

Path Integration in Mammals

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ABSTRACT: It is often assumed that navigation implies the use, by animals, of landmarks indicating the location of the goal. However, many animals (including humans) are able to return to the starting point of a journey, or to other goal sites, by relying on self-motion cues only. This process is known as path integration, and it allows an agent to calculate a route without making use of landmarks. We review the current literature on path integration and its interaction with external, location-based cues. Special importance is given to the correlation between observable behavior and the activity pattern of particular neural cell populations that implement the internal representation of space. In mammals, the latter may well be the first high-level cognitive representation to be understood at the neural level. © 2004 Wiley-Liss, Inc.

KEY WORDS: path integration; navigation; landmarks; self-motion cues; hippocampus; cognitive map

INTRODUCTION

Navigation, the capacity to plan and execute a goal-directed path (Gallistel, 1990) is generally viewed as being linked to the recognition of places that are labeled by landmarks. The simplest form of navigation, however, is the ability of many diverse animals, including humans, to return to the starting point of a journey without making use of familiar position cues. Instead, the agent estimates its position in a continuous manner with respect to a reference point, such as its nest, by relying on signals that derive from its own locomotion. An outstanding example of this comes from the desert ant, *Cataglyphis fortis*, which can return directly to the nest after an outward journey (over featureless terrain) of hundreds of meters (Wehner and Srinivasan, 1981). This process was originally called dead reckoning, by analogy with the deduced (“ded”) reckoning historically used by sailors to navigate across featureless open sea. More recently it has come to be called path integration (PI) (Mittelstaedt and Mittelstaedt, 1982) to reflect the assumption that the process takes place by the addition of successive small increments of movement onto a continually updated representation of direction and distance from the starting point.

Path integration—first postulated by Darwin (1873) and described by Murphy (1873), in reply to Darwin, as the integration of inertial signals—

appears to operate in a great number of diverse species with a fixed home base, both vertebrate and invertebrate, during the exploration of a new environment or in commuting between the home and familiar resource sites. It may also provide continuous information to the animal about where it is located on its internal representation of space (Gallistel, 1990), particularly in the intervals between visual fixes (e.g., in darkness). PI functions automatically and constantly, whenever the agent moves in continuous space. Thus, a central place forager may, for instance, interrupt its excursion to return home at any place and at any moment of its journey.

Ethologists have studied PI mainly through homing behavior in the context of foraging, and in particular of hoarding, where the animal explores the environment and returns home immediately after finding and collecting food items. Figure 1 illustrates this approach in golden hamsters, which were tested after a two-leg outward journey away from the nest. Despite the absence of any spatial cue from the familiar environment except the nest exit and the arena border, the animal returned to the place from which it had initiated its excursion. Homing without the help of external references could only occur through cues that derive from locomotion. Therefore, on the basis of these self-generated references, the animal must have updated its position with respect to its point of departure throughout its excursion, and could return home at any time.

Homing through PI is often assumed to be fairly direct but it can, in fact, occur along variable, indirect paths. This is particularly the case in test conditions in which the animal has to pinpoint its goal on the open arena floor, and possibly explores the test space in search of external cues. In an experimental arena with a peripheral home base, homing is generally more direct, most likely because the animal has learned to follow the planned homing direction to the arena periphery and then to search for the nest entrance along the arena border (Siegrist et al., 2003). Let us emphasize that, for reasons discussed below, PI in itself exerts a functionally important control over navigation only as long as the animal can combine it with learned strategies and/or spatial cues from the familiar environment.

One of the greatest difficulties in the study of PI is to prove that the animal does not use any external references. Three methods can be used to achieve this. The first method is to eliminate or mask all potential cues from the distal and proximal environment, including directional information from the earth's magnetic field

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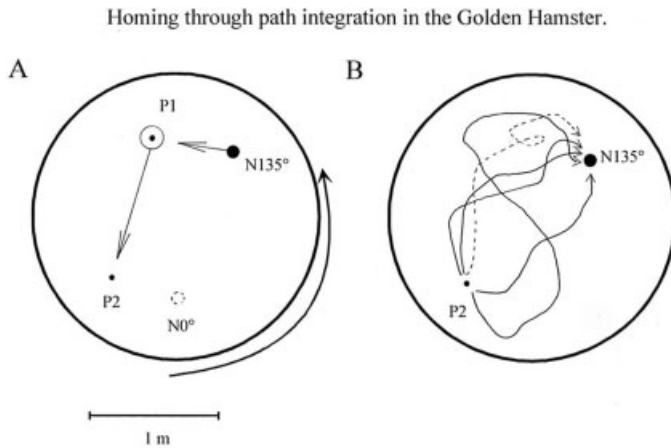


FIGURE 1. Homing through PI in the golden hamster (*Mesocricetus auratus* W.) **A:** Outward journey. Before the start of a trial, the arena is rotated by 135°, so that the (underground) nest box is rotated from its standard 0° position (N0°) to the N 135° position. The subject leaves the nest exit at its current, rotated position and performs a hoarding excursion under infrared light. Olfactory and/or tactile cues have been eliminated by stirring the thick sawdust substrate on the floor and by displacing plastic sheets along the wall of the arena. Following a dimly illuminated bait, the animal proceeds to point P1, where it walks along two full circles (open circle), and then goes on to P2, where it is offered food and fills its pouches. **B:** Return paths. Out of nine homing paths, eight are orientated toward the current nest location. Only those return paths are represented (continuous and hatched lines) in which the animal did not make contact with the arena wall. Path integration takes place throughout the excursion, so that the return trip can be fairly direct as well as convoluted. The fact that three return paths follow a detour similar to that of the outward trip cannot be explained by substrate cues. The return itineraries are never superimposed on the outward trajectory, and there is no concentration of the homing paths in the region where the animals had performed a number of rotations.

(Etienne et al., 1986). Strategies for such masking include testing the animal under infrared (IR) light or surrounding the testing environment with undifferentiated walls, and cleaning the surface of the apparatus so as to render olfactory cues ineffective. The second method is to set external cues and PI in a twofold (Etienne et al., 1986, 1988) or threefold (Etienne et al., 1990) conflict with each other. In such conflict situations, if an animal relies on self-motion cues, it should behave according to these rather than according to references from the proximal and/or distal environment. The third method is to manipulate the input into the PI system and observe the corresponding changes in behavior and neural activity. For example, Mittelstaedt and Mittelstaedt (1982) tested the ability of gerbils to retrieve their pups from within a circular arena by returning to their nest at the arena border. When the gerbils were slowly rotated on a platform (with an angular acceleration below the vestibular threshold, and thence not detected by the animals) while taking up a pup, they returned "home" in a direction that deviated from the nest by the amount they had been rotated themselves. In other words, they homed using an internal (and in this case disrupted) sense of direction rather than external references. Likewise, in a neural recording study of place cells, Jeffery et al. (1997) rotated rats slowly and observed a corre-

sponding rotation of the place cell representation (see below), the animals' vestibular system having not integrated the subthreshold inertial signal produced by angular acceleration. To confirm the use of PI independently of external references, the three above-mentioned procedures can also be combined with one another.

This article begins with a description of how animals sense and/or calculate the direction and distance in which they progress, and then presents some computational models of how they estimate their position with respect to the starting point of their excursion. Taking a comparative perspective, we also briefly mention certain aspects of PI in insects such as bees and desert ants, in which this navigational strategy is highly developed and has been studied most extensively. Turning to mammals, we then examine how and where self-motion signals are processed by the nervous system, where in the brain PI may be implemented, and how, in conjunction with external references, it controls the firing patterns of single neurons in the network of structures thought to be involved in navigation. Particular importance is given to the problem of how external, location-based and self-motion cues are combined to optimize navigation.

Because of its relative simplicity, PI is a potentially tractable problem on both the behavioral and neurobiological levels. The scope of what has to be represented, i.e., the animal's location with respect to a particular reference point, is well defined and amenable to formal analysis. Likewise, the primitives of PI, the (continuously ongoing) estimation of the distance traveled and in what direction, are well established. The questions for neurobiologists are how and where in the brain distance and direction are ascertained and represented, how these primitives are combined with one another to yield the neural representation of position, and how this representation is finally "read out" in order to guide homing.

PLACE CELLS AND HEAD DIRECTION CELLS

Before turning to more general analyses of PI, we begin by discussing what is known about the network of neural structures thought to underlie spatial representation in mammals, since study of these structures has provided important advances in our understanding of PI. Most of the work on mammalian spatial cognition has been conducted in rats, but recent functional imaging studies suggest that a similar network underpins human spatial cognition (Maguire et al., 1998). The cornerstone of the representation of local large-scale space appears to be the hippocampus and nearby structures (O'Keefe and Nadel, 1978; Morris et al., 1982; O'Keefe et al., 1998), which are needed for the solution of a wide variety of navigation tasks. Recordings of single hippocampal cells in freely exploring animals find that they exhibit activity that is highly localized in space (O'Keefe and Dostrovsky, 1971), generating firing patterns known as "place fields" (Muller, 1996) (Fig. 2A). The ensemble activity (Wilson and McNaughton, 1993) of these place cells codes for the animal's current location within a familiar environment, leading to the influential hypothesis that the hippocampus is the site of a "cognitive map" of the animal's environment (O'Keefe and Nadel, 1978). Although this notion has been greatly

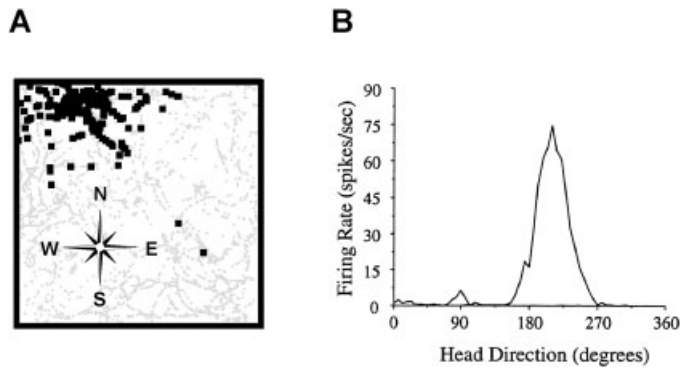


FIGURE 2. A: Raw data showing the activity of a hippocampal place cell as a rat foraged in a square box of 72×72 cm (adapted from Jeffery and O'Keefe, 1999). The path of the rat is indicated in grey. Every time the cell fired, a small black square was placed at the position where the rat was at that moment. It can be seen that this cell fired almost exclusively when the rat was in the Northwest corner of the box. B: A head direction cell (adapted from Golob and Taube, 1999). The direction the rat's head was facing is plotted on the x-axis, and the firing rate of the cell on the y-axis. This cell fired maximally when the rat was facing at about 220° .

debated (Redish, 2001), most investigators agree that spatial representation is at least one function of the hippocampus.

The place cells mainly appear to use the immediate boundaries of the environment to determine where to fire (O'Keefe and Burgess, 1996), but they also need information about direction, since environments (especially in the laboratory) may be symmetrical and not inherently polarized. The source of the directional information onto place cells most likely lies in the head direction system, a network of structures near the hippocampus whose cells display firing that correlates strongly with the direction the animal is facing at a given moment (Taube et al., 1990; Taube, 1998). Head direction cells always fire "in register," i.e., with the same relative angular directional firing preferences, regardless of which environment the animal is in, suggesting that they coherently signal the directional heading of the rat.

Place cells and head direction cells appear to form an internal map and internal compass, respectively. They respond to experimental manipulations of PI in a way that parallels the behavior of the animals; for example, both place and head direction cells can update their firing using only movement-related cues (Gothard et al., 1996; Knierim et al., 1996; Taube et al., 1996; Jeffery et al., 1997). This suggests that observation of these cells may provide a simple way of testing how a manipulation of PI affects the animal's computation of its position and heading. Furthermore, as discussed below, the head direction system and the hippocampus and its associated structures may actually comprise a major component of the neural substrate for a PI system (Samsonovich and McNaughton, 1997).

ESTIMATION OF DIRECTION AND DISTANCE

Mammals with a fixed home base rely on a variety of external cues and/or on path integration to navigate in their home range.

Position information from both familiar external references (Cheng and Spetch, 1998) and self-motion cues (Mittelstaedt and Mittelstaedt, 1982) is gained by assessing direction and distance through separate mechanisms. In this review, the nature and role of spatial references from the environment are discussed mainly with respect to their interaction with self-motion cues, our main concern being the role of self-motion cues in guiding PI.

In mammals, self-motion cues (often called "idiothetic" cues; Mittelstaedt and Mittelstaedt, 1982) derive from several sensory sources, including visual (linear and radial optic flow), vestibular (translational and rotational accelerations), and proprioceptive (feedback information from muscles, tendons, and joints). Recent studies have indicated an important role for the vestibular system in path integration, as animals and humans with vestibular damage show navigational impairment in the absence of landmarks (Cohen, 2000; Slackman et al., 2002; Wallace et al., 2002). Other types of information may play a part as well, such as short-term copies of locomotor commands (efference copies) and inertial signals due to acceleration from extr vestibular gravity receptors (Mittelstaedt, 1999; for review, see Berthoz et al., 1999; Etienne et al., 1996). Note that PI occurs independent of the modality of locomotion, as shown by walking bees (Bisetzky, 1957) and swimming rats (Benhamou, 1997). Therefore, signals that derive from rotations and translations must undergo substantial information processing before being transmitted to the path integrator.

The behavioral and neurophysiological studies referred to in this article analyze path integration in the absence of external self-induced motion cues such as visual flow. According to converging behavioral data from humans (Kearns et al., 2002; Telford et al., 1995; Harris et al., 2000), and single-cell recordings in rats (Sharp et al., 1995; Blair and Sharp, 1996), the contribution of visual flow to PI is much less obvious than the role played by non-visual feedback from locomotion in conditions where both categories of route-based information are available.

DIRECTION

In order to path integrate, animals need to maintain a continuous record of the direction in which they are moving. This information can be obtained either by reference to a fixed landmark of known orientation, or by measuring rotations since the last known heading (with or without an external reference). For instance, bees and ants estimate direction through visual motion cues, by measuring the angles in which they progress with respect to the sun azimuth and correlated skylight patterns (Wehner, 1994). By contrast, spiders measure rotations through proprioceptive feedback from strain receptors on the legs (Zill and Seyfarth, 1996) and add the rotation signal to the last known heading to estimate their current heading. The picture for mammals is more complicated, with evidence pointing toward the mutual integration of both environmental and movement-detection systems, preference being given to one or other type of information depending on its salience or reliability (see below).

In a familiar environment, even macroscopic mammals use predominantly stable (Jeffery, 1998) distal landmarks with a known

bearing as directional references (O'Keefe and Nadel, 1978). In the absence of visual references, the animals can rely on other categories of external information together with self-motion cues. Among the latter, inertial signals from the semicircular canals play a specific role in assessing angular motion. This has been shown by experiments in which rodents (Mittelstaedt and Mittelstaedt, 1982; Etienne et al., 1988) and humans (Metcalf and Gresty, 1992; Israel et al., 1995) had to reproduce or compensate for passive rotations around their vertical axis. Angular velocity, the output of the semicircular canals, is time-integrated at a higher level of the nervous system to allow the subject to estimate its heading (Israel and Siegler, 1999).

During active walking, proprioceptive and further cues from locomotion complement vestibular information. For example, hamsters update direction more accurately, and over a larger range of rotations, when they walk actively around a foraging site than when they are rotated on a platform where they collect food items (Etienne et al., 1988).

Head direction cells, whose activity is assumed to reflect an animal's computation of its current heading, are strongly influenced by a single salient cue in an otherwise symmetrical environment (Taube et al., 1990). Such a cue also influences both place cells in rats (Muller and Kubie, 1987; Knierim et al., 1995; Jeffery, 1998) and homing behavior in hamsters (Etienne et al., 1996), suggesting that animals may use visual landmarks to compute their heading when they can. If, however, the visual cues are removed or otherwise unavailable (e.g., in darkness), a stable firing pattern continues to be maintained by both place cells (Quirk et al., 1990; Jeffery et al., 1997) and head direction cells (Golob and Taube, 1999), and animals can still navigate effectively (Etienne et al., 1996). Some of this ability may be supported by nonvisual environmental cues such as odors (Goodridge et al., 1998; Save et al., 2000). However, head direction cells can maintain a constant firing direction even when the animal enters novel territory (Taube and Burton, 1995; we return to a detailed discussion of this experiment later), and place cell firing can be rotated by rotating the animal independently of environmental cues (Jeffery et al., 1997), showing that movement-related directional information can be recruited in the absence of vision.

How is information about angular motion processed? Recently it has been found that cells in the dorsal tegmentum code for angular velocity (Sharp et al., 2001; Bassett and Taube, 2001), information they receive from the semicircular canals via the vestibular nuclei. The picture that seems to be emerging is that information about angular acceleration in the horizontal plane is collected and converted to an angular velocity signal by the semicircular canals, then passed on to the dorsal tegmentum and integrated again on its way through the mammillary nuclei and thalamus (Bassett and Taube, 2001). This provides an angular distance measure that updates the head direction signal appropriately. Meanwhile, periodic visual fixes, arriving from the cortex, act to reset the head direction signal if it has drifted by a small amount (see below).

Visual and movement information may come together in one of the multimodal head direction areas, which receive a convergence of cortical inputs (presumably carrying visual information) and

subcortical inputs (presumably carrying movement information). Cells in the anterior thalamus show anticipatory firing, signaling not the present heading of the rat but rather the heading it will attain up to 40 ms in the future (Blair et al., 1997). This suggests an influence of extrapolated motion and/or efference copy, an interpretation that is supported by the observation that cells in the anterior thalamus fail to fire in their preferred directions if the animal is restrained, and hence unable to execute motor commands (Taube et al., 1996). Thus, it is plausible that this structure may serve to organize and/or transfer motion-related information. Mizumori and colleagues have suggested that this information is then carried, along with possible posterior parietal inputs, to the retrosplenial cortex. Here it is integrated with visual information from the geniculostriate and tectocortical pathways and then passed to the hippocampus to organize the place fields (Cooper and Mizumori, 1999, 2001). In contrast, Taube and colleagues have suggested that the site of visual-idiothetic integration may be the postsubiculum, which receives anatomical (van Groen and Wyss, 1990) and functional (Goodridge and Taube, 1997) inputs both from the anterior thalamus and from higher-order visual areas, including the retrosplenial cortex.

Regardless of the site of convergence of these two information sources, a challenge for computational modeling is to explain how such disparate information sources could be bound together to give a unified direction signal. Skaggs et al. (1995) and Zhang (1996) have provided models in which the animal's current heading is represented by the activity of a collection of head direction cells that are interconnected in a virtual "ring," with cells representing neighboring directions being mutually excitatory, but progressively less so with increasing angular distance, and cells representing opposite directions being mutually inhibitory. The cells whose current activity is the greatest are the ones indicating the current head direction of the animal. Both motion cues and landmarks influence the system by shifting the region of greatest activity toward a different part of the ring, the strongest cue gaining control of the representation and hence resolving any conflict. Other models of head direction computation also depend on the idea of local excitation and global inhibition, with a rotational input that shifts the center of activation (for review, see Redish, 1999).

DISTANCE

To assess its position, as well as its orientation or head direction with respect to the starting point of its excursion, a navigator needs to estimate translations as well as rotations. Bees rely on optic flow to measure translations (Srinivasan et al., 2000), while ants gauge distance mainly through proprioceptors located on joints between the insect's main body parts (Wohlgenuth et al., 2001). Measuring the ground distance, and not the distance actually walked, desert ants are able to compensate for undulations in the terrain in order to calculate the straight-line distance back to the nest (Wohlgenuth et al., 2001). Spiders cover the straight-line homing distance to their nest in darkness, without the help of any external reference; they cover the correct distance under the control of proprioceptive motion cues only (Görner and Möller, 2001).

Hamsters (Séguinot et al., 1993), dogs (Séguinot et al., 1998), and humans (Loomis et al., 1993) are capable of estimating the beeline distance in which they walk through self-motion cues. During active walking without vision, the assessment of path length depends less on inertial information than on nonvestibular motion cues, such as proprioceptive feed back and efference copies. This has been observed in rodents, which update their position much more accurately during actively performed translations than during passive shifts (Mittelstaedt and Mittelstaedt, 1982; Etienne et al., 1988). Similar conclusions can be drawn from experiments on normal (Mittelstaedt and Mittelstaedt, 2001) and labyrinthine-defective (Glasauer et al., 1994, 1999) human subjects who had to estimate and reproduce the length of a path or to cover the distance to a previously seen visual target. However, recent data indicate that blindfolded humans are able to reproduce passive translations by driving a robot or to indicate the distance to a target while being driven on a trolley (Israel et al., 1997). Thus, mammals do use inertial information to estimate distance. There still is no general agreement on how this occurs. Linear acceleration acts exclusively on the vestibular otoliths, which function as general accelerometers and therefore respond to tilt as well as to linear acceleration. According to a recent hypothesis, the nervous system would use internal models to distinguish between gravity and linear acceleration (Merfeld et al., 1999).

Very little is known at a neuronal level about the integration of sensory information in the determination of the straight-line distance moved, mainly because a linear homologue of the head direction system has not been identified, and possibly does not exist as a separate entity (Maurer, 1998). Physiological studies show that neurons in the place system can receive information about linear translations. Gothard et al. (1996, 2001) have found that place cells use PI as well as visual cues to compute the correct distance from a boundary in a linearly constrained environment. When the rat began an outward journey from a boundary, its place cells appeared principally to be driven by the distance of the rat to the wall behind it, presumably computed using PI. However, as the animal moved further from this boundary the visual cues took over, often at a distinct transition point, so that by the time it reached the far end of the linear track, its place cells were primarily driven by the distance to the boundary the rat was heading toward (i.e., by vision). Place cells also code weakly for the speed of the animal as it traverses the environment (Hirase et al., 1999). In addition, a cell or axon firing strongly in response to the speed of the animal has been reported in the hippocampus (O'Keefe et al., 1998), suggesting that the nervous system does compute a precise speed signal. Whether there is an explicit neural "odometer" in the brain remains to be determined. It may be that absolute distance from the home base is not represented explicitly, but that distance estimations are combined directly with the head direction signal to update either a vector, or a point on a cognitive map. We return to this point in the section on PI and the representation of space.

COMPUTATION OF POSITION VECTORS AND GOAL VECTORS

For an agent to be able to keep updating its position (the position vector) on the basis of motion cues, there must be a continuous gathering of information on how far and in which directions it has traveled. Thus, information on both translations and rotations must be constantly recorded and combined. What computations underlie this process? According to the mathematical formulation of PI, the line integral of the angular component is performed along the actual path to yield the navigator's current coordinates in any chosen frame of reference. Mittelstaedt and Mittelstaedt (1982) proposed that animals update their position in a Cartesian system, with their nervous system breaking down each rotation into its two orthogonal (sine and cosine) components and integrating (summing up) these components over the total path. However, the nervous systems of invertebrates and vertebrates may not perform explicit trigonometric operations. The combining of direction and distance to yield a vector means that PI involves information processing that is isomorphic with (Gallistel, 1990), but not necessarily identical to trigonometry.

The measurement of rotations and translations is inevitably accompanied by errors, particularly when rotations are estimated without the help of an external reference (Benhamou et al., 1990). Furthermore, PI being an incremental recursive process, in which changes in the current estimate of the position are added to the position vector of the previous step, these errors are necessarily cumulative (Etienne et al., 1988). Benhamou et al. (1990) therefore added an explicit representation of Gaussian noise to a trigonometric formulation of PI (Benhamou et al., 1990).

Müller and Wehner (1988) pointed out that the homing direction of ants and other species is affected by a systematic "inward" error (Fig. 3), and suggested that such an observation cannot be explained by noise alone, but indicates that the algorithm for computing the position is approximate rather than exact. The observed biases may therefore provide a clue on how the animal calculates direction and distance. To explain the findings in ants, Müller and Wehner (1988), following a seminal attempt at formalization of PI by Jander (1957), proposed a recursive arithmetical algorithm of PI that is described as a "distance-weighted mean-direction calculation," which is (negatively) weighted by the insect's distance from the nest: "While proceeding from one step of unit length to the next, the ant adds some measure of the angular distance between its n th step and the direction of the mean vector pertaining to its $(n-1)$ th step to this previous vector, and does so by scaling down all successive angular contributions in proportion to the distance it has moved away from the nest" (Wehner and Wehner, 1990).

Figure 3 illustrates the inward error that vertebrates as well as invertebrates commit after an L-shaped outward journey. The astonishing similarity of this error across unrelated taxa suggests that the same approximate (but generally efficient) PI algorithm has evolved in different phyla. The systematic error may be adaptive because it leads back to the beginning of the outward journey, where the animal may encounter familiar landmarks (Wehner and Wehner, 1990). Error-based algorithms provide an interesting ap-

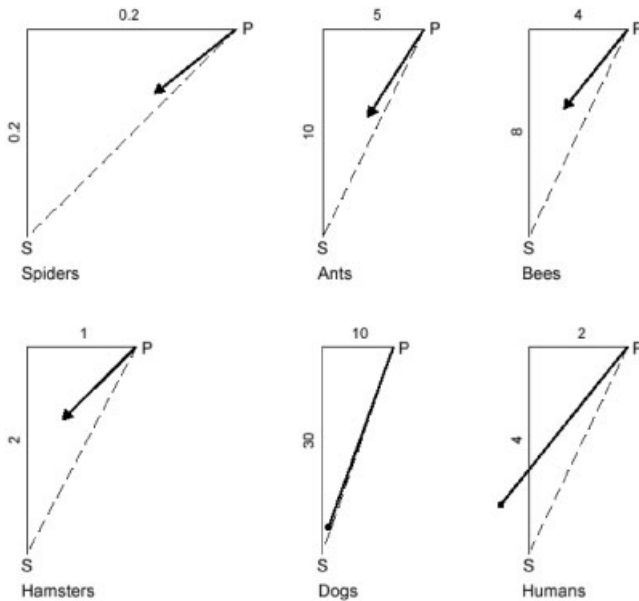


FIGURE 3. Systematic PI errors in invertebrates and mammals. All species followed an L-shaped outward journey (thin line) from their retreat or an arbitrary starting point S to point P, and then attempted to return to the starting point. Throughout the excursion, spiders (Goerner, 1958), hamsters (Séguinot et al., 1993), and humans (Loomis et al., 1999) were deprived of visual, auditory, olfactory, and tactile spatial references from the environment, while ants (Müller and Wehner, 1988) and bees (Lindauer, 1963) could use the sun as a directional reference. Dogs (Séguinot et al., 1998) were blindfolded and ear-phoned during the outward trip, but not during the return, and could not rely on olfactory cues. The heavy arrows indicate the return direction to S measured when the subject was at a standard distance from the start point of the return. (For bees, this direction was deduced from their dance axis.) The heavy lines with a dot indicate the return vector. The presentation of some of the data is adjusted.

proach to the study of information processing and have also an important heuristic role. Deriving from empirical data, they lead to precise and therefore verifiable predictions of how an animal computes a desired parameter and therefore behaves in a particular situation. However, the general validity of these models may be questioned. For instance, the model failed to describe the homing trajectories of hamsters after a more convoluted outward trip that started with a loop around the point of departure (Séguinot et al., 1993; Maurer and Séguinot, 1995).

In recent times, a number of attempts have been made to describe PI in terms of arithmetical models (Fujita et al., 1990), flow diagrams (Mittelstaedt, 2000), and especially neural networks (Hartmann and Wehner, 1995; Guazzelli et al., 2001; Wittman and Schwegler, 1995; McNaughton et al., 1996; Samsonovich and McNaughton, 1997; Maurer, 1998; Arleo and Gerstner, 2000; Stringer et al., 2002). Most network models take into account available evidence that external references as well as PI are needed to complement each other, suggesting the binding process discussed in the next section. One of these integrative networks is presented later. Again, the main value of connectionist models is in their heuristic content (Etienne, 1998).

So far, we have dealt with models that aim to formalize the basic steps of the path integration process: namely, the continuous estimation of self-motion cues in order to compute momentary changes in location and orientation (head direction). The subject's current position may be represented by the resultant vector of the summation of all the intermediate short-range (or infinitesimal) vectors that were processed since the departure from home. Again, what the animal's nervous system is actually adding up, or integrating, and how precisely this summation or integration is performed, remains unknown. However, the sequence of computations that have to be performed at the neural level can nevertheless be seen as analogous to those of vector addition and subtraction.

Vector addition allows a navigator not only to home, but also to return to a profitable resource site. Central place foragers like bees (von Frisch, 1967; Collett and Collett, 2000) and hamsters (Etienne et al., 1998) store nest-to-food-goal vectors in long-term memory. They can then commute between the nest and each of the food locations, along a direct path or through various detours, without the help of external cues. Relying on PI only, they seem to subtract in a continuous manner the (short-term) nest-to-current-position vector from the (long-term) nest-to-food-site vector, up to zero vector, i.e., until they reach the goal. Likewise, dogs can be shown the location of a bait within a large symmetrical enclosure, led blindfolded and ear-phoned along a detour to the other side of the test space, and then released to search for the (strongly camouflaged) bait. The animals find the bait along a goal directed path in 90% of the trials (Cattet and Etienne, in press). However, these seemingly astonishing performances depend on rigid computational rules. For example, neither ants (Wehner and Menzel, 1990) nor hamsters (J. Georgakopoulos, in preparation) can proceed directly from one familiar food goal to another by selecting the appropriate long-term vectors and combining them with one another.

Navigation that involves the free combination of goal vectors has so far been demonstrated only in humans, in a report on a 2-year old congenitally blind child (Landau et al., 1984). During a preliminary training phase, the child was walked from a base point to each of three objects in a rectangular room. In subsequent test trials, the child was able to find the routes between the three objects on her own. At each goal, the infant recognized the corresponding goal object through tactile information, so that PI could be associated with and therefore confirmed by external references. In a further experiment at the age of 43 months, the child was also able to commute between places without objects. Thus, to commute between two particular targets, the child must encode the three training paths using PI, store these paths as long-term vectors in a vector map, and then select and combine the two correct stored vectors. Let us emphasize that adult subjects probably navigate on the basis of the same allocentric computations. However, they also update the direction and distance to particular locations according to simpler and therefore more economic rules, on the basis of short-term subject-centred vectors which are not interrelated at the level of an integrated map system (Wang and Spelke, 2000).

BINDING OF LANDMARK INFORMATION AND SELF-MOTION CUES

A recurring problem in cognitive psychology concerns how different information sources—arriving via different sensory modalities and contributing different computational elements—are integrated to form a unified representation. In the domain of navigation, landmark information and motion cues continuously interact in a complementary fashion. Landmark information is taken up episodically, involves complex perceptual and learning processes and remains fairly stable, but it is not always available to an animal. In contrast, PI works automatically and continuously and depends on hardwired rules of information processing. However, we have already seen that, as a recurrent process of computation, PI has the major drawback of being progressively degraded by the accumulation of errors. It is beneficial, then, for the navigational system(s) to use both sources of information, depending on which is more appropriate at the time.

How do external references and self-motion cues interact to guide behavior? In conditions in which navigation has to be very precise, such as during the final approach to a goal, PI is too error-prone to be wholly relied upon, and so stable (Biegler and Morris, 1993), necessitating the use of external landmarks. During the outward journey to a known food source, foraging hamsters (Etienne, 2003), like ants (Collett and Collett, 2000), need external cues to stop at the goal site. Without these cues, the animals continue their outward progression, in spite of the fact that the current state of their path integrator corresponds to the goal coordinates. During homing, when their path integrator indicates proximity to the nest, both species switch from a fairly linear homeward progression to circular movements in search of familiar cues near the nest entrance (Séguinot et al., 1993; Müller and Wehner, 1994).

Behavioral data (Biegler and Morris, 1993) and recordings of head direction and place cells in rats show that visual cues, the most used spatial references from the environment, control navigation only if they are experienced by the rat as stable (Jeffery, 1998). Conversely, visual control may be weakened after experience of instability (Knierim et al., 1995, 1996). The animals may also use nonvisual stimuli as external references and associate these references with particular locations and/or directions. Once the associations have been established, rats show a great flexibility in the use of spatial cues from different sensory modalities. However, in conditions where different types of references are set at variance with each other, the animals show a hierarchy of preferences: vision predominates over olfaction, and olfaction over motion cues (Maaswinkel and Whishaw, 1999).

When directional information from visual and self-motion references (olfactory and other proximal cues being neutralized) is conflicting, rodents seem to estimate the credibility of each category of cue and give more credit to the more reliable type of information. In circular test arenas, mice (Alyan and Jander, 1994) and hamsters (Etienne et al., 1990) return to their nest along compromise directions, distal landmarks predominating over the directional component of PI as long as both types of information

do not diverge by more than 90°. By contrast, whenever the conflict between the two categories of spatial information is increased, hamsters seem no longer to trust the hitherto stable visual world. They either regress to PI (probably the older strategy at both ontogenetic and phylogenetic levels) or else home in a random direction (Fig. 4, upper row).

Data from single-cell recordings in similar conflict conditions follow the same principles as behavioral results. For both place and head direction cells, if the angular discrepancy between visual and self-generated motion cues is relatively small and/or induced slowly, then the visual cues predominate, whereas if it is induced by sudden large movements of the landmark then the movement cues predominate, or the cells behave more erratically (Rotenberg and Muller, 1997; Knierim et al., 1998) (Fig. 4, lower row). In intermediate situations, the cells compromise between using visual and other motion cues with such conflicts sometimes causing an apparent reorganization of the place cell representation (Sharp et al., 1995; Blair and Sharp, 1996; Knierim et al., 1998). Such a hierarchy of control is adaptive, since in the real world, small discrepancies are more likely to be induced by progressively accumulated errors in the path integrator, whereas sudden large discrepancies are more likely to be due to movement of the visual stimulus. However, not all data from conflict situations follow the same pattern, for reasons that may be linked to the location of the recorded spatially selective neurons, or are not yet understood (e.g., Wiener, 1993; Chen et al., 1994).

The data about conflict situations between the linear components of self-motion and visual references are limited. In the Gothard et al. studies discussed earlier (Gothard et al., 1996, 2001), it was found that (as in the case of directional cues) small mismatches between path integration and vision were accommodated by smooth alterations in the firing locations of the place cells, while for large mismatches the cells jumped from a representation driven by one information source to that driven by the other. For intermediate mismatches, a mixture of these effects was observed. The possible site of such interaction remains unknown at present.

In natural conditions, external references and self-motion cues usually cooperate rather than compete with one another. Because of this, a drifting path integrator can be reset by stable landmarks so that it can guide navigation more accurately when these landmarks become unavailable again. The resetting process implies that the navigator (1) establishes its current location and orientation through its actual perception of external references, and (2) changes the state of its path integrator in accordance with the position fix. Recently, this process has been demonstrated for homing behavior in hamsters, in a situation of conflict between path integration and distal landmarks (Etienne et al., 2000). In all trials, the test arena and peripheral nest box were rotated before the animal had initiated the hoarding trip. From the rotated nest, the hamster was guided to a food source on the open arena floor along a two-leg outward journey. If the hoarding excursion took place in continuous darkness, the animal homed toward the current, rotated nest location and therefore relied on PI. If, however, the room lights were briefly turned on at the end of the first outward leg and then turned off again, the hamster returned toward the standard, unrotated nest location. The fix had therefore changed

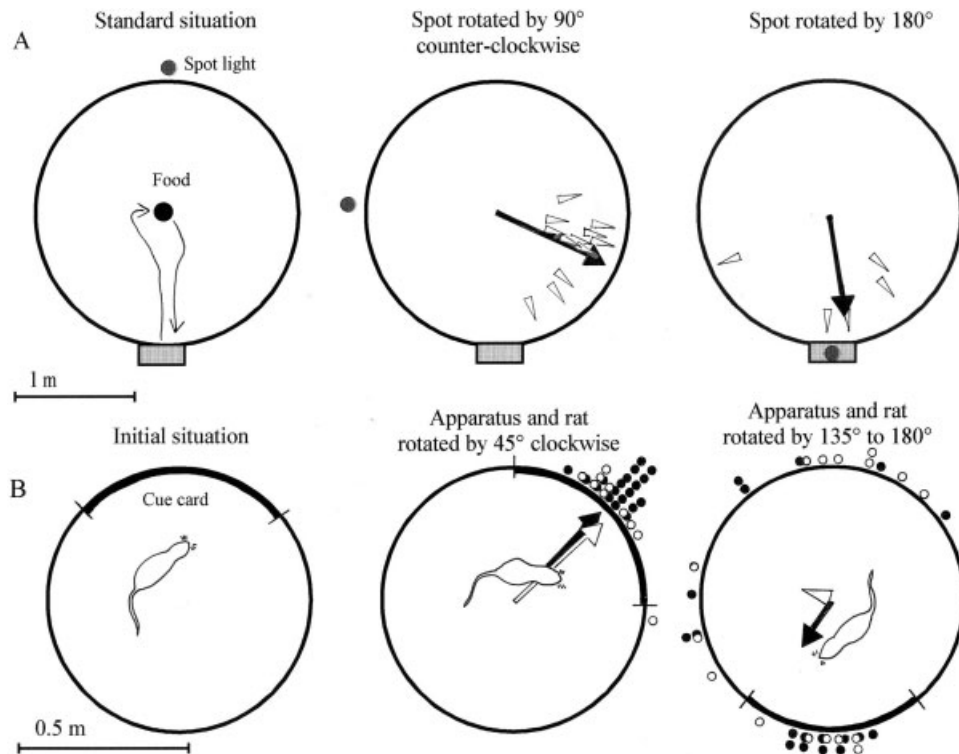


FIGURE 4. Behavior, place cells, and head direction cells in conflict conditions between self-motion cues and a visual reference. **A:** Homing in hamsters. Each animal lives in an arena with a peripheral nest box (small rectangle), with a dim spotlight presented during the (active) night phase, opposite to the nest. In control trials (standard situation), the subject follows a bait to a food source, fills its cheek pouches, and returns to the nest. By rotating the spotlight, a conflict is created between self-motion cues and the light cue. The open arrowheads indicate the mean homing directions from each individual, and the black arrow the mean homing direction of the whole experimental group. Going with motion cues means returning to the nest, and going with the spot light means walking 180° away from the light.

B: Place fields and preferred directions of single cells. The activity of place and head-direction cells (from the anterior thalamic nuclei) is recorded as the rat forages for food in a high-walled apparatus with a single salient cue card. The abrupt rotation of the apparatus and rat introduces a conflict in directional information from the cue card and from motion cues. The dots and small circles on the middle and right graphs represent the mean rotation score of the place field and the preferred direction of particular cells, and the arrows represent the corresponding mean rotation score for the total number of recorded cells (with respect to the cells' place field and preferred direction in the initial situation). Full symbols represent place fields, and open symbols preferred directions. (Modified after Knierim et al., 1998).

the animal's representation of its location and head direction. Furthermore, the visually induced new coordinates were fed into the integrator, so that, during the second outward leg, the animal could update its location and head direction with respect to the standard nest location. Further experiments with a central nest (Fig. 1A) allowed us to confirm that a fix on a rich landmark panorama induces a total reset, comprising both head direction and location, and not just head direction (i.e., the sense of direction) alone.

We have seen that place and head direction cells use predominantly visual cues to establish and maintain their place fields and preferred directions, but that they update their firing pattern through self-motion cues when visual information is not available. The most relevant data in this respect were obtained from head direction cells. When a rat reenters a familiar test environment, it has to be exposed to its visual surroundings in order to reset its head direction system. If the lights are then turned off, the cells maintain their direction specific firing for a given time span; their activity then starts drifting, as expected, if we assume that the updating process occurred through the an-

gular components of self-motion cues (Mizumori and Williams, 1993). Likewise, in a cylindrical test apparatus with a single cue card, the head direction cells may maintain their directional preference after the removal of the cue card, but this preference drifts slowly over time. When the visual cue is replaced in its original position, the cells' preferred firing direction in general shifts back to the originally established relationship with the visual reference (Goodridge et al., 1998). In contrast, Knierim et al. (1998) found that during the dark phase of a light/dark/light experiment, the preferred directions of head direction cells started to drift and only occasionally returned to their initial preference when the lights were turned on again. Thus, the resetting process does not necessarily occur after the reintroduction of the visual cues in their former position.

Place and head direction cells receive polymodal inputs, and the resetting processes may be controlled by nonvisual cues. This is the case, for example, with blind rats that explored a test space with three different landmarks (Save et al., 1998). The animals' place cells developed place fields with normal characteristics, provided the animals had physically contacted the intra-apparatus objects.

Subsequently, the rats continued to make frequent contact with the objects, most likely to clear the path integrator of errors.

The interaction between landmark information and PI poses a general computational problem. Perception is bound to an egocentric frame; visual landmarks, for instance, are projected onto the subject's visual field and thus their position is at first computed with respect to the current position and orientation of the eyes. To be used in conjunction with path integration and possibly integrated into a geocentric map, the nervous system has to transform the landmarks' egocentric into geocentric coordinates (Gallistel, 1990; Gallistel and Cramer, 1996). For mammals, it has been suggested that the transition from an egocentric to a geocentric mode of coding occurs in certain regions of the parietal cortex (Burgess et al., 1998).

PI AND THE REPRESENTATION OF SPACE

In order to navigate flexibly in a given environment, taking short-cuts and detours where necessary, an agent needs to represent this environment by some kind of neural map in which particular locations are interconnected by Euclidean or topological relationships. Such a representation would allow the animals to manipulate spatial relationships computationally, and therefore to plan optimal routes in real space. Furthermore, the processes of place representation and path integration exist in a mutually reinforcing relationship. While PI may underpin a navigator's map, its performance in turn may be influenced by the subject's representation of the current surroundings. This may be the case for rodents (Siegrist et al., 2003) and has clearly been shown for humans. Blindfolded subjects compute the bearing of a landmark using self-motion cues more accurately when they are aware of their environment, or asked to imagine their surroundings, than when PI occurs without any conscious representational support (Rieser, 1999). The close relationship between PI and place representation lends support to the gradually developing idea, discussed in detail below, that mammalian PI may be dependent on the hippocampus.

As discussed earlier, O'Keefe and Nadel (1978) proposed that mammals possess a map, the so-called "cognitive map," that resides in the hippocampus. They suggested further that their putative cognitive map might be represented by the activity of the hippocampal place cells (O'Keefe and Nadel, 1978; Nadel, 1999). Different locations could be represented by different neural signatures and adjacent places by broadly similar neuronal ensemble activity, allowing for a continuous representation of space. Additionally, because they are influenced by signals deriving from translational and directional components of movement, place cells are a possible site for integration of these signals and thus a candidate for the mammalian path integrator (O'Keefe and Nadel, 1978; McNaughton et al., 1996; Samsonovich and McNaughton, 1997; Whishaw et al., 1997). The idea of the hippocampus as both a map and a path integrator has since evolved in response both to experimental studies and to computational modeling. Whishaw et al. (1995) suggested that the impairment of fornix-lesioned rats in performing a watermaze navigation task might be due to an impairment in path integration. In a careful series of follow-up stud-

ies, they have demonstrated that rats with lesions to either the fimbria/fornix or hippocampus itself cannot use path integration to return home across a circular arena (Whishaw and Maaswinkel, 1998; Maaswinkel et al., 1999; Whishaw and Gorny, 1999). Contradicting these results, however, are findings reported by Alyan and McNaughton (1999) of intact PI in hippocampectomized animals, a discrepancy that has not yet been explained. Further supporting a PI role for the hippocampus, hippocampal lesions impair angular PI by head direction cells (Golob and Taube, 1999) and vestibular lesions, which disrupt the place cell representation (Taube et al., 1996), also impair path integration (Cohen, 2000; Wallace et al., 2002).

On the computational side, McNaughton et al. (1996) devised a PI-based network model of spatial representation that involves primarily the hippocampus. Within this structure, a pre-wired network of place cells implements a map-like representation of each particular environment. While the rat moves around in real space, its position is updated on this matrix on the basis of movement-related information, successive sets of place cells being activated according to the cells' ensemble code (Wilson and McNaughton, 1993). Attractor dynamics (Samsonovich and McNaughton, 1997) control and stabilize the cells' ensemble activity and therefore the representation of the animal's current position. Thus, the activity of a given place cell depends on the activation of cells with adjacent receptive fields and a PI signal that tells the network which way the animal is moving, and therefore what cell(s) ought to be activated next. Visual (and other external) spatial information is only secondarily associated to and stored in the place cell matrix. However, once particular self-position coordinates and landmarks have been associated with one another, the landmarks control the retrieval of the correct internal map when the subject enters a familiar environment, and then set the origin for PI and clear the PI system from errors.

Appealing though it has been, the conception of a representation of space that is primarily based on PI (McNaughton et al., 1996), with landmark information acting only secondarily, is at variance with data showing that place (O'Keefe and Burgess, 1996; Muller, 1996) and head direction (Taube, 1998) cells are controlled primarily by positional and directional cues from the familiar environment. The notion of a cohesive attractor-based representation has also had to be modified in light of accumulating data suggesting that place cells do not always act as a unified population, but sometimes as a collection of independent individuals (O'Keefe and Burgess, 1996; Tanila et al., 1997; Skaggs and McNaughton, 1998; Jeffery, 2000; Lever et al., 2002). Furthermore, experiments with conflicting proximal and distal visual references showed not only that different subsets of place cells can be controlled by a different type of cues, but also that a small proportion of place fields split in half, each of the two halves responding to a different cue category (Knierim, 2002).

In contrast, there is a general agreement that the place cell ensemble can update the representation of location using motion cues that indicate direction (Jeffery et al., 1997) and distance (Gothard et al., 1996) as well as landmark information (O'Keefe and Speakman, 1987). The question that remains unanswered is whether these information sources are conveyed to the hippocam-

pus via a mediating structure—a path integrator—or whether they arrive at the hippocampus independently and are combined there by the place cells, in which case it could be argued that the hippocampus *is* the path integrator (at least in rodents). Recent findings suggest that cortical areas such as the retrosplenial (or posterior cingulate) cortex (Cooper and Mizumori, 1999; Nadel, 1999) and the parietal cortex (Save et al., 2001) may play a role in PI. At the present state of our knowledge, further research is needed to determine the outputs from various subsystems linked to path integration, together with the final brain region on which these outputs converge.

According to a number of investigators (Gallistel, 1990; McNaughton et al., 1996; Etienne, 1998), PI may well play a leading role in the construction of a map. This has mainly been suggested by behavioral observations, and it is compatible with data from single-cell recordings. When exploring a new environment, rats and other rodents center their excursion on a basic reference point, their fictive or real “home base” (Golani et al., 1993). As soon as it enters the new surroundings, the animal presumably uses PI continuously to compute its position vector in relation to this reference point. Frequent returns to the home base reset the path integrator to its zero state, so that each exploratory trip starts with an error-free path integrator. During these trips, the animal may register the state of its integrator at functionally relevant locations, and associate the current view of landmarks (and/or the presence of nonvisual cues) with the corresponding position vector. PI is also a likely candidate for interlinking places in both real and represented space.

On the physiological level, place fields become rapidly established in a new environment (Hill, 1978). This might be expected if the fields are hardwired, and selected primarily by PI when the environmental cues are either unavailable or have not yet been learned. However, the place fields start by being less precise and robust than at a later stage. This could be explained by the progressive recruitment of place cells which implement the representation of the new environment (Samsonovich and McNaughton, 1997), and by the association between stored position vectors and external references.

A study by Taube and Burton (1995) shows how visual references and motion cues interact to control the directional preferences of head direction cells, which we assume to be the internal compass. Rats entered the first compartment of an unfamiliar dual chamber apparatus, a cylinder with a salient cue card. The card set the animals’ internal compass. The rats then walked along an U-shaped passageway to a second compartment, a rectangle, that contained a different cue card. Throughout this trip, angular PI allowed the cells to maintain their formerly established directional preference with some accuracy. This enabled the head direction system to register the bearing of the second landmark within a unitary directional reference frame: an essential condition for building a consistent internal representation of a particular environment. Further experiments with the same rats showed that their head direction cells tended to follow the rotation of the cue card in the cylinder, but returned to their initial preferences when the animals returned to the passageway. These data illustrate that in a complex environment, which is structured into different parts and

thus can never be seen all at once, visual cues set and reset, and angular motion cues update, the preferred direction of head direction cells. This process provides a means by which an animal could navigate within a visually disconnected environment.

In conclusion, while it is not yet known how the nervous system combines its distance and direction signals to produce a path integration signal, neurobiological studies have pointed to a possible role for the hippocampal spatial representation in mediating such computations. By this view, the signals produced by the movement of the animal are used to update a position estimate which is instantiated by the collective activity of the place cells. In this way, even though the motion signals arrive via a number of different modalities, the place cells can use these to produce a common code that represents the animal’s position on a moment-by-moment basis. The notion that the nervous system can extract abstract representations (in this case “place”) from the incoming sensory data stream offers a solution to the general problem of how information from different sensory modalities is bound together for computational purposes.

The studies we have outlined in the present review have raised a set of well-defined questions: How is information from multiple sensory modalities combined to produce the computational “primitives” of direction and distance? How are these primitives, in turn, combined to yield position information? How are places coded by the association between self-generated position vectors and landmarks to yield a higher-order representation of space? Does this representation in turn influence the performance of PI? Can PI be seen as an Ariadne thread that links not only the starting point of a journey to its final destination, but that also connects locations with landmarks and different landmark-place associations with each other? Since even animals of the level of insects have solved at least the simplest of these problems in the path integration domain, the study of this faculty and its interaction with external references may open the doors to the understanding of higher order cognitive processes.

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