ICP Imperial College Press
www.icpress.co.uk

**Special Report**

# MULTIMODAL SENSORY INTEGRATION AND CONCURRENT NAVIGATION STRATEGIES FOR SPATIAL COGNITION IN REAL AND ARTIFICIAL ORGANISMS

ANGELO ARLEO[*] and LAURE RONDI-REIG[†]

[*]*Université Pierre et Marie Curie-Paris 6,*
*CNRS, UMR 7102, Laboratoire de Neurobiologie des Processus Adaptatifs,*
*F-75005 Paris, France*
[*]*angelo.arleo@snv.jussieu.fr*

[†]*Collège de France, CNRS, UMR 7152, Laboratoire de Physiologie de la*
*Perception et de l'Action, F-75005, Paris, France*
[†]*laure.rondi-reig@college-de-france.fr*

Flexible spatial behavior requires the ability to orchestrate the interaction of multiple parallel processes. At the sensory level, multimodal inputs must be combined to produce a robust description of the spatiotemporal properties of the environment. At the action-selection level, multiple concurrent navigation policies must be dynamically weighted in order to adopt the strategy that is the most adapted to the complexity of the task. Different neural substrates mediate the processing of spatial information. Elucidating their anatomo-functional interrelations is fundamental to unravel the overall spatial memory function. Here we first address the multisensory integration issue and we review a series of experimental findings (both behavioral and electrophysiological) concerning the neural bases of spatial learning and the way the brain builds unambiguous spatial representations from incoming multisensory streams. Second, we move at the navigation strategy level and present an overview of experimental data that begin to explain the cooperation-competition between the brain areas involved in spatial navigation. Third, we introduce the spatial cognition function from a computational neuroscience and neuro-robotics viewpoint. We provide an example of neuro-computational model that focuses on the importance of combining multisensory percepts to enable a robot to acquire coherent (spatial) memories of its interaction with the environment.

*Keywords*: Spatial navigation; behavioral strategies; multimodal information; path integration; hippocampal place cells; head-direction cells; grid cells; neuro-mimetic models; neuro-robotics.

## 1. Introduction

Spatial cognition involves the ability of a navigating agent (be it an animal or an autonomous artifact) to acquire spatial knowledge (e.g., spatiotemporal relations between environmental cues or events), organize it properly, and employ it to adapt

---

[*]Corresponding author.

its motor response to the specific context (e.g., performing flexible goal-oriented behavior to solve a navigation task). Similar to other high-level brain functions, spatial cognition calls upon parallel information processing mediated by multiple neural substrates that interact, either cooperatively or competitively, to promote appropriate spatial behavior.

At the sensory level, different perceptual modalities provide the navigator with a manifold description of the currently experienced spatial context. The integration of these multimodal signals (that are processed by interrelated brain regions) into a coherent representation is at the core of spatial cognition. A large body of experimental work has been done to elucidate the neural mechanisms subserving the establishment and maintenance of spatial representations in animals and humans. Section 2 reviews some experimental findings issued from this research, and focuses on those that concern the interrelation between different sensory modalities.

At the action selection level, determining and maintaining a trajectory from one place to another, i.e. navigating, according to Gallistel [51], involves multiple concurrent processes, and requires the ability of the subject to adapt its goal-directed strategy to the complexity of the task. The process of dynamically weighing the behavioral contribution of distinct navigation policies depends on contextual variables, like the available sensory inputs and their relative importance, and the motivational state of the animal. Section 3 focuses on this issue and reviews some experimental findings concerning the cooperative-competitive interaction of multiple spatial navigation strategies.

Similar to animals, autonomous navigating artifacts (e.g., mobile robots) need to interact with their environment, process multimodal sensory signals, and learn both low-level sensory-motor couplings and more abstract context representations supporting spatial behavior. Therefore, in parallel to experimental neuroscience, a large body of research in autonomous robotics has focused on spatial learning-related issues (e.g., self-localization, space representation, and way-finding techniques). Most of the classical control architectures engineered so far (e.g. see Refs. [6, 41, 77, 152]) provide task-specific (*ad-hoc*) solutions and are not as general and adaptive as animals' spatial learning systems. Therefore, a novel approach to designing autonomous navigating artifacts is being explored, whose principles take inspiration from known behavioral and neurophysiological mechanisms underlying animals' spatial learning capabilities. This approach, termed neuro-mimetic robotics or simply neuro-robotics, focuses more on adaptiveness and flexibility than on optimality and completeness, and stresses the idea that the agent must acquire its own worldview by means of its experience [18]. The last section of this paper (Sec. 4) focuses on neuro-mimetic spatial learning and on the importance of combining multisensory information for robust coding of the spatial contexts experienced by the robots.

## 2. Acquiring Representations of Space

The variety of sensory modalities conveying spatial information can be dichotomized into two main categories, namely *idiothetic* and *allothetic* cues. Idiothetic stimuli

are self-motion related signals and include vestibular (inertial), kinesthetic (e.g., information from muscle and joint receptors), motor command efferent copies, and sensory flow information (e.g., optic field flow signals informing the navigator about its own movements). Allothetic signals provide information about the external environment and include visual, olfactory, auditory, and somatosensory (e.g., tactile or texture) cues. In other words, idiothetic stimuli provide the navigator with movement-generated (i.e., dynamic) spatial information, whereas allothetic signals describe the static spatial relations between environmental cues (e.g., configurations of visual landmarks). Learning spatial memories requires the extraction of coherent information from such a redundant and multidimensional sensory input space. This learning process implies, for instance, maintaining idiothetic and allothetic cues congruent (e.g., minimization of interferences or conflicts) both during the exploration of a novel environment and across subsequent visits to a familiar environment.

A given sensory modality is labeled as allothetic or idiothetic to characterize the *type of information* it conveys. On the other hand, if we want to characterize the *way this information is represented* by the navigator, we need to introduce the concept of reference coordinate system (or simply reference frame). This system defines the framework in which spatial information (e.g., the position of an object) can be represented relative to an origin point. Depending on the anchorage of the origin of the reference coordinate system, the same information can be encoded *egocentrically* or *allocentrically*. If the reference frame is centered on the subject (e.g., on a body part such as the head) the representation is said egocentric. If the origin of the framework is a fixed point of the environment (e.g., a corner of the room), the representation is called allocentric. As shown in Fig. 1(A), the same allothetic spatial information (e.g., the position of a visual cue in the environment) can be represented either egocentrically (e.g., relative to the body of the navigator) or allocentrically (e.g., relative to the room corner). Likewise, as shown in Fig. 1(B), idiothetic signals (e.g., vestibular information) can be employed to describe self-motion information either egocentrically or relative to an allocentric reference frame. Egocentric coding can be simple to build but it varies as the navigator moves in the environment (because the reference frame translates and rotates as the subject moves). Allocentric coding requires more complex processing (e.g., to relate the visual cue position to the world-centered origin), but it is invariant with respect to the subject's position and orientation in the environment.

## 2.1. *Spatial learning on the basis of allothetic and idiothetic signals*

Animals employ both idiothetic and allothetic cues to build and maintain memory traces of the spatial components (e.g., their body position and orientation) of experienced events.

On one hand, they are capable of estimating their current location relative to a starting point (i.e., homing vector) by integrating linear and angular self-motion signals over time [Figs. 2(A), (B)]. This process, termed *path integration* or dead reckoning [42, 44, 46, 95–97], relies upon idiothetic cues like vestibular and kinesthetic
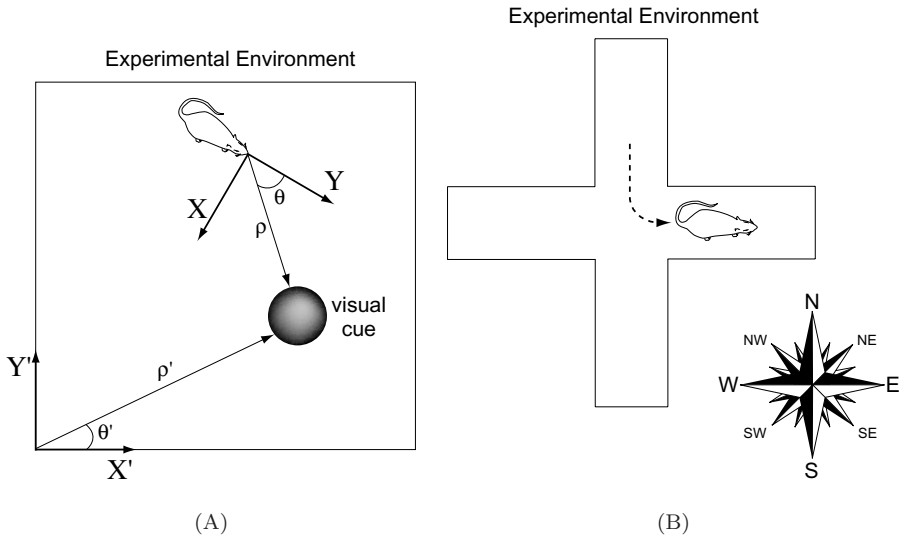
Fig. 1.   Encoding spatial information within a reference coordinate system. (A) The circular object provides an allothetic (visual) spatial cue to the navigator (rat). The latter can represent the spatial position of the external cue within the egocentric reference frame X-Y (centered on its head), that is estimate the distance $\rho$ between its head and the object, as well as the angle $\theta$ between its heading and the direction to the object. Alternatively, the rat can encode the same spatial information within the allocentric coordinate system X'-Y' (centered on the bottom-left corner of the experimental environment), that is estimate the distance $\rho'$ and the angle $\theta'$. (B) In this example, the navigator can employ idiothetic information (e.g., vestibular signals) to represent the change of its motion direction within an egocentric reference frame, that is "I turned to my left". Alternatively, it can refer to the allocentric directional system based on the geomagnetic north, that is "I turned eastward".

signals, motor command efferent copies, and sensory (e.g., optic) flow information. On the other hand, self-localization can also occur solely on the basis of allothetic cues like vision, auditory, olfactory, and tactile signals. Indeed, locations can be characterized by specific allothetic sensory patterns (e.g., configurations of visual cues), such that memorizing these sensory patterns can enable a subject to recognize familiar places.

Idiothetic and allothetic spatial information have complementary strengths and weaknesses. Since path integration does not depend on external references, it allows a subject to self-localize in an unfamiliar environment from its very first exploring excursion [58]. Also, path integration is a basic mechanism suitable for all types of environments (i.e., with or without external cues) and navigators (e.g., agents that cannot exploit their interaction with the external world effectively). A limitation of path integration is its vulnerability to cumulative drift over time. Indeed, the idiothetic-based dynamics, consisting of integrating translational and rotational signals over time, is prone to systematic as well as nonsystematic errors that quickly disrupt the position estimate [44, 96]. This holds for both biological and artificial navigating systems.
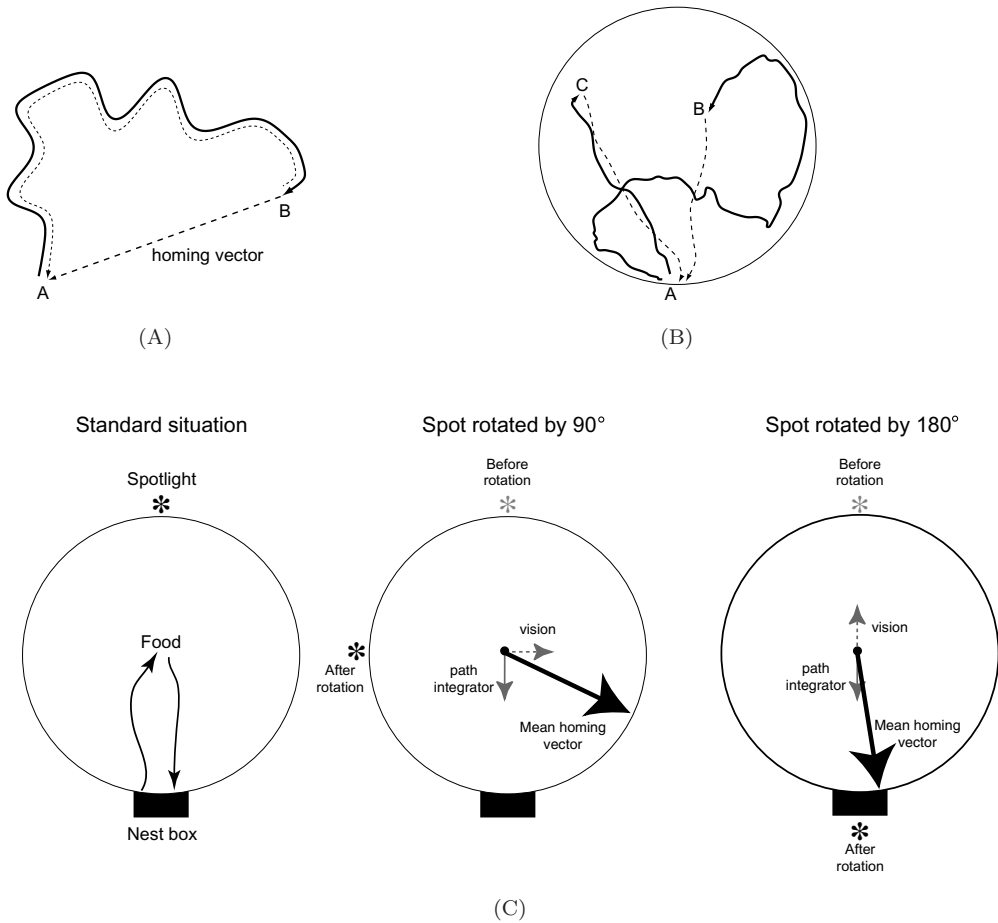
Fig. 2. Homing behavior based on path integration (PI). (A) Difference between path reversal (i.e., inverting the sequence of movements performed from a starting point A to a current location B), and path integration (i.e., integrating translations and rotations over time to generate a homing vector leading the animal directly to the departure point A). The solid line represents the outward journey; the dotted line indicates the return journey based on path reversal; the dashed line is the homing vector obtained by path integration. Adapted from Etienne *et al.* [44]. (B) Two examples of homing behavior performed by two hamsters. After having been guided by a bait from the nest location A to points B and C (solid lines), the two animals return home following direct trajectories (dashed lines). The experiment was performed in the dark in a circular arena of 2 m of diameter. Adapted from Etienne *et al.* [44]. (C) Hamsters' homing behavior in conflict situations. During training (left), a distal spotlight (asterisk) provides a stable landmark to the animal performing hoarding excursions to a feeder. In probe trials, the spotlight is rotated by either 90° (center) or 180° (right). Animals are guided from the nest to the feeder in darkness conditions, then the spotlight is turned on, which creates a conflict between self-motion (continuous gray arrows) and visual (dashed gray arrows) information. Large arrows indicate the homing vectors followed by the animals and show that in the case of 90° conflicts the visual landmark signal tends to dominate over self-motion, whereas for a 180° mismatch the path integration component becomes predominant. Adapted from Etienne and Jeffery [42].

Allothetic spatial information permits the formation of local[a] sensory views directly suitable for self-localization [94]. Also, if the spatial configuration of the environmental cues (e.g., distal landmark arrays) remains fairly stable over time, the position assessment process is not affected by cumulative errors. However, allothetic (e.g., visual) cues are not always available to the navigator (e.g., in darkness conditions). Additionally, since self-localization based on allothetic cues involves sensory pattern recognition, perceptual aliasing phenomena may occur, that is distinct areas of the environment may be characterized by equivalent local patterns. For instance, visual sensory aliasing can lead to singularities (i.e., ambiguous state representations) in a purely vision-based space coding [141].

Therefore, neither idiothetic nor allothetic cues are sufficient by themselves to establish reliable spatial memories (e.g., see Refs. [12, 70, 113 and 124]). One solution is to combine allothetic and self-motion signals into a unified representation. The combination of allothetic and idiothetic information may yield a mutual benefit in the sense that idiothetic cues may compensate for perceptual aliasing (e.g., discriminate between two locations in a visually symmetrical environment) and, conversely, environmental landmarks may be used to occasionally reset the integrator of self-motion signals. Idiothetic information might provide the spatial framework suitable for "grounding" the knowledge gathered by a navigating animal [74, 94]. According to this hypothesis, allothetic local views might be tied onto this framework as the exploration of a novel environment proceeds. But how are conflicts between self-motion and landmark cues solved? How is this idiothetic-allothetic coupling established and maintained consistent over time?

Ethologists have largely investigated the interaction between self-motion information and landmark cues for spatial navigation [42]. Numerous behavioral studies involve homing tasks in which animals perform hoarding excursions and then return home with the collected food. One method to distinguish the idiothetic and allothetic determinants of the animals' homing behavior consists of setting a conflict between environmental (proximal or distal) and self-motion cues. Then, observing the homing vector makes it possible to assess the relative influence of allothetic and idiothetic information. Etienne *et al.* [43] have examined the homing behavior of golden hamsters during hoarding trips within a circular open arena [Fig. 2(C)]. During training, a stable distal spotlight provided a unique visual landmark on an otherwise dark background. Other allothetic cues (e.g., tactile and olfactory stimuli) were masked. In probe trials, hamsters were guided in the dark from the nest (a box located at a fixed peripheral position) toward a feeding location at the center of the arena. During the uptake of food, visual and self-motion information were set in conflict by rotating the spotlight (either by 90° or 180° relative to its standard position) and turning it on. The authors report that animals tended to return home following homing vectors whose visual component dominated over the self-motion

---

[a]The term "local' indicates "locally invariant", that is constant within a limited region of the environment.

component in the case of 90° conflicts [Fig. 2(C) center]. By contrast, when the divergence between the two types of information was further increased (i.e., 180°) the path integration component became predominant [Fig. 2(C) right]. In another series of experiments, Etienne *et al.* [45] tested the realignment of the path integrator relative to distal landmarks. The arena and the peripheral home base were both rotated before each hoarding excursion. Then, in the darkness, the hamsters were guided from the rotated nest toward a feeding location along a two-leg (L-shaped) journey. Under this condition, the animals mainly relied on their internally generated homing vector and returned to the new rotated home base. By contrast, if the environmental lights were briefly turned on at the end of the first outward leg and then switched off again, the animals tended to return to the original unrotated home location, suggesting that a reset of the path integrator had occurred on the basis of the (unchanged) distal visual cues.

## 2.2. *The neural bases of spatial learning*

In addition to behavioral studies, an extensive body of electrophysiological work has been done to investigate the neural bases of animals' spatial learning capabilities. Extracellular single-cell recordings have largely focused on the properties of pyramidal neurons in the hippocampal formation. This limbic region has been thought to mediate spatial memory functions ever since location-sensitive cells [Fig. 3(A)] in the hippocampus of freely moving rats were found [111]. These neurons, termed hippocampal place (HP) cells, are likely to provide a spatial representation in allocentric (i.e., world centered) coordinates, thus providing a "cognitive map" to support flexible navigation [113]. Furthermore, since the spatially selective responses of HP neurons might result from the projection of contextual (relational) memories onto the two-dimensional locomotion space of the animal, a role for the hippocampal formation in a larger class of memories, namely declarative memory, has been postulated (e.g., see Refs. [21] and [48]). In humans, damages to the medial temporal lobe (and in particular to the hippocampus, e.g., bilateral temporal lobectomy patient H.M. or degenerative temporal lobe pathologies such as Alzheimer's disease) produce anterograde and retrograde memory deficits that tend to impair, among others, the ability to learn spatial navigation tasks and to memorize context-dependent experienced events (i.e., episodic memory) [21, 37].

The hippocampal formation is well suited for subserving the integration of multimodal spatial information. It receives afferents from numerous subcortical regions (e.g., brainstem, amygdala, septum) via the fornix fiber bundle, and it is the recipient of highly processed sensory-motor signals conveyed by neocortical areas (e.g., the parietal cortex [20]), and mainly via the entorhinal cortex, which plays an important role in mediating the hippocampal-neocortical interactions [166]. Furthermore, recent electrophysiological findings have brought evidence for a key contribution of the entorhinal cortex to the spatial memory function [50, 59, 95, 134, 146]. Indeed, neurons in the medial entorhinal cortex have been found that exhibit

spatially-selective discharges with multiple receptive fields (in contrast to most HP cells) that cover the environment with regularly spaced hexagonal patterns [59]. It has been suggested that these neurons, termed grid cells, could mediate the encoding of metric spatial information necessary for the path integration process (see Ref. [95], for a review).
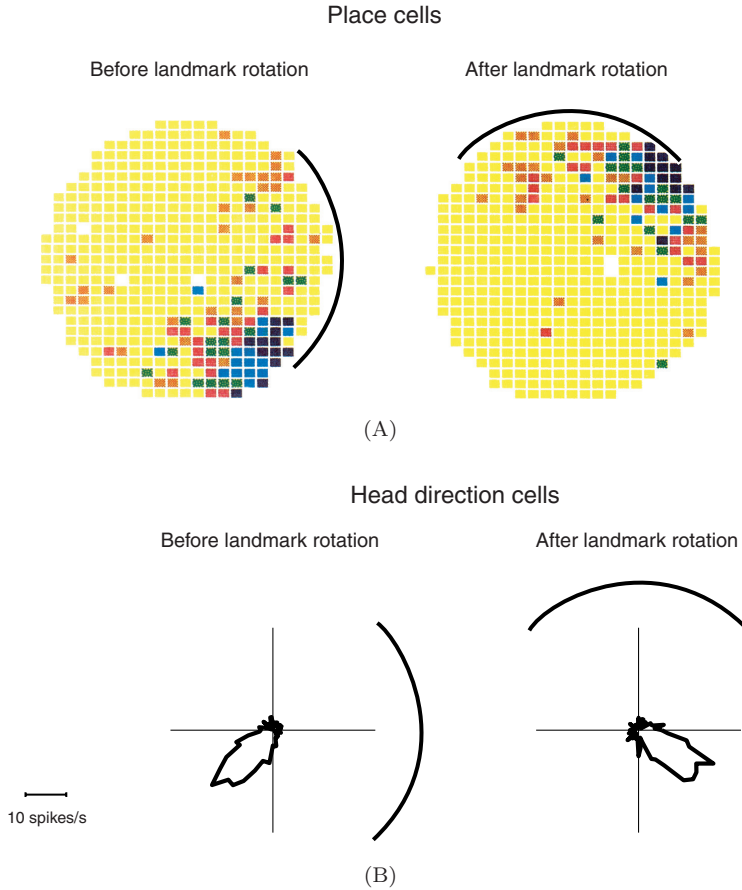


Fig. 3.   (A) Sample of receptive field of a place cell recorded from the rat hippocampus. The plots show the mean discharge of the neuron (blue and yellow denote peak and baseline firing rates, respectively) as a function of the animal position within the environment (a cylindrical arena with a cue card attached to inner wall). The location-selective response of the cell is controlled by the cue card in that rotating the card by $90°$ induces an equivalent rotation of the receptive field. Adapted from Muller and Kubie [107]. (B) Sample of tuning curve of a head direction cell recorded in the rat anterodorsal thalamic nucleus. The polar plots indicate that the cell has a unique "preferred" direction and that the response of the cell is controlled by the visual landmark. Data by Arleo and Wiener. (C) Interrelation between visual and self-motion cues in controlling place (left) and head direction (right) cells. Plots indicate the angular deviations of the responses of place and head direction cells relative to the visual landmark in the case of small ($45°$) and large ($135°$–$180°$) conflicts, and for fast and slow induction of the conflict. The angular deviation of $0°$, indicating the absolute control of the visual landmark over the cells' response, is plotted at the 12:00 position. Dots indicate individual trials, whereas arrows are averages over all trials. Adapted from Knierim *et al.* [75].
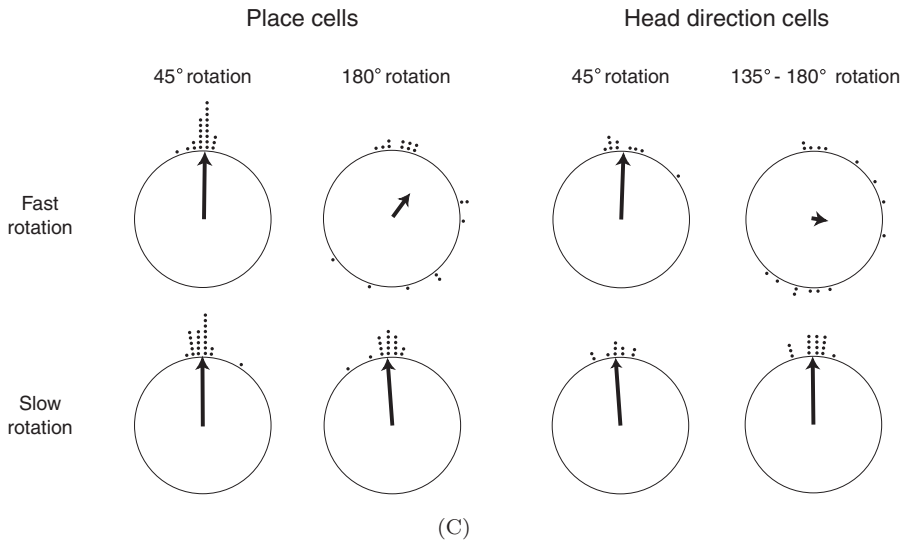
Fig. 3. (*Continued*)

Binding of multiple spatial representations may occur via correlational learning. Akin with Hebb [62], it is now admitted that correlated spiking of pre- and post-synaptic neurons can result in the strengthening or weakening of synapses, depending on the temporal order of spiking (e.g., see Refs. [1, 10, 11, 86, 119, 160]). The activity-dependent long-term synaptic plasticity in the hippocampus constitutes a neurochemical mechanism suitable for this type of learning [100]. Both pharmacological and genetic approaches have shown that hippocampal NMDA (N-methyl-D-Aspartate) receptors (NMDARs) are required for the induction of hippocampal long-term potentiation (LTP), a temporally correlational learning process that can be understood in terms of Hebbian synaptic modification [30, 105, 156]. NMDAR-mediated plasticity in the recurrent connections of the CA3 hippocampal region is crucial for the rapid encoding of novel experiences [81]. CA3-NR1-knockout mice are deficient in acquiring novel place/reward information, and CA1 HP cells in these animals are significantly impaired when recorded in a novel environment [108–110].

Complementing the allocentric place responses of hippocampal neurons, head direction (HD) cells provide an allocentric representation of the orientation of the animal (see Ref. [163], for a review). The discharge of these neurons is highly correlated with the direction of the head of the animal in the azimuthal plane, regardless of the orientation of the head relative to the body, of the animal's ongoing behavior and of its spatial location. Each HD cell is selective for one specific "preferred" direction [Fig. 3(B)], and the preferred directions of a population of HD cells tend to be evenly distributed over 360°. Direction-sensitive neurons have been found in numerous brain regions centered on the limbic system, including postsubiculum [123, 150], anterodorsal thalamic nucleus [15, 147], lateral mammillary nucleus [144], retrosplenial cortex [28], dorsal striatum [161], and dorsal tegmental nucleus [142].

Similar to the HP cell system, the HD circuit receives multimodal afferent information, including angular self-motion signals from the medial vestibular nucleus and visual inputs from neocortical areas (e.g., parietal cortex).

Thus, the discharges of HP and HD cells are determined by the interaction between allothetic and idiothetic cues. Several studies have attempted to identify the nature of the signals relevant for the establishment and maintenance of their firing properties (see Refs. [13] and [95]).

The responses of HP and HD cells are anchored to visual landmarks of the environment [16, 75, 107, 112, 114, 149, 164, 170]. A classical experimental apparatus employed to record HP and HD cells consists of a black cylindrical arena in which the rat freely moves while searching for chocolate pellets. The high walls of the cylinder prevent the animal from seeing outside the arena. A large white card, attached to the inner wall of the otherwise black cylinder, is used as a unique salient visual cue. Data show that rotating the white card causes an equal rotation of the receptive fields of HP and HD cells [Fig. 3(A), (B)]. More generally, experimental findings indicate that distal (background) visual cues tend to dominate over proximal (foreground) visual cues in controlling HP [31] and HD cells [169, 171]. The dominance of background cues may be due to the fact that they provide more stable references than proximal landmarks as the animal moves around. Consistent with this hypothesis, the more stable an animal perceives an allothetic cue to be, the higher the influence of the cue upon HP and HD cell dynamics [14, 69, 74].

Despite their dependence on allothetic signals, both HP and HD cells can maintain stable location and direction tuning for several minutes in the absence of environmental landmarks [27, 87, 107, 114, 121, 149], which suggests a role for internal movement-related cues. HP and HD cells continue to discharge when the animal moves about in complete darkness (see Ref. [162], on persistent activity in limbic neurons). Also, the location-selective responses of HP cells can develop in blind animals exploring a novel environment [65]. Save *et al.* [137] studied the HP cell activity in blind rats and found receptive fields and response specifics (e.g., spike parameters) very similar to those recorded from sighted rats. The only major difference concerned the mean peak firing rates that were prominently lower in HP cells from blind animals [137]. Vestibular information seems to be very important for maintaining the selectivity properties of HP and HD cells [143]. Also, motor signals influence the dynamics of both types of cells, since HP and HD neurons exhibit a dramatic attenuation of their responses if the animal is tightly restrained [49, 147].

Recently, electrophysiological recordings of HP and HD neurons shed light on the interaction between idiothetic and allothetic cues and their relative importance under different experimental conditions. Knierim *et al.* [75] made self-motion and visual cues incongruent (by rotating the animal and a salient familiar landmark relative to each other) and recorded both HP and HD cells before and after the onset of the conflict [Fig. 3(C)]. For small angular mismatches (45°) between idiothetic and landmark information, the responses of HP and HD cells remained anchored to the

visual stimulus. When larger discrepancies (180°) were induced by slow continuous rotations, the landmark still controlled the cell responses. By contrast, for sudden large (180°) rotations, either HP and HD cells followed the landmark, or self-motion cues predominated, or a reorganization (remapping) of HP fields occurred. Jeffery and O'Keefe [70] further examined HP cell responses in the presence of 180° conflicts and found that the ability of visual cues to dominate self-motion signals might depend on the "confidence" of the idiothetic information. When animals were prevented from visual update for about three minutes while the conflict was introduced, the visual landmark tended to predominate. Conversely, when animals underwent visual isolation during only 30 seconds, a marked attenuation of the visual control was observed.

Finally, HD cells maintain their directional coding even after the removal of external landmarks, but their preferred directions may drift slowly over time [148]. When the visual cue is put back to its standard position, HD cells tend to realign their preferred directions with the external reference [56]. However, this resetting does not always occur during subsequent light-dark-light recording phases [75].

## 3. The Cooperative-Competitive Interaction of Multiple Spatial Strategies

As mentioned in the introduction of this paper, efficient spatial navigation calls upon the ability of the subject to select the strategy that is most appropriate to the complexity of the task (see Fig. 4; see also the review by Trullier *et al.* [155]). For instance, reaching a goal that is either visible or identified by a visible cue (beacon) calls for a simple reactive behavior: orient towards the target (or beacon)
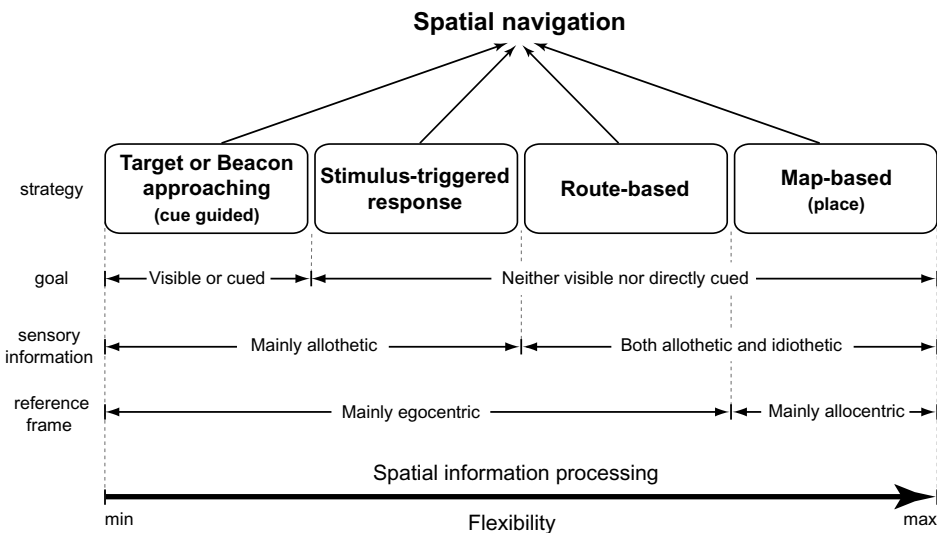


Fig. 4. Taxonomy of spatial navigation strategies.

and approach it. This procedure, named *target approaching* (or *beacon approaching*, or *cue strategy*), requires the acquisition of a single egocentric stimulus-response association and demands limited spatial information processing. If the target is neither directly visible nor identified by a beacon, the subject can learn an ensemble of Pavlovian associations to solve the task, which means that the subject employs a *stimulus-triggered response* strategy. This procedure is suitable when the trajectory to a hidden target is identified by an ensemble of choice points where the spatial context (e.g., visual landmarks or geometric configurations) can be associated to specific directions of body movement. However, since the sensory-motor associations of the learned ensemble are treated independently, this strategy does not allow the subject to anticipate subsequent stimuli. One strategy that allows for such anticipation is *route-based navigation*, in which the subject learns the spatiotemporal relationships among the intermediate events of a sequence. This procedure enables the navigator to predict the next stimulus based on the current stimulus-action association. A route can be thought of as a learned sequence of egocentric stimulus-response-stimulus (S-R-S) associations. Within each S-R-S association, the most prominent element can be either the stimulus itself or the motor response requirement. In the former case we have "guidance" (or taxon navigation), in the latter, we have an automated sequence of self-movements. Navigating using such a learned sequence of movements is a skill called "praxis". Tolman [153] suggested that animals do not solve navigation tasks solely on the basis of sensory-motor associations or fixed motor programs. Rather, they are capable of learning a sort of navigation map encoding the spatiotemporal relationships between their position in the environment, their movements, and the location of rewarding sites. *Map-based navigation*, also referred to as "place" or "locale" navigation [113, 124], requires complex processing (e.g., allocentric relational learning), but it may allow the subject to perform true flexible goal-oriented behavior (e.g., planning new or alternative trajectories, inferring shortcuts, solving multiple-goal tasks).

## 3.1.  *A coexistence of functionally distinct strategies*

The aforementioned navigation strategies come from interwoven processes that continuously concur to determine the animal's spatial behavior. The following experiment was designed in order to determine the relative contribution of three of these four strategies in rodents tested in a T-maze paradigm. The animals were first trained to find food located at the end of the right arm of the T. The rewarded goal was distinguished from the unbaited arm by its spatial location (map-based or place strategy), the presence of a tactile cue (cue guided strategy), and by the direction of the body turn required by the animal at the choice point (stimulus-triggered response strategy). Subsequently, probe trials were introduced occasionally in order to characterize the strategy used by each animal in order to solve the task. In this particular experiment, normal animals exhibited a strategy distribution of about 30% map-based, 25% cue and 45% response [8]. Thus, a task of spatial navigation

can be solved on the basis of more than a single strategy. It is worth mentioning that strategy preferences can vary with the length of the training process [24, 116].

How are these different strategies of navigation acquired and used? During the navigation process, multisensory information (i.e., allothetic and idiothetic) can be organized in two different reference frames (i.e., allocentric and egocentric) therefore leading to the simultaneous acquisition of different strategies. A rat learning in the Morris water maze to swim to a visible platform that remains at a fixed location will learn at the same time to navigate to the corresponding place [158]. This capability has been demonstrated in a simple task in which the animal can use idiothetic cues as well as proximal and distal allothetic landmarks to reach a visible platform [Fig. 5(A)]. After the platform is hidden from view under the water, the rat readily finds the correct position of the platform using either praxis navigation [Fig. 5(B1)] or place navigation according to distal cues [Fig. 5(B3)]. Animals that previously learned to go to the platform location according to proximal cues were looking for the platform in the wrong place [Fig. 5(B2)] therefore showing a hierarchical organization of the different strategies in terms of flexibility. The simultaneous acquisition of these different strategies gives the animal the possibility to adapt its behavior to challenges and changes within the environment. For example, when sudden darkness eliminates the access to distant visual cues, the animal can still return to a recently visited part of the environment identifiable by the recalled locomotory movements [47]. This finding is in agreement with the Whishaw and Mittleman [158] experiment, suggesting that even not required strategies can be acquired during a task of spatial navigation [19]. These results have to be compared to recent data suggesting that the complexity of the task might also account for the strategy used. In mice, using the starmaze task, which can be solved by using either map-based or route-based strategies, Rondi-Reig *et al.* [130] recently demonstrated that both map-based and route-based strategies involved the hippocampus. Both strategies were used during the entire training period and animals could flexibly switch from one to another [130].

The coexistence of different strategies of navigation raises several questions. How does the brain store and coordinate the different strategies in the different brain systems? What are the parameters influencing the use of one strategy over the others?

## 3.2. *The shift between strategies as a resultant of multiple parallel memory systems*

### 3.2.1. *Multiple and parallel memory systems*

A large number of structures are involved in the neuronal network implicated during spatial navigation, including (non-exhaustively) the hippocampus [113]; the parahippocampus [40]; the entorhinal cortex [59, 95]; the parietal cortex [20, 151]; the frontal cortex [157]; the striatum [34, 79, 161]; and even a new possible player, the cerebellum [78, 99, 120, 127, 129].
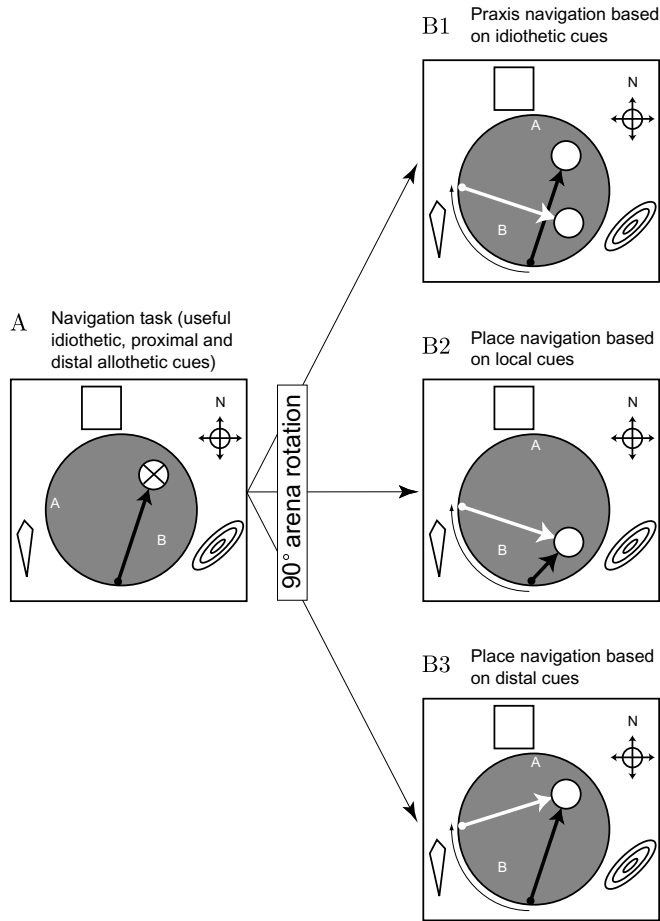
Fig. 5.   Different navigation strategies within a circular enclosure in a square room are depicted. Adapted from Bures and Fenton [19]. The movement trajectory is shown as a vector. Allothetic cues are provided by distal room landmarks outside the enclosure. Three are shown, along with a compass that indicates the inertial coordinate frame of the earth. There are also arena-bound proximal landmarks such as objects, odors, and textures that can be accessed. They are represented by A and B. (A) A rat can learn to go directly from a start point (●) to a goal using distal or proximal allothetic cues or idiothesis. Here the goal is also visible (marked by an X), and thus the animal can also find the target by cued navigation, simply going to the X. (B) When the arena is rotated by 90°, it is possible to detect which navigation strategy is used by the rat. If the rat learned the target position by computing the orientation from the start at the arena periphery (B1), it will look for the goal at different room- and arena-defined places but always according to the vector 60° to the tangent at the start regardless of whether the start is in the room-defined south (black vector) or an arena-defined place 90° away (white vector). This behavior (i.e., navigating using a learned series of movements) is a skill called praxis and is one of the subtypes of the route-based strategies. Navigation learned according to cues on the arena (B2) will lead the rat to the goal between cues A and B regardless of the start position or the placement of the arena cue configuration. Similarly, navigation according to room cues (B3) will lead the rat to search for the goal in the northeast area regardless of the start or the presence of the arena cues. Note that the place navigation according to distal cues has the advantage over the two other strategies to give the correct position of the platform regardless to the starting position (black or white vectors) and despite the 90° arena rotation.

To detail the contribution of these different structures is beyond the scope of this paper (see for example Thinus-Blanc [151], for a detailed review). The cooperative or competitive interactions of these different systems have been reviewed by White and McDonald [159]. Here, we focus on the hippocampal formation, which plays a role in the organization of a spatial representation, and on the cerebellum, which seems to be essentially involved in the organization of the motor behavior adapted to the specific spatial context [23, 126]. In the following, we report on recent findings and current debated questions concerning the functions mediated by these two structures during spatial learning and navigation.

Many different studies in humans and animal models have led to a consensus that, among the different structures involved in spatial navigation, the hippocampus subserves the place learning function [37, 39, 104, 113]. Strong support for the role of the hippocampus in place learning comes from convergent findings of hippocampal lesions, both in humans and in various other mammalian species, and electrophysiological recordings of hippocampal neurons [HP cells, Fig. 3(A)].

A current debate concerns the role of the hippocampus in more than the map-based strategy. It has been proposed that the hippocampus plays a critical role when distinct personal experiences must be encoded in relation to one another and linked temporally [159]. Based on the strategy taxonomy defined above (Fig. 4), this would lead to the possibility that the hippocampus may be relevant to both map-based and route-based strategies. There exist some evidence, from recordings of hippocampal neural activity, showing that the hippocampal network can encode episodic memories, i.e., memories requiring spatial or sequential (temporal) organization [168, 169]. Yet, other works suggested that not in all conditions hippocampal place cell activity patterns are indicative of episodic encoding [17, 57, 82].

Nonspatial memory requiring relational and temporal coding has been shown to be dependent on CA1-NMDA receptors [66, 128]. This combination of coding and cellular properties suggested that the CA1-NMDA dependent mechanisms could contribute to the construction of a "memory space" composed of multiple episodes spatially or sequentially linked together and therefore sustain multiple strategies of navigation requiring such an organization. Rondi-Reig *et al.* [130] have demonstrated that mice lacking hippocampal NMDA receptors and presenting a decrease of these receptors in the deep cortical layers are indeed deficient in acquiring the memory of successive stimulus-response-stimulus behaviors requiring the execution of a specific sequence of body rotations associated to an ensemble of choice points (sequential egocentric strategy) in addition to a deficit in the map-based strategy [130]. This strengthens the hypothesis of the implication of the hippocampus in a general memory acquisition process, where memories are composed of multiple spatiotemporal events.

Concerning the cerebellum, the question is now to understand which navigation component it is relevant for. Several findings have pointed toward the role of the cerebellum in the procedural part of the navigation process [78, 120, 127,

129]. Recent data obtained with subjects asked to navigate through a virtual three-dimensional labyrinth showed a strong activation in the medial temporal area including the parahippocampal region, the hippocampus, and the thalamus. The cerebellum was also active in those subjects. The authors proposed that the stronger activation in the thalamic-basal ganglia-cerebellar loop points toward a more automatic support of memory and attentional processes possibly mediating memorization of spatial maps [71]. The possible implication of the cerebellum in the organization of the spatial representation *per se* is matter of strong debate [126]. We recently employed the L7-PKCI transgenic mice model [32], which presents a specific inactivation of the long-term synaptic depression (LTD) at the parallel fiber–Purkinje cell synapses, to investigate the potential role of this cellular mechanism during spatial navigation [23]. In order to dissociate the relative importance of the declarative and procedural components of navigation, we adopted two different behavioral paradigms: the Morris water maze (MWM) and a new task called the Starmaze [130]. In both cases, the animal had to find a fixed hidden platform from random departure locations, which requires the declarative capability of learning a spatial representation of the environment. Yet, in contrast to the MWM task, the Starmaze allows the animal to only swim within alleys guiding its movements. This helps to execute goal-directed trajectories effectively, and reduces the procedural demand of the task. Our data bring evidence for a deficit of L7-PKCI mice in the acquisition of an adapted goal-oriented behavior, i.e., in the procedural component of the task. This finding supports the hypothesis that cerebellar LTD may subserve a general sensory-motor adaptation process shared by motor and spatial learning functions [23].

### 3.2.2. *The shift between strategies*

Several parameters influence the strategy shift process. For example, practice-related changes between strategies have been observed in rodents as well as in humans. In rats, place and stimulus-triggered response strategies involve two different systems of memory including the hippocampus and the striatum (caudate nucleus and putamen), respectively [90–92, 104]. According to McDonald and White [91] and Packard and McGaugh [115], rats can reach a target by relying on the contribution of the hippocampal or the striatal neural systems depending on whether the animal is in an early or late phase of training. In the early phase of training, the hippocampus is involved in the rapid acquisition of spatial information, allowing rats to reach a target from any starting position [104]. The striatum is involved in a slower process that relies on rewarded stimulus-response behavior [113, 159].

Similar findings have been found with humans [67]. Normal subjects were told to retrieve virtual objects located at the end of virtual arms of a radial maze. These objects were located down a set of stairs and were not visible from the center of the maze. Landscape and trees could be viewed at a distance and used for place navigation. Subjects could also count the visited arms either clockwise or counterclockwise, which corresponds to a more automated strategy. In the early phase
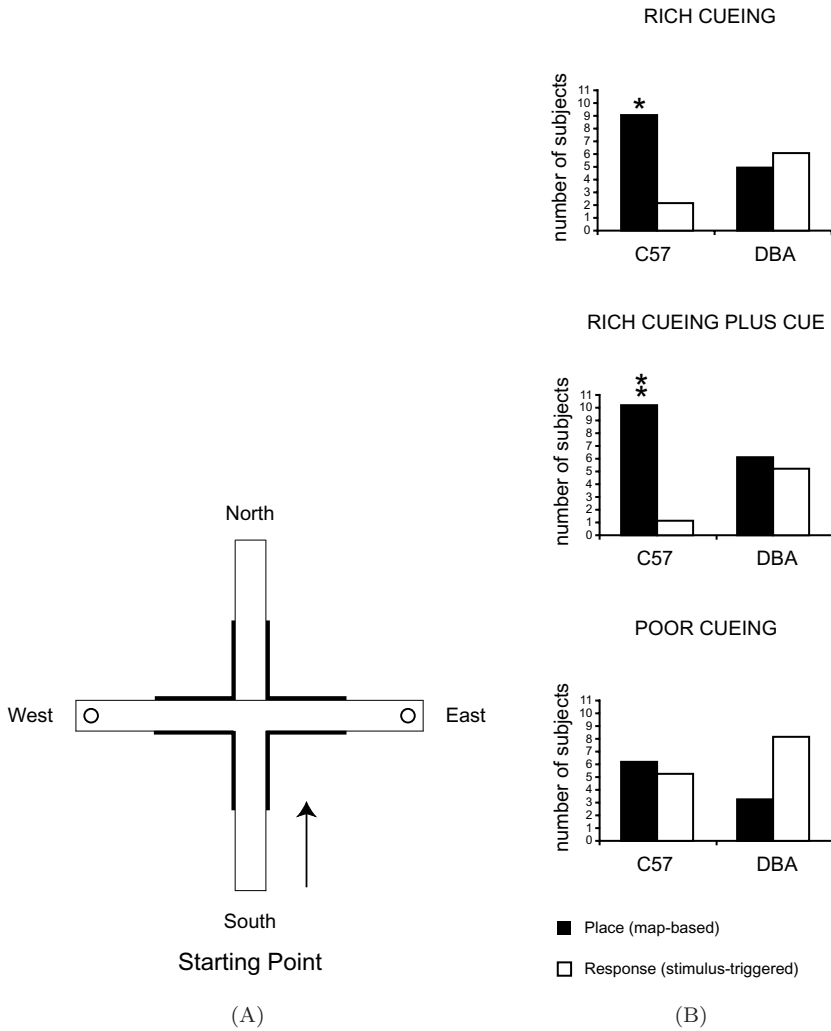
Fig. 6.   From Passino *et al.* [118]. (A) Schematic representation of a cross-maze with four identical arms (north, south, east, and west) and transparent Plexiglas high walls fixed on both sides of each arm. During training, access to the north arm was blocked; animals were placed at the starting point of the south arm and were allowed to consume the food pellet located at the end of the east arm. During the probe trial, access to the south arm was blocked; animals were released from the north arm, and were allowed to choose either the east arm (place learning) or the west arm (response learning). Two different strains of mice, C57BL/6 and DBA/2, were used for this experiment. C57BL/6 and DBA/2 mice present significant differences in hippocampal anatomo-functional properties (see Ref. [118], for details). In spatial navigation tasks, C57BL/6 mice tend to be more efficient than DBA/2 mice when (hippocampal-dependent) processing of contextual information is required, whereas DBA/2 mice tend to show better performances in tasks requiring the formation of simple stimulus-response associations. (B) Number of C57BL/6 and DBA/2 showing place or response learning under rich, rich plus cue and poor cueing condition. Rich cueing corresponds to a room of $12\,m^2$ with numerous items. Rich cueing plus cue was similar to the precedent context except that an additional poster was attached to the wall in the direction of the west arm in which the reward was delivered. In the poor cueing condition, all the items were removed. Statistical significant place versus response differences: $p < 0.001$ and $p < 0.05$.

of training, half of the subjects used spatial landmarks to navigate (place navigation) and these subjects showed increased activation of the right hippocampus. The other half used the counting strategy and showed sustained increased activity within the caudate nucleus during navigation. By the end of the test, 72% of the subjects were employing the counting strategy and only 28% were using the place strategy, demonstrating a shift from place navigation to a more automated strategy.

Burgess *et al.* [22] combined virtual reality and functional imaging and showed that the human hippocampus is activated when memory for location is required in a complex three-dimensional space, but not within a simple two-dimensional array. Similarly, in young children self-reorientation first occurs solely according to the geometry of the room. Children tend to ignore a large colored cue presented on one wall that under the same conditions enables adults to orient correctly [63]. However, this effect is weakened when a larger room is used [80]. In adult mice, the presence of intra-maze and extra-maze cues favors place learning, whereas a poor cueing environment favors stimulus-response learning [see Ref. [118], Fig. (6)].

Taken together, these results point toward a crucial role of the complexity of the environment in which the navigation is performed. As suggested by the experiment performed by Iaria *et al.* [67], the subjects eventually employed the strategy leading to fewer errors during navigation. Therefore, even if multiple strategies are acquired simultaneously, the subject tends to rely on the more advantageous one, that is, the one leading to the best chance to reach the goal without making errors. In simple environments, the behavioral response can be easily automated and therefore relies on a system promoting simple stimulus-response. A complex environment requires more flexible behavior, a process that depends on a brain system including the hippocampal formation.

## 4. Spatial Learning in Neuro-Mimetic Robots

The perspective of developing autonomous control systems emulating the spatial navigation capabilities of animals has given rise to a large number of bio-inspired (or neuro-mimetic) robotic models (see Ref. [5], for a review). Most of these control architectures rely on artificial neural networks (ANNs), massively parallel distributed systems suitable for nonsymbolic processing of complex information [61, 64]. The elementary constituents of ANNs are formal computing units (artificial neurons), each of which receives and transmits a large number of afferent and efferent connections. The computational power of an ANN derives from the large interconnectivity between its formal neurons. Learning occurs through short- and long-term modification of the strength (or weight) of these connections (modeling synaptic plasticity). Thus, ANNs offer a suitable tool for designing adaptive (experience-dependent) control systems, on the basis of highly simplified models of the anatomo-functional properties of the neural substrates involved in spatial navigation (e.g., hippocampal formation).

Most of the existing models for neuro-robotic spatial learning mainly rely on vision to build space representations (see, for instance, [22, 52, 139, 154]). The neuro-mimetic model by Arleo *et al.* [3, 4, 7] provides an example of spatial learning system stressing the importance of integrating idiothetic and allothetic cues to establish stable place and head direction coding (Fig. 7). In the model, the place and direction representations drive a downstream population of action cells mediating motor commands and guide goal-oriented behavior. In particular, reward-based learning is employed to acquire a navigation map allowing the agent to reach hidden goals while avoiding obstacles. Here we only survey the place cell learning component of the model and we focus on the interrelation between exteroceptive and self-motion information.

The mobile robot used for the experimental validation of the model is shown in Fig. 8. Allothetic sensory inputs were provided by a two-dimensional vision system and by eight infrared sensors detecting proximal objects (i.e., tactile-like information). Idiothetic signals were provided by wheel rotation encoders that allowed the
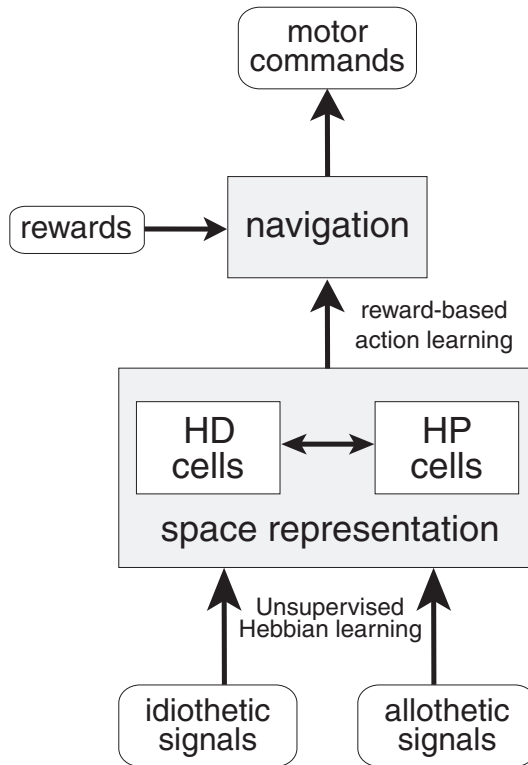


Fig. 7.   Overview of the spatial learning model proposed by Arleo and Gerstner [3]. The system processed idiothetic and allothetic sensory inputs in parallel. The spatial information extracted from these two processing streams was combined by means of LTP-LTD Hebbian learning to generate place and directional coding. Goal-oriented navigation was then achieved by mapping places onto allocentric locomotor actions by means of reward-based learning.
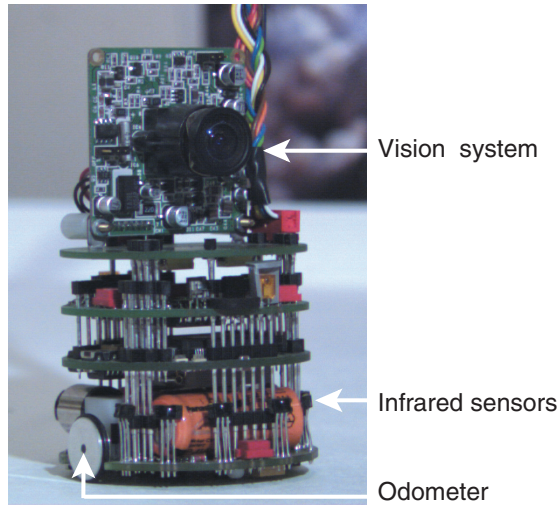
Fig. 8.   The mobile Khepera miniature robot (commercialized by K Team S.A.) used for the experimental validation of the model. The Khepera robot has a cylindrical shape with a diameter of 55 mm, and, in the configuration used for the experiments, was about 90 mm tall. A two-dimensional vision system (image resolution: $768 \times 576$ pixels, view field: $90°$ pitch, $60°$ yaw) and eight infrared proximity sensors (detection range: 40 mm) provided the robot with allothetic sensory inputs. Wheel rotation encoders (odometers) estimated linear and angular movements and provided idiothetic signals.

robot to estimate its linear and angular movements (similar to self-motion kines-thetic and vestibular-derived signals). A low-level reactive module was taking control whenever the infrared proximity sensors detected an object and endowed the robot with obstacle-avoidance capabilities. On the other hand, the spatial learning model was used to develop the high-level controller determining the robot's spatial behavior.

## 4.1.   *Combining vision and path integration for robust space coding*

In the model, space learning occurred via two processing streams that drove two HP cell populations producing two parallel spatial representations: an allothetic place code based on visual information, and an idiothetic representation obtained by path integration.

Vision-based place coding consisted of a three-step process. First, low-level features were extracted by sampling each image taken by the robot [Fig. 9(A)] by means of a family of local visual filters [Fig. 9(B)]. Second, the responses of the filters were combined to drive a population of units whose activity became correlated to more complex spatial relationships between visual features. These units were called "view cells" because they provided a neural encoding of the views perceived by the robot. However, the activity of the view cells was not invariant with respect to the robot's gaze direction and position. Therefore, the third step to achieve vision-based space coding consisted of combining multiple gaze-dependent views at each robot's
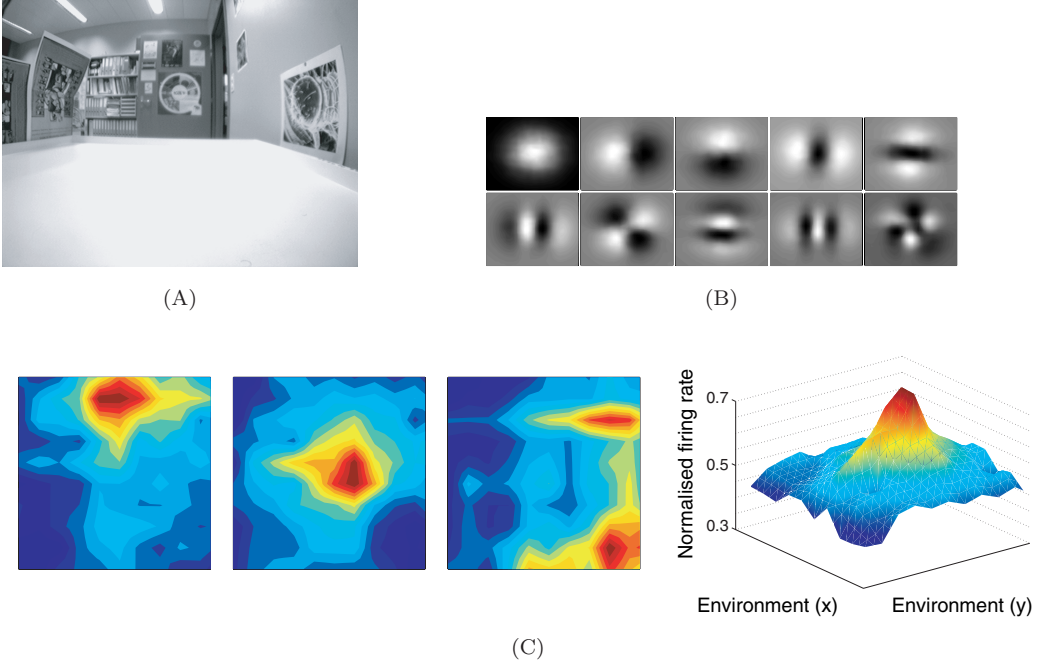
(A)



(B)



(C)

Fig. 9. Vision-based place (ViP) representation. (A) A sample image taken by the robot while exploring an open-field square environment (the $800 \times 800$ mm open-field arena was placed within a standard laboratory background and the robot's behavior was monitored by means of a video camera above the arena). (B) The receptive fields of a set of filters used to sample the images and detect low-level visual features (the ten filters corresponded to the first ten principal components, numbered from left to right, top to bottom, obtained by applying the learning algorithm proposed by Sanger [134]). The model was also tested by employing a set of Gabor filters and a retinotopic sampling method [7]. (C) Some samples of vision-based place fields. The squares represent overhead views of the environment. The mean firing rate of each recorded cell is plotted as a function of the locations visited by the robot (red regions denote high activity). Most of the recorded cells showed clean location-correlated firing (e.g., first two plots). However, due to visual aliasing, some cells exhibited multipeak receptive fields (third plot from the left). The three-dimensional diagram suggests that visually driven place cells tended to have rather high baseline firing rates. (D) Accuracy of the vision-based place representation. The diagram has been obtained by separating the environment into an $18 \times 18$ grid matrix (i.e., each sampled area was about $44 \times 44$ mm). First, the robot was let visit the center of each cell of the grid and it had to use its vision-based place map to estimate its position. Population vector decoding was employed to map the ensemble place cell activity onto a spatial location [53, 131]. Second, the position reconstruction error associated to each sampled area was computed by comparing the vision-based position estimate with the location of the center of the matrix cell. This process was iterated $n = 10$ times (each time corresponding to a different spatial learning session) to calculate the mean position error associated to each sampled area. This mean error function is shown by the three-dimensional diagram. By averaging this error function over the $18 \times 18$ grid matrix, we obtained a mean position error over the whole environment of about 60 mm. (E) For each position visited by the robot, the reliability of the visual space coding was assessed by measuring the dispersion of the ensemble activity around the center of mass (computed by population coding). The diagram shows the correlation between this (normalized) dispersion measure and the (normalized) vision-based position reconstruction error (number of data points: 4600, correlation coefficient: 0.67). The robot utilized such an online reliability criterion to select those local views that are suitable for calibrating its path integrator.
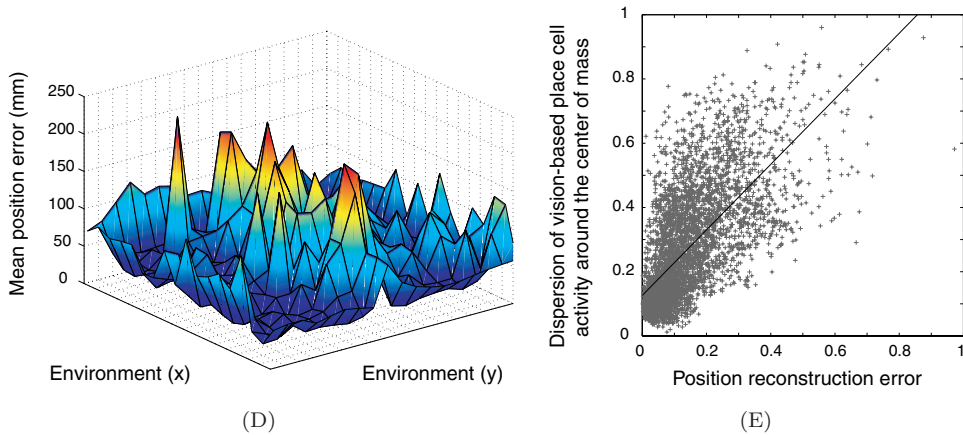
(D)                                    (E)

Fig. 9.   (*Continued*)

position. This combination produced a local view coding for the spatial relationships between the perceived visual cues and generated allocentric location-selective activity in a population of vision-driven place (ViP) cells, [Fig. 9(C)]. The model postulated a possible role for the lateral entorhinal cortex in allothetic space coding, suggesting it as a possible locus for the vision-based place field representation [3].

As aforementioned, unimodal spatial information is prone to perceptual aliasing and can lead to ambiguous space representations. Indeed, due to visual aliasing, the vision-based HP cells of the model happened to have multiple subfields and could not always differentiate spatial locations effectively [Fig. 9(C), third plot from the left]. As a result, the accuracy of the vision-based representation was not uniformly distributed over the surface explored by the robot [Fig. 9(D), (E)]. In the model, path integration was employed to compensate for ambiguities in the visually driven place coding. The robot integrated its linear and angular displacements over time to generate an environment-independent representation of its position relative to a starting point. Such a dead-reckoning mechanism was used to drive a population of place cells (named "path integration place", PiP, cells) whose activity depended on self-motion signals only (i.e., it provided a space coding based solely on idiothetic information). In the model, the place fields of the PiP neurons had preconfigured metric interrelations within an abstract allocentric framework being mapped onto the environment according to the robot's entry position and the absolute directional reference provided by HD cells. In agreement with previous hypotheses [125, 132, 140], the model postulated that the PiP network might find its anatomical counterpart in the medial entorhinal cortex [3]. Indeed, early experimental reports [122] showed that the place field topology of location-sensitive cells in the medial entorhinal cortex does not change across different environments. More recently, the discovery of grid cells in the medial entorhinal cortex by Hafting *et al.* [59] has provided a relevant piece of evidence about the role of this brain area in encoding a path integrator-based spatial map [95].

In the model, the efferents of the ViP and PiP networks (i.e., of the two place cell populations driven by vision and path integration, respectively) converged onto a third downstream network of hippocampal place (HP) cells. Hebbian learning was employed to induce long-term synaptic potentiation (LTP) and depression (LTD) at the level of the ViP-HP and PiP-HP synapses. This learning mechanism allowed the system to couple allothetic (ViP) and idiothetic (PiP) spatial codes based on their correlation during the agent-environment interaction. This process generated a stable HP space representation consisting of localized place fields similar to those found in hippocampal CA3-CA1 regions [Fig. 10(A)]. These place fields were less noisy than those solely driven by vision (i.e., ViP receptive fields) and did not exhibit multi-peak fields, meaning that the system was able to overcome the sensory aliasing problem of purely vision-based representations.
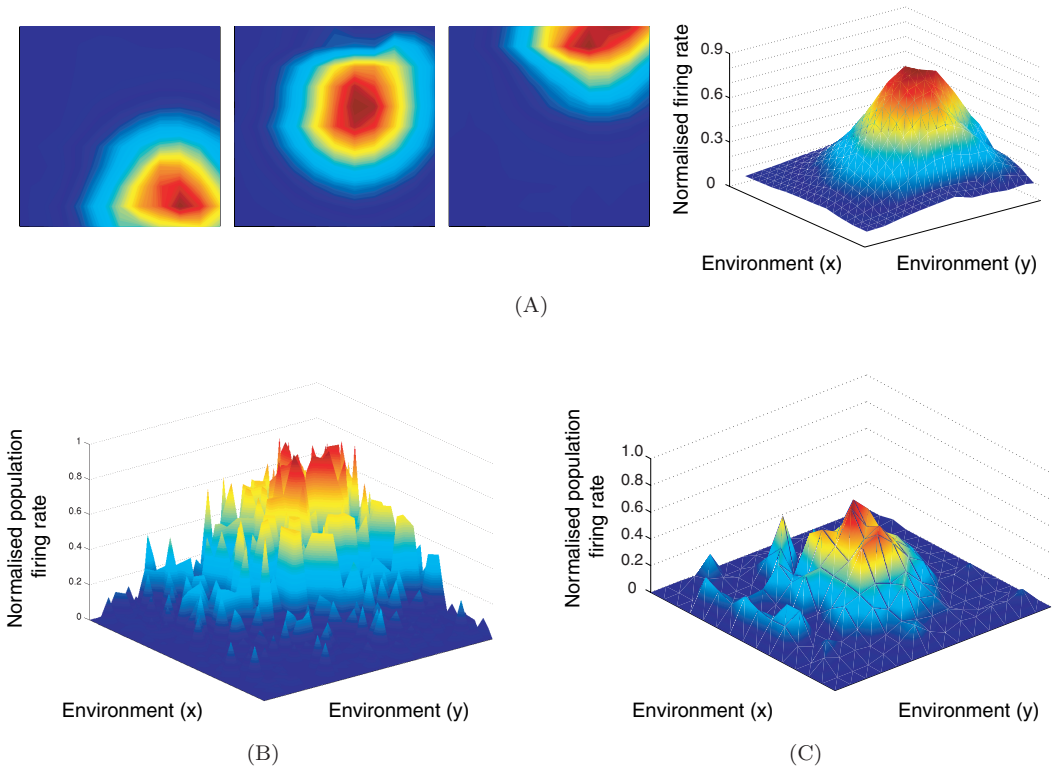


(A)



(B)



(C)

Fig. 10. Space representation based on multisensory inputs. (A) Examples of place fields obtained by combining vision and path integration. They did not exhibit multiple subfields and they were less noisy than those solely driven by vision (the three dimensional diagram shows very low baseline firing). (B) The robot used the ensemble place cell activity to self-localize. The diagram shows an example of population activity when the robot was located at the upper-right corner of the arena. (C) In the absence of visual information (e.g., in the dark), place cell firing could be sustained by the input provided by the path integration signal. The figure illustrates the population activity recorded in the dark when the robot was approximately at the center of the arena.

The goal of the spatial learning model was to generate a large population of overlapping place fields covering the two-dimensional space uniformly and densely. The robot utilized the ensemble HP cell activity to self-localize [Fig. 10(B)]. At each time step, a population vector decoding scheme [53, 165] computed the center of mass of the ensemble activity pattern to estimate the robot's current position. Using the population activity, rather than single cell activity, helped in terms of stability and robustness of the self-localization process.

In the model, a place map could emerge and persist even in the absence of visual information (e.g., in darkness conditions). This property was consistent with the experimental observation that hippocampal place fields can arise in darkness [121]. Because the activity of the modeled HP cells relied on convergent excitation from both vision and path integration, their mean peak firing rates were lower in vision-less conditions than when the robot could use visual spatial cues [Fig. 10(C)]. The reduced firing activity of the HP units of the model in darkness conditions is in agreement with the experimental findings indicating that HP cells recorded from blind rats exhibit lower discharge frequencies than those observed in sighted animals [137].

## 4.2.  *Coherence between allothetic and idiothetic information*

### 4.2.1.  *Exploring a novel environment*

The robot initially explored an unfamiliar environment by relying upon path integration only. As exploration proceeded, local views (encoded by the visually driven HP cells) were coupled (by means of LTP/LTD correlational learning) to the spatial framework provided by the path integrator such that vision and self-motion signals could cooperate to form the hippocampal space code (i.e., the CA3-CA1 place representation). However, to maintain this allothetic-idiothetic coupling coherent over time, the robot had to prevent the path integrator from accumulating errors. In order to do that, the robot adopted an exploration strategy consisting of looped excursions (i.e., outward and homing journeys) centered at the starting location [Fig. 11(A)]. During an outward excursion, the robot acquired new spatial knowledge and updated its space code. After a while, it started following its homing vector and as soon as it arrived and recognized a previously visited location (not necessarily the starting location), it utilized the vision-based representation to realign the path integrator. Once vision had calibrated the path integrator, a new outward excursion was initiated. By iterating this procedure, the robot could keep the dead-reckoning error bounded [Fig. 11(C)], and propagate exploration over the entire environment (the probability of calibrating the path integrator at locations other than the starting region increased over time). Behavioral findings concerning the locomotion of rodents exploring novel environments [35] show a typical exploratory pattern consisting of looped excursions centered at their home base [Fig. 11(B)]. The model postulated that maintaining the idiothetic and allothetic signals mutually consistent might be one of the factors determining such a loop-based exploratory behavior.
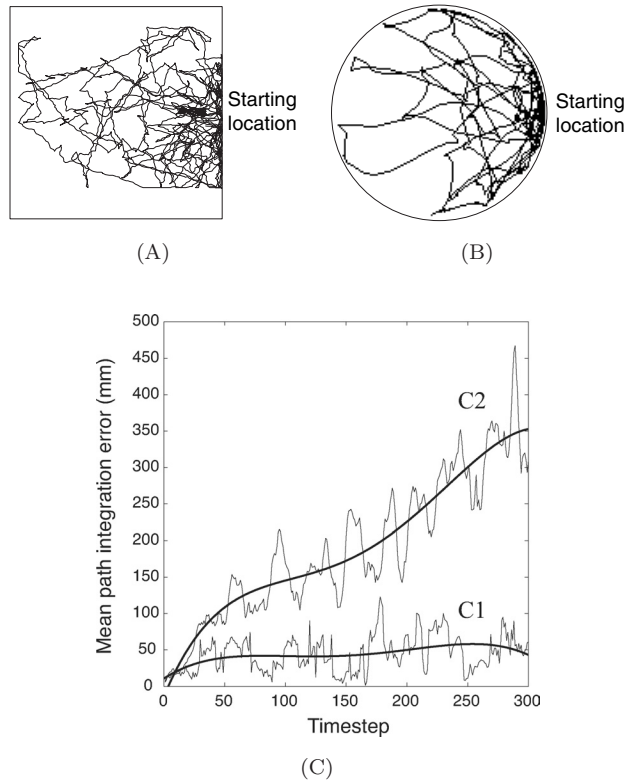
Fig. 11. Exploratory behavior and path integration calibration. (A) To establish a coherent allothetic-idiothetic coupling, the robot started exploring a novel environment (in this example a square arena) by means of looped excursions centered at the starting location. (B) Example of a rat's behavior at the beginning of exploration in a novel circular environment (data courtesy C. Brandner, Institute of Psychology, University of Lausanne, Switzerland). (C) Uncalibrated (C2 curves) and calibrated (C1 curves) mean path integration error (thin lines are raw data, whereas thick lines are polynomial fittings). At each timestep ($x$-axis) the robot updated its orientation and moved one step further. The difference between the actual position of the robot and the estimate provided by the path integrator was measured at each timestep. The C2 curves show that this path integration error (averaged over $n = 5$ trials) tended to grow over time. By contrast, if the system used the vision-based place representation to calibrate the path integrator occasionally, this error remained bounded over time (C1 curves).

### 4.2.2. *Importance of landmark stability*

The LTP-LTD Hebbian learning used to combine allothetic and idiothetic representations made stable visual configurations more likely to be correlated to self-motion signals than unstable ones [Fig. 12(A)]. As a consequence, only those visual configurations that were taken as stable by the robot could influence the dynamics of the space coding process [4]. Stable landmarks could polarize the space representation across different entries in an environment. This polarization could help the robot to realign the allothetic and idiothetic components of its spatial code and, then, to reactivate a previously learned description of a familiar environment.
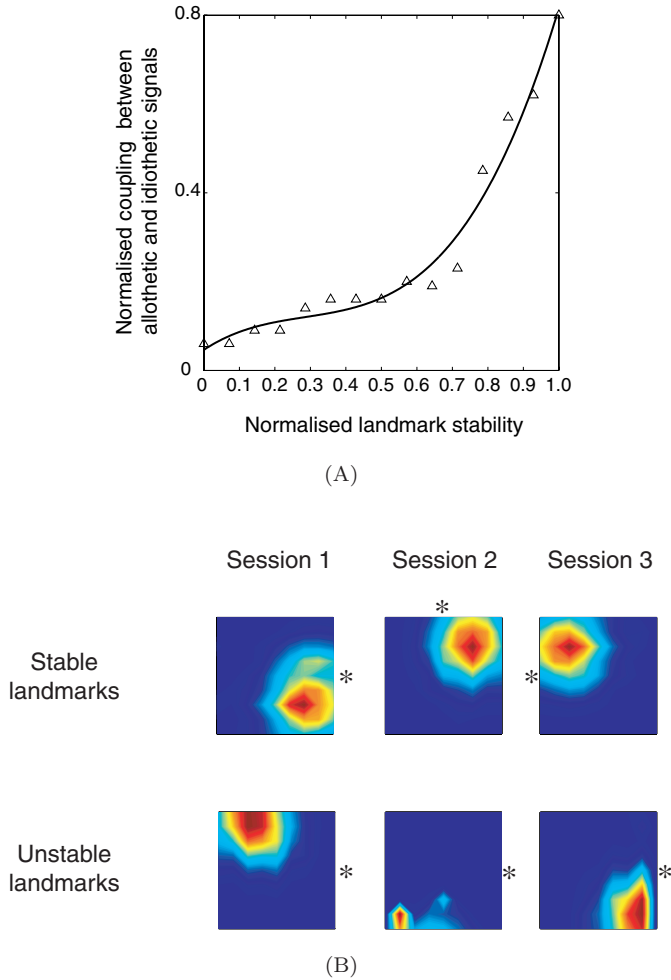
(A)



(B)

Fig. 12.    Interaction between visual and self-motion signals. (A) Due to Hebbian learning, the larger the stability of a visual cue configuration, the strongest its coupling with the path integration-based representation (triangles are sampled data, the curve is a polynomial fitting). (B) Intersession responses of one formal place cell after spatial learning. At the beginning of each probe session, the robot was disoriented. Top: Visual cue configurations that remained stable during spatial learning were able to polarize the place code at the beginning of each probe session. The place cell reoriented its receptive field according to the $90°$ visual cue rotations (the asterisk indicates the centroid of the visual cue configuration). Bottom: Unstable visual cues did not allow the disoriented robot to reactivate coherent representations across sessions and remapping occurred.

Failure of such a reactivation process might result in creating a new superfluous representation [75].

In a series of robot experiments conducted by Arleo and Gerstner [4], the constellation of visual cues was kept stable during spatial learning. Then, the path integrator was reinitialized randomly (simulating a disorientation procedure) and the robot was placed back in the familiar environment. Since the system learned a stable coupling between the idiothetic and allothetic signals, the robot could use

the visual information to anchor its allocentric spatial representation, reset its path integrator, and reactivate the previously learned place map [Fig. 12(B) top row]. In a second series of experiments, the constellation of visual cues underwent arbitrary rotations during spatial learning. Thus, the Hebbian learning scheme failed to establish stable correlations between idiothetic and allothetic inputs. As a consequence, when the robot was disoriented and placed back in the explored environment, it was unable to reactivate the learned spatial representation properly and intersession remapping occurred (i.e., HP cell response patterns varied across subsequent visits of the same environment, Fig. 12(B) bottom row). These results are in agreement with those reported by Knierim *et al.* [74] who recorded HP cells and HD cells from freely moving rats.

Finally, note that since the realigning procedure relied on the allothetic-idiothetic coupling established by the robot via Hebbian learning, impairing this latter mechanism would also lead to unstable intersession representations (i.e., remapping). This result is consistent with experimental findings showing that animals with impaired hippocampal LTP exhibit stable place cell firing patterns within sessions, but unstable mapping between separate runs [9].

### 4.2.3. *Conflict situations*

In the above experiments, the robot used external visual fixes to recalibrate an otherwise untrustworthy path integrator (e.g., after disorientation or because of cumulative integration error). Here we consider the situation in which stable allothetic inputs and *reliable* idiothetic signals provide conflicting spatial information. In the model, the relative importance of coupled external and internal spatial cues was a function of: (i) the degree of confidence of the robot about self-motion related spatial information (i.e. the path integrator); (ii) the degree of discrepancy between allothetic and idiothetic spatial information. A series of tests was run inspired by the behavioral experiments by Etienne *et al.* [43], who studied the homing behavior of hamsters in perceptual conflict situations (see Sec. 2 for a review of these experiments). First, we let the robot learn the coupling between a stable visual configuration and its path integrator. Then, during testing, we created both a 90° and a 180° conflict between external and internal cues and examined the homing behavior of the robot. Results in Fig. 13(A) (top row) show that when a 90° conflict occurred the visual component tended to influence the robot's homing trajectory more than self-motion signals. By contrast, for 180° conflicts (bottom row) the system's response was twofold: if the robot had not been disoriented, then its homing behavior was mainly determined by self-motion signals (bottom row, central plot); on the other hand, if the robot had been disoriented, then it relied on allothetic spatial information even for large discrepancies (i.e., 180°) between allothetic and idiothetic cues (bottom row, right plot). Finally, Fig. 13(B) shows the average response of the robot to a 180° conflict situation as a function of the degree of confidence about its path integrator. The diagram indicates that as long as self-motion information was given confidence above
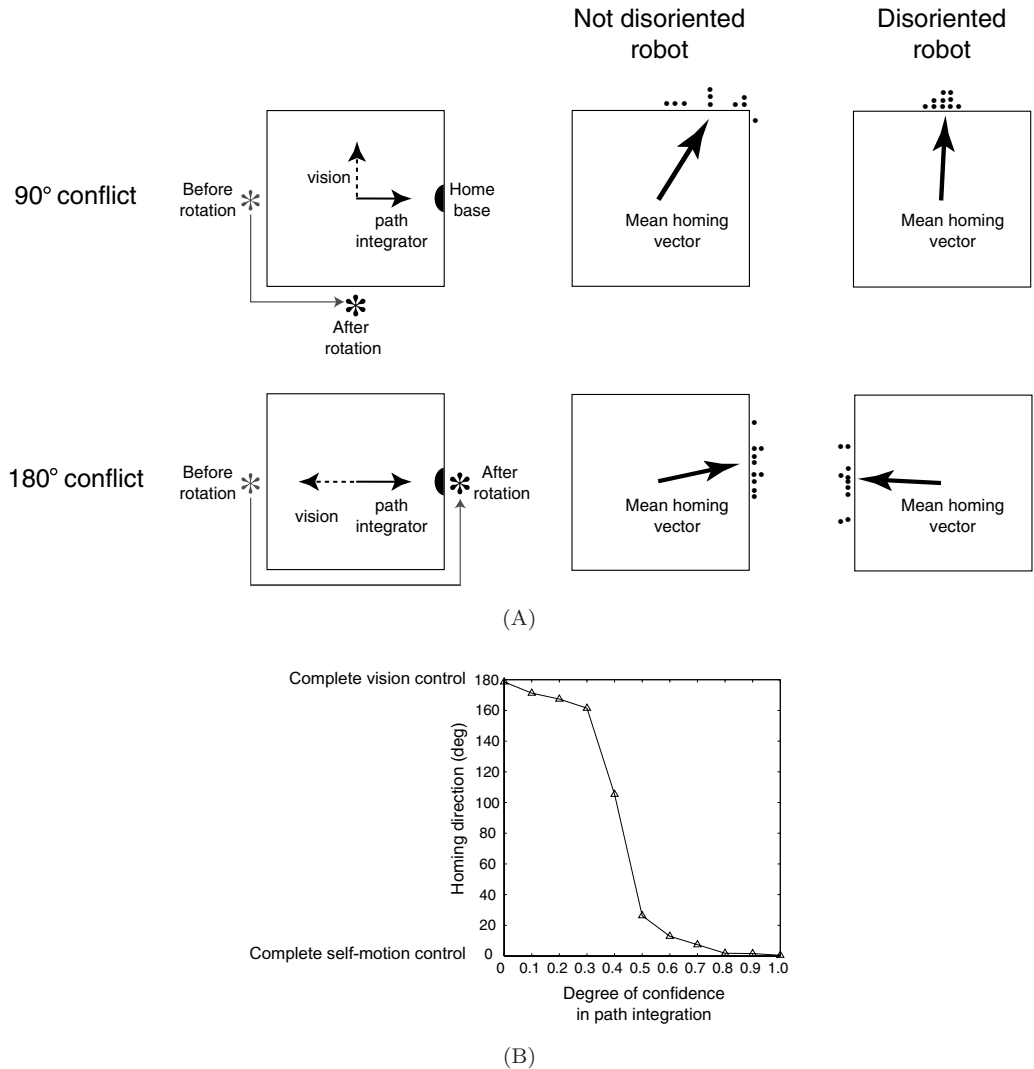
(A)



(B)

Fig. 13.   Conflict situations between vision and path integration. (A) During spatial learning, the visual cue configuration was maintained stable. The protocol for the probe trials included: (i) An outward journey during which the robot moved directly from its home base to the center of environment in the dark. (ii) A "hoarding" phase during which the robot actively rotated on the spot for a random amount of time (both the amplitude and the sign of the rotation were selected randomly). During hoarding, the visual cue configuration was rotated by either $90°$ or $180°$ and the light was switched on. (iii) A backward journey during which the robot had to compute the homing vector to return home. A conflict occurred between vision and path integration (dashed and continuous arrows, respectively, in the first column). The thick arrows in the second and third columns indicate the resulting mean homing behavior of the robot averaged over ten trials (black dots). In the case of nondisoriented robot (second column), the familiar visual cues tended to influence the robot's behavior when a $90°$ conflict occurred. By contrast, the visual control vanished when the conflict was further increased (i.e., $180°$). If the robot was disoriented during the hoarding phase (third column), visual cues predominated for both $90°$ and $180°$ conflicts. (B) The response of the robot to a $180°$ conflict depended on its confidence about the path integrator. In these experiments, the confidence of the robot about the spatial information provided by its self-motion signals was simply decreasing nonlinearly as a function of the time of the last calibration of the path integrator.

chance, the robot tended to use it to perform homing behavior. If the confidence fell below chance, then a priority switch occurred and the visual information became predominant.

## 5. Discussion

This paper provides an extensive (though non-exhaustive) overview of the large body of research on spatial cognition and navigation. It puts the emphasis on the manifold nature of these complex functions, at the level of both the neural information coding mediating spatial learning, and the decisional processes regulating the selection of navigation strategies.

The multisensory integration issue, which is relevant to the acquisition of robust spatial representations, is addressed in the first part of the paper (Sec. 2). We review a series of experimental findings that shed light on how the brain elaborates appropriate descriptions of the multimodal spatial information gathered through exploration. The presented approaches span from molecular neurobiology experiments (e.g., pharmacological and genetic manipulations), to electrophysiological work (mainly single unit extracellular recordings), and to behavioral studies. We focus on the ability of animals to maintain coherent couplings between self-motion (i.e., idiothetic) signals and environmental landmark (i.e., allothetic) information. Their capability of solving perceptual conflict situations (e.g., following environmental manipulations) is also addressed. Besides, we discuss the properties of hippocampal place (HP) and head-direction (HD) cells, central neurons discharging selectively as a function of the position and orientation of the head of the animal, respectively. We review several electrophysiological studies that aim at elucidating how the response of these neurons is determined by the interrelation between allothetic and idiothetic cues.

The ensemble activities of HP cells, HD cells, and the recently discovered entorhinal grid cells, are suitable to encode spatial representations of the environment. According to the cognitive map theory [113], HP and HD cells are likely to constitute the neural bases of spatial cognition in mammals. Nevertheless, the link between the electrophysiological properties of these neurons (i.e., single-cell observation level) and the ability of animals to perform flexible spatial navigation (i.e., behavioral level) is not straightforward. A large body of evidence (e.g., Refs. [29, 68, 72, 93, 101, 102, 103, 116, 135, 136, 145] has related the hippocampal function to spatial navigation strategies that require a representation of the environment (e.g., map-based navigation, see taxonomy given in Sec. 3, Fig. 4). Most of these studies are based on behavioral impairments after hippocampal lesions. A direct demonstration of the functional relationship between place cell firing patterns and map-based spatial behavior was only recently provided by Lenck-Santini *et al.* [83–85], who corroborated and extended the earlier findings by O'Keefe and Speakman [114].

Similarly, numerous studies have investigated the extent to which head-direction (HD) cell activity is directly linked to spatial orientation behavior (e.g., see Refs. [36, 55, 98, 106]; see also chapters 10–13 in Ref. [163]). The experiments by Dudchenko

and Taube [36] suggested that HD cell firing patterns are indeed correlated to spatial responses on a radial maze, supporting the hypothesis that HD cells might provide a directional framework suitable for guiding spatial behavior. However, subsequent work by Golob *et al.* [55] and Muir and Taube [106] partially disproved this hypothesis, showing no relationship between the stability of the HD cell directional representation and the performance of rats on a task requiring the use of a map-based navigation strategy. Thus, it seems that HD cell activity and spatial behavior are not tightly coupled in all spatial tasks, and this relevant issue requires further investigation.

The second part of this paper (Sec. 3) focuses on the selection of navigation strategies. We review a series of experimental studies attempting to unravel the cooperative-competitive interaction between the multiple brain systems involved in this selection process. A rather comprehensive taxonomy of spatial navigation strategies is provided (Fig. 4) to characterize the multiple solutions available to a subject in order to achieve a navigation task (our proposal extends previous ones by Trullier *et al.* [155] and Redish [123]). This taxonomy is not meant to say that the complex manifold of navigation strategies can be dissected into a discrete set of independent tokens. Rather, it is a mere analytical tool to help us to interpret spatial behavior. How are coexistent functionally distinct strategies learned and employed by animals? How do multiple brain areas compete/cooperate to promote the efficient selection of navigation strategies? These questions (among others) are addressed in this paper, and the roles of the hippocampus, striatum, and cerebellum in spatial navigation are prominently discussed. Also, we report some experimental findings showing that the shift between strategies can depend on the phase of training (e.g., early *vs* late training trials) [91, 104, 115, 117, 159]. It is worth mentioning that strategy shifts can also take place within a trial (and not only across trials) (e.g., see Ref. [33]). Moreover, Hamilton *et al.* [60] reported that a sequence of distinct navigation strategies may actually occur even during tasks that are usually labeled as pure cue-response tasks. Another fundamental issue concerns the relationship between the strategy selection process and the complexity of the task to be learned. We review some experimental findings showing that adaptive spatial behavior consists in adopting (when available) the most advantageous solution (e.g., optimal in terms of the performance *vs* employed resources ratio) to solve a navigation task. Likewise, numerous other factors can play a role in regulating strategy selection, such as stress [73], chemical factors [88, 89] and gender-specific factors [76]. How these multiple factors interact to each other when a choice has to be made among different existing solutions remains an open question.

The third part of this paper (Sec. 4) addresses the spatial memory function from a computational neuroscience and neuro-robotics viewpoint. Neuro-computational models are suitable for investigating the functional link between findings on the neuronal level (e.g., HP and HD cell firing activity) and on the behavioral level (e.g., spatial behavior performance). For instance, hippocampal models can show that the information contained in the HP and HD cell ensemble activity is indeed sufficient for

navigation problems such as the Morris water-maze task, provided that their position and direction representations are combined with learning capability regulated by reward-dependent signals [138]. We present an example of neuro-mimetic spatial learning system [3, 7] to show how models can permit (i) a scale up from single HP and HD cell firing activity to large neural population dynamics, and (ii) the investigation of hypotheses about the anatomo-functional interactions between multiple systems subserving spatial behavior. The presented model does not focus on the biophysical properties of HP and HD neurons (e.g., intrinsic electroresponsiveness). It rather addresses the issue of how the discharges of HP and HD cells are controlled by multisensory cues, stressing the importance of integrating multimodal information to elaborate robust spatial memories. How can the interrelations between idiothetic and allothetic cues be learned and mapped onto stable HP and HD codes? How can exploratory behavior be adapted to optimize the interaction between the navigator and the environment? These are some of the main issues addressed by the presented model, which mainly aims at establishing suitable spatial representations for supporting goal-directed behavior. By contrast, in this paper, we do not discuss any neuro-mimetic navigational model (e.g., see reviews by Arleo [2] and Chavarriaga [25]). To our knowledge, the coexistence of multiple navigation strategies and their cooperative/competitive interactions have been addressed by a few biologically plausible models only. For instance, Chavarriaga *et al.* [26] put forth a model of strategy selection process underlying the navigation behavior of rats. The model accounts for parallel navigation systems (including the hippocampus, the ventral and the dorsolateral striatum) competing to each other (based on a softmax probabilistic mechanism) to select the appropriate action depending on both the task and the training process [159]. An alternative view is proposed by Girard *et al.* [54], in which a weighing mechanism (as opposed to a competitive rule) generates a cooperative behavioral response mediated by the basal ganglia-thalamo-cortical loop.

To conclude, this paper reviewed some of the achievements of the past decades in understanding spatial cognition. The prominent subfunctions (i.e., multisensory integration, episodic and procedural memory, action selection) were addressed at different description levels (e.g., from cellular adaptation mechanisms, such as LTP/LTD, to behavioral response learning, such as goal-directed navigation). The need for an integrative neuroscience approach promoting interdisciplinary research efforts (e.g., in neurobiology, behavioral genetics, cognitive neuroscience, computational neuroscience, and neuro-robotics) was postulated in order to infer a functional linking between these multilevel observations.

## References

[1] Abbott LF, Nelson SB, Synaptic plasticity: Taming the beast, *Nat Neurosci* **3** Suppl:1178–1183, 2000.

[2] Arleo A, Spatial learning and navigation in neuromimetic systems, *Modeling the Rat Hippocampus*, Germany, Verlag-Dissertation, 2000.

[3] Arleo A, Gerstner W, Spatial cognition and neuro-mimetic navigation: A model of hippocampal place cell activity, *Biol Cybern* **83**:287–299, 2000.

[4] Arleo A, Gerstner W, Spatial orientation in navigating agents: Modeling head-direction cells, *Neurocomputing* **38–40**:1059–1065, 2001.

[5] Arleo A, Gerstner W, Head direction cells and place cells in models for navigation and robotic applications, in Wiener SI, Taube JS (eds.), *Head Direction Cells and the Neural Mechanisms of Spatial Orientation*, MIT Press, 2005.

[6] Arleo A, del R Millán J, Floreano D, Efficient learning of variable-resolution cognitive maps for autonomous indoor navigation, *IEEE Trans Robot and Autom* **15**:990–1000, 1999.

[7] Arleo A, Smeraldi F, Gerstner W, Cognitive navigation based on nonuniform Gabor space sampling, unsupervised growing networks, and reinforcement learning, *IEEE Trans Neural Netw* **15**:639–652, 2004.

[8] Barnes CA, Nadel L, Honig WK, Spatial memory deficit in senescent rats, *Can J Psychol* **34**:29–39, 1980.

[9] Barnes CA, Suster MS, Shen J, McNaughton BL, Multistability of cognitive maps in the hippocampus of old rats, *Nature* **388**:272–275, 1997.

[10] Bear MF, Bidirectional synaptic plasticity: From theory to reality, *Philos Trans R Soc Lond B Biol Sci* **358**:649–655, 2003.

[11] Bear MF, Malenka RC, Synaptic plasticity: LTP and LTD, *Curr Opin Neurobiol* **4**:389–399, 1994.

[12] Berthoz A, Viaud-Delmon I, Multisensory integration in spatial orientation, *Curr Opin Neurobiol* **9**:708–712, 1999.

[13] Best PJ, White AM, Minai A, Spatial processing in the brain: The activity of hippocampal place cells, *Annu Rev Neurosci* **24**:459–486, 2001.

[14] Biegler R, Morris RG, Landmark stability is a prerequisite for spatial but not discrimination learning, *Nature* **361**:631–633, 1993.

[15] Blair HT, Sharp PE, Anticipatory head direction signals in anterior thalamus: Evidence for a thalamocortical circuit that integrates angular head motion to compute head direction, *J Neurosci* **15**:6260–6270, 1995.

[16] Bostock E, Muller RU, Kubie JL, Experience-dependent modifications of hippocampal place cell firing, *Hippocampus* **1**:193–205, 1991.

[17] Bower MR, Euston DR, McNaughton BL, Sequential-context-dependent hippocampal activity is not necessary to learn sequences with repeated elements, *J Neurosci* **25**:1313–1323, 2005.

[18] Brooks RA, New approaches to robotics, *Science* **253**:1227–1232, 1991.

[19] Bures J, Fenton AA, Neurophysiology of Spatial Cognition, *News Physiol Sci* **15**:233–240, 2000.

[20] Burgess N, Jeffery KJ, O'Keefe J, Integrating hippocampal and parietal functions: A spatial point of view, *The Hippocampal and Parietal Foundations of Spatial Cognition*, Oxford University Press, pp. 3–29, 1999.

[21] Burgess N, Maguire EA, O'Keefe J, The human hippocampus and spatial and episodic memory, *Neuron* **35**:625–641, 2002.

[22] Burgess N, Donnett JG, Jeffery KJ, O'Keefe J, Robotic and neuronal simulation of the hippocampus and rat navigation, *Philos Trans R Soc Lond B Biol Sci* **352**:1535–1543, 1997.

[23] Burguière E, Arleo A, Hojjati M, Elgersma Ĭ, De Zeeuro CI, Berthoz A, Rondi Reig L, Spatial navigation impairment in mice lacking cerebellar LTD: A motor adaptation deficit? *Nat Neurosci* **8**:1292–1294, 2005.

[24] Chang Q, Gold PE, Switching memory systems during learning: Changes in patterns of brain acetylcholine release in the hippocampus and striatum in rats, *J Neurosci* **23**:3001–3005, 2003.

[25] Chavarriaga R, *Spatial Learning and Navigation in the Rat: A Biomimetic Model*, Swiss Federal Institute of Technology Lausanne, 2005.

[26] Chavarriaga R, Strosslin T, Sheynikhovich D, Gerstner W, A computational model of parallel navigation systems in rodents, *Neuroinformatics* **3**:223–241, 2005.

[27] Chen LL, Lin LH, Green EJ, Barnes CA, Mc Naughtom BL, Head-direction cells in the rat posterior cortex. II. Contribution of visual and ideothetic information to the directional firing, *Exp Brain Res* **101**:24–34, 1994a.

[28] Chen LL, Lin LH, Green EJ, Barnes CA, Mc Naughton BL, Head-direction cells in the rat posterior cortex. I. Anatomical distribution and behavioral modulation, *Exp Brain Res* **101**:8–23, 1994b.

[29] Cho YH, Giese KP, Tanila H, Silva AJ, Eichenbauon H, Abnormal hippocampal spatial representations in alphaCaMKIIT286A and CREBalphaDelta-mice, *Science* **279**:867–869, 1998.

[30] Collingridge GL, Kehl SJ, McLennan H, Excitatory amino acids in synaptic transmission in the Schaffer collateral-commissural pathway of the rat hippocampus, *J Physiol* **334**:33–46, 1983.

[31] Cressant A, Muller RU, Poucet B, Failure of centrally placed objects to control the firing fields of hippocampal place cells, *J Neurosci* **17**:2531–2542, 1997.

[32] De Zeeuw CI, Hansel C, Bian F, Koekkoek SKE, Van Alphen AM, Linden DJ, Obevdick J, Expression of a protein kinase C inhibitor in Purkinje cells blocks cerebellar LTD and adaptation of the vestibulo-ocular reflex, *Neuron* **20**:495–508, 1998.

[33] Devan BD, White NM, Parallel information processing in the dorsal striatum: Relation to hippocampal function, *J Neurosci* **19**:2789–2798, 1999.

[34] Devan BD, Goad EH, Petri HL, Dissociation of hippocampal and striatal contributions to spatial navigation in the water maze, *Neurobiol Learn Mem* **66**:305–323, 1996.

[35] Drai D, Kafkafi N, Benjamini Y, Elmer G, Golani I, Rats and mice share common ethologically relevant parameters of exploratory behavior, *Behav Brain Res* **125**:133–140, 2001.

[36] Dudchenko PA, Taube JS, Correlation between head direction cell activity and spatial behavior on a radial arm maze, *Behav Neurosci* **111**:3–19, 1997.

[37] Eichenbaum H, The hippocampus and declarative memory: Cognitive mechanisms and neural codes, *Behav Brain Res* **127**:199–207, 2001.

[38] Eichenbaum H, Cohen NJ, *From Conditioning to Conscious Recollection*, New York, 2001.

[39] Eichenbaum HE, Stewart C, Morris RGM, Hippocampal representation in spatial learning, *J Neurosci* **10**:331–339, 1990.

[40] Ekstrom AD, Kahana MJ, Caplan JB, Fields TA, Isham EA, Newman EL, Fried I, Cellular networks underlying human spatial navigation, *Nature* **425**:184–188, 2003.

[41] Elfes A, Sonar-based real-world mapping and navigation, *IEEE J Robot and Autom* **3**:249–256, 1987.

[42] Etienne AS, Jeffery KJ, Path integration in mammals, *Hippocampus* **14**:180–192, 2004.

[43] Etienne AS, Teroni E, Hurni C, Portenier V, The effect of a single light cue on homing behaviour of the golden hamster, *Anim Behav* **39**:17–41, 1990.

[44] Etienne AS, Berlie J, Georgakopoulos J, Maurer R, Role of dead reckoning in navigation, in Healy S (ed.), *Spatial Representation in Animals*, Oxford University Press, pp. 54–68, 1998a.

[45] Etienne AS, Boulens V, Maurer R, Rowe T, Siegrist C, A brief view of known landmarks reorientates path integration in hamsters, *Naturwissenschaften* **87**:494–498, 2000.

[46] Etienne AS, Maurer R, Berlie J, Reverdin B, Rowe T, Georga Kopoulos J, Seguinot V, Navigation through vector addition, *Nature* **396**:161–164, 1998b.

[47] Fenton AA, Wesierska M, Kaminsky Y, Bures J, Both here and there: Simultaneous expression of autonomous spatial memories in rats, *Proc Natl Acad Sci USA* **95**:11493–11498, 1998.

[48] Fortin NJ, Agster KL, Eichenbaum HB, Critical role of the hippocampus in memory for sequences of events, *Nat Neurosci* **5**:458–462, 2002.

[49] Foster TC, Castro CA, McNaughton BL, Spatial selectivity of rat hippocampal neurons: Dependence on preparedness for movement, *Science* **244**:1580–1582, 1989.

[50] Fyhn M, Molden S, Witter MP, Moser EI, Moser MB, Spatial representation in the entorhinal cortex, *Science* **305**:1258–1264, 2004.

[51] Gallistel CR, *The Organization of Learning*, MIT Press, Cambridge, 1990.

[52] Gaussier P, Revel A, Banquet JP, Babeau V, From view cells and place cells to cognitive map learning: Processing stages of the hippocampal system, *Biol Cybern* **86**:15–28, 2002.

[53] Georgopoulos AP, Schwartz AB, Kettner RE, Neuronal population coding of movement direction, *Science* **233**:1416–1419, 1986.

[54] Girard B, Cuzin V, Guillot A, Gurney KN, Prescott TJ, A basal ganglia inspired model of action selection evaluated in a robotic survival task, *J Integr Neurosci* **2**:179–200, 2003.

[55] Golob EJ, Stackman RW, Wong AC, Taube JS, On the behavioral significance of head direction cells: Neural and behavioral dynamics during spatial memory tasks, *Behav Neurosci* **115**:285–304, 2001.

[56] Goodridge JP, Dudchenko PA, Worboys KA, Golob EJ, Taube JS, Cue control and head direction cells, *Behav Neurosci* **112**:749–761, 1998.

[57] Griffin AL, Eichenbaum H, Hasselmo ME, Spatial representations of hippocampal CA1 neurons are modulated by behavioral context in a hippocampus-dependent memory task, *J Neurosci* **27**:2416–2423, 2007.

[58] Griffin AS, Etienne AS, Updating the path integrator through a visual fix, *Psychobiology* **26**:240–248, 1998.

[59] Hafting T, Fyhn M, Molden S, Moser MB, Moser EI, Microstructure of a spatial map in the entorhinal cortex, *Nature* **436**:801–806, 2005.

[60] Hamilton DA, Rosenfelt CS, Whishaw IQ, Sequential control of navigation by locale and taxon cues in the Morris water task, *Behav Brain Res* **154**:385–397, 2004.

[61] Haykin S, *Neural Networks, A Comprehensive Foundation*, NJd, MacMillan, Englewood Cliffs, 1994.

[62] Hebb DO, *The Organization of Behavior*, John Wiley, New York, 1949.

[63] Hermer L, Spelke ES, A geometric process for spatial reorientation in young children, *Nature* **370**:57–59, 1994.

[64] Hertz J, Krogh A, Palmer RG, *Introduction to the Theory of Neural Computation*, Addison-Wesley, Redwood City, CA, 1991.

[65] Hill AJ, Best PJ, Effects of deafness and blindness on the spatial correlates of hippocampal unit activity in the rat, *Exp Neurol* **74**:204–217, 1981.

[66] Huerta PT, Sun LD, Wilson MA, Tonegawa S, Formation of temporal memory requires NMDA receptors within CA1 pyramidal neurons, *Neuron* **25**:473–480, 2000.

[67] Iaria G, Petrides M, Dagher A, Pike B, Bohbot VD, Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: Variability and change with practice, *J Neurosci* **23**:5945–5952, 2003.

[68] Jarrard LE, Selective hippocampal lesions: Differential effects on performance by rats of a spatial task with preoperative versus postoperative training, *J Comp Physiol Psychol* **92**:1119–1127, 1978.

[69] Jeffery KJ, Learning of landmark stability and instability by hippocampal place cells, *Neuropharmacology* **37**:677–687, 1998.

[70] Jeffery KJ, O'Keefe JM, Learned interaction of visual and idiothetic cues in the control of place field orientation, *Exp Brain Res* **127**:151–161, 1999.

[71] Jordan K, Schadow J, Wuestenberg T, Heinze HJ, Jancke L, Different cortical activations for subjects using allocentric or egocentric strategies in a virtual navigation task, *Neuroreport* **15**:135–140, 2004.

[72] Kentros C, Hargreaves E, Hawkins RD, Kandal ER, Shapiro M, Muller RV, Abolition of long-term stability of new hippocampal place cell maps by NMDA receptor blockade, *Science* **280**:2121–2126, 1998.

[73] Kim JJ, Baxter MG, Multiple brain-memory systems: The whole does not equal the sum of its parts, *Trends Neurosci* **24**:324–330, 2001.

[74] Knierim JJ, Kudrimoti HS, McNaughton BL, Place cells, head direction cells, and the learning of landmark stability, *J Neurosci* **15**:1648–1659, 1995.

[75] Knierim JJ, Kudrimoti HS, McNaughton BL, Interactions between idiothetic cues and external landmarks in the control of place cells and head direction cells, *J Neurophysiol* **80**:425–446, 1998.

[76] Korol DL, Role of estrogen in balancing contributions from multiple memory systems, *Neurobiol Learn Mem* **82**:309–323, 2004.

[77] Kuipers BJ, Byun YT, A robot exploration and mapping strategy based on a semantic hierarchy of spatial representations, *Robot and Autonom Sys* **8**:47–63, 1991.

[78] Lalonde R, Visuospatial abilities, in *International Review of Neurobiology*, Academic Press, New York, pp. 191–215, 1997.

[79] Lavoie AM, Mizumori SJ, Spatial, movement- and reward-sensitive discharge by medial ventral striatum neurons of rats, *Brain Res* **638**:157–168, 1994.

[80] Learmonth AE, Newcombe NS, Huttenlocher J, Hermer L, Spelke ES, Toddlers' use of metric information and landmarks to reorient a geometric process for spatial reorientation in young children, *J Exp Child Psychol* **80**:225–244, 2001.

[81] Lee I, Kesner RP, Differential contribution of NMDA receptors in hippocampal subregions to spatial working memory, *Nat Neurosci* **5**:162–168, 2002.

[82] Lenck-Santini PP, Save E, Poucet B, Place-cell firing does not depend on the direction of turn in a Y-maze alternation task, *Eur J Neurosci* **13**:1055–1058, 2001a.

[83] Lenck-Santini PP, Save E, Poucet B, Evidence for a relationship between place-cell spatial firing and spatial memory performance, *Hippocampus* **11**:377–390, 2001b.

[84] Lenck-Santini PP, Muller RU, Save E, Poucet B, Relationships between place cell firing fields and navigational decisions by rats, *J Neurosci* **22**:9035–9047, 2002.

[85] Lenck-Santini PP, Rivard B, Muller RU, Poucet B, Study of CA1 place cell activity and exploratory behavior following spatial and nonspatial changes in the environment, *Hippocampus* **15**:356–369, 2005.

[86] Malenka RC, Bear MF, LTP and LTD: An embarrassment of riches, *Neuron* **44**:5–21, 2004.

[87] Markus EJ, Barnes CA, McNaughton BL, Gladden VL, Skaggs WE, Spatial information content and reliability of hippocampal CA1 neurons: Effects of visual input, *Hippocampus* **4**:410–421, 1994.

[88] Marriott LK, Korol DL, Short-term estrogen treatment in ovariectomized rats augments hippocampal acetylcholine release during place learning, *Neurobiol Learn Mem* **80**:315–322, 2003.

[89] Matthews DB, Ilgen M, White AM, Best PJ, Acute ethanol administration impairs spatial performance while facilitating nonspatial performance in rats, *Neurobiol Learn Mem* **72**:169–179, 1999.

[90] McDonald RJ, White NM, A triple dissociation of memory systems: Hippocampus, amygdala, and dorsal striatum, *Behav Neurosci* **107**:3–22, 1993.

[91] McDonald RJ, White NM, Parallel information processing in the water maze: Evidence for independent memory systems involving dorsal striatum and hippocampus, *Behav Neural Biol* **61**:260–270, 1994.

[92] McDonald RJ, White NM, Hippocampal and nonhippocampal contributions to place learning in rats, *Behav Neurosci* **109**:579–593, 1995.

[93] McHugh TJ, Blum KI, Tsien JZ, Tonegawa S, Wilson MA, Impaired hippocampal representation of space in CA1-specific NMDAR1 knockout mice, *Cell* **87**:1339–1349, 1996.

[94] McNaughton BL, Chen LL, Markus EJ, Dead reckoning, landmark learning, and the sense of direction: A neurophysiological and computational hypothesis, *J Cog Neurosci* **3**:190–202, 1991.

[95] McNaughton BL, Battaglia FP, Jensen O, Moser EI, Moser MB, Path integration and the neural basis of the "cognitive map," *Nat Rev Neurosci* **7**:663–678, 2006.

[96] Mittelstaedt H, Mittelstaedt ML, Homing by path integration, in Papi F, Wallraff HG (eds.), *Avian Navigation*, Springer, Berlin Heidelberg, 1982.

[97] Mittelstaedt ML, Mittelstaedt H, Homing by path integration in the mammal, *Naturewissenschaften* **67**:566–567, 1980.

[98] Mizumori SJ, Williams JD, Directionally selective mnemonic properties of neurons in the lateral dorsal nucleus of the thalamus of rats, *J Neurosci* **13**:4015–4028, 1993.

[99] Molinari M, Petrosini L, Grammaldo LG, Spatial event processing, *Int Rev Neurobiol* **41**:217–230, 1997.

[100] Morris RG, Frey U, Hippocampal synaptic plasticity: Role in spatial learning or the automatic recording of attended experience, *Philos Trans R Soc Lond B Biol Sci* **352**:1489–1503, 1997.

[101] Morris RG, Garrud P, Rawlins JN, O'Keefe J, Place navigation impaired in rats with hippocampal lesions, *Nature* **297**:681–683, 1982a.

[102] Morris RG, Anderson E, Lynch GS, Baudry M, Selective impairment of learning and blockade of long-term potentiation by an N-methyl-D-aspartate receptor antagonist, AP5, *Nature* **319**:774–776, 1986a.

[103] Morris RG, Schenk F, Tweedie F, Jarrard LE, Ibotenate lesions of hippocampus and/or subiculum: Dissociating components of allocentric spatial learning, *Eur J Neurosci* **2**:1016–1028, 1990.

[104] Morris RGM, Garrud P, Rawlins JNP, O'Keefe I, Place navigation impaired in rats with hippocampal lesions, *Nature* **297**:681–683, 1982b.

[105] Morris RGM, Anderson E, Lynch G, Baudry M, Selective impairment of learning and blockade of long-term potentiation by an N-methyl-D-aspartate receptor antagonist, AP5, *Nature* **319**:774–776, 1986b.

[106] Muir GM, Taube JS, Head direction cell activity and behavior in a navigation task requiring a cognitive mapping strategy, *Behav Brain Res* **153**:249–253, 2004.

[107] Muller RU, Kubie JL, The effects of changes in the environment on the spatial firing of hippocampal complex-spike cells, *J Neurosci* **7**:1951–1968, 1987.

[108] Nakazawa K, McHugh TJ, Wilson MA, Tonegawa S, NMDA receptors, place cells and hippocampal spatial memory, *Nat Rev Neurosci* **5**:361–372, 2004.

[109] Nakazawa K, Sun LD, Quirk MC, Rondi Reig L, Wilson MA, Tonegawa S, Hippocampal CA3 NMDA receptors are crucial for memory acquisition of one-time experience, *Neuron* **38**:305–315, 2003.

[110] Nakazawa K, Quirk MC, Chitwood RA, Watanabe M, Yeckel ME, Sun LD, Kato A, Carr CA, Johnston D, Wilson MA, Requirement for hippocampal CA3 NMDA receptors in associative memory recall, *Science* **297**:211–218, 2002.

[111] O'Keefe J, Dostovsky J, The hippocampus as a spatial map, Preliminary evidence from unit activity in the freely-moving rat, *Brain Res* **34**:171–175, 1971.

[112] O'Keefe J, Conway DH, Hippocampal place units in freely moving rats: Why they fire where they fire, *Exp Brain Res* **31**:573–590, 1978.

[113] O'Keefe J, Nadel L, *The Hippocampus as a Cognitive Map*, Clarendon Press, Oxford, 1978.

[114] O'Keefe J, Speakman A, Single unit activity in the rat hippocampus during a spatial memory task, *Exp Brain Res* **68**:1–27, 1987.

[115] Packard MG, McGaugh JL, Inactivation of hippocampus or caudate nucleus with lidocaïne differentially affects expression of place and response learning, *Neurobiol Learn Mem* **65**:65–72, 1996a.

[116] Packard MG, McGaugh JL, Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning, *Neurobiol Learn Mem* **65**:65–72, 1996.

[117] Packard MG, Knowlton BJ, Learning and memory functions of the basal ganglia, *Annu Rev Neurosci* **25**:563–593, 2002.

[118] Passino E, Middei S, Restivo L, Bertaina-Anglade V, Ammassan-Teule M, Genetic approach to variability of memory systems: Analysis of place vs. response learning and fos-related expression in hippocampal and striatal areas of C57BL/6 and DBA/2 mice, *Hippocampus* **12**:63–75, 2002.

[119] Pastalkova E, Serrano P, Pinkhasova D, Wallace E, Fenton AA, Sacktor TC, Storage of spatial information by the maintenance mechanism of LTP, *Science* **313**:1141–1144, 2006.

[120] Petrosini L, Molinari M, Dell'Anna ME, Cerebellar contribution to spatial event processing: Morris water maze and T-maze, *Eur J Neurosci* **9**:1882–1896, 1996.

[121] Quirk GJ, Muller RU, Kubie JL, The firing of hippocampal place cells in the dark depends on the rat's recent experience, *J Neurosci* **10**:2008–2017, 1990.

[122] Quirk GJ, Muller RU, Kubie JL, Ranck JB Jr, The positional firing properties of medial entorhinal neurons: Description and comparison with hippocampal place cells, *J Neurosci* **12**:1945–1963, 1992.

[123] Ranck JBJ, Head-direction cells in the deep cell layers of dorsal presubiculum in freely moving rats, *Soc Neurosci Meet* **10**:599, 1984.

[124] Redish AD, *Beyond the Cognitive Map, From Place Cells to Episodic Memory*, MIT Press, London, 1999.

[125] Redish AD, Touretzky DS, The role of the hippocampus in solving the Morris water maze, *Neural Comput* **10**:73–111, 1998.

[126] Rondi-Reig L, Burguière E, Is the cerebellum ready for navigation? *Prog Brain Res* **148**:199–212, 2005.

[127] Rondi-Reig L, Caston J, Delhaye-Bouchaud N, Mariana J, Cerebellar functions: A behavioral neurogenetic perspective, in *Neurobehavioral Genetics: Methods and Applications*, CRC, 1999.

[128] Rondi-Reig L, Libbey M, Eichenbaum H, Tonegawa S, CA1-specific N-methyl-D-aspartate receptor knockout mice are deficient in solving a nonspatial transverse patterning task, *Proc Natl Acad Sci USA* **98**:3543–3548, 2001.

[129] Rondi-Reig L, Le Marec N, Caston J, Mariani J, The role of climbing and parallel fibers inputs to cerebellar cortex in navigation, *Behav Brain Res* **132**:11–18, 2002.

[130] Rondi-Reig L, Petit G, Tobin C, Tonegawa S, Mariani J, Berthoz A, Impaired sequential-egocentric and allocentric memories in forebrain specific NMDA receptor knockout mice during a new task dissociating strategies of navigation, *J Neurosci* **26**:4071–4081, 2006.

[131] Salinas E, Abbott LF, Vector reconstruction from firing rates, *J Comput Neurosci* **1**:89–107, 1994.

[132] Samsanovich A, McNaughton B, Path integration and cognitive mapping in a continuous attractor neural network, *J Neurosci* **17**:5900–5920, 1997.

[133] Sanger TD, Optimal unsupervised learning in a single-layer linear feed forward neural network, *Neural Networks* **2**:459–473, 1989.

[134] Sargolini F, Fyhn M, Hafting T, Mc Naughton BL, Witter MP, Moser Mb, Moser EI, Conjunctive representation of position, direction, and velocity in entorhinal cortex, *Science* **312**:758–762, 2006.

[135] Save E, Poucet B, Involvement of the hippocampus and associative parietal cortex in the use of proximal and distal landmarks for navigation, *Behav Brain Res* **109**:195–206, 2000.

[136] Save E, Poucet B, Foreman N, Buhot MC, Object exploration and reactions to spatial and nonspatial changes in hooded rats following damage to parietal cortex or hippocampal formation, *Behav Neurosci* **106**:447–456, 1992.

[137] Save E, Cressant A, Thinus-Blanc C, Poucet B, Spatial firing of hippocampal place cells in blind rats, *J Neurosci* **18**:1818–1826, 1998.

[138] Schultz W, Dayan P, Montague PR, A neural substrate of prediction and reward, *Science* **275**:1593–1599, 1997.

[139] Schölkopf B, Mallot HA, View-based cognitive mapping and path planning, *Adaptive Behavior* **3**:311–348, 1995.

[140] Sharp PE, Complimentary roles for hippocampal versus subicular/entorhinal place cells in coding place, context, and events, *Hippocampus* **9**:432–443, 1999.

[141] Sharp PE, Kubie JL, Muller RU, Firing properties of hippocampal neurons in a visually symmetrical environment: Contributions of multiple sensory cues and mnemonic processes, *J Neurosci* **10**:3093–3105, 1990.

[142] Sharp PE, Tinkelman A, Cho J, Angular velocity and head direction signals recorded from the dorsal tegmental nucleus of gudden in the rat: Implications for path integration in the head direction cell circuit, *Behav Neurosci* **115**:571–588, 2001.

[143] Stackman RW, Taube JS, Firing properties of head direction cells in the rat anterior thalamic nucleus: Dependence on vestibular input, *J Neurosci* **17**:4349–4358, 1997.

[144] Stackman RW, Taube JS, Firing properties of rat lateral mammillary single units: Head direction, head pitch, and angular head velocity, *J Neurosci* **18**:9020–9037, 1998.

[145] Steele RJ, Morris RG, Delay-dependent impairment of a matching-to-place task with chronic and intrahippocampal infusion of the NMDA-antagonist D-AP5, *Hippocampus* **9**:118–136, 1999.

[146] Steffenach HA, Witter M, Moser MB, Moser EI, Spatial memory in the rat requires the dorsolateral band of the entorhinal cortex, *Neuron* **45**:301–313, 2005.

[147] Taube JS, Head direction cells recorded in the anterior thalamic nuclei of freely moving rat, *J Neurosci* **15**:70–86, 1995.

[148] Taube JS, Head direction cells and the neurophysiological basis for a sense of direction, *Prog Neurobiol* **55**:225–256, 1998.

[149] Taube JS, Muller RU, Ranck Jr JB, Head-direction cells recorded from the postsubiculum in freely moving rats. II. Effects of environmental manipulations, *J Neurosci* **10**:436–447, 1990.

[150] Taube JS, Muller RU, Ranck JB, Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis, *J Neurosci* **10**:420–435, 1990.

[151] Thinus-Blanc C, *Animal Spatial Cognition*, World Scientific, Singapore, 1996.

[152] Thrun S, Learning maps for indoor mobile robot navigation, *Artif Intel* **99**:21–71, 1998.

[153] Tolman EC, Cognitive maps in rats and men, *Psychol Rev* **55**:189–208, 1948.

[154] Trullier O, Meyer JA, Animat navigation using a cognitive graph, *Biol Cybern* **83**:271–285, 2000.

[155] Trullier O, Wiener SI, Berthoz A, Meyer JA, Biologically based artificial navigation systems: Review and prospects, *Prog Neurobiol* **51**:483–544, 1997.

[156] Tsien JZ, Huerta PT, Tonegawa S, The essential role of hippocampal CA1 NMDA receptor-dependent synaptic plasticity in spatial memory, *Cell* **87**:1327–1338, 1996.

[157] Vallar G, Lobel E, Galati G, Bevthoz A, Pizzamiglio L, Le Bihan D, A fronto-parietal system for computing the egocentric spatial frame of reference in humans, *Exp Brain Res* **124**:281–286, 1999.

[158] Whishaw IQ, Mittleman G, Visits to starts, routes, and places by rats (Rattus norvegicus) in swimming pool navigation tasks, *J Comp Psychol* **100**:422–431, 1986.

[159] White NM, McDonald RJ, Multiple parallel memory systems in the brain of the rat, *Neurobiol Learn Mem* **77**:125–184, 2002.

[160] Whitlock JR, Heynen AJ, Shuler MG, Bear MF, Learning induces long-term potentiation in the hippocampus, *Science* **313**:1093–1097, 2006.

[161] Wiener SI, Spatial and behavioral correlates of striatal neurons in rats performing a self-initiated navigation task, *J Neurosci* **13**:3802–3817, 1993.

[162] Wiener SI, Arleo A, Persistent activity in limbic system neurons: Neurophysiological and modeling perspectives, *J Physiol Paris* **97**:547–555, 2003.

[163] Wiener SI, Taube JS, *Head Direction Cells and the Neural Mechanisms of Spatial Orientation*, MIT Press, 2005.

[164] Wiener SI, Berthoz A, Zugaro MB, Multisensory processing in the elaboration of place and head direction responses by limbic system neurons, *Brain Res Cogn Brain Res* **14**:75–90, 2002.

[165] Wilson MA, McNaughton BL, Dynamics of the hippocampal ensemble code for space, *Science* **261**:1055–1058, 1993.

[166] Witter MP, Organization of the entorhinal-hippocampal system: A review of current anatomical data, *Hippocampus* **3**:33–44, 1993.

[167] Wood ER, Dudchenko PA, Eichenbaum H, Cellular correlates of behavior, *Int Rev Neurobiol* **45**:293–312, 2001.

[168] Wood ER, Dudchenko PA, Robitsek RJ, Erchembaum H, Hippocampal neurons encode information about different types of memory episodes occurring in the same location, *Neuron* **27**:623–633, 2000.

[169] Zugaro MB, Berthoz A, Wiener SI, Background but not foreground, spatial cues are taken as references for head direction responses by rat anterodorsal thalamus neurons, *J Neurosc* **21**:RC154(151–155), 2001.

[170] Zugaro MB, Arleo A, Berthoz A, Wiener SI, Rapid spatial reorientation and head direction cells, *J Neurosci* **23**:3478–3482, 2003.

[171] Zugaro MB, Arleo A, Dejean C, Burguieve E, Khamassi M, Wiener SI, Rat anterodorsal thalamic head direction neurons depend upon dynamic visual signals to select anchoring landmark cues, *Eur J Neurosci* **20**:530–536, 2004.