# Local and global navigational coordinate systems in desert ants

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## SUMMARY

While foraging, the desert ant *Cataglyphis fortis* keeps track of its position with respect to its nest through a process of path integration (PI). Once it finds food, it can then follow a direct home vector to its nest. Furthermore, it remembers the coordinates of a food site, and uses these coordinates to return to the site. Previous studies suggest, however, that it does not associate any coordinates remembered from previous trips with familiar views such that it can produce a home vector when displaced to a familiar site. We ask here whether a desert ant uses any association between PI coordinates and familiar views to ensure consistent PI coordinates as it travels along a habitual route. We describe an experiment in which we manipulated the PI coordinates an ant has when reaching a distinctive point along a habitual route on the way to a feeder. The subsequent home vectors of the manipulated ants, when displaced from the food-site to a test ground, show that also when a route memory is evoked at a significant point on the way to a food site, *C. fortis* does not reset its PI coordinates to those it normally has at that point. We use this result to argue that local vector memories, which encode the metric properties of a segment of a habitual route, must be encoded in a route-based coordinate system that is separate from the nest-based global coordinates. We propose a model for PI-based guidance that can account for several puzzling observations, and that naturally produces the route-based coordinate system required for learning and following local vectors.

Key words: insect cognition, navigation, spatial learning, inverse model.

## INTRODUCTION

On a sunny day, if a foraging desert ant *Cataglyphis fortis* is given a biscuit crumb, it will immediately take a direct path to its nest. If instead it is caught and transported to unfamiliar ground before being given the crumb, then the forager travels the direction and distance that would have taken it home had it not been transported (Santschi, 1913; Wehner and Srinivasan, 2003). At the end of this 'home vector', the ant then starts a search centred where its nest should have been (Wehner and Srinivasan, 1981). Its ability to set an appropriate homeward direction shows that the forager monitors changes in its position as it travels away from the nest. The monitoring is achieved through a process of path integration (PI) (Mittelstaedt, 1983) using a sun-based compass (Wehner and Rossel, 1985) and an odometer that probably receives proprioceptive input from the legs (Collett et al., 2006; Ronacher et al., 2000; Wittlinger et al., 2006). We call the PI information that an individual has about its position relative to the nest its 'global coordinates'. Desert ants and honeybees use these global coordinates to remember the position of food sites with respect to their nests (Collett et al., 1999; von Frisch, 1967). When a desert ant or honeybee travels repeatedly along a route between its nest and a food site, it forms habitual 'local vector' memories encoding the directions and distances of segments of the route (Collett et al., 1998; Collett et al., 1996). PI often then also appears to provide a cue that indicates the expected end of such a segment (Collett et al., 2002; Knaden et al., 2006; Srinivasan et al., 1997; Collett and Collett, 2009). We ask here what the relationship may be between the nest-centred global coordinates used to generate home vectors and to remember food sites, and the encoding of metric information for the use of local vector memories along segments of a habitual route.

A habitual route could conceivably be encoded as a set of significant global coordinates that mark the endpoints of route segments. A forager could then set its course along a route by subtracting its current global coordinates from the stored coordinates of the endpoint of its current segment. But to use global coordinates in this way, an individual would have to ensure that it had the appropriate global coordinates at the start of a segment. Experiments suggest that honeybees and desert ants can use PI to determine the end of a habitual route segment, even if manipulations alter the amount of PI they have experienced between the nest and the start of the segment (Collett et al., 2002; Srinivasan et al., 1997; Collett and Collett, 2009). If during such experimental manipulations an ant did use global coordinates to encode a route segment and monitor its progress along the segment, then it could reproduce the habitual segment only if, before beginning the segment, it had reset its coordinates to a memory of the appropriate habitual value (Cartwright and Collett, 1987; Srinivasan et al., 1997). Do ants reset their global coordinates at familiar locations?

When travelling homewards along a habitual route, desert ants do not reset the global coordinates at familiar landmarks (Andel and Wehner, 2003; Collett et al., 1998; Knaden and Wehner, 2005). A previous study also showed that an ant does not reset its global coordinates at a habitual food site (Collett et al., 2003): the home vectors always reflected the route the ant had just taken rather than a remembered value. In that study, however, the route was entirely within a channel, and so there was no positive evidence that any landmarks on the way to the feeder were recognized or used. We have repeated this experiment, but under conditions in which ants are clearly guided by *en route* features. If ants were to reset their global coordinates when using the landmarks, it would be plausible for local vectors to be encoded in the global coordinates that monitor

the ant's position with respect to the nest. But an absence of resetting in the present study would suggest that when an ant monitors its progress along a route segment, it uses a coordinate system distinct from the global coordinates.

In the Discussion we present a model describing how a secondary coordinate system could allow individuals to use PI information to produce straight trajectories along both novel paths and familiar routes. This model proposes how the lengths of habitual route segments may be learnt in order to form local vector memories.

## MATERIALS AND METHODS

The experiments were performed on the island of Djerba, Tunisia, during June 2006 using the same *Cataglyphis fortis* (Forel 1902) nest as in the accompanying paper (Collett and Collett, 2009). The nest was enclosed by a plastic barrier with a single gate through which movement could be controlled. The inside of the barrier was coated with Fluon™ to prevent the ants escaping, while a sloping sand ramp was built around the outside so that foragers could return freely to the nest. The exit opened next to a 10 m long, 6 cm high barrier, also coated with Fluon™, which foragers followed on their way to a feeder (Fig. 1A). The orientation of the barrier was the same as the orientation of the channel in our other study (Collett and Collett, 2009).

A feeder, consisting of a slice of watermelon on a 1 cm high plate, was placed 6 m perpendicular to the far end of the barrier so that the trained ants made a 90 deg. turn on reaching the end of the barrier. To the left of the route from the barrier to the feeder were two low bushes 20–30 m away (see accompanying paper), but beyond the feeder there were no prominent natural landmarks for at least 100 m. The barrier constraining the first leg of the route was potentially visible to an ant travelling over open ground to the feeder, and so might provide cues for navigation. The feeder itself was marked by a small landmark (10 cm high and wide) to help guide the ants' final approach. Ants were marked with individual colour codes. The home vectors were tested after a week's training.

The exit point of the nest enclosure led into a small tray with doors at each end that could be closed to trap an ant briefly. During some tests we manipulated the global PI state that the ant had when it reached the end of the barrier. Once the ant was inside the tray, the doors were closed and the tray with the ant inside was picked up and displaced 4 m along the barrier. The ant was then released to travel the remaining 6 m along the barrier on its own. Training occurred between 08:00 h and 18:00 h for 2 weeks with occasional brief interludes of testing. To minimize any possible learning during such tests, an individual experienced test conditions for no more than one trip per day. In Fig. 2, the ants were not tested more than once in each condition.

A grid of 1 m squares made from fine string was laid out beyond the barrier to permit the ants' food-ward trajectories to be recorded on squared paper. Another grid was laid out approximately 100 m to the South to provide a test area on which home vectors were recorded. Ants taken from the feeder were released on the test grid with a crumb of biscuit. The direction of a food-ward trajectory was measured as the angle, clockwise from the direct line from the barrier to the feeder, to the first point at which the ant was 2 m distant from the end of the barrier. For the analysis of distances, digitized trajectories were truncated at the point where it was judged that they indicated the beginning of search. These points were judged by eye, but were made blind to the distance carried along the barrier.
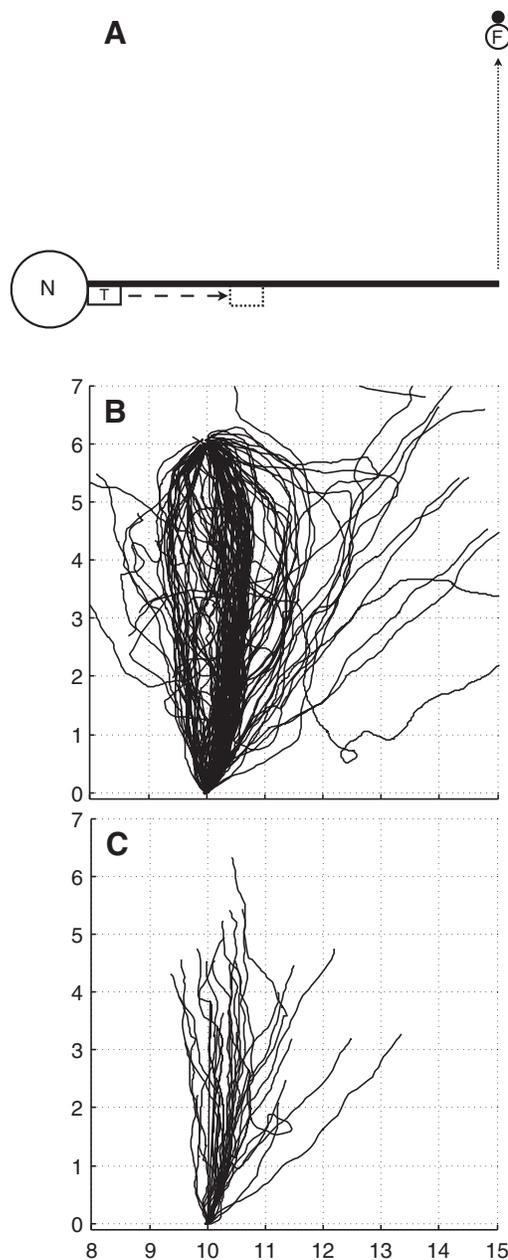


Fig. 1. Food-ward trajectories. (A) The training route. F, feeder; N, nest; T, tray. (B) Forager trajectories from the end of the barrier during training. (C) Trajectories with the feeder and feeder landmark removed. Grid lines are spaced at 1 m.

## RESULTS

The ants' trajectories from the end of the barrier to the feeder show an initial tendency towards under-turning (Fig. 1B), having a mean direction after 2 m of $10\pm15$ deg. ($N=105$) clockwise from the direct path. The end portions of the trajectories curve in towards the feeder. The initial parts of the trajectories are little affected by the removal of the feeder and feeder landmark. The mean direction after removal is $17\pm14$ deg. ($N=45$) over the first 2 m (Fig. 1C). But the final curve to reach the feeder is replaced by more tortuous search-like movement.

### Route memories

In order to examine whether ants could follow their habitual route even if they had a reduced amount of PI before reaching the end

of the barrier, we carried ants over the first 4 m of their route. The ants were then released to walk the remaining 6 m along the barrier before turning onto open ground for the second leg of the route to the feeder. To reduce the visual cues at the feeder during tests, we temporarily removed the feeder landmark leaving only the feeder – a very slightly elevated (1 cm) plate. The mean initial direction of the food-ward trajectories of ants that walked the entire 10 m length of the barrier (Fig. 2A) was 13±23 deg. ($N$=25), while the mean for ants carried 4 m (Fig. 2B) was 11±13 deg. ($N$=33). These directions were indistinguishable from each other (Watson–Williams $F$-test: $P$>0.5, $F$=0.311). The directions of the food-ward trajectories were therefore guided by memories from along the route.

Although we can be confident that the ants are recognizing and using landmarks or panoramas for guidance along their route, it is not possible to determine the nature of the memories in the present case. Previous results would suggest that the ants formed a local vector memory using compass cues (e.g. Collett et al., 1998; Knaden et al., 2006; Collett and Collett, 2009). But because the 6 cm high barrier in the present experiment provides a visual cue over the open ground, during tests as well as in training, it could potentially provide snapshot-based cues about position or direction (Collett and Collett, 2009).

### Does the global coordinate system re-align with familiar landmarks?

One potential memory that might be associated with the end of the barrier is a habitual global PI coordinate. If the global coordinate system were realigned with such a global coordinate memory, it would then be possible for the ants to use global PI to produce trajectories that were independent of the actual distance walked along the barrier. But signs of such resetting would be identifiable: the global PI coordinates of ants reaching the feeder after being carried the first 4 m along the barrier should then not reflect the shorter distance walked, but would be the same as those of ants walking the habitual 10 m along the barrier. To test for this possibility, we collected each ant at the feeder after recording its trajectory from the barrier, and recorded its home vector when it was released on a distant test field (Fig. 2).

The end of the home vector indicates the approximate position of the origin of the global PI coordinate system (Wehner and Srinivasan, 1981), thereby revealing the ant's global coordinates at the point of capture, and thus whether its global coordinates have been reset. The directions of the homeward trajectories show the well-known systematic error (Müller and Wehner, 1988), making a more acute angle relative to the line from feeder to barrier than is geometrically correct. In many of the ants, there is also a puzzling initial segment roughly in the feeder to end-of-barrier direction. But, critically, unlike the food-ward trajectories, the home vectors from the two manipulations differ significantly. Ants carried 4 m along the barrier have shortened home vectors and the direction of their trajectories is shifted towards the perpendicular from the feeder to the barrier (directions to endpoints, Watson–Williams $F$-test: $P$<0.000001, $F$=32, d.f.=1,53). Thus, even though the ants do recognize and use remembered features along their route for guidance to the feeder, they do not reset their global PI coordinates to any habitual state.

### DISCUSSION

A foraging desert ant or honeybee uses a PI-based global coordinate system to monitor its position with respect to the nest. It can use these nest-centred coordinates to remember and return to the
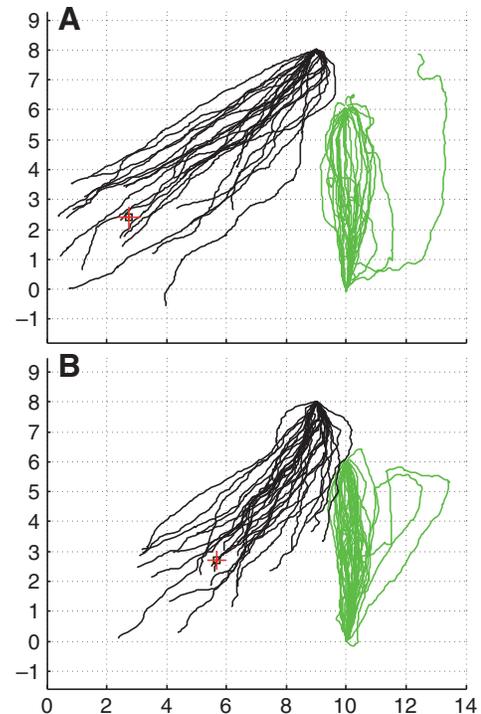


Fig. 2. Food-ward and homeward trajectories. (A) Ants that have walked the full 10 m along the barrier. Food-ward trajectories are shown in green. Subsequent homeward trajectories were recorded on a test ground, but are shown here starting slightly displaced from the endpoints of the food-ward trajectories, in black. The mean endpoint of the trajectories is indicated by a square. Crosses indicate the standard errors. The position of the fictive nest would be at (–1,2). (B) Ants that were carried for the first 4 m along the route before being released. The position of the fictive nest would be at (3,2).

location of a valuable resource (Collett et al., 1999; Riley et al., 2005; von Frisch, 1967; Wehner et al., 1983). We do not know whether a forager also remembers the global coordinates of other significant points in a familiar area. But we now do know that desert ants do not reset their current global coordinates to any global coordinate memories, even at significant places where landmarks are recognized and used for navigation. The global coordinate system appears to be updated independently of any landmark-associated knowledge.

### PI output coordinates as a basis for local coordinates

Desert ants can learn the direction (Collett et al., 1998; Collett and Collett, 2009) and distance (Knaden et al., 2006; Collett and Collett, 2009) of a segment of a habitual route. There is good theoretical reason to believe that local vector memories of such segments would not be encoded as a difference between global coordinates (Fig. 3A). The scatter generally observed in home vectors (Sommer and Wehner, 2004; Ziegler and Wehner, 1997) implies considerable noise in the PI system. The scatter scales with the distance travelled. As a consequence, the greater the length of the route before a segment, the more inaccurate a local vector encoded in such a way would be. Moreover, shorter local vectors would be particularly inaccurate. Observations, however, suggest that accuracy along a local vector scales with the length of the local vector (Cheng et al., 1999; Srinivasan et al., 1997). The lack of resetting found here, and in earlier studies (Andel and Wehner, 2003; Collett et al., 1998;
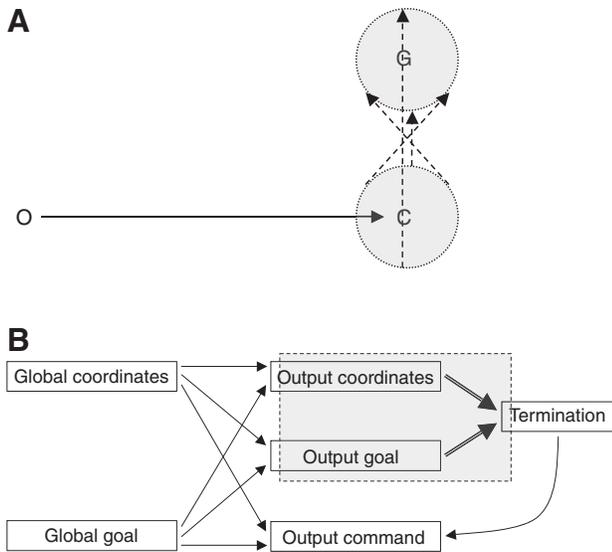
**A**



**B**



Fig. 3. Course setting using global coordinates. (A) After having travelled from the nest at O to the current position at C, a forager makes a comparison to reach the goal at G. The circles around C and G schematize the variation in the global coordinates resulting from noise in PI. The four dashed lines illustrate the range of possible variation in direction and distance of the output from the comparison. The greater the distance travelled from O, the larger the circles will be. The closer C and G are together, the greater is the scatter in the output directions. (B) Model of the production and use of a PI output vector coordinate system. An initiation comparison between current global coordinates and the global coordinates of a goal produces the three components of an output vector: a directional output command, an output coordinate system and an output goal. As an ant moves, there are then further comparisons (occurring within the shaded box) between the output coordinates and the output goal.
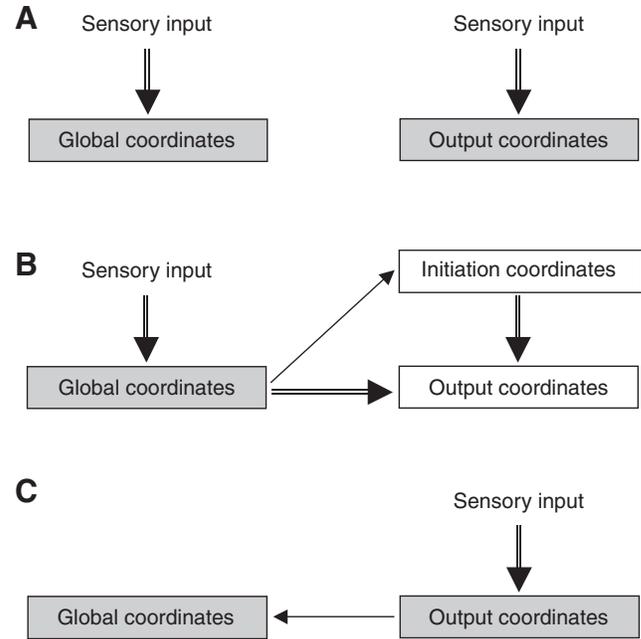
**A**



**B**



**C**



Fig. 4. Three possible relationships between the global and the output coordinates. Integrators are indicated by shading in the boxes. (A) Each coordinate system has its own integrator, each with input from a compass and odometer. (B) Only the global coordinate system has an integrator. The output coordinates could then be produced from the global integrator by using a memory of the global integrator state on initiating the output vector: current output coordinates = (initialization PI – current PI). (C) An output vector integrator receives input from an odometer and compass. Every time a new output vector is generated, the old output coordinates are added to a global integrator. The global integrator then would not have direct input from a compass and odometer, but only occasional input from the output vector integrator.

Collett et al., 2003; Knaden and Wehner, 2005), provides the evidence for a second line of argument that when an ant monitors its progress along a local vector, it must do so in a local coordinate system that is distinct from the global coordinates. A third piece of evidence comes from a recent study with honeybees, which suggests that local and global coordinates may use separate integrators (Dacke and Srinivasan, 2008). How might the local and global coordinate systems be related?

A *Cataglyphis* forager can use its global coordinates to compensate after an unfamiliar detour to redirect itself towards its nest (Schmidt et al., 1992) or towards a remembered food location (Collett et al., 1999). To set the new course, it must compare its current coordinates with the coordinates of its goal (Collett and Collett, 2000; Collett et al., 1999). The comparison is likely to use an 'inverse model' to generate the appropriate trajectory to reach the goal (Kawato, 1999). The resultant of the comparison can be thought of as a 'PI output vector'. One possibility is that, as the goal is approached, there is a sequence of diminishing PI output vectors, with a zero output vector at the goal. These output vectors would become increasingly inaccurate as the goal is approached, and noise in the comparison process could result in a change in direction at every comparison (Fig. 3A). Such successive comparisons could account for the frequent changes in direction observed during search. But they would produce neither the straight home vectors generally observed nor the sudden transitions to search that occur at the 'abknicht point' (Wehner and Srinivasan, 1981).

A straight home vector could be generated from an output vector if the initiation comparison between global coordinates produces a directional command that is followed along the entire length of the output vector. The abknicht point that marks the beginning of search would occur when the directional command is abandoned. Further evidence for a persistent directional command is that, when ants compute a PI-guided trajectory to a food site at the end of a detour, if the terrain does not match the accustomed terrain around the feeder they may continue in the computed direction far beyond the position of the food site [(Collett et al., 1999) and in honeybees (Collett et al., 2002)]. The directional output command produced at the end of the detour appears to retain control in this case, without further comparisons between global coordinates.

Generally, desert ants and honeybees do search at appropriate distances when guided by PI (Riley et al., 2005). To determine when the endpoint has been reached and the directional command should be relinquished, a 'termination comparison' would also be required. We propose that, at the same time as the guidance command is produced, an output vector coordinate system is initiated. This output coordinate system would be centred at the location where the initiation comparison is made, and the resultant of the comparison would provide the goal state for the output coordinates (Fig. 3B). An ant would then monitor its progress in an output coordinate system, in addition to monitoring the global coordinates. The updating of position within the two coordinate frames could involve two separate integrators, as may possibly be the case for honeybees (Dacke and

Srinivasan, 2008), or they could share a single integrator (Fig. 4). A termination comparison would provide a stop signal to the output command once the output coordinates have reached the output goal. An output coordinate system would provide distance information with respect to the point at which it is initiated – exactly the distance information that would be required for a local vector initiated at the same point.

The distance information in a local vector memory would not be involved in setting the direction of travel, but only in providing a termination signal to the directional command. It could be learnt from the output coordinates in at least two ways. An ant could learn the normal range of output coordinates experienced along the segment. It would then follow the local vector directional command as long as its current output coordinates fall within those familiar bounds. Alternatively, distance could be encoded as a goal state, learnt from the output coordinates at which new actions are initiated. In this case, an ant would terminate the local vector directional command if the command differs greatly from the resultant between its local vector goal and its current output coordinates. For either scheme, an ant would not have to follow the guidance cues from the output vector in order to use the output coordinates to monitor the distance travelled along a local vector.

An ant is likely to learn the direction of a local vector from some kind of average of the compass directions it experiences whilst travelling within a panorama-defined segment (Collett and Collett, 2009). We have suggested here that it could learn the length of any local vector that starts where a PI output vector is regularly produced. Since output vectors would generally be produced at locations where there would be a distinct change in panoramic context, such as at the end of a detour, changes in context along a route would generally be reliable triggers of a learnt local vector (Collett et al., 2002).

### Navigational implications of multiple coordinate systems

The use of a separate coordinate system for the metric route memories leaves the global coordinate system uncorrupted by the misidentification of a landscape feature. The independence from landscape features means that while the global PI coordinate system allows insects to navigate from novel sites and across unfamiliar terrain, it does not support general way finding between landmarks (e.g. Gould, 1986). This limitation contrasts with the situation in mammals, which can use landmark information to up-date PI coordinates (Etienne et al., 2004; Hartley et al., 2003; O'Keefe and Nadel, 1978). The richness of desert ant navigation seems to be derived from multiple, relatively simple and modular systems (Collett and Collett, 2006). The ensemble of vector- and snapshot-based navigational strategies gives ants a robust navigational system that can exploit the benefits of familiar features while being resilient to errors of mis-recognition.

### REFERENCES

**Andel, D. M. and Wehner, R.** (2003). Path integration in desert ants, *Cataglyphis*: redirecting global vectors. In *Proceedings of the 29th Göttingen Neurobiology Conference 2003* (ed. N. Elsner). Stuttgart: Thieme Verlag.

**Cartwright, B. A. and Collett, T. S.** (1987). Landmark maps for honeybees. *Biol. Cybern.* **57**, 85-93.

**Cheng, K., Srinivasan, M. V. and Zhang, S. W.** (1999). Error is proportional to distance measured by honeybees: Weber's law in the odometer. *Anim. Cogn.* **2**, 11-16.

**Collett, M. and Collett, T. S.** (2000). How do insects use path integration for their navigation? *Biol. Cybern.* **83**, 245-259.

**Collett, M. and Collett, T. S.** (2006). Insect navigation: no map at the end of the trail? *Curr. Biol.* **16**, 48-51.

**Collett, M. and Collett, T. S.** (2009). The learning and maintenance of local vectors in desert ant navigation. *J. Exp. Biol.* **212**, 895-900.

**Collett, M., Collett, T. S., Bisch, S. and Wehner, R.** (1998). Local and global vectors in desert ant navigation. *Nature* **394**, 269-272.

**Collett, M., Collett, T. S. and Wehner, R.** (1999). Calibration of vector navigation in desert ants. *Curr. Biol.* **9**, 1031-1034.

**Collett, M., Harland, D. and Collett, T. S.** (2002). The use of landmarks and panoramic context in the performance of local vectors by navigating honeybees. *J. Exp. Biol.* **205**, 807-814.

**Collett, M., Collett, T. S., Chameron, S. and Wehner, R.** (2003). Do familiar landmarks reset the global path integration system of desert ants? *J. Exp. Biol.* **206**, 877-882.

**Collett, M., Collett, T. S. and Srinivasan, M. V.** (2006). Insect navigation: measuring travel distance across ground and through air. *Curr. Biol.* **16**, R887-R890.

**Collett, T. S., Baron, J. and Sellen, K.** (1996). On the encoding of movement vectors by honeybees: are distance and direction represented independently? *J. Comp. Physiol. A* **179**, 395-406.

**Dacke, M. and Srinivasan, M. V.** (2008). Two odometers in honeybees? *J. Exp. Biol.* **211**, 3281-3286.

**Etienne, A. S., Maurer, R., Boulens, V., Levy, A. and Rowe, T.** (2004). Resetting the path integrator: a basic condition for route-based navigation. *J. Exp. Biol.* **207**, 1491-1508.

**Gould, J. L.** (1986). The locale map of honey bees: do insects have cognitive maps? *Science* **232**, 861-863.

**Hartley, T., Maguire, E. A., Spiers, H. J. and Burgess, N.** (2003). The well-worn route and the path less traveled: distinct neural bases of route following and wayfinding in humans. *Neuron* **37**, 877-888.

**Knaden, M. and Wehner, R.** (2005). Nest mark orientation in desert ants *Cataglyphis*: what does it do to the path integrator? *Anim. Behav.* **70**, 1349-1354.

**Kawato, K.** (1999). Inverse models for motor control and trajectory planning. *Curr. Opin. Neurobiol.* **9**, 718–727.

**Knaden, M., Lange, C. and Wehner, R.** (2006). The importance of procedural knowledge in desert-ant navigation. *Curr. Biol.* **16**, R916-R917.

**Mittelstaedt, H.** (1983). The role of multimodal convergence in homing by path integration. *Fortschr. Zool.* **28**, 197-212.

**Müller, M. and Wehner, R.** (1988). Path Integration in desert ants, *Cataglyphis fortis*. *Proc. Natl. Acad. Sci. USA* **85**, 5287-5290.

**O'Keefe, J. and Nadel, L.** (1978). *The Hippocampus as a Cognitive Map*. Oxford: Oxford University Press.

**Riley, J. R., Greggers, U., Smith, A. D., Reynolds, D. R. and Menzel, R.** (2005). The flight paths of honeybees recruited by the waggle dance. *Nature* **435**, 205-207.

**Ronacher, B., Gallizzi, K., Wohlgemuth, S. and Wehner, R.** (2000). Lateral optic flow does not influence distance estimation in the desert ant Cataglyphis fortis. *J. Exp. Biol.* **203**, 1113-1121.

**Santschi, F.** (1913). Comment s'orientent les fourmis. *Rev. Suisse Zool.* **21**, 347-425.

**Schmidt, I., Collett, T. S., Dillier, F. X. and Wehner, R.** (1992). How desert ants cope with enforced detours on their way home. *J. Comp. Physiol. A* **171**, 285-288.

**Sommer, S. and Wehner, R.** (2004). The ant's estimation of distance travelled: experiments with desert ants, *Cataglyphis fortis*. *J. Comp. Physiol. A* **190**, 1-6.

**Srinivasan, M. V., Zhang, S. W. and Bidwell, N. J.** (1997). Visually mediated odometry in honeybees en route to the goal: visual flight control and odometry. *J. Exp. Biol.* **200**, 2513-2522.

**von Frisch, K.** (1967). *The Dance Language and Orientation of Bees*. London: Oxford University Press.

**Wehner, R. and Rossel, S.** (1985). The bees' celestial compass-a case-study in behavioral neurobiology. *Fortschr. Zool.* **31**, 11-53.

**Wehner, R. and Srinivasan, M. V.** (1981). Searching behavior of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J. Comp. Physiol.* **142**, 315-338.

**Wehner, R. and Srinivasan, M. V.** (2003). Path integration in insects. In *The Neurobiology of Spatial Behaviour* (ed. K. J. Jeffery), pp. 9-30. Oxford: Oxford University Press.

**Wehner, R., Harkness, R. D. and Schmid-Hempel, P.** (1983). Foraging strategies in individually searching ants, *Cataglyphis bicolor* (Hymenoptera, Formicidae). In *Information Processing in Animals* (ed. M. Lindauer), pp. 1-79. Stuttgart: Fischer.

**Wittlinger, M., Wehner, R. and Wolf, H.** (2006). The ant odometer: stepping on stilts and stumps. *Science* **312**, 1965-1967.

**Ziegler, P. E. and Wehner, R.** (1997). Time-courses of memory decay in vector-based and landmark-based systems of navigation in desert ants, *Cataglyphis fortis*. *J. Comp. Physiol. A* **181**, 13-20.