops, and again this is what was observed.

Uncertainty is an inherent property of the odometer, the compass and the path integrator and, therefore, its amount surely cannot be measured and taken into account by the ants. Thus, it seems to be a successful strategy to take the uncertainty into account by widening the systematic search after longer foraging excursions as shown in this experiment. However, it might well be that in the very same training situation an ant behaves as if it decreased the size of its uncertainty range (e.g. during an upwind approach to the feeder, see Wolf and Wehner 2000). Other experiments, in contrast, have shown that during continuous training the ants are not able to increase the accuracy of their outbound or inbound runs (see III.4.7).

4.4.3 Conclusions

To sum up, the results of this experiment provide clear evidence that errors during path integration accumulate during the outbound run and, therefore, longer outbound runs account for larger overall errors. The ant's systematic search behavior is not a fixed program that is just reeled off after the animal has completed its home vector. Rather, the search program is highly adaptive and enables the ants to take errors into account that have accumulated during path integration. There might be further impacts on that program to those revealed in this experiment which still have to be elucidated. In the long run, the result presented here might be helpful for more detailed models and the length of the foraging excursion might be one essential factor for the calibration of probability density functions describing this behavior.

4.5 Experiment 5: Inbound runs

4.5.1 Do ants deviate from the shortest track back to the nest?

As a first step, I investigated whether the ants respond to the deviation at their capture position from the beeline between feeder and nest. Whereas for the 50%-in ants no significant correlations were found, the result for the 25%-in ants was quite different: there exist striking negative correlations — as predicted — between this deviation and the direction of their remaining home run (III.3.5.5). How can these results be explained?

The results seem surprising, since the path integration process is based upon the principle of making a beeline back to the nest (e.g. Mittelstaedt and Mittelstaedt 1973; Wehner et al. 1983; Wehner 1992). Furthermore, all models describing the path integration process rely on this property of the path integrator (e.g. Mittelstaedt 2000; Merkle et al. 2006b). (Large) landmarks have been shown to influence the homeward courses of desert ants and, therefore, can lead to changes of the straight homing paths (Collett et al. 1992; Wehner et al. 1996; Kohler and Wehner 2005) but due to the setup used here they cannot be held responsible for this result. However, Wolf and Wehner (2000, 2005) showed that desert ants proceeding to a known food source deviate from the direct global vector course with the direction of the blowing wind, and then start their 'final approach' against the direction of the wind. This way the ants use the odor plume emanating from the feeder quite effectively. Additionally, the authors could prove that the distance of the upwind approach depends on the length of the foraging trip. Thus, this strategy is one of the probably high number of tools that desert ants employ to deal with their uncertainty. During experiment 4, I investigated another one of these 'compensation tools', in this case for the home run to the nest. On the other hand, it must be mentioned that desert ants do only develop specific routes if landmarks are present (see experiment 8 and Wehner et al. 1996), an ability that has also been shown for other ants such as *Melophorus bagoti* (Kohler and Wehner 2005; Wehner et al. 2006).

Now, might it be possible that wind also influences the home runs of the desert ants?

Though this interpretation seems unlikely, since there is probably no odor plume emanating from the nest as is from a feeder, I investigated it. At a

first look, the data presented here seem to support this hypothesis. There are some snags, however: after each run, I put the direction and strength of the wind on record (Merkle and Wehner, unpublished). When considering these data, two results catch one's eye: first, 7 of the 50%-in and 25%-in ants did not deviate from the beeline between nest and feeder at all. During six of these seven runs the wind was blowing from either of the two directions perpendicular to the beeline feeder-nest. Second, although the wind was blowing all the time from directions in the eastern half, i.e. within the range from north-north-east to south-south-east, the directions of the deviations from the beeline showed no tendency to either direction. One would have expected a majority of ants to deviate to the west in order to approach the nest and this was not the case (altogether 51 ants to west and 43 to east, Wilcoxon signed rank test: p=0.416). Therefore, the wind can be ruled out as main factor causing this behavior.

One possible explanation for this behavior is that there happens to be some scattering with regard to the ants' steering mechanism that guides them towards the nest (in the theoretical model, the mechanism that tries to keep the Y-value as close to zero as possible, II.2.2).

This might not be an inaccuracy of the path integrator itself, but rather the inability to keep the correct course, since the desert ants obviously compensate this behavior during the last part of their inbound run. This compensation, which is something different than the 'error compensation strategy' described in experiment 4 and by (Wolf and Wehner 2000, 2005), seems to take place during the second half of the homeward run, as the differences regarding the 50%-in and 25%-in ants suggest. The ants just do not keep the direct course, but the path integrator moves along and keeps integrating as accurate as possible. Before starting the 'final approach' the ants correct their directions. Considering my egocentric path integration model, a strategy could be performed and tested via the interactions of X and Y-value, e.g. that reaching a certain amount of X triggers the 'final approach'. At this point the finding of experiment 1 that there might be a substantial deviation at the beginning from the homeward run that gets compensated during the run is worth mentioning again. It is one more hint that at different stages during the inbound run the ants vary with regard to their performance with regard to keeping the direct course.

Continuing these considerations, it again becomes obvious how important it might be for further research to try to analyze empirical data as viewed by the arthropod itself.

4.5.2 Does the capturing of ants on their inbound runs have any impact on the accuracy of the path integrator?

Both 50%in ants and 25%-in ants were trained to the same distance of 20m. But they significantly differed in terms of their accuracy, 50%-in ants being less accurate than the 25%-in ants, if measured via the end of the home run (III.3.5.5).

Considering the end point of the home vector, the accuracy of the 50%-in ants was similar to that of both 10-m and 20-ants that did not differ from each other (see III.3.5.3). The accuracy of 25%-in ants, in contrast, matched

that of 5-m ants. If the accuracy was measured via the systematic search center, the 50%-in ants again did not differ from the 20-m ants, whereas the 25%-in ants were less accurate than the 5-m ants, but matched the 10-m ants (III.3.5.5)

The results of experiment 4 clearly showed that the distance to cover was positively correlated with the error performed by the ants. Therefore, one may conclude that errors accumulate during the path integration process. The 50%-in ants had covered the same distances during outbound and inbound run as the 20-m ants tested in experiment 4. In the training as well as in the test area all obvious landmarks had been eliminated, since they had been proven to be used as navigational tools (for desert ants e.g. Collett et al. 1998; Collett 1996; Collett et al. 1999, 2003a; Wehner 2003; Bisch-Knaden and Wehner 2003a). Thus, the accuracy of the 50%-in ants should — according to the ongoing error accumulation — resemble that of the 20-ants and this is exactly what was observed. Moreover, this result suggests that the capture and transfer of the ants to the test field in all probability does not effect their path integrator. The last conclusion is that the first 50% of the homebound run does either not provide the ants with additional cues or they do not use them during this part of their home run.

Now, why were the 25%-in ants more accurate than the 20-m ants, although, as for the 50%-in ants, the total length of outbound and inbound run was the same? Obviously, some cues achieved on the familiar route to the nest within the training area increased the accuracy of the ants' path integrator. Whereas it has been known for a long time that desert ants as well as bees employ obvious *big* landmarks that are visible from wide distances to pinpoint the nest entrance (e.g. Wehner and Räber 1979; Cartwright and Collett 1983; Wehner 2003), some studies (Wehner 1968; Seidl and Wehner 2006) have shown that variations in terms of the ground or soil may help desert ants to find their way as well. Since the ground structure did not vary to a greater extent during the whole outbound and inbound route, the question comes up why the 50%-in ants obviously did not use the same cues to improve their accuracy. This discrepancy can be explained via the actual state of the path integrator: Seidl and Wehner (2006) showed that homing desert ants accept ground marks as nest-defining cues after having completed 100%, 83%, or 66% of the homevector, whereas at a state of 22% they were ignored completely. Transferring this data to my nomenclature, the respective groups would have been called 0%-in, 17%-in, 34%-in, and 78%-in ants. The 25%-in ants of this experiment passed the spot where Seidl and Wehner had tested their 34%-in ants. The 50%-in ants, in contrast, possibly had not reeled off their homevector to a state where they would begin making use of ground landmarks. They rather had to reel off the second half of their home runs in the test field where the cues they might have used before were not present, whereas the 25%-in ants had only to cover the last quarter of their home runs in the test field, i.e. they had at least the third quarter of the home run to improve their bearings home to the nest. In a number of experiments, Wehner et al. (1996) demonstrated that skyline landmarks are applied mainly when the ants are close to their nest entrance; this results corroborates the conclusion drawn here. Fukushi (2001) showed that wood ants sometimes use skyline landmarks rather than employing the path integrator.

The presence of nest mates could be another cue ants use to adjust their bearings. However, though the numbers of ants traveling to and fro between the nest was rather high, this explanation can be ruled out, since the sole presence of conspecific nest mates cannot help to improve the direction the ants were heading towards. Nevertheless, the presence of nest mates might increase the confidence in the path integrator, as we shall see below.

4.5.3 What does the capturing during the inbound run do to the systematic search behavior?

Ants that reeled off larger parts (50%-in and 25%-in ants) or even the entire home vector in the training area showed narrower search patterns as compared to those ants that had to run off their complete vector in the remote test field (20-m ants, III.3.5.5). This holds true for all three groups of ants (50%-in, 25%-in, and 0%-in ants) that were under investigation here. Especially the 0%-in ants catch one's eye: they returned from a 20 m distance, but temporarily achieved the real vicinity of the nest, and — after their transfer to the training area — revealed almost the same search patterns as 5-m ants, i.e. ants that were trained to a feeder in only 5 m distance from the nest, but that had to run off the homevector in the test field, and, thus, did not reach the real nest position. Even those ants that were allowed to run off only the first part of their homevector in the training area (50%-in and 25%-in ants) revealed a significant reduction of the range of their search patterns.

Hence, although the latter two groups never reached the vicinity of the real nest, again some cues achieved on the familiar route back to the nest within the training area obviously increased the ants' confidence in the nest position as defined by the path integrator. I mentioned before that there might be other cues than the length of outbound and inbound runs that influence the ant's systematic search patterns. These cues seem to be achieved during the whole return trip to the nest, as the narrower search patterns of the 50%-in ants suggest; but they are obviously somehow concentrated close to the real nest, which may explain the extremely narrow search patterns of 0%-in ants and the only marginal differences between 50%-in and 25%-in ants. Since big landmarks have been shown to be mainly important for finding the nest entrance (e.g. Wehner et al. 1996), and are mainly used when the ants have run a tremendous portion of their home vector and the same finding holds true for ground cues (see first part of experiment 5 and Seidl and Wehner 2006), the results presented here brought clear proof that cues achieved close to the nest are also more important for the confidence in the path integrator and the range of the systematic search pattern than those acquired during parts of the home run that were located farther away from the nest. These cues are most likely soil conditions, but could also be horizon landmarks or the presence of nestmates.

The forager force of *C. fortis* is rather small (Knaden and Wehner 2003). Thus, it seems not very likely that the presence of nest mates indicates the vicinity of the nest, as Knaden and Wehner (2003) suggest. On the other hand, this does not rule out the explanation that the frequent encounter with nest mates increases the confidence in the path integrator. This confidence, as outlined above, seems to be controlled by other, or at least additional cues

than the path integrator itself.

However, at this point it must be mentioned again that the search of all ants was tracked in the remote test field. Therefore, whatever the cues were that increased the confidence of the ants in their path integrator, they were not present during the ants' search anymore. The calibration of the confidence in the path integrator by some kind of route- or nest-defining properties and the fact that obviously no 'recalibration' in the test field, where these cues are missing, does occur, is striking as the path integrator itself is not set to zero even by conspicuous landmarks (Collett et al. 2003a; Collett and Graham 2004; Knaden and Wehner 2005b).

4.5.4 Conclusions

The results of experiment 5 indicate that desert ants not always make a beeline back to the nest, but rather deviate from the correct course during the inbound run and reduce these deviations during the last part of the inbound run, probably performing a 'final approach' to the nest. Familiar characteristics during the inbound run, such as nest- or route specific cues or the presence of nest mates can help desert ants to adjust their bearings and, therefore, to reduce errors of the path integrator that have accumulated during the foraging excursion. In experiment 4, I have shown that the systematic search program of desert ants is highly adaptive. Here, I have expanded these findings by giving evidence that not only the characteristics of the foraging trip but also nest- and route-specific cues influence the pattern displayed by the systematic search program.

4.6 Experiments 6 and 7: Outbound runs

4.6.1 Do ants continue their foraging trip when captured during their outbound runs?

Most of the 50%-out ants returned to the nest upon their release in the test field (III.3.5.7). This was also observed before (Collett et al. 1999; Bisch-Knaden and Wehner 2003b) and might indicate a lower motivation to head towards a feeder than to return to the nest. In this context, an additional observation I made during my field stay in 2004 seems worth mentioning. As outlined in III.2.2.3, ants that were captured and released with a biscuit crumb in the test area, very rarely did not take the biscuit crumb. Since one cannot be sure whether the motivation to return to the nest without food in the mandibles is as high as compared to the ants that took the bait, these ants were not tested. Twice I did not bring the ants back to the nest but rather allowed them to start a run without food in the test area (these runs were not put on record). The ants set out for the correct nest position without searching for food and also commenced systematic search behavior when they were close to the assumed position of the nest.

Experiments with different species of arthropods brought evidence that their behavior and some 'specific' abilities depend on their motivational state, i.e. on the fact whether they are heading for a feeder or returning to the nest: honey bees do not take shortcuts to the feeder, but to the hive (Menzel et al. 1998), *Formica* ants solve problems with their route better during inbound

than outbound runs (Schneirla 1934), and desert ants store landmark information close to the nest over their entire lifetime (Ziegler and Wehner 1997), whereas food site based landmark information vanishes from the memory within 24 hours, most likely caused by a decay in foraging motivation (Loch and Wehner 1997). Furthermore, in desert ants the state of the path integrator decides whether the memory of panoramic, i.e. distant landmarks gets activated (Wehner et al. 1996; Bregy and Wehner 2003).

All these findings suggest a higher motivation to return to the nest than to approach a known feeding site again, shown by the exclusive application of specific abilities on the inbound runs. In this experiment, I tested them via a straightforward approach and the suggestions could be confirmed.

Harris et al. (2005) provided evidence that in wood ants the feeding state (fed or unfed) primes the decision whether to conduct an outbound or an inbound run by activating specific landmark memories. Since if conspicuous landmarks are absent, the feeding state on its own obviously is not sufficient to make foraging ants continuing their outward trips after being captured, I trained them through a landmark corridor. When they were tested in the test field, they had the same corridor of landmarks and exactly the same position relative to that corridor (see Materials and Methods). This way I could test whether landmarks could increase the foraging motivation of the ants. Such was the case, since the ratios between ants continuing their foraging trip and those returning to the nest significantly differed between experiments 6 and 7.

Thus, the influence of landmarks seems to be one essential factor with respect to the foraging motivation of *C. fortis*. Why did 21 out of 38 ants still return and search for the nest immediately? There might be two reasons: (1) still, the capturing during the outbound run had a big effect on the motivation of the ant and in many causes could not be 'overridden' by the landmark corridor; (2) there are other factors that may indeed influence the motivation of desert ants. Since not many experiments have been conducted hitherto, where desert ants have been captured on their outbound runs, the question which of these two hypotheses comes true remains elusive.

Bisch-Knaden and Wehner (2003b) showed that homeward-directing landmarks - even if they are close to the feeder - are learned during the ants' home runs. They explain this behavior by the variance of foraging excursions (of course, the second approach to the feeder will be a different straight one as compared to the first one) and that, therefore, it might be the more effective strategy to acquire this knowledge during the home run. However, they could not totally rule out the possibility that ants have learned landmarks guiding them to the feeder. Can the result presented here give more hints for solving this problem? At a first glance, it seems obvious that the presence of the landmarks in the test field triggers a local vector to the feeder which the ants follow. But this question should be approached with more caution: it is still possible that the ants acquired their knowledge during their inbound runs (during training the landmarks were present on inbound and outbound runs) and just reel off an inverse of their homebound vector. A similar explanation for some surprising findings has been proposed by Dyer et al. (2002).

Finally, since during experiments 4 and 5 and the research conducted by

Seidl and Wehner (2006) the importance of route-specific cues was shown, I address the question if the presence of these cues — that were, of course, missing in the test area — might also have increased the number of ants continuing their foraging trip. I reject this explanation for the simple reason that (1) those cues are obviously only acquired during the part of the route which is closer to the nest and (2) that those cues cannot be seen from farther distances.

4.6.2 Are there differences in the accuracy of the path integrator between outbound and inbound runs?

Only tendencies were found in view of the accuracy of the path integrator between outbound and inbound runs, measured as Euclidean distance ED (III.3.5.7). Probably due to the strongly varying sample sizes, these tendencies were not significant. Nevertheless, it seems worth to interpret two of them on a speculative basis.

It is striking that 50%-out-LM ants were more accurate when heading for the feeder than for the nest. This could be due to the presence of the landmarks which help them to navigate to the feeder (Loch and Wehner 1997; Bisch-Knaden and Wehner 2003a). In contrast, ants that returned to the nest did not experience the landmarks at all, since they did not perform the first half of the home run. These findings confirm the relevance of landmarks for desert ants during foraging, but still cannot solve the question of how they finally are acquired, raised by Bisch-Knaden and Wehner (2003a).

A similar argument could hold true for the difference between 50%-out and 50%-out-LM ants heading for the nest. The fact that 50%-LM-out ants were less accurate than the 50%-out ants might be a hint how important landmarks - that the 50%-out-LM ants, though trained to them, did not encounter in the test field, since they did not continue their foraging runs — can be for exact path integration. However, such interpretations seem to be speculative due to the small sample size of the 50%-out ants, and therefore will not be taken up.

The ED determined via the systematic search center displayed no differences at all between the groups (III.3.5.7), again indicating that the systematic search center may be the more realistic and stable value to determining the ants' guess of the nest position. An explanation could be that capture and transfer to the test field affects the home runs more than the systematic search; however, this can be rejected, since the Euclidean distances for the assumed positions of the nest or the feeder are larger if determined via the systematic search. Not all of the ants that had headed for the feeder engaged in systematic search behavior for the feeder; this finding corroborates the conclusions drawn with respect to the motivation to visit the feeder again or to return to the nest, respectively.

4.6.3 Systematic search behavior

The ranges of the systematic search did not vary between the groups (III.3.5.7). Therefore, following the conclusions drawn during experiments 4 and 5, it might be possible that the ants use their knowledge about the

length of their runs not only for their inbound runs but also during their outbound runs to find feeders as effectively as possible. The hypothesis that the length of the foraging excursion influences the systematic search pattern is confirmed, since 50%-out ants that returned to the nest showed smaller search pattern than 20-m ants (whose path lengths were 2 times higher).

4.6.4 Conclusions

To conclude, the results show that — as proposed by different authors (Frisch 1965; Etienne et al. 1998; Collett et al. 1999; Collett and Collett 2000) — the path integrator works for the outbound runs as accurately as for the inbound runs, but that the motivational cues differ. The motivation to approach a feeder can be increased by landmarks; however, there must be additional factors that are able to increase the motivation to return to a feeding site. Since no experiments with outbound runs of desert ants have been conducted so far by others, no comparisons were made at this stage.

4.7 Experiments 8: Ontogeny of the foraging behavior

4.7.1 General

Different studies have shown that desert ants (Wehner and Duelli 1971; Collett et al. 1999; Wehner et al. 2002) as well as bees (Otto 1959) are able to recalibrate their global vectors. Furthermore, there exists evidence that desert ants can store their vectors over longer periods (Ziegler and Wehner 1997), possibly over an entire worker's lifespan, as Wehner et al. (2002) suspect. They conclude that a calibration occurs whenever an ant encounters food at a new spot and that this way the global vector leading to known feeding sites gets changed or more accurate all the time. During the studies mentioned above the ants had to face the problem of differences between their inbound and outbound routes, i.e. they were either forced into channels during the first part of their home run that led them to directions that differed from the correct homing direction (Collett et al. 1999) or they were transferred after having reached the feeder and, therefore, after playing out their homevectors, were far away from the correct nest position and had to commence their systematic search, in the course of which they finally encountered the nest (Wehner et al. 2002). During that time the ants adjusted their global vectors in both experiments (Collett et al. 1999; Wehner et al. 2002). Though the adjustments were different in the different experimental paradigms, in both experiments it became obvious that (1) desert ants do adjust their global vectors as well as their systematic search patterns and (2) that they are not able to learn outbound routes that are not the reversal of their inbound routes.

Since the ecological reason for such an ability seems quite clear and has been discussed before, it might also be an adaptive strategy in an ecological sense to straighten and improve the accuracy of inbound and outbound runs to a known feeding site; experiment 3 revealed first hints that this is indeed possible. Wood ants *Formica rufa* increase the straightness by which they approach a known feeder slightly, although the overall foraging time does not change remarkably (Graham et al. 2003). Thus, experiment 8 aimed

at testing whether desert ants can also recalibrate their global vector when they do not have to solve the conflict of different outbound and inbound runs. In this experiment I addressed the question whether the calibration occurs also for the situation described above, resulting in both less tortuous and more accurate outbound and inbound runs. Although the ants were not far away from the nest when they started their systematic search, they only rarely arrived exactly at the entrance of their nest. Thus, it might be helpful to recalibrate the global vector to a small extent and thereby increase the foraging efficiency. Casual transfers to the test field should give a better understanding of the meaning of nest- and route-specific cues during the inbound runs. In addition, these transfers might be helpful in finally answering the question of potential effects of capturing and transferring of ants.

4.7.2 Outbound runs

All outbound runs were recorded in the training area. There was a striking difference with respect to the tortuosity of outbound runs that were performed after a preceding displacement to the test area (III.3.6.1). This result is surprising, especially if you consider that their accuracy was not influenced. Now, ants that were released at the nest entrance after performing the inbound run in the test field, entered the nest immediately, and stayed there for at least 10 min, whereas ants returning from the feeder in the training field entered the nest, and — with no exception — appeared at the nest entrance again after less than one minute to commence the next foraging run. Is it possible that such a short time span (10 min) may be able to decrease the straightness of foraging runs?

Previous studies dealing with this subject did not investigate the tortuosity of these runs. It might be possible that the confidence in the direction of the vector leading to the feeder decreases over time and therefore the ants do not approach the feeder as straightforward as they do when they have been in the nest for a longer time. Under natural conditions, the probability to find food again at a certain space is decreasing over the time (Wehner et al. 1983). Therefore, it might be better to perform more tortuous outbound runs after longer 'foraging breaks' to increase the probability to find food that is randomly dispersed. However, there are some doubts if such a short time span can reduce the confidence in a vector that much. Since all studies that investigated the memory on desert ants (e.g. Ziegler and Wehner 1997; Cheng and Wehner 2002; Cheng 2000; Narendra et al. 2007) were based upon longer time periods (hours or days), the answer to this question remains elusive.

Another explanation could be that ants did not have their route- or nest-specific cues at hand during the preceding home run (in the test field). This might also be a factor for decreasing confidence in the global vector, since it has been shown that that they are mainly acquired during the home run (Seidl and Wehner 2006). On the other hand, one would expect this result coinciding with a decreasing accuracy and increasing tortuosity of home runs performed in the test field and this was not the case, as will be outlined later.

The outbound runs are not only straighter if no manipulations occurred before, but straightness also increases over time. That is, the ants seem

to become more and more confident in the position where they have found some food. This result backs up the hypothesis that I just drew from the differences of tortuosities for runs without manipulations before and runs after manipulations. It might also be a useful adaption to approach a feeding site the straighter the safer it is that there is still food available.

Considering all these thoughts it seems obvious that tortuosity is not related to the accuracy of the path integrator. Whereas there is no increase in its accuracy (see next paragraph) the tortuosity changes with the number of runs. Thus, the tortuosity — at least during the outbound runs — is not a fixed routine used by the ants to reach a certain goal, but is rather highly adaptive and seems to be adjusted by the circumstances. One of those circumstances is undoubtedly the number of previously successful foraging excursions. The time that has elapsed since the last successful trip might be another candidate but this presumption has to be tested again.

Do the ants improve the accuracy of their outbound runs? There is no doubt that desert ants do not become more accurate if they were trained during their outbound runs (III.3.6.1). Wehner et al. (2002) found a vector recalibration at the latest after the fourth foraging excursion and no calibrations thereafter. Therefore, if there were an improvement due to the training, it should have become visible during the 19 outbound runs I analyzed. One might also argue that the frequent manipulations somehow influenced the ants' behavior, thereby covering potential gradual improvements. This point can be rejected, since no improvement was found during runs 2-6, i.e. before any manipulation took place.

Now, why does the training in no way improve the accuracy of outbound runs? First, the accuracy is quite high already. Even the second approach to the feeder, i.e. the first one after encountering the feeder, is quite good and, although sometimes the ants have to commence a kind of systematic search for the feeder, they find it quite easily. Thus, it might not be necessary to use memory space for this kind of adjustments (Dukas 1999; Cheng et al. 2006) that can only slightly increase the efficiency. The effort might just be too high as compared to the improvements that would be, say, a few seconds seconds time spent less during the outbound run. Second, the situation does merely resemble the natural situation that *Cataglyphis* has to handle in the desert. No feeding site will provide the ants with food for several days (Wehner et al. 1983). Therefore, as it is essential that the ants can recalibrate their global vector to find a new feeding site when the last one does not exist any more, it does not seem as important to increase the accuracy of outbound runs to a known feeding site that have been very high from the beginning. Desert ants also increase their section fidelity (Wehner et al. 2004), but this increase mainly depends on the foraging success and this result is in concordance with the training procedure. Since Wehner et al. (2004) could show that they ever and ever forage in the same section as long as they find food during the excursion, a training procedure might be the most extreme case of this kind of situation.

4.7.3 Inbound runs

Inbound runs in the test field were as tortuous as those in the training field. In addition, their tortuosity does not get reduced over time (III.3.6.2). Thus, the transfer obviously had no effect on the confidence of the ants in their home run. How can this result be explained?

First of all, the motivation is totally different as compared to the motivation during the foraging run (Wehner et al. 1996; Loch and Wehner 1997). During foraging the ants aim at finding food as effectively as possible; it does not depend on the location of the spot. As an example, it might even be better to find food close to the nest and thereby to shorten the total foraging effort than to take the longer way to the feeding site. Second, a feeder or a feeding site can vanish, whereas a nest stays at the same spot all the time. Third, the ants whose home runs were tested in the test field almost always took a biscuit crumb and started heading to the nest immediately. Thus, the confidence in the home vector should be the same all the time. This interpretation is backed up by the fact that, in general, inbound runs are less tortuous than outbound runs, as was compared for the outbound and inbound runs 2 to 5 (III.3.6.3). Thus, inbound runs obviously are very straight from the very beginning, and there is no need to improve them. Even after outbound run 5, when the outbound runs had become less tortuous they could not match the inbound runs. So, it takes a long time for outbound runs to get as straight as inbound runs. However, in experiment 3 (III.3.4.1) I have shown that this is indeed possible. The ants that were trained for at least 24 h, were even straighter on their outbound than inbound runs. However, it seems to take many runs to the same feeder to reach the same straightness during outbound runs as reached during inbound runs from the beginning. Finally, the result shows clearly that the tortuosity on the inbound run does not represent the ants' confidence in the path integrator; the result is confirmed if considering the data for the tortuosities of the inbound runs obtained in experiment 4 (see appendix 4.4.)

The inbound runs performed in the test field did not significantly differ from those performed in the training field with respect to their accuracy (III.3.6.2). This result conflicts with the evidence that the ants use ground-specific structures during their inbound runs. How can that result be explained? In all experiments, where these nest- or route-specific cues have been shown, the ants were trained for long times. This holds true for the experiment conducted by Seidl and Wehner (2006) (duration of training: 1 or 2 days) as well as for my experiments 4 and 5 (at least 24 h). Thus, these ants had performed a high number of runs (at least 30, see Åkesson and Wehner 2002) while obviously learning to use soil or ground structures effectively. In this respect the results of experiment 8 suggest that it takes a longer time to start effective use of ground structures than is necessary to learn large, panoramic landmarks (Wehner and Räber 1979; Bisch-Knaden and Wehner 2003b; Bregy and Wehner 2003). Further experiments, where high numbers of outbound and inbound runs in known and unknown territory are recorded, could test this suspicion.

The inbound runs did also not become more accurate during the repeated training procedure. Thus, it is as clear, as was pointed out for the outbound

runs, that no effective training occurs at all but that desert ants mainly rely on their path integration system to return to the nest or to the feeder if no large landmarks or other cues are available. This strategy might also be due to the costs of memory capacity (see also Cheng et al. 2006). On the other hand, similar arguments as outlined above work here: it is essential for an ant to come home to the nest after having found food, even if the food was found randomly or the feeding site was encountered for the first time. The ants cannot afford to improve their inbound runs over time; they must be as accurate as possible from the very beginning, and this is exactly what was observed.

Now, let us again take a look at experiment 3, where significant differences between the accuracy of the inbound runs of trained and untrained ants were found. This result conflicts with all the results that were revealed by experiment 8 including the arguments raised here. As explained when discussing experiment 3 (III.4.3.3), this result might be related to the different procedure between trained and untrained ants: the former group captured at the feeder, in most cases had already taken up a biscuit crumb, whereas the latter group was captured during the outbound run. This is the only explanation for the somehow surprising result of experiment 3. Here again, it should be mentioned that this result inspired me to conduct experiment 8. However, the results of experiment 8 gave clear evidence that - as all the time suggested and at least partially proven before (Cheng and Wehner 2002; Cheng et al. 2006; Narendra et al. 2007) - the ants are not able to increase the accuracy of the path integration system by training procedures.

4.7.4 Do desert ants develop specific paths to the feeder or to the nest?

Desert ants (Wehner et al. 1996; Kohler and Wehner 2005; Wehner et al. 2006) as well as other arthropods (e.g. Collett et al. 1996, 2002, 2003b) are able to develop specific paths that lead them to nest or feeder. Nowadays we know that procedural knowledge plays an essential role in the orientation of desert ants (Knaden et al. 2006; Wehner et al. 2006). Thus, desert ants do not learn complete paths all the time, but sometimes they learn specific sections of their route. Up to now, all this research on route fidelity of desert ants has been conducted with natural (in Australia tussocks of Buffel grass *Cenchrus ciliaris*, Kohler and Wehner 2005) or artificial landmarks (Wehner et al. 1996). If such landmarks are present it is even possible to get ants to follow such routes, if they were captured at the nest and transfered to the feeder. Andel and Wehner (2004) made homing ants running away by applying a similar procedure.

In this experiment I addressed the question whether desert ants also develop paths (I do not use the phrase route here, since this is usually used whenever landmarks come into play) if they are deprived of additional information by large landmarks (at this point, we know that small nest- or route-specific cues seem to play a role within the path integration system that has long been neglected). In addition, the experiment should reveal whether the ants also develop different outbound and inbound paths in a 'landmark-free' area. That they do approach a feeder against the blowing

wind has been shown by Wolf and Wehner (2000, 2005). Notice that due to the experimental setup, the wind could not influence the ants' paths in this experiment, since the beeline between nest and feeder was adjusted in a way that the ants were always approaching the feeder against and the nest with the direction of the wind. Most of the ants showed no preference for one side of the path during inbound or outbound runs (III.3.6.4). These results indicate that desert ants do not develop specific paths to the feeder, if no obvious (large) landmarks are available. The variations for ants that had somehow preferred areas for foraging or returning to the nest, respectively, showed high variances. Thus, it can either be that (1) the route- or nest-specific cues that are used to increase the accuracy of the path integrator are not sufficient to trigger the learning of specific routes or (2) that it again takes a very long time until these routes can be developed. It could also be another hint that soil conditions may play an important role for the orientation of *C. fortis*, since they could be used as a route-specific cues without developing particular routes. On the other hand, then substantial differences between inbound runs and the test and the training field should have appeared and this was not observed.

One might argue that the variance observed here is not that high as compared to the study mentioned (Kohler and Wehner 2005). On the other hand, small route-specific cues can only be seen from short distances. If they were used to develop specific paths, the variances of those paths would be much lower than they actually are; again, this argumentation does not hold true if they rely mainly on soil conditions. Furthermore, a considerable number of desert ants did not even develop a preferred side for foraging or heading back and, therefore, it can be ruled out that these ants developed specific paths to nest or feeder.

Theoretically, these questions could be solved by recording the outbound and inbound runs of individually marked ants for several days. On the other hand, over days desert ants loose some of their knowledge (Ziegler and Wehner 1997). Therefore, it may be difficult to conduct the suggested experiments.

4.7.5 Conclusions

To sum up, although a couple of previous studies have shown that the outbound trips of desert ants are flexible and can be changed and recalibrated due to several factors (feeding success, different outbound and inbound routes), they do not get more accurate when approaching a feeder over and over again, whereas their tortuosity gets reduced with increasing number of successful foraging excursions. This might display the ants' increasing confidence in the position of the known feeding site. The results also showed that repeated training does not increase the accuracy or the straightness of inbound paths of desert ants, but that the inbound runs are very straight from the beginning; for several reasons this strategy seems adaptive. Furthermore, the nest and route specific cues whose existence has been shown before, seem to require a high number of repeated training runs to get acquired and used by the ants.

Supposed that the ants' path integrator is a simple 'calculator' which

starts again with a new foraging excursion — as it is, to current knowledge — one would not expected desert ants to improve the accuracy of outbound or inbound runs during repeated training. This experiment proved this hypothesis.

Summary

Path integration enables desert arthropods to find back to their nest on the shortest track from any position. To perform path integration successfully, speeds and turning angles along the preceding outbound path have to be measured continuously and combined to determine an internal global vector leading back home at any time. A number of experiments have given an idea how arthropods might use allothetic or idiothetic signals to perceive their orientation and moving speed. When the global vector has been run off but the nest has not yet been reached, the arthropods engage in systematic search behavior. This behavior consists of a series of search loops of ever increasing size and finally leads to a search density profile peaking at the starting location.

In the theoretical part of this work, the model descriptions of mathematically precise path integration that have been developed so far are reviewed, and the hitherto not used variant of egocentric cartesian coordinates is proposed and explained. Its simple and intuitive structure is demonstrated in comparison to the previous path integration models. Measuring two quantities, forward moving speed and angular turning rate, and implementing them into a linear system of differential equations provides the necessary information during foraging run, reorientation process (e.g. at a feeding site) and return path to the nest. In addition, several possible types of systematic errors that can cause deviations from the correct homeward course are easily implemented and illustrated by means of the model. Such deviations have been observed for several species of desert arthropods in different experiments, but their origin is still under debate. The two most important error mechanisms in this respect are the Müller-Wehner-error, an approximative path integration model that accumulates systematic miscalculations in path integration whenever the animal walks different from the correct inbound and outbound direction, and the leaky integrator, a mechanism that predicts a linear underestimation of the distance to the nest with an exponential rate; both error types have been shown to occur in specific experimental paradigms with desert ants *Cataglyphis fortis*. Using the egocentric path integration model, simple indices are proposed that might allow to rule out or corroborate certain error types by conducting experiments.

Experiments were conducted with desert ants *C. fortis*. Those experiments, in which natural outbound runs as well as the following inbound runs and systematic search behaviors were observed and analyzed, revealed that natural outbound runs do not differ remarkably among different ants. This holds true for their spatial conformation as well as for overall path length and distance covered during foraging. Consequently, no significant correlations between all factors determing the shape of the outbound runs and the errors that were measured via different variables for inbound run as well as systematic search were found. Besides, the extension of the systematic search does not differ remarkably. However, due to the only slight differences of the natural outbound runs, such correlations cannot be totally excluded.

The error postulated by Müller and Wehner seems to be of no or minor importance during natural foraging excursions; the principle of the leaky in-

tegrator, on the other hand, might be able to explain some shortcomings of the path integration mechanism with respect to distance estimation. Repeated training increases the straightness of outbound runs. In experiments, where desert ants were trained to different distances, it became obvious that the longer the distances of foraging excursions, the larger the errors occurring during path integration (again measured via home run and systematic search), and that the ants adapt their systematic search strategy to their increasing uncertainty by extending the search pattern.

Additional experiments, during which the distance was kept constant, revealed that not only the characteristics of the foraging trip influence the accuracy of path integrator and systematic search behavior, but that also nest- or route specific cues have an impact on the orientation and the systematic search patterns of desert ants. If desert ants are disturbed during their outbound runs, most of them immediately set out in direction back to the nest, even without having food in their mandibles. External cues, in the respective experiment huge landmarks placed on the route between nest and feeder, increased the number of ants that continued its preceding foraging run; but still the majority headed back towards the nest. For a number of ants successive outbound and inbound runs (ontogeny-experiment) were recorded and analyzed. As a result, their outbound runs to a known feeding site get straighter over time, whereas the inbound runs are very straight from the very beginning and no increase of their straightness could be observed. For both outbound and inbound runs also no improvement in terms of accuracy of the path integrator was found; obviously the ants perform path integration in the same fashion all the time. Even if trained to a feeder for a long time in an area free of landmarks, desert ants do not develop specific paths, as they have been observed for other species of desert arthropods.

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Appendix

1   Abbreviations

ACF	autocorrelation function (III.2.5.1)
d	radial distance from start to end point of outbound or inbound run (III.2.4.2 and 2.5.1)
DIR	directional deviation from correct homing direction, measured via the systematic search center (III.2.4.3)
DIR_{MW}	directional deviation from homing direction predicted by the model of Müller and Wehner, measured via the systematic search center (III.2.5.1)
DIRM	directional deviation from correct homing direction during inbound run, measured by means of minimization method (III.2.4.2)
$DIRM_{MW}$	directional deviation from homing direction as predicted by Müller and Wehner during inbound run, measured by means of minimization method (III.2.5.1)
*DIR*0.5, ..., ..., ..., *DIR*12	directional deviation from correct homing direction during inbound run, measured at intersection of 0.5 m, 1 m, 2 m, 8 m, 12m-circle (III.2.4.2 and 2.5.5)
$DIR0.5_{MW}$, ..., ..., ..., $DIR12_{MW}$,	directional deviation from homing direction predicted by the model of Müller and Wehner during inbound run, measured at intersection of 0.5 m, 1 m, 2 m, 8 m, 12 m-circle (III.2.5.1)
DIS	deviation from correct homing distance, measured via end point of home run or systematic search center (III.2.4.2 and 2.4.3)
DIS_{LI}	deviation from correct homing direction as predicted by the Leaky Integrator, measured either via end point of home run or systematic search center (III.2.5.1)
ED	Euclidian distance between either end point of home run and correct nest position or systematic search center and correct nest position (III.2.4.2 and 2.4.3)
ED_{LI}	Euclidian distance between end point of home run or systematic search center and nest position as predicted by the Leaky Integrator (III.2.5.1)
ED_{MW}	Euclidian distance between end point of home run or systematic search center and nest position as predicted by the model of Müller and Wehner (III.2.5.1)
*EXT*100, ..., *EXT*20	extension of the systematic search with path length 100 m, 40 m, 20 m (III.2.4.3)
IR	interquartile range (III.2.4.4)
L	overall path length of outbound or inbound path (III.2.4.2 and 2.5.1)

LI	Leaky Integrator (II.3 and III.2.5.1)
LU	linear underestimation of ω (II.3)
M	median (III.2.4.4)
MA	mean angle (III.2.4.4)
MW-direction	homing direction predicted by the model of Müller and Wehner (III.2.5.1)
MW-error	error found in the experiments of Müller and Wehner (1988) (II.3)
MW-model	model of Müller and Wehner (II.3)
NLU	partially saturated underestimation of ω (II.3)
NLUs	fully saturated underestimation of ω (II.3)
OM	integrated curvature of outbound run (III.2.5.1)
OM3	integral of cubed curvature of outbound run (III.2.5.1)
P_c	correct position of the (fictive nest) (III.2.5.1 and 3.1.2)
P_{MW}	nest position according to the model of Müller and Wehner (III.2.5.1)
PD	processing delay of ω (II.3)
TOR	tortuosity during outbound or inbound run, measured as path length / radial distance (III.2.4.2 and 2.5.1)
*TOR*02, *TOR*57	tortuosity (length/distance) calculated for meters 0-2 or 5-7 during inbound run (III.2.4.2 and 2.5.1)
5-m ants	ants that were trained to a feeder 5 m south of the nest and captured at the feeder (III.2.3.4)
10-m ants	ants that were trained to a feeder 10 m south of the nest and captured at the feeder (III.2.3.4)
20-m ants	ants that were trained to a feeder 20 m south of the nest and captured at the feeder (III.2.3.4)
50%-in ants	ants that were trained to a feeder 20 m south of the nest and captured during the inbound run 10 m (50%) before reaching the nest (III.2.3.5)
25%-in ants	ants that were trained to a feeder 20 m south of the nest and captured during the inbound run 5 m (25%) before reaching the nest (III.2.3.5)
50%-out ants	ants that were trained to a feeder 20 m south of the nest and captured in the middle (50%) of their outbound run (III.2.3.6)
50%-out-LM ants	ants that were trained to a feeder 20 m south of the nest with landmarks on their route and then captured in the middle (50%) of their outbound run (III.2.3.7)

2 Supplement: Model for egocentric path integration (II.2)

Two more examples of an arthropod's foraging excursions (II.2) are given in Fig. A.
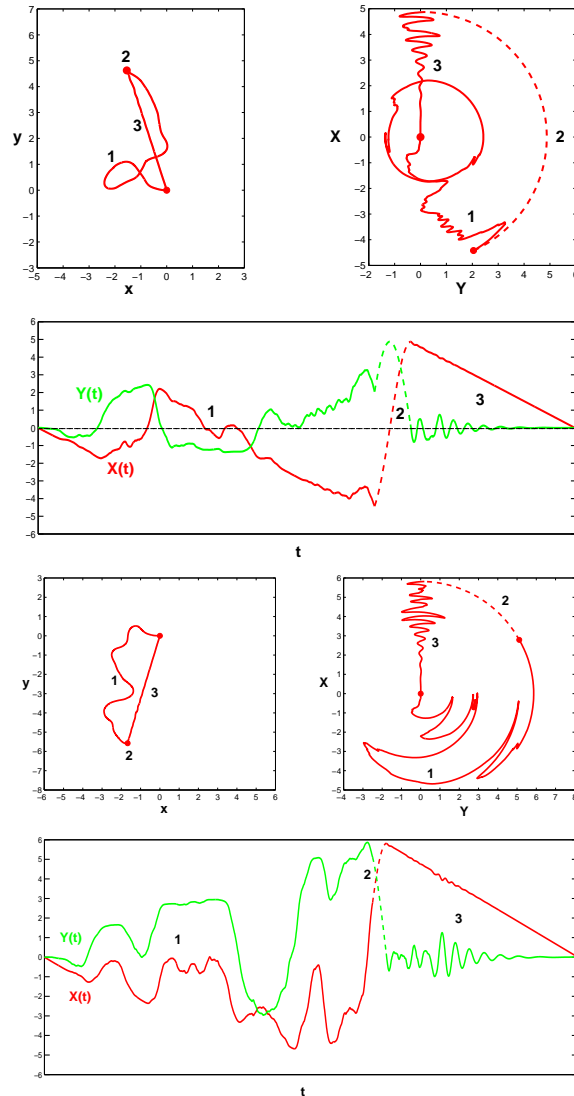
Figure A: Model simulations of two natural outbound paths and the successful return paths back to the nest due to precise path integration, according to the 3-Phase-model. Parameters used for calculations are, (1) for the outbound path $T_\omega = 1.0$ s, $\beta_\omega = 1$ s$^{1/2}$, and constant forward speed $v \equiv v_0 = 0.2$ m/s, (2) constant $\omega_{\text{rot}} = 1$ s^{-1} during rotation and (3) for homing the same as in (1) but a feedback constant $c = 1/0.5$ s^{-1} for beacon steering. Top left: Plots of the actual paths in cartesian (x, y)-coordinates of an observer. Position of the nest at $(0, 0)$ and the end of the foraging run are marked by filled circles. Top right: Corresponding plots of the nest position in the same scale in relative cartesian (X, Y)-coordinates, where the origin denoting the home position is marked by a filled circle. Note that the animal's head's direction is the X–axis pointing upwards, while the lateral Y–axis points to the left. Bottom: Corresponding plots of X and Y over time.

3 Supplement: Materials and Methods (III.2)

The tortuosities of 130 natural outbound runs were calculated either by means of the length L of the path divided by its distance d (TOR) or by using the ratio of the two eigenvectors that point into perpendicular directions (see III.2.5.1). The results of the two methods were highly correlated (Spearman correlation coefficient: $r_s = 0.672, p < 0.001, N = 130$, Fig. B).
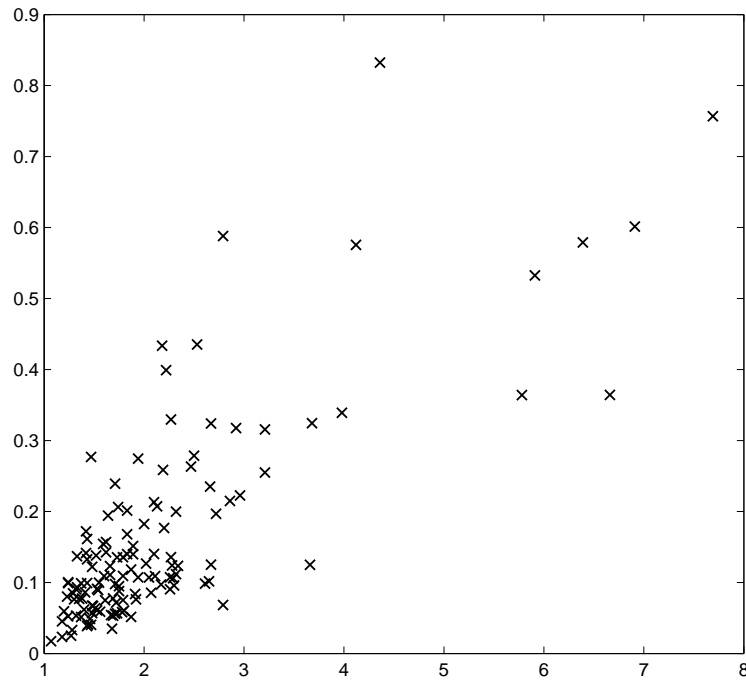

Figure B: Tortuosities of 130 natural outbound runs, measured as L/d (TOR, x-axis) and the ratio of the eigenvalues (y-axis).

4 Supplement: Results (III.3)

4.1 Müller-Wehner-error $> 5°$

For some of the ants of experiment 1 the theoretically correct homing direction and the homing direction predicted by MW (MW-direction) differed by at least 5°. For these ants the whole test procedure was repeated as described in III.2.5.1 for the MW-error. As already mentioned, the corresponding tests confirmed the results presented in III.3.2.3 (Tables A, B, C).

	N	deviation from correct homing direction	deviation from MW-direction	p-value
$|DIR0.5|, |DIR_{MW}0.5|$	64	29.17°(10.39-53.58°)	25.60°(9.94-47.39°)	0.253
$|DIR1|, |DIR_{MW}1|$	64	18.83°(8.50-42.36°)	19.19°(7.88-37.36°)	0.846
$|DIR2|, |DIR_{MW}2|$	64	11.60°(4.22-25.85°)	15.90°(79.75-28.67°)	**0.014**
$|DIR8|, |DIR_{MW}8|$	51	6.22°(2.15-8.78°)	11.92°(7.27-17.51°)	**<0.0001**
$|DIRM|, |DIR_{MW}M|$	64	5.71°(1.88-9.85°)	9.00°(4.73-16.44°)	**<0.0001**
$|DIR|, |DIR_{MW}|$ (SS)	51	11.37°(4.77-18.62°)	13.11°(5.63-18.13°)	0.633

Table A: Sample sizes, deviations (M and IR, in parentheses) from correct homing direction and MW-direction as well as p-values (Wilcoxon-text) are given for the directions determined by the crossing of the concentric circles with diameters 0.5 m, 1 m, 2 m, 8 m, and via the minimization method for the home runs as well as for the center of the systematic search (SS) for all ants of experiment 1 for whose home runs the correct homing direction and MW-direction differed by more than 5°. P-values that are significant on a 5%-level are printed in bold types.

	N	deviation from P_c	deviation from P_{MW}	p-value
ED, ED_{MW} (HR)	64	1.77m(1.20-2.69m)	2.33m(1.67-3.09m)	**0.002**
ED, ED_{MW} (SS)	51	1.59m(1.04-2.56m)	2.25m(1.64-3.07m)	**0.003**

Table B: Sample sizes, Euclidean distances (M and IR, in parentheses) from correct nest position P_c (ED) and nest position according to MW P_{MW} (ED_{MW}), respectively, and p-values (Wilcoxon-test) are given for the assumed nest positions — determined via the end point of the home run HR or the systematic search center SS — for all ants of experiment 1 for whose home runs the correct homing direction and the MW-direction differed by more than 5°. P-values that are significant on a 5%-level are printed in bold types.

	N	number of ants closer to correct homing homing direction	number of ants closer to MW-direction	p-value
$DIR0.5$	64	19	45	**0.0012**
$DIR1$	64	22	42	**0.019**
$DIR2$	64	29	35	0.456
$DIR8$	51	33	18	**0.036**
$DIRM$	64	30	34	0.538
DIR (SS)	51	21	30	0.210

Table C: Sample sizes and numbers of ants whose directions during the home run were closer to the correct homing direction and the MW-direction, respectively, and corresponding p-values (Wilcoxon signed-rank-test) are given for the directions determined by the crossing of the concentric circles with diameters 0.5m ($DIR0.5$), 1 m ($DIR1$), 2 m ($DIR2$), 8 m ($DIR8$) and via the minimization method ($DIRM$) for the home runs as well as for the center of the systematic search (DIR (SS)) for all ants of experiment 1 whose home runs the respective homing directions differed by more than 5°.

4.2 Müller-Wehner-error > 10°

The same procedure as described in appendix 4.1 was applied for those ants of experiment 1 for which correct homing direction and homing MW-direction differed by at least 10°. Again, the results confirmed the results presented in III.3.2.3 (Tables D, E, F).

	N	deviation from correct homing direction	deviation from MW-direction	p-value
$|DIR0.5|, |DIR_{MW}0.5|$	19	25.24°(9.81-41.49°)	23.56°(12.21-28.63°)	1.0
$|DIR1|, |DIR_{MW}1|$	19	17.49°(8.17-30.63°)	15.56°(8.84-30.67°)	0.355
$|DIR2|, |DIR_{MW}2|$	19	6.31°(3.57-24.95°)	24.58°(13.55-36.12°)	**0.001**
$|DIR8|, |DIR_{MW}8|$	17	6.24°(2.01-13.16°)	18.73°(12.67-27.34°)	**0.004**
$|DIRM|, |DIR_{MW}M|$	19	5.68°(1.92-7.71°)	16.25°(10.25-26.87°)	**0.001**
$|DIR|, |DIR_{MW}|$ (SS)	15	14.12°(3.45-22.56°)	14.96°(6.51-23.60°)	0.460

Table D: Sample sizes, deviations (M and IR, in parentheses) from correct homing direction and MW-direction as well as p-values (Wilcoxon-test) are given for the directions determined by the crossing of the concentric circles with diameters 0.5m, 1 m, 2 m, 8 m, and via the minimization method for the home runs as well as for the center of the systematic search (SS) for all ants of experiment 1 for whose home runs the correct homing direction and the MW-direction differed by more than 10°. P-values that are significant on a 5%-level are printed in bold types.

	N	deviation from P_c	deviation from P_{MW}	p-value
ED, ED_{MW} (HR)	19	1.80m(0.83-2.38m)	3.03m(2.48-3.35m)	**0.001**
ED, ED_{MW} (SS)	19	0.65m(1.29-2.32m)	2.35m(2.00-4.44m)	**0.003**

Table E: Sample sizes, Euclidean distances (M and IR, in parentheses) from P_c (ED) and P_{MW} (ED_{MW}), respectively, and p-values (Wilcoxon-test) are given for the assumed nest positions — determined via the end point of the home run HR or the systematic search center SS — for all ants of experiment 1 for whose home runs the correct homing direction and the MW-direction differed by more than 10°. P-values that are significant on a 5%-level are printed in bold types.

	N	number of ants closer to correct homing direction	number of ants closer to MW-direction	p-value
$DIR0.5$	19	6	13	0.169
$DIR1$	19	5	14	0.073
$DIR2$	19	12	7	0.332
$DIR8$	17	10	7	0.547
$DIRM$	19	10	9	0.860
DIR (SS)	15	6	9	0.404

Table F: Sample sizes and numbers of ants whose directions during the home run were closer to the correct homing direction or the MW-direction, respectively and p-values (Wilcoxon signed-rank-test) are given for the directions determined by the crossing of the concentric circles with diameters 0.5m ($DIR0.5$), 1 m ($DIR1$), 2.0m ($DIR2$), 8.0m ($DIR8$) and via the minimization method ($DIRM$) for the home runs as well as for the center of the systematic search (DIR (SS)) for all ants of experiment 1 for whose home runs the respective homing directions differed by more than 10°.

4.3   Integrated curvature: runs with varying distance

For outbound runs with varying distances the integrated curvature $\int \omega(t)\,dt = \phi_{\mathrm{end}} - \phi_0$ and the integral of the cubed curvature $\int \omega^3(t)\,dt$ was calculated (III.3.3.3) and tested for correlations with the accuracy of home run (ED, $DIR8$, $DIRM$) and systematic search (ED, DIR) and the extension of the systematic search during the first 100m ($EXT100$). As usual, for comparisons with DIR the original values (negative or positive) and for ED and $EXT100$ absolute values of $\int \omega(t)$ or $\int \omega^3(t)$ were used. No significant correlations were found (Table G: integrated curvature, Table H: integral of cubed curvature).

	N	r_s	p-value
ED (HR)	60	0.138	0.294
$DIR8$ (HR)	44	0.109	0.480
$DIRM$ (HR)	60	-0.047	0.720
ED (SS)	58	-0.084	0.529
DIR (SS)	58	0.096	0.471
$EXT100$ (SS)	57	0.154	0.252

Table G: Sample sizes and tests for correlations (Spearman correlation coefficient) between $\int \omega(t)$ and accuracy of home run (ED (HR), $DIR8$ (HR), $DIRM$ (HR)), systematic search (ED (SS), DIR (SS)), and extension of systematic search ($EXT100$ (SS)) of natural outbound runs with varying distances.

	N	r_s	p-value
ED (HR)	60	0.062	0.635
$DIR8$ (HR)	44	0.168	0.274
$DIRM$ (HR)	60	-0.017	0.895
ED (SS)	58	-0.010	0.940
DIR (SS)	58	-0.040	0.768
$EXT100$ (SS)	57	0.140	0.300

Table H: Sample sizes and tests for correlations (Spearman correlation coefficient) between $\int \omega^3(t)\,dt$ and accuracy of home run (ED (HR), $DIR8$ (HR), $DIRM$ (HR)), systematic search (ED (SS), DIR (SS)), and extension of systematic search ($EXT100$ (SS)) of natural outbound runs with varying distances.

4.4 Additional results of experiment 4

The values describing the accuracy of inbound run and systematic search of 5-m, 10-m, and 20-m ants (experiment 4, see III.2.5.4 and 3.5.1) are shown in Tables I and J.

	5-m ants	10-m ants	20-m ants
$|DIR8|$	7.30°(4.34-18.92°)	8.56°(3.35-15.01°)	3.23°(1.96-6.07°)
$|DIRM|$	5.94°(2.65-10.43°)	7.37°(2.93-11.49°)	3.312°(1.35-5.24°)
DIS	0.86m(-0.14-1.67m)	0.61m(-0.15-2.53m)	-1.20m(-2.99-0.16m)
TOR	1.34(1.22-1.51)	1.34(1.22-1.47)	1.17(1.12-1.20)

Table I: $|DIR8|$, $|DIRM|$, DIS, and TOR for the inbound runs of 5-m, 10-m, and 20-m ants are shown. Given are M, IR (in parentheses), and sample size N.

	5-m ants	10-m ants	20-m ants
$|DIR|$	12.53°(4.67-22.76°)	9.46°(5.25-17.40°)	9.73°(5.12-12.47°)
DIS	0.85m(-0.26-1.53m)	0.51m(-0.82-2.70m)	-1.80m(-3.90-0.91m)

Table J: $|DIR|$ and DIS for the systematic search of 5-m, 10-m, and 20-m ants are shown. Given are M, IR (in parentheses), and sample size N.

4.5 Additional results of experiment 5

4.5.1 Values for inbound run and systematic search

The values describing the accuracy of inbound run and systematic search of 50%-in and 25%-in ants (experiment 5, see III.2.5.4 and 3.5.1) are shown in Tables K and L.

	50%-in ants	25%-in ants
$|DIR8|$	9.76°(3.49-15.23°), N = 31	14.93°(9.66-28.43°), N = 30
$|DIRM|$	7.88°(4.92-13.24°), N = 50	11.93°(5.92-18.10°), N = 35
DIS	-1.74m(-2.86-0.41m), N = 50	0.35m(-0.44-1.32m), N = 35
TOR	1.33(1.19-1.47), N = 50	1.50(1.39-1.85), N = 35

Table K: $|DIR8|$, $|DIRM|$, DIS, and TOR for the inbound runs of 50%-in and 25%-in ants are shown. Given are M, IR (in parentheses), and sample size N.

	50%-in ants	25%-in ants
$|DIR|$	14.85°(8.37-25.66°), N = 48	33.98°(15.05-49.38°), N = 49
DIS	-1.94m(-3.35-0.41m), N = 48	-0.70m(-2.94-0.83m), N = 49

Table L: $|DIR|$ and DIS for the systematic search of 50%-in and 25%-in ants are shown. Given are M, IR (in parentheses), and sample size N.

4.5.2 Deviation from beeline at point of capture

Home runs and systematic search patterns of 50%-in and 25%-in ants were analyzed in views of directional deviations ($|DIR8|$, $|DIRM|$, $|DIR|$) and Euclidian distances (ED) (see III.3.5.1). The values determined if (1) either the deviation from the beeline between nest and feeder at the point of capture was neglected or (2) taken into account, are given in Tables M and N.

	without deviation	with deviation
$|DIR8|$ (HR)	9.69°(4.66-16.30°), N = 31	9.76°(3.49-15.23°), N = 31
$|DIRM|$ (HR)	8.75°(4.57-13.28°), N = 50	7.88°(4.92-13.24°), N = 50
ED (HR)	2.80m(2.01-3.59m), N = 50	2.78m(1.85-3.64m), N = 50
$|DIR|$ (SS)	15.44°(7.59-24.09°), N = 48	14.85°(8.37-25.66°), N = 48
ED (SS)	4.03m(2.80-5.87m), N = 48	3.82m(2.89-5.92m), N = 48

Table M $|DIR8|$, $|DIRM|$, ED of the home runs HR and $|DIR|$ and ED calculated via the systematic search center SS of 50%-in ants are given without and with consideration of the deviation from the beeline at the point of capture.

	without deviation	with deviation
$|DIR8|$ (HR)	18.93°(6.06-27.72°), N = 30	14.93°(9.66-28.43°), N = 30
$|DIRM|$ (HR)	14.18°(7.46-21.28°), N = 35	11.93°(5.92-18.10°), N = 35
ED (HR)	1.69m(0.90-2.19m), N = 35	1.79m(0.93-2.37m), N = 35
$|DIR|$ (SS)	30.96°(13.66-54.92°), N = 49	33.98°(15.05-49.38°), N = 49
ED (SS)	3.54m(2.11-4.64m), N = 49	3.64m(2.48-4.60m), N = 49

Table N: $|DIR8|$, $|DIRM|$, ED of the home runs HR and $|DIR|$ and ED calculated via the systematic search center SS of 25%-in ants are given without and with consideration of the deviation from the beeline at the point of capture.

4.6 Additional results of experiment 6

The values describing the accuracy of inbound run and systematic search of the 50%-out ants (experiment 6, see III.2.5.4 and 3.5.1) are shown in Tables O and P.

	50%-out ants (nest)	50%-out ants (feeder)
$|DIR8|$	7.84°(1.55-13.74°), N = 22	6.92°(***), N = 3
$|DIRM|$	7.84°(2.55-11.81°), N = 35	6.06°(1.96-20.04°), N = 6
DIS	-1.62m(-2.80–1.00m), N = 35	-4.36m(-2.21–1.54m), N = 6
TOR	1.50(1.36-1.69), N = 35	2.37(1.96-2.57), N = 6

Table O: $|DIR8|$, $|DIRM|$, DIS, and TOR for the runs of 50%-out ants heading for the nest, or for the feeder, respectively are shown. Given are M, IR (in parentheses), and sample size N. ***: no interquartile range given due to small sample size.

	50%-out ants (nest)	50%-out ants (feeder)
$|DIR|$	14.74°(6.34-21.23°), N = 34	14.46°(4.11-34.20°), N = 4
DIS	-2.84m(-4.14–0.98m), N = 34	-3.34m(-4.81–2.08m), N = 4

Table P: $|DIR|$ and DIS for the systematic search of 50%-out ants heading for the nest, or for the feeder, respectively are shown. Given are M, IR (in parentheses), and sample size N.

4.7 Additional results of experiment 7

The values describing the accuracy of inbound run and systematic search of the 50%-out-LM ants (experiment 7, see III.2.5.4 and 3.5.1) are shown in Tables Q and R.

	50%-out-LM ants (nest)	50%-out-LM ants (feeder)
$|DIR8|$	9.62°(4.57-24.85°), N = 20	13.75°(2.97-29.42°), N = 12
$|DIRM|$	13.75°(5.69-25.37°), N = 21	12.72°(9.36-22.62°), N = 13
DIS	-3.32m(-4.48–2.47m), N = 21	-1.78m(-2.72–0.23m), N = 13
TOR	1.60(1.44-2.07), N = 21	1.31(1.20-1.55), N = 13

Table Q: $|DIR8|$, $|DIRM|$, DIS, and TOR for the runs of 50%-out-LM ants heading for the nest, or for the feeder, respectively, are shown. Given are M, IR (in parentheses), and sample size N.

	50%-out-LM ants (nest)	50%-out-LM ants (feeder)
$|DIR|$	9.71°(4.28-19.39°), N = 21	2.35°(5.80-20.65°), N = 12
DIS	-3.48m(-4.81–2.08m), N = 21	-3.64m(-5.07–1.65m), N = 12

Table R: $|DIR|$ and DIS for the systematic search of 50%-out-LM ants heading for the nest, or for the feeder, respectively are shown. Given are M, IR (in parentheses), and sample size N.

5   CD

5.1   Application 1: Matlab routine (simulated run)

5.2   Applications 2 and 3: Matlab routines (natural runs)

5.3   Applications 4 and 5: Implementation of Müller-Wehner-error

5.4   Applications 6 and 7: Implementation of Leaky Integrator