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A Hierarchy of Associations in Hippocampo-Cortical Systems: Cognitive Maps and Navigation Strategies

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In this letter we describe a hippocampo-cortical model of spatial processing and navigation based on a cascade of increasingly complex associative processes that are also relevant for other hippocampal functions such as episodic memory. Associative learning of different types and the related pattern encoding-recognition take place at three successive levels: (1) an object location level, which computes the landmarks from merged multimodal sensory inputs in the parahippocampal cortices; (2) a subject location level, which computes place fields by combination of local views and movement-related information in the entorhinal cortex; and (3) a spatiotemporal level, which computes place transitions from contiguous place fields in the CA3-CA1 region, which form building blocks for learning temporospatial sequences.

At the cell population level, superficial entorhinal place cells encode spatial, context-independent maps as landscapes of activity; populations of transition cells in the CA3-CA1 region encode context-dependent maps as sequences of transitions, which form graphs in prefrontal-parietal cortices. The model was tested on a robot moving in a real environment; these tests produced results that could help to interpret biological data. Two different goal-oriented navigation strategies were displayed depending on the type of map used by the system.

Thanks to its multilevel, multimodal integration and behavioral implementation, the model suggests functional interpretations for largely unaccounted structural differences between hippocampo-cortical systems. Further, spatiotemporal information, a common denominator shared by several brain structures, could serve as a cognitive processing frame and a functional link, for example, during spatial navigation and episodic memory, as suggested by the applications of the model to other domains, temporal sequence learning and imitation in particular.

1 Introduction _

In recent years, the understanding of the hippocampo-cortical connectivity (Witter et al., 2000; Lavenex & Amaral, 2000; Amaral & Witter, 1989) and evidence from a variety of experimental approaches indicate that each of the component fields of the hippocampal system (parahippocampal region, entorhinal cortex, hippocampus proper) may serve different yet complementary functions. Both anatomical and experimental results suggest the existence of at least three main processing levels of complex temporospatial information: a first level in the perirhinal and postrhinal cortex for pattern location association, a second level in the entorhinal cortex for the integration of visuospatial and self-motion information into a coarse spatial code, and a third level for temporospatial and contextual integration in the trisynaptic loop, which forms a major input to the subiculum. Moreover, two parallel streams (conveying respectively "what" and "where" information) have been delineated by tracers all the way through parahippocampal and entorhinal systems. Local connections within and between these streams potentially lead to increased associativity and integration of the information that reaches the different rostrocaudal or mediolateral regions of the hippocampal system (Lavenex & Amaral, 2000). Yet contrasting with these latter partial connections, a layered projection of the "What" and "Where" streams leads to a considerable convergence and a loss of anatomical topology at the level of the dentate gyrus (DG) and the CA3 fields (Witter et al., 2000; Lavenex & Amaral, 2000; Amaral & Witter, 1989). These two structures are also in receipt of important modulating signals from the septum of the basal forebrain cholinergic system and the dopaminergic system. The functional meaning of these structural characteristics is poorly understood. A biologically realistic and functionally integrated model should help to clarify the properties of the different subsystems and their contribution to global functions attributed to the hippocampus, such as spatial processing and navigation, or episodic memory.

The hippocampus of the rat has been hypothesized to host a spatial representation of the animal's environment (O'Keefe & Nadel, 1978). The main evidence in support of this theory is the existence of hippocampal place cells (PC, pyramidal neurons whose firing is strongly correlated with the location of a freely moving rat in its environment) (O'Keefe & Dostrovsky, 1971). The activity of each cell is selective of the current location of the animal. This cell-specific region of intense discharge is named the firing field, by analogy to the receptive field of cortical neurons. The firing fields of PCs can be seen in all parts of the environment accessible to the rat, so that collectively, active PCs and their specific firing profile provide a potent signature of the environment and, plausibly, the components of a map. If the shape of the apparatus (Muller & Kubie, 1987; Lever, Willis, Cacucci, Burgess, & O'Keefe, 2002), the color of the objects within the apparatus (Bostock, Muller, & Kubie, 1991; Kentros, Hargreaves, Kandel, Shapiro, & Muller, 1998), or the orientation of the apparatus relative to background (Cressant, Muller, & Poucet, 2002; Skaggs, Knierim, Kudrimoti, & McNaughton, 1995; Tanila, Sipila, Shapiro, & Eichenbaum, 1997) are changed, "remapping" takes place: some cells active in one apparatus become silent, and inversely. The fields of the cells active in both apparatuses are unrelated. This phenomenon suggests that the hippocampus learns and holds distinct maps for distinct environments.

The hallmark of our hippocampal model was a dynamical spatiotemporal (and not just spatial) representation of the space and task environment through the computation and encoding of transitions in the CA field (transition cells), the inclusion of this hippocampal structure into a larger corticalsubcortical network, and the storage of the maps at cortical level. These characteristics provided for a straightforward solution to the theoretical difficulty to switch from a spatial cognitive map to its motor implementation during goal-oriented navigation (Banquet, Gaussier, Quoy, Revel, & Burnod, 2004; Gaussier, Revel, Banquet, & Babeau, 2002; Banquet, Gaussier, Revel, Moga, & Burnod, 2001). Even though different implementations of neural fields (Amari, 1977) and chaotic attractors (Tsuda, 2001) were used (Quoy, Banquet, & Dauce, 2001; Dauce, Quoy, & Doyon, 2002), the model presented here differs from a classical attractor model in that no recurrent connections were implemented in CA3.

Our main goal in this letter is to delineate within a coherent frame the distinct complementary contributions, in spatial processing and navigation, of the parahippocampal region (perirhinal, PR; parahippocampal, PH; and entorhinal, EC cortices) and of the hippocampus (HS) proper, based on anatomical and experimental observations, and to make testable predictions. Our model comprises successive levels of association of different types and of increasing complexity. These associative neural nets, functionally paired to pattern-encoding and recognition networks, provided increasingly multimodal and abstract representations of the inputs. The differences between the associations performed by the local recurrent cortical circuits of pyramidal cells and the extensive, global CA3 associations (Cohen & Eichenbaum, 1993) were attributed to the distinct structures of hippocampal and cortical networks. Object-location associations (here landmarks), encountered in the parahippocampal cortex (Rolls & Treves, 1998), combined to form local views; in conjunction with idiothetic inputs (here, *idiothetic information* means all direct self-motion information, including optic flow, vestibular signals, corollary discharge, and somatosensory feedback), these views created position-dependent activity in the medial EC (Quirk, Muller, Kubie, & Ranck, 1992; Sharp, 1999) and HS. The wealth of experiments on spatial and navigation tasks in rodents and primates provided a test bench for model development and analysis.

The recording of at least two types of PCs (hippocampal and entorhinalsubicular) suggests the encoding by distinct neural populations of two types of maps for the same environment. Classically, PCs with well-delimited place fields have been recorded in CA3-CA1 pyramidal cells and DG granule cells (Jung & McNaughton, 1993). More recently, place cell-like activity has been recorded in the superficial (Quirk et al., 1992; Sharp, 1999) and deep layers (Frank, Brown, & Wilson, 2000; Mizumori, Ward, & Lavoie, 1992) of medial entorhinal cortex (MEC), as well as in the subiculum (SUB) (Sharp & Green, 1994). The firing fields of these pyramidal neurons have no clear-cut boundaries but a graded decay starting from spatially stable maxima. No remapping of these fields takes place when the geometry of the environment is changed; rather, there is a topological adaptation to the shape of the environment (Quirk et al., 1992; Sharp, 1999). The relatively weak and coarse place codes found in superficial EC are refined in the hippocampus proper to create a finely grained representation of position in DG, transformed into larger, overlapping place fields in CA3-CA1, and further embedded in the context of a trajectory in deep EC (Frank et al., 2000). Our model reproduced two types of place fields, entorhinal and hippocampal, starting from real views taken from the environment by the camera of a moving robot and also provided mechanistic and functional interpretations and predictions. The hypothesis of a hierarchy of associativity allowed us to consider the spatial information precoded in EC as the source for both a DG refined spatial code and a CA3-CA1 temporospatial code. Recent results confirmed the main assumption of our model (Banquet et al., 1997; Revel, Gaussier, Leprêtre, & Banquet, 1998) of two distinct functions of EC-DG and CA3-CA1 for the processing of spatial and temporal order information. After selective DG or CA1 lesions, a double dissociation in the separation of respectively small-grain spatial patterns and temporospatial patterns (Gilbert, Kesner, & Lee, 2001) supported this view.

Collectively, the corresponding two types of place cells encoded two types of coexisting hippocampo-cortical maps, associated with distinct navigation strategies during robotic experiments. The first was a "universal" context-independent map (Sharp, 1999) computed by superficial entorhinal neural populations with weak position-dependent activity, based on "landscapes" of PC potentials proper to each location. The classical concept of spatial map was extended here to the acquisition of a coarse yet specific location-action mapping, close to the concept of cognitive map. The second type was a context-dependent map computed by the CA3-CA1 association networks based on place field transitions encoded by transition cells. A transition cell or set (representing a population in the model) was a minimal representation of changing subsets of active CA3 neurons during navigation. The transition cells formed the building blocks of the neural representations of temporospatial sequences, graphs, and contextual maps putatively stored in parietal or prefrontal cortex. While the first type of map could be characterized as spatial and stable, this second type could be characterized as temporospatial and dynamic. Universal and contextual maps were both modulated by the "head direction system," thus achieving external coherence aligned to the external world, as well as internal coherence by the alignment of views from multiple directions.

Our model built on previous models of place cells (O'Keefe, 1991; Sharp, Blair, & Brown, 1996; Burgess, Recce, & O'Keefe, 1994; McNaughton, Knierim, & Wilson, 1994; Touretzky & Redish, 1996), and yet made several original contributions. First, the use of transitions to guide actions provided a straightforward transition between spatial representation and navigation. Second, a theoretical analysis of the process of place field and map learning resulted in a single analytical equation (equation 2.10) that summarized the spatial properties of the network and was useful to understand the relations between the landmarks and the geometrical properties of the place fields. Third, visual information was automatically extracted from the environment by a biologically inspired vision system combined with path integration to provide a mechanistic and functional integration and interpretation of the two types of place fields. Stable invariant but coarse spatial codes were combined with context- and task-dependent dynamic codes (transitions) to produce robust and flexible temporospatial representations. At the population level, the map concept was extended to a mathematical mapping between the spaces of representations and actions, which could be shared by both spatial and cognitive maps. Finally, the most significant subsystems of the parahippocampal region and the hippocampus proper were functionally integrated in order to implement, beyond the simple simulation of a model, a robot control system during navigation experiments that were more recently conducted in parallel in rat and robot (Paz-Villagran, Save, & Poucet, 2003, 2004).¹ This letter emphasizes the anatomical and physiological support and detailed mathematical formulation of the different model subsystems and the corresponding experimental predictions; it also proposes a functional significance for the different types of PCs and corresponding maps by establishing a link between map types and navigation strategies. Nevertheless, the letter focuses on the input stages (PR, PH) and

¹ Koala robot built by K-team, equipped with a CCD camera mounted on a servomotor to take panoramic views of the environment; the visual field varied from 60 to 300 degrees with a maximal resolution of (256 x 1200) pixels. A magnetic compass simulated the vestibular system.

the early stages (EC, DG) of hippocampal processing, which form a sound basis for the development of the whole system. The functions of CA3, CA1, and subiculum are only sketched here. In spite of its apparently limited scope, the further developments of the model proved its general relevance for hippocampal and brain processing, since the same architecture receiving different input modalities was successfully used for learning purely temporal or spatiotemporal sequences (Banquet, Gaussier, Revel, et al., 2001; Banquet, Gaussier, Quoy, Revel, & Burnod, 2002), as well as learning by imitation (Gaussier, Moga, Banquet, & Quoy, 1998; Banquet, Gaussier, Revel, et al., 2001; Andry, Gaussier, Moga, Banquet, & Nadel, 2001) and could be adapted to any type of information in different formal spaces (e.g., word list learning). This result is in agreement with the detection of spatiotemporal information in a large variety of brain structures more or less directly related to the hippocampal system. This information could help to monitor the specific processing performed by these structures and provide a functional link between them.

We first outline the anatomical and physiological bases, the architecture, and the functioning of the model in the methodological section, before presenting the results and a discussion.

2 Methods _

2.1 Anatomical and Physiological Basis of the Model. The parahippocampal region, first level in the hierarchy of associativity of the hippocampo-cortical loop, receives convergent inputs from neocortex unimodal and polymodal association areas, and yet preserves some modal segregation (Lavenex & Amaral, 2000; Suzuki, Zola-Morgan, Squire, & Amaral, 1993; Witter et al., 2000). Selective lesions of PR and PH induced mild navigation deficits (Wiig & Bilkey, 1994, 1995; Liu & Bilkey, 1998), qualitatively different from hippocampal deficits, or no deficit at all (Kolb, Buhrmann, McDonald, & Sutherland, 1994; Glenn & Mumby, 1998; Bussey, Muir, & Aggleton, 1999). Conversely, PR and PH removal disrupted the animal's ability to detect the changed position of a specific object in a familiar environment (Aggleton, Vann, Oswald, & Good, 2000). Accordingly, these lesions enduringly impaired DMS/DNMS (delay match/nonmatch to sample) tasks based on object-location associations in monkey (Suzuki et al., 1993; Zola-Morgan, Squire, Amaral, & Suzuki, 1989; Zola-Morgan, Squire, & Ramus, 1994) and equivalent navigation tasks in rats (Eichenbaum, Otto, & Cohen, 1994; Wiig & Bilkey, 1994). These tasks can be considered to depend on a simple stimulus-response strategy. The PR lesions induced more severe visual recognition deficits than EC lesions, and their effect was doubly dissociated from that of HS (Aggleton et al., 2000). The PH and posterior EC lesions produced a more severe spatial deficit than lesions of the rostral PR and EC (Parkinson, Murray, & Miskin, 1988). PR-PH areas remain cortically oriented because stimulus responsive

1344

cells are more frequent there than in EC. In the model, these two structures were represented by two one-dimensional layers representing pattern and direction that combined in a landmark-encoding two-dimensional array.

A second wave of association and pattern encoding was hypothesized to take place in EC superficial layers that receive inputs from PR, PH, and other polysensory areas. EC deep layer V receives, via subiculum, hippocampal backprojections that close the major hippocampal loop (see Figure 1) through a unidirectional internal projection to superficial EC layers (Kohler, Eriksson, Davies, & Chan-Palay, 1986; Jones, 1993; Witter et al., 2000). EC deep layers also send external projections to the cortex, thus closing the hippocampo-cortical loop. Preferentially, layer II projects to DG and CA3 and layer III to the CA3-CA1 region. The direct EC projections on the CA3-CA1 region are at least as strong as the projections relayed through DG (Yeckel & Berger, 1990). An inhibitory barrier on EC layer II prevents any important traffic in the trisynaptic loop except for high-frequency (7 Hz) firing (Jones, 1993).

Like PR or PH lesions, selective EC lesions induce more severe deficits in DNMS than selective HS lesions (Eichenbaum et al., 1994). More important, extensive EC lesions reduce the fraction of hippocampal cells presenting location-specific firing, and the stability of the place fields after maze rotation (Miller & Best, 1980) causes spatial deficits comparable to hippocampal deficits (Miller & Best, 1980; Olton, Walker, & Wolf, 1982; Goodlett, Nichols, Halloran, & West, 1989; Schenk & Morris, 1985), thus confirming the importance of EC spatial information in hippocampal spatial processing. In an attempt to overcome the limitations of lesion studies, Vann (Vann, Brown, Erichsen, & Aggleton, 2000) found a highly significant increase in C-fos expression in all HS and SUB subfields, in proportion to the (radial maze) task demands on spatial capacities for self-location and navigation. The parahippocampal region showed a lower yet highly significant increase in the C-fos label, with the exception of PR, which reacted only to novel stimuli. Simple spatial rearrangement of familiar icons increased C-fos expression in PH and parts of HS. Finally, place cell-like activity has been recorded in the superficial (Quirk et al., 1992; Sharp, 1999) and deep layers (Frank et al., 2000; Mizumori et al., 1992) of MEC, and in SUB (Sharp & Green, 1994). Furthermore, prospective and retrospective coding and path equivalence (tendency to fire at same relative locations along different paths) in deep EC suggest a coding by these neurons of the similarities between different trajectories at the same relative location with respect to a starting point (rather than precisely coding locations per se), thus relating location and behavior (Frank et al., 2000), and suggesting a dominance of path integration-related information in deep EC layers. In the model, EC (superficial) cells generated place-specific activity by implementing an unsupervised pattern learning on PR-PH inputs.

The role of the dentate gyrus (DG) in spatial processing is ambiguous. DG is essential for subtle (but not coarse) spatial pattern discrimination, and

a double dissociation exists between DG lesions associated with deficits in fine spatial discrimination and CA1 lesions associated with deficits in temporospatial sequence learning (Gilbert et al., 2001). Selective destruction of the DG granule cells preserves the spatial selectivity of CA3 cells but induces a spatial learning deficit (McNaughton, Barnes, Meltzer, & Sutherland, 1989). Some coherence emerges from these results if two facts are emphasized: the presence of a weak spatial code in EC and the direct and indirect connections of EC to downstream structures CA3, CA1, and SUB, susceptible to functioning independently (Yeckel & Berger, 1990). Accordingly, our model assumed that EC weak spatial code is used for a refined spatial localization by DG (orthogonalization) and also for spatiotemporal sequence learning by CA3-CA1. This hypothesis predicts that selective bilateral EC lesions should impair both a fine spatial discrimination by DG and a temporal spatial sequence learning by CA1. At present, it is known that deficits in maze performance follow bilateral EC lesions but not bilateral DG lesions in rats (Jarrard, Okaichi, Steward, & Goldschmidt, 1984). Other relevant spatiotemporal characteristics of DG processing are implemented in the model:

- 1. The anatomical topography reflected by the LEC-MEC subdivision is lost at the DG-CA3 stage due to the laminated projection (Amaral, 1993) of superficial EC neurons on the distal DG-CA3 dendrites. The highly convergent EC projections on DG granules and their divergent widespread distribution on the DG field were believed to further foster intermodal integration.
- 2. The dominance of feedforward DG activation, in the absence of any significant direct recurrent connectivity between granule cells, was thought to be responsible for the sharp delimitation of DG place fields (Jung & McNaughton, 1993) and was implemented in the model by a full feedforward convergent EC-DG connectivity and a winner-take-all (WTA) long-range competition between active neurons (orthogonalization).
- 3. Excitatory interneurons (mossy cells), modeled by a local recurrent activation of granule cell assemblies, implemented a delay in DG cell activity that created a sliding window of activation, including past and present events, encoded as an event transition by CA3.
- 4. The convergence onto CA3 of the direct distal inputs from the perforant pathway and the indirect spatially restricted proximal DG projections onto CA3 (each granule cell contacts at most 15 CA3 pyramidal cells) enforced a pattern of activation on CA3.

Temporal processing and delay activity believed to take place in DG are also a part of HS function:

- 1. During single stimulus response, an initial monosynaptic activation of the pyramidal cells in CA3-CA1 through direct EC projections was followed by a weaker activation of the same cells through the DG-CA3 trisynaptic route (Yeckel & Berger, 1990). Thus, with spatially close place fields corresponding to temporally overlapping subsets of active PCs, coding for sequentially visited locations could also support the coding of place transitions at the level of neural populations (Banquet, Gaussier, Revel, et al., 2001).
- 2. A remarkably long time constant of the CA3 NMDA receptors (150 msec) and their capacity for short-term potentiation endow CA3-CA1 with a memory range adapted for learning transitions or short event sequences.
- 3. A familiarity-dependent, increasing place field overlap in the CA3-CA1 region (Mehta, Barnes, & McNaughton, 1997) could correspond to an earlier anticipation of upcoming fields, when the rat is at the border of the current field.
- Some hippocampal cells discharge according to the stage of a task, independent of the animal's location (Eichenbaum, Kuperstein, Fagan, & Nagode, 1987; Wiener, Paul, & Eichenbaum, 1989; Wiener & Korshunov, 1995).
- 5. Recent developments (Gilbert et al., 2001) in pattern separation paradigms (Chiba, Kesner, & Gibson, 1994; Gilbert, Kesner, & DeCoteau, 1998) confirm a double dissociation between a DG finely grained spatial pattern separation and a CA3-CA1 (spatial) temporal order pattern separation.

2.2 Network Model. The network architecture includes two onedimensional input layers. A PR "What" layer, receiving pattern codes from temporal areas TE, and a PH "Where" layer, receiving object direction and location codes from posterior parietal cortex (plus V4 in primates), are dedicated, respectively, to the recognition of novel items and their spatial arrangement. These input layers converge on a merging module PR-PH, coding landmark constellations. Pattern selection-recognition in an EC module results in a weak place code that combines visual and movement-related information. A DG module performs a feedforward self-organizing, competitive separation of patterns (orthogonalization) and their transient storage in working memory. Current direct and delayed indirect inputs to CA3 allow the computation of transitions. These transitions are associated with their corresponding movement vector by convergence of place information and path integration on SUB. An analytical formulation of place coding and recognition, based on a comparison (match-mismatch) between current and memorized views of an environment, summarizes the performances of the different networks.

2.2.1 Network Input. This letter does not aim at a detailed presentation of the process of visual pattern learning (Gaussier, Joulain, Banquet, Leprêtre, & Revel, 2000). In the first visual processing stages, the identification of focal features at the center of subareas partitioning a scene resulted from gradient and curvature extraction, end stop, and corner detection, among others. The gradient extraction was followed by a convolution with filters (e.g., difference of gaussians) for the detection of corners. A serial search resulted from the emergence of a new winner feature-coding neuron after the inhibition of the previous winner. Typically, the pattern and location of 20 to 30 areas were extracted from a panoramic scene.

In mammals and more so in primates, ocular saccade and pop-out attention play an important role during scene exploration. In our model, sequential snapshots of a scene identified separately "what" (a significant feature and its context) and "where" (azimuth) information, which was then recombined into landmarks. A localization-navigation paradigm (visually based in particular) involves a similarity measure between learned and current views. Such a match mechanism at the level of features allowed a more robust scene recognition than a global correlation (without feature extraction) because the recognition level depended only on the correct recognition of the selected features in their context and on their relative displacement compared to the learned image (see the analytical equation of the model, equation 2.10).

A one-shot learning of the patterns took place within the connections between input pathways and "What" layer, where the pattern was recognized or a new code recruited. The absence of identification of symbolic objects avoided the binding problem related to this process. A given configuration of landmarks (constellation) allowed the recognition of a place. The whole process simulated a spotlight mechanism, whatever its nature (attention, saccade, head direction), performed by the rotation of the camera.

2.2.2 Model of Perirhinal-Parahippocampal Cortices: "What" and "Where" Input Association. In the model (see Figure 2), for a given landmark 1, the effect of lateral diffusion on activity Θ_j of neuron j on the "Where" PH layer was expressed as a nonnormalized gaussian activity profile: $\Theta_j = \exp -\frac{\left((\theta_k^l - \frac{2\pi}{N}j) \mod 2\pi\right)^2}{2\sigma^2}$ where θ_k^l represents the azimuth of the *l*th landmark and $\frac{2\pi}{N}j$ the preferred direction of neuron j. N represents the number of neurons (120) on the PH "Where" network. The influence on Θ_j of the activity related to *l*th landmark decays exponentially as a function of the angular distance between neuron j preferred direction of *l*th landmark corresponds to the preferred direction of neuron j), $\Theta_j = 1$. The activity level of each "Where" neuron represented an internal measure of the angular distance between the azimuth of the current head gaze direction and the preferred direction of the neuron j of the angular distance between the azimuth of the current head gaze direction and the preferred direction of the neuron j by $\Theta_j = 1$. The activity level of each "Where" neuron represented an internal measure of the angular distance between the azimuth of the current head gaze direction and the preferred direction of this neuron. The lateral diffusion of activation to neighbor neurons implied that a neuron did not need to be precisely tuned to the direction of a given landmark in order to become active. Neurons N_{jk} belonging to the *j*th neighborhood and projecting to the PR-PH cells of the *k* column are defined by

$$N_{jk} = \left\{ j : \left| k . \frac{j_{\max}}{k_{\max}} - j \right| < d N_{\theta} \right\}.$$

 $|k.\frac{l_{\max}}{k_{\max}} - j| < dN_{\theta}$ determined the neighborhood of the *j*th "Where" neuron that projected to neuron *lk* in the PR-PH network; $\frac{j_{\max}}{k_{\max}}$ was the ratio between the number of neurons in the "Where" layer and the number of columns in the PR-PH network; dN_{θ} determined the size of the neighborhood of "Where" cells that project to a single PR-PH cell.

This encoding of object direction is consistent with a polar coordinate system. Ultimately, object direction was referred to the body axis orientation, which itself referred to an external reference. This external reference allowed that landmark information be aligned with the environment and also independent of the orientation of the agent. In vivo, the head direction system, scattered in different brain structures and integrated into the hippocampal system in the subiculum (Sharp, Blair, Etkin, & Tzanetos, 1995) or in a HS-SUB-EC loop (Redish & Touretzky, 1997), is believed to perform this function.

The activity of pattern-encoding PR and direction-encoding PH converged on the PR-PH two-dimensional array that merged "What" and "Where" streams to code landmarks by a product (pi, AND operator). PR-PH is a "necessary" zone of convergence for "What" and "Where" information. This convergence has been proven by the recording of neurons in different structures (PH, EC, CA3) that respond specifically for one object in a given location (Rolls & Treves, 1998). Therefore, several possible structures or neuron populations could correspond to the PR-PH network. It could be PH since strong connections exist between PR and PH or even a subpopulation of neurons in EC superficial layers that include both stellate and pyramidal cells. AND operations in biological networks can be performed by the staged merging of excitatory synapses on dendritic trees (Shepherd, 1993). All the cells of a column of the PR-PH matrix received inputs from the same neighborhood in the "Where" layer. These neighborhoods partially overlapped. In summary, four characteristics of the network deserve to be emphasized:

- Although full feedforward connectivity between "Where" and PR-PH networks led to accurate performance, PR-PH units received only a fraction of "Where" units in order to increase the capacity of the network.
- 2. Only maximally active inputs were learned by the PR-PH neurons.

- 3. Due to input codes, the level of activation of product neurons reflected the angular distance of the corresponding landmark to the current head gaze direction.
- 4. Assuming that the visual system cannot recognize several patterns in parallel, we use an automatic spotlight system to explore sequentially the visual scene according to a saliency map. This sequential exploration makes "What" and "Where" information temporally correlated and bound. The time-sliced sensory sweep performed by the visual system is corrected by the PR-PH working memory, which bridges the temporal gap introduced by the sequential exploration (EC delay neurons). A similar mechanism has been demonstrated for visual saccades in posterior parietal cortex.

The discrete equation of the PR-PH neurons activity X_{kl}^{prph} is

$$X_{kl}^{prph}(t+dt) = \left[X_{kl}^{prph}(t) + I_{kl} - X_{kl}^{prph} \cdot \sum_{m} In_{m} \cdot W_{m,kl}^{In-prph}\right]^{+}$$
(2.1)

 $[x]^{+} = \begin{cases} x & \text{if } x > 0\\ 0 & \text{otherwise} \end{cases}$

The excitatory component of equation 2.1 includes I_{kl} , a global input to neuron kl detailed below, and $X_{kl}^{prph}(t)$, a memory term allowing the buildup of a landmark constellation and fluctuating between 0 and 1.

The inhibitory term in equation 2.1 induces a reset of the representation of a learned landmark constellation. In_m represents the activity of m^{th} inhibitory interneuron triggered by a sensorimotor reset signal at $T, 2T, 3T, \ldots, nT$, where T is a constant period for a visual panoramic exploration of the scenery; $W_{m,kl}^{In-prph}$ represents fixed weights between the inhibitory interneuron m and a PRPH pyramidal cell kl.

 I_{kl} , the global input to neuron kl of the PR-PH matrix, is computed as a product:

$$I_{kl} = \left(\max_{i \in N_{li}} L_i . W_{i,kl}^{pr-prph}\right) . \left(\max_{j \in N_{lj}} \Theta_j . W_{j,kl}^{ph-prph}\right).$$
(2.2)

 $W_{i,kl}^{pr-prph}$ ($W_{j,kl}^{ph-prph}$) are the connection weights between any *i*th landmark (*j*th azimuth) input to the *kl* PR-PH neuron; L_i and Θ_j represent the "What" and "Where" network inputs, respectively. The synaptic weights between input unit *j* and PR-PH neurons learn in one trial, in the absence of inhibitory reset and only for maximal input lines:

$$W_{j,ki}^{ph-prph} = (L_i) . (\Theta_j) . f(I - I_n).$$
 (2.3)

 $i = \arg(\max_{p \in N_{li}} L_p), j = \arg(\max_{q \in N_{kj}} \Theta_q); I_n \text{ is an inhibitory reset activity that prevents learning in case of reset;$ *I*is:

$$I = \frac{(\max_{i \in N_{li}} L_i) + (\max_{j \in N_{kj}} \Theta_j)}{2}.$$
 (2.4)

f(x) = 1 if x > 0.99 and 0 otherwise; this thresholded Heaviside function corresponds to a learning modulation common to all active neurons.

The Max operator in equations 2.2 through 2.4 expressed a competition between "Where" neurons belonging to the same neighborhood of inputs to PR-PH neurons. Thus, the optimally tuned "Where" neuron could get control of PR-PH neuron activation and learn the corresponding patternazimuth conjunction.

In summary, the PR-PH network has two functions: to bind the "What" and "Where" information in order to create a landmark and to bridge the temporal gap between successive landmarks (working memory) in order to create a landmark constellation or view that is directly learned or recognized as a place by EC.

2.2.3 Entorhinal Cortex and Place Coding. In the second wave of integration and association—between sensory (visual) inputs and path integration—the emergence of place cell–like activity in EC is accounted for in the model by a summation (OR operator) that complements the AND operator of the PR-PH network to globally perform a sigma pi. The activity X_j^{ec} of an EC pyramidal neuron j coding for places is given by

$$X_j^{ec} = f_{\overline{D_j}} \left(\sum_{kl \in N_{kl}} W_{kl,j}^{prph-ec} . X_{kl}^{prph} \right),$$
(2.5)

where $f_{\overline{D}}(x)$ represents an output function that performs a learningdependent tuning of EC neuron response such that the response, which is weak and mildly specific before learning, becomes larger for specific inputs after learning:

$$f_{\overline{D_j}}(x) = \overline{D_j} . r. e^{\frac{(-V_{ig} + 0.01).(1 - x/r)^2}{\sigma_j . (D_j - 1.01)^2}}.$$
(2.6)

The three parameters (\overline{D} , r, Vig) modulated height, width, and slope of the gaussian function: (1) \overline{D} , a neuron tuning factor increased with learning; (2) Vig, a vigilance parameter was the inverse of the activity level resulting from the comparison between memorized and new input patterns; and (3) r, a scaling factor, allowed the output integration on EC to work at constant energy in spite of the fluctuations in input levels.

1351

A local competition was implemented:

$$X_j^{ec} = \begin{cases} X_j^{ec} & \text{if } X_j^{ec} = \max_{i:|i-j| < d_1 \max} X_i^{ec} \\ 0 & \text{otherwise.} \end{cases}$$

 d_1 max is a parameter determining the distance on which neurons compete on EC.

The learning equation at the synapses between PR-PH and EC neurons implemented a pseudo-Hebbian rule:

$$\frac{d W_{kl,j}^{prph-ec}}{dt} = -\lambda_1 \cdot W_{kl,j}^{prph-ec} \cdot f\left(X_{kl}^{prph}\right) + \lambda_2 \left(1 - \sum_{kl \in N_{kl}} W_{kl,j}^{prph-ec}\right) \cdot f\left(X_{kl}^{prph}\right) \cdot X_j^{ec}.$$
(2.7)

 $f(X_{kl}^{prph}).X_j^{ec}$ is the product of pre- and postsynaptic terms of the Hebbs rule; weight normalization is $W_{kl,j}^{prph-ec} = \frac{W_{kl,j}^{prph-ec}}{\sum_{kl\in N_kl} W_{kl,j}^{prph-ec}}$; λ_i is the gains of depression or potentiation; and f is the PR-PH output function, as defined in equation 2.1.

2.2.4 DG Delay Cells versus CA3-CA1 Transition Cells. DG has already been simulated as a neural network performing spectral timing and pattern learning (Banquet et al., 1997), which can function independent of the global architecture.² The solutions of the dynamic equations of the model provided a family of bell-shaped curves. In order to spare computing resources, this part of the architecture modeled the temporal function of the DG network by a basis of radial functions (gaussian),

$$X_{j,l}^{dg}(t) = \frac{m_0}{m_j} \exp{-\frac{((t-\tau_l)-m_j)^2}{2\sigma_j}},$$
(2.8)

where m_j denotes the particular time constant of neuron j, with standard deviation σ_j , m_o being the faster referential time constant; l the label of the recognized input pattern that triggers its associated neural cluster including neurons with different time constants; and τ_l the instant of activation of the lth cluster. In navigation tasks, precise timing is usually not necessary. Then m_j , τ_l , σ_j were the same for all cells, and σ_j was large. DG neurons were combined with excitatory mossy cell interneurons to form delay loops. The

² Spectral timing is a weighted decomposition of time by a neural population endowed with a whole spectrum of neural time constants (Grossberg & Merrill, 1992)

pattern separation function (orthogonalization) of DG granule cells uses the same computations as EC neurons except that a winner-takes-all (WTA) competition encompassed the whole DG field.

In this model, the CA3-CA1 region computed a third type of association besides the association of object and location in PR-PH and of visual-allothetic (landmark) and movement-related-idiothetic (path integration) information in EC-SUB. This association learned transitions between events (in this case, visited places). This temporal-sequential aspect was implemented thanks to the hetero-association capacities of the CA3-CA1 network between direct and indirect pathways, combined with a DG delay memory due to local excitatory loops between mossy cells (excitatory interneurons) and granule cells (see Figure 4A) that created a sliding memory window (Banquet, Gaussier, Revel, et al., 2001; Gaussier et al., 2002). Encoding transitions does not preclude the simultaneous coding of places in the CA3-CA1 region (a place can be viewed as a transition from a place to itself). In further developments of the model, these transitions formed the building blocks of place field chunks, akin to Worden's (1992) fragment fitting embedded in different trajectories as recorded in deep EC neurons (Frank et al., 2000), and of spatiotemporal sequences (Banquet, Gaussier, Quoy, Revel, & Burnod, 2004; Banquet et al., 2002; Banquet, Gaussier, Revel, et al., 2001; Banquet, Gaussier, Quoy, & Revel, 2001). These transitions simplified the Hebbian learning of the temporospatial sequences and the implementation of the corresponding cognitive graph maps in the sensorimotor system, thanks to an appropriate and unambiguous association between a transition and a movement vector. Whatever the trajectory between two places, path integration computed a single displacement vector.

The neural implementation (see Figure 4A) featured a group of CA3 neurons combining information on the current place recognition from EC (distal dendrite inputs) with information on the previously stored input (proximal dendrite inputs). The activity of transition-prediction neurons, $X_{i,j}^{CA3}$, resulted from a summation of the activity of the two inputs, separately insufficient to trigger the activity. The transition prediction was achieved by reinforcing (Hebbian learning) the link between the DG delayed input and the CA3 assembly coding the transition, such that the delayed activity became sufficient by itself to activate CA3 neurons. Correct predictions reinforced learning; otherwise weights were depressed, and another (learned or new) node became active.

 $X_{i,i}^{CA3}$ is the activity of CA3 TCs:

$$X_{i,j}^{CA3} = \left[\sum_{k} \left(W_{k,ij}^{dg-CA3} \cdot X_{k}^{dg}\right) + W_{j,ij}^{ec-CA3} \cdot X_{j}^{ec}\right]^{+}$$
(2.9)

 $[x]^+$ is as defined in equation 2.1.

Description	Symbol Value
Number of neurons in "Where" layer "Where" layer diffusion range	N = 12 (simulation); $N = 180$ (robot) $\sigma^2 = \frac{15}{2.\log(0.1)}$
Saturation point of sigma pi neuron ac- tivity	$B_X = 1$
Number of inhibitory interneurons	m = 1/20 principal neurons
Decay factor of sigma pi activity	$0 < \lambda_0 << 1$
Decay factor of sigma pi activity	$\lambda_1 = 0.99$
Sigma pi to EC weights decay factor	$\lambda_2 = 0.001$
Sigma pi to EC weights learning gain	$\lambda_3 = 1$
Number of input pathways to a sigma pi neuron	$m_{\rm max} = 10$
EC neuron tuning factor	$\overline{D_i} = 0.1$ before learning, $\overline{D_i} = 0.9$ after
Novelty detection tuning factor	Vig = 1 in novel situation, $Vig = 0.1$ otherwise
PR-PH neuron population size	$N_{kl} = 90$ (simulations)
PR-PH neurons competition range	$d_1 \max = 10$ (simulations)
EC neurons competition range	$d_1 \max = 10 \text{ (simul)}, d_1 \max = 120 \text{ (robot)}$
DG neurons competition range	$d_2 \max = 40$ (DG group size)
Θ to PR-PH neuron neighborhood	$dN_{\theta} = 2$ (simulation), $\bar{d}N_{\theta} = 30$ (robot)
PR-PH to EC neuron neighborhood	$d N_{kl} = 20$ (simulation)

Table 1: Model Parameters.

 $W_{k,ij}^{dg-CA3}$ is the strength of the link between the *k* DG neuron and the (*ij*) CA3 neuron; X_k^{dg} is the activity of the *k* DG cell; X_j^{ec} is the activity of the EC neuron *j* connected to an (*ij*) CA3 neuron; and $W_{j,ij}^{ec-CA3}$ is the strength of the link between them. The weight modification rule between an *i* DG granule cell and an *ij* CA3 pyramidal cell is:

$$W_{i,ij}^{dg-CA3} = \begin{cases} \frac{X_i^{dg}}{\sum_i (X_i^{dg})^2} & \text{if } X_j^{ec} \neq 0\\ \text{unmodified} & \text{otherwise.} \end{cases}$$

Direct EC-CA3 inputs are unconditional and not learned in the model. The parameter values used during the simulation and robotic experiments are listed in Table 1.

2.3 Functioning of the Network and Experimental Paradigms. Our model combines an abstract mathematical analysis of the overall network properties, a simulation of these principles by a realistic neural network architecture (see Figure 1), and an implementation of the model as a control system for robot navigation. We now describe the functioning of the network during navigation and then establish a correspondance between the analytical and simulation levels. The neural network implemented four steps.

Step 1. Visual scenes of an environment were automatically extracted by the single CCD mobile camera of the robot visual system. This part of the model is not detailed in this article (Gaussier et al., 2000). The pan of the camera varied in different experiments from 180 to 300 degrees. For each landmark extracted, a compass measured the azimuth of the head gaze direction relative to an absolute reference as a substitute for the robot's vestibular system. In a landmark-bounded area, as in navigation experiments, the angle between these landmarks and a stable and salient distant landmark could be used as an absolute reference. Thus, the angular measure of the different landmarks refering to the body axis and to the absolute reference remained stable regardless of the agent's orientation. At any position, a given pattern in the current head gaze direction (fixation point) of the agent was encoded and learned by a neuron *i* with activity l_i in the "What" layer. Simultaneously, a neuron *j* in the "Where" layer optimally tuned to this direction presented directional activity θ_i . The same pattern also activated (to a lesser degree) related "Where" cells tuned for neighboring directions because of their bell-shaped tuning curve.

Step 2. The activity of the "What" and "Where" layers was then combined in an $N_l \times N_{\theta}$ multimodal layer PR-PH (see Figure 2) by a product operation. In our model, the temporary memory buffer capacity of PH and EC neurons (Suzuki et al., 1993; Zola-Morgan, Squire, Clower, & Rempel, 1993; Egorov, Hamam, Fransen, Hasselmo, & Alonso, 2002; Fransen, Alonso, & Hasselmo, 2002) served to transiently store sequential snapshots that built up constellations of landmarks forming local views. Two indices identified each PR-PH unit. Unit *ik* received input from pattern unit l_i and preferred direction unit θ_k (including its neighborhood) (see Figure 2).

Step 3. A population of EC neurons summed up the neural activities of a landmark constellation, thus computing a sigma pi operation (sum of products) in collaboration with the PR-PH multimodal layer. This integration of a set of landmarks was sufficient to generate place-dependent activity in superficial EC. The diffuse overlapping EC place fields let several EC nodes encode simultaneously, albeit at different degrees, for a single place. In the model, a movement induces a reset of the previous landmark constellation in PR-PH nodes. However, a new place was encoded only if the mismatch between the previous and new view was sufficient. In a more recent version, path integration combined continuously with PC information at the level of the subiculum and fed back this combined information to deep EC layers (Banquet et al., 2004).

Step 4. Distribution of information to the whole DG field and strong convergence on DG granule cells allowed a WTA competition over the entire DG field, providing a single winner for a given location. Excitatory coupling between mossy cells and granule cells implemented a working memory on DG used to compute transitions on CA3. When a temporal derivative on the EC output (or novelty detection, more recently) detected a novel pattern, the temporal conjunction of the delayed input in the indirect pathway and of

the current input through the direct pathway encoded a transition pattern in CA3 pyramidal cells that was learned in the proximal connections between mossy fibers and CA3 pyramidal cells. The convergence-divergence of connections between the different processing stages was parametrically determined by the size of the input neighborhoods of the principal neurons. This convergence was a factor 4 between the "Where" map and PR-PH network, a factor 5 between PR-PH and EC, and from all-to-one between EC and DG, so that both the high degree of convergence of EC inputs on granule cells (a factor of 400 in animal) and the extensive receptive field of DG neurons could be accounted for.

Training and performance were simultaneous. In rats, the incentive to explore their environment prevails over the immediate satisfaction of basic drives. During an exploration phase, independent of any reward, Hebbian learning of places (by conjunction of inputs and EC place cell activation), and also of maps (by spatiotemporal contiguity between successive locations) made an environment familiar and also eventually located the goal objects. Learning modified the synaptic strength of the connections and also induced an increased selectivity of the output function of the PCs. Spatial tuning of PCs is suggested by the increased response of PCs within a single session in the same environment (Mehta et al., 1997), or an increase in reliability across sessions. Goal-oriented navigation in maze or open environments depended on the cortical map of this environment learned during an exploration phase. Goal-reaching paradigms confirmed the learning of reward location (place-reward association) and reinforced the trajectories leading to the goal. Robotic experiments were preceded by simulations in artificial setups.

During the exploration or recognition of an environment, the shift between successive PCs was monitored by a novelty-dependent septal modulation (Hasselmo, Schnell, Berke, & Barkai, 1995). The system was confronted with continuously drifting visual inputs. Septal modulation favored either a network reconfiguration in the presence of novel inputs or associative learning and pattern storage when no novelty was detected. The decrease in EC and DG activity triggered by a mismatch between stored and novel inputs raised a vigilance level. This increase in vigilance sharpened the EC-DG output functions, favoring the emergence of a new activation pattern, thus avoiding the system's being trapped in the same PC attractor (see Figure 6). A progressive degradation of the PC firing occurred when the robot moved from the center of the field to the periphery, and then a sudden change when a low-activity threshold was crossed. This PC switch is comparable to the map switch hypothesized by other authors (Redish, Rosenzweig, Bohanick, McNaughton, & Barnes, 2000; Samsonovich & McNaughton, 1997). This drift-and-shift process (degradation of the views and takeover of a new PC population) provided for a coherent partitioning of space into distinct place fields during exploration. In a familiar environment, the same process implemented a successive activation of PCs during the transition from one place field to the next. NMDA receptor blockade

or selective knock-out mice have recently permitted a dissociation between short-term (NMDA-independent) and long-term (NMDA-dependent) place field stability (Kentros et al., 1998; McHugh, Blum, Tsien, Tonegawa, & Wilson, 1996; Rotenberg, Mayflower, Hawkins, Kandel, & Muller, 1996).

As a theoretical formulation of the model, analytical equation 2.10 is not used in the simulations, unlike other network equations. It summarizes the spatial properties of the PR-PH-EC-DG network processing, with a loss of dynamical and online learning properties. Nevertheless, this equation is useful to understand the relationships between the landmarks and the geometrical properties of the place fields. Each term of the equation corresponds to a fundamental property of one of the network equations that support the simulations. In this equation, the activity of the place cell *i* when the agent is at the location (*x*, *y*) is analytically given by

$$P_i(x, y) = 1 - \frac{\sum_{k=1}^{N_i} V_{i,k} f(|\Delta \Theta|, v_k(x, y))}{\pi N_i}.$$
(2.10)

PC activity is expressed as the complement to one of a mismatch factor between stored views and the current view. $|\Delta\Theta|$ is computed as the minimum between $|\Theta_{i,k} - \theta_k(x, y)|$ and $2\pi - |\Theta_{i,k} - \theta_k(x, y)|$ and is always smaller than or equal to π ; πN_i is a mismatch normalization factor, π being the maximal angular mismatch for a given landmark and N_i the number of visible landmarks when the agent is at the place field *i*, which corresponds to place cell activity P_i . All the angles are measured in radians from an absolute direction (the north for instance). $\Theta_{i,k}$ represents the azimuth of the landmark k from the learned place i; $\theta_k(x, y)$ is the azimuth of the same landmark k for the current robot location (x, y); $V_{i,k}$ (respectively, v_k), an all-or-none weighting factor depending on the landmark visibility and/or recognition from learned *i* (respectively current (x, y)) location, is set to 1 when the landmark k is seen from the learned (respectively, current) location *i*, and 0 otherwise. When learned landmarks are not recognized, we can have $V_{i,k} = 1$ and $v_k = 0$. *f* is a nonlinear function that accounts for landmark recognition:

$$f(\theta, v_k) = \begin{cases} \theta & \text{if } v_k = 1 \\ \pi & \text{if } v_k = 0. \end{cases}$$

Three of the four possible combinations of the pair ($V_{i,k}$, v_k) are relevant for mismatch computation:

- 1. (1, 0): Landmark *k* was seen from learned place *i* but is not seen or recognized from the current place; $f(\theta, 0) = \pi$. The mismatch π associated with this landmark is maximal.
- 2. (1, 1): Landmark *k* was seen from learned place *i* and is recognized from the current location. The contribution to mismatch is $|\Delta \Theta|$.

3. (0, 1): Landmark *k* is seen from the current place, but was not seen from the learned place *i*. It does not contribute to the mismatch term $(V_{i,k} = 0)$. Equation. 2.10 gives a function P_i that tends asymptotically to 1 when the azimuths $\theta_k(x, y)$ associated with the current location are close to the stored $\Theta_{i,k}$.

The network implementation complies with equation 2.10. Landmarks are learned in the connectivity patterns between visual inputs and the "What" layer. Therefore, match-mismatch is reflected in the activity level of "What" nodes that results from the dot product between the input and the learned weight pattern. The landmark node with maximal activity in the "What" layer identifies the input. This network operation implements the $(V_{i,k}, v_k)$ pair in equation 2.10. If no stored landmark corresponds to the input, a new node is dedicated to this novel landmark, and its azimuth is also learned. Only the connection weights between the maximally active "Where" nodes and PR-PH nodes are learned, for the sake of simplicity. Thus, after learning, the dot product between a bell-shaped activation pattern in the "Where" layer and the weight pattern on an active PR-PH neuron (determining the activation level of this neuron) reflects the azimuth difference between learned and recognized landmark. This network step implements the $|\Delta \Theta|$ term in equation 2.10. In this way, the level of activity of a PR-PH landmark node reflects the level of similarity between the learned and the current view for this landmark. A landmark constellation is encoded in a few EC nodes and learned in the synaptic weights of the PR-PH to EC pathways. This network step implements the summation in equation 2.10.

3 Results _

Some results derive from simulations with artificial inputs (see Figures 2 and 6), yet most of them come from robotic experiments conducted with real visual inputs in natural indoor environments (see Figures 3, 4, 5, 7, and 8). They express the functions of the different hippocampal subsystems (see Figure 1), which are presented incrementally, going from land-marks to local views, place fields, and transitions. Two paradigms were used. In self-localization paradigms, the robot was passively moved in different locations of an open environment, where different place fields could arise from panoramic views of the environment. In goal-oriented navigation paradigms, within open or maze environments, or a combination of both, random exploration allowed the buildup of cortical maps and the discovery of the goal(s) locations on these maps.

3.1 Landmark Constellations and Local Views. Visual patterns L_i automatically extracted from the environment by the single CCD mobile camera of the robot visual system during exploration or artificially provided at



Figure 1: Schematic representation of the hippocampal circuits. Superficial layers of lateral (L) and medial (M) entorhinal cortex (EC) receive information from the perirhinal (PR) and parahippocamapl (PH) cortices, respectively. EC layer II transmits information to the dentate gyrus (DG) granule cells, and CA3 pyramidal cell distal dendrites, through the perforant pathway. The CA3 proximal dendrites receive mossy fibers from the DG granule cells. CA3 pyramidal neurons connect to other CA3 neurons by recurrent collaterals and to CA1 by Schaffer collaterals. Distal CA1 dendrites also receive direct connections from EC layer III. CA1 connects to subiculum (SUB) and directly to deep EC layers. Subicular connections to EC layer V close both the intrahippocampal loop through a one-way connection from layer V to EC superficial layers, and the hippocampocortical loops through indirect connections to the same associative cortical areas that send inputs to EC layer II. Direct connections link subiculum to prefrontal cortex (PF) and accumbens (AC). Septal modulatory inputs (not represented on this figure) target mostly DG, CA3, and CA1. Semicircular connections represent modifiable synapses.

time T0 to the system during preliminary simulations (see Figure 2) were learned by a neuron *i* with activity l_i in the "What" layer PR representing the perirhinal cortex. For each landmark extracted, a compass (a substitute for the robot's vestibular system) measured the azimuth Θ_j of the landmark relative to the head-body axis of the robot referred to a stable external reference, thus making the measure independent of the robot orientation. This azimuth was encoded by a neuron *j* optimally tuned to this pattern direction with directional activity θ_j in the "Where" PH layer, representing parahippocampal (posthippocampal in rat) cortex (see Figure 1). The same pattern also activated (to a lesser degree) "Where" cells with a bell-shaped tuning for neighboring directions. The activity of the "What" and "Where" layers was then combined in an $N_l \times N_{\theta}$ multimodal layer PR-PH with units kl (see Figure 2) by a product operation.



Figure 2: (A) Simplified model architecture representing "What" (PR) and "Where" (PH) inputs merging (AND operator) in a PR-PH layer with a short-term memory capacity (recurrent loops). Only active links have been displayed. Several landmark-encoding cells simultaneously active in the PR-PH layer correspond to a constellation of landmarks collected by visual exploration, and form a view of the environment from a given place. (B) Simulation results of these first three networks of the architecture. Pattern L_i and azimuth Θ_j merge to form a landmark in the PR-PH network. During the exploration of a scene from a particular place at times T0, T01, T02, T03, and T04, PR-PH working memory allows the buildup of a landmark constellation correponding to a view.

At times T0-T04 (see Figure 2), a landmark constellation forming a local view representing the visual configuration of the environment from the current location was incrementally stored in the PR-PH working memory, which is a property of PH and EC neurons (Suzuki et al., 1993; Zola-Morgan et al., 1993; Egorov et al., 2002; Fransen et al., 2002). The population code of these views was next decoded in EC.

3.2 Entorhinal Location-Dependent Activity. A specific location is defined by the configuration and orientation of the landmarks corresponding to this location. This information from the PR-PH network was integrated in the EC network (see Figure 3A) and learned in the synaptic connections between PR-PH and EC. A remarkable property of this system resides in its built-in generalization capacity. A neuron coding for a location *A* responds when the robot is precisely in *A*, but also to a lesser degree for a neighborhood of *A*. In this way, a field is created around each learned location, providing continuity and also overlap in the space code.

When the robot visually explored the experimental room from different locations (similar to a rat passively moved from place to place), place fields corresponding to each location covered the space of the room. With a short-range, soft competition among pyramidal cells, large, overlapping place fields represented a weak place code, similar to that of EC neurons. Nevertheless, as for hippocampal place fields, the firing maxima were stable and evenly distributed. The learning of several locations led to a paving of the space, where neurons reactive to different locations coded for different areas of the environment (see Figure 3B). The shape of the place fields adapted to the geometry of the environment (Gaussier et al., 2002).

3.3 Hippocampal Dentate and CA3 Transition Cells. The coarse spatial information computed in several EC cells converged on DG granule cells, where it underwent a sharp competition. Then the elaborated spatial information was transmitted to proximal dendrites of CA3 pyramidal cells; EC information also reached CA3 neurons through direct connections to distal dendrites (see Figure 4A). CA3 connected to CA1 pyramidal cells (Schaffer collaterals) and CA1 to subiculum (SUB).

In DG, place fields became clearly delimited (Jung & McNaughton, 1993), evenly distributed in space, and comparable to place fields recorded in HS proper (see Figure 4B). In CA3, the temporal conjunction of a delayed DG place cell activity (maintained through recurrent activation of granule cells by the mossy cells) and of the current PC activity provided by the direct connections to CA3 gave rise to transition cells, which encoded the transition between two place fields in relation to transition-dependent direction and self-motion information (path integration). Once learned, these transitions helped to prime and predict accessible locations from the current one and to detect novelty as a violation of expectations.

The following key features of PC firing were reproduced:

 Typical place cell firing patterns were elicited in the first moments (Hill, 1978) of the exposure of the robot to a new environment. In agreement with Redish and Touretzky (1997, 1998), we did not need any preconfigured reference frame as in the CA3 charts hypothesized by McNaughton (McNaughton et al., 1996; Samsonovich & McNaughton, 1997). A weak and randomly distributed initial set of weights in the network synapses was sufficient to get this result (see Figure 4B).

- The place field pattern stabilized during the first instants of exploration and was reproducible from session to session provided that the environment was not changed.
- Little directional specificity of place fields was found in an open field (Muller, Kubie, & Saypoff, 1991) when the system was configured with a large visual angle (300 degrees). Yet, with a smaller visual angle as in frontal vision (180 degrees), view cells were obtained, as in monkey.
- In these natural indoor experiments, about 15 to 30 landmarks were identified and used by the system in a typical panoramic image, although not all of them were necessary. In theory, either two correctly recognized landmarks referring to an absolute direction or three

Figure 3: (A) The neurons coding for a landmark constellation in PR-PH converge on EC superficial layers, where they activate position-dependent cells. In a first approximation, EC superficial layers sending inputs to DG and CA3 and EC deep layers receiving subicular inputs have not been dissociated. Their functional integration is granted by the existence of a one-way link from deep to superficial EC pyramidal cells. (B) Examples of firing rate maps of typical EC cells. The upper maps represent an overhead view of square and cylindrical recording chambers in which the rat's position is correlated with the firing rate of MEC cells (darker spots represent locations of higher firing rate) averaged over the recording session. When the shape of the recording chamber was changed from a square to a cylinder, MEC firing patterns topologically transformed (as by compression). Reproduced from Quirk et al. (1992, Figure 13) with permission. The lower maps result from experiments where robots were passively moved to different locations of a room. They represent activation patterns of simulated MEC pyramidal neurons with positional firing, induced by real visual inputs sampled by the vision system of a robot at different locations in an experimental room. A diffuse but stable place cell-like tuning of the 25 EC cells covers the whole space. Each rectangle represents an overhead view of the experimental room. The numbers on the *x*- and *y*-axes represent the distances in meters. The cues available were composed of the usual furniture of a laboratory room (for example, desks, chairs, shelves). As in experimental data, each PC presents focal stationary maxima corresponding to a particular location in the experimental room but no clear-cut boundaries and a progressive graded decay.

Figure 4: (A) The complete, simplified architecture of the hippocampal model is represented. DG forms a pattern-encoding network with a working memory that maintains a delayed representation of the previous input. The CA3 heteroassociative net associates previous and current input transmitted respectively through indirect and direct perforant path connections to CA3 in order to compute event transitions. CA1-SUB performs a pattern-encoding and





recognition of these transitions and closes the intrahippocampal loop through its connections to deep EC layers. This loop closure is not simulated here, but see Banquet et al., (2004). (B) The experimental firing-rate maps illustrate that the firing pattern of hippocampal place cells changed when the room shape changed. (Reproduced from Quirk et al., 1992, Figure 13 with permission.) The lower maps represent activation patterns of simulated hippocampal neurons with positional firing, induced by the same conditions as in Figure 3B. When a sharp competition between PCs was implemented by a WTA network, the activity of the PCs did not present a large overlap anymore. Clearly separated place fields still covered the entire space. landmarks referring to a relative direction (given by a landmark) are sufficient for unambiguous place recognition. Environment perturbations such as suppression or occlusion of some landmarks did not affect the spatial distribution of the place fields (Knierim, Kudrimoti, & McNaughton, 1995; McNaughton et al., 1996; O'Keefe & Speakman, 1987).

3.4 Primates' View Cells. Cells with view and/or object rather than place-dependent activity are most often recorded in monkey (Rolls & O'Mara, 1995). Figure 5 compares recordings of monkey view cells (A) with results (B) obtained by reducing the angle of the robot vision from 300 to 180 degrees. The previously isotropic, orientation-independent response of place cells became dependent on which particular part of space (and/or object) the robot was looking at. Simultaneously, cell activity became relatively independent of the location of the animal, as found for view cells. Thus, a frontal vision in primates, compared to the panoramic vision of rats, could partially account for the preeminence of view cells in monkey and the difficulty in recording PCs. This does not imply that a one-eyed rat, with a reduced field of vision, will present view cells rather than PCs, due to the compensation by idiothetic information. This result was obtained from robotic experiments implementing a biologically realistic vision system separating frontal from panoramic vision (Gaussier, Joulain, Banquet, & Revel, 1998; Gaussier et al., 1999, 2000, 2002). On the basis of the same principles, Rolls's group developed a similar model using simulated visual inputs that also accounted for the spatial field specificities of primate view cells and rodent place cells (de Araujo, Rolls, & Stringer, 2001; Stringer, Rolls, & Trappenberg, 2004).

3.5 Maps and Navigation Strategies

3.5.1 Shift Between Places During Simulated Random Navigation. Autonomous learning and performance were not dissociated. A vigilance parameter (active during both stages) depending on the match-related level of PC activity featured ACh septal modulation (Hasselmo et al., 1995). This parameter decided whether a new panorama was different enough from the stored ones to be learned as a new place, and favored either novel event encoding or expression of previously learned patterns in the absence of novelty detection. It also induced the shift between place fields during navigation by tuning a PC output function. This spatiotemporal contiguity between successive place fields was at the basis of Hebbian latent learning of a contextual map, during exploration.

In Figure 6, the same local view (landmark constellation) and the associated place field (PF1) were learned or recognized through times T1-T2, in spite of the decreased amplitude of neural activity at T2 due to a drift of landmark azimuths, or even a drop of some landmarks. Conversely, a shift



Figure 5: Place versus view cells. (A) View cell recordings in monkey's hippocampus. (Reproduced from Rolls & O'Mara, 1995, Figures 3–4, with permission.) (B) Results from an experiment where the pan of the camera of the robot was reduced from 300 to 180 degrees in order to replicate the frontal view of the primates. Activity was recorded from two model view cells responding to oriented views of a scene. Circles represent positions where the views were taken from. An arrow inside a circle indicates the learned position and direction. The length of the bars represents cell response amplitude as a function of the head (camera) orientation. The responses of the model view cells, as in the monkey experiment, were relatively independent of the location where the view was taken from, but depended on the view captured by a particular direction of gaze. Bars represent not spike frequencies but average activities of the cells.

from PF1 to PF2 occurred at T3. In fact, at the end of T2, the activation (SUM) of the PC corresponding to PF1 decreased below a threshold, triggering a burst of activity in the vigilance (VIG) module, a reset of the current EC-DG pattern, and the selection of a new code corresponding to PF2, at T3-T4-T5.



Figure 6: Results from a simulation with artificial inputs. Identification by EC and DG of two place fields (PF1 at T1,T2,T6 and PF2 at T3,T4,T5). After PF1 learning or recognition at T1, the landmarks recognition decreased (weaker output at T2 in EC-DG and in the activation-integrator, SUM). As a consequence of an increasing mismatch between the current constellation and the memorized constellation corresponding to PF1, the activation of the neural population coding for the PF1 constellation crossed a threshold at the end of T2. A phasic vigilance burst (VIG) induced an output function modulation in EC-DG and a different PC was learned or recognized at T3. When the simulated animal crossed back PF1 border at T6, the landmark constellation corresponding to PF1 was reactivated due to its prior learning during exploration.

Later, at T6, long-term learning ensured the activation of the PC coding for PF1 and the recognition of the place when the animal moved back to the former place field (PF1). Thus, a progressive degradation of the PC firing occurred when the robot moved from the center of the field to the periphery,

and then a sudden change when a low-activity threshold was crossed. This PC switch is comparable to the map switch hypothesized by other authors (Redish et al., 2000; Samsonovich & McNaughton, 1997).

At variance with random navigation, which is a simulation result, the navigations with maps, presented next, are behavioral results obtained from experiments with the Koala robot.

3.5.2 Universal Maps and Route Navigation. A collection of coarse and weak EC place codes (see Figure 7A) formed a landscape of overlapping PC potentials resulting from the variable coactivation for each location of a specific subset of neurons. We consider this landscape of potentials as a generalization of the classical concept of map, tested in the following unsupervised learning paradigm. When a goal was discovered during random exploration, the robot associated a few places around the goal with specific actions leading to the goal. Thus, a local behavioral attractor was learned around the goal, supporting a gradient-descent strategy toward the goal (see Figure 7B). A capacity to generalize permitted reaching the goal from a novel (unlearned) place in the open environment. The large size of PCs in EC verified in a robotic experiment, combined with a graded decrement of their bump activity, provided for a true generalization of learning to any place in an open environment. Indeed, each novel place was associated with a weighted combination of the actions associated with the most active PCs corresponding to neighboring learned places in order to generate smooth trajectories. At any location, the direction to the goal could also be provided by the single most similar place where a view-action association had been previously learned (see Figure 7B). Further, multiple goals could be simultaneously active as multiple attractor basins that were size-modulated by the strength of the corresponding drives (Gaussier et al., 2000).

3.5.3 Contextual Maps and Planning. A set of such places and transitions could be learned during random exploration (see Figure 8A) of an environment by strengthening the connections between the corresponding transition cells (Hebbian latent learning at the cortical level). Some of these connections could also be reinforced after leading to a goal-reward (see Figure 8B). A combination of several such paths formed a task-contextdependent map similar to a graph (see Figure 8). Muller first developed a conceptual graph model based on PCs (Muller et al., 1991) that was also simulated (Redish & Touretzy, 1998). In contrast, in our model, transitions computed in CA3-CA1 formed the building blocks of the global graph-map learned and stored at the cortical level. In conjunction with goal diffusion through the graph-map in prefrontal cortex, these transitions provided for a straightforward solution to the shift from space representation to navigation, in particular path desambiguation, monitoring several goals, and the invention of shortcuts. The navigation strategy based on this type of map implemented sequences of transitions leading to a goal in a proactive, planning mode of navigation combining previous latent learning of a global map in the prefrontal or parietal cortices and a guidance by the diffusion of activation from the goal location throughout the map (Gaussier et al., 2002; Banquet, Gaussier, Revel, et al., 2001; Banquet et al., 2002, 2004)

4 Discussion _

Before discussing these results, the scope of the model must be clearly delineated: neural computations at cell and population levels, in parahippocampal cortices and the hippocampus, were related to spatial processing and navigation. The model aimed to establish a link between mechanisms, functions, and behavior and to separate the specific contributions of these cortical and subcortical structures that are not yet clearly understood. The head direction system was only implicitly modeled by referring directional information of landmarks to the head-body axis and to an external reference. The simulations and robotic experiments dissociated the contribution of the different modalities or structures and the static-dynamic aspects in spatial processing. In spite of this limited scope, the model is relevant for hippocampal and brain processing in general. Indeed, the same architecture receiving different input modalities was successfully used for

Figure 7: (A) Results of an experiment where the robot learned different locations in a room. The *x*,*y* plane represents the space of the experimental room. The z-axis represents the normalized level of activity of the place cells. The manifolds in different gray levels represent the overlapping activities of four different place cells, with maxima in different locations, recorded during a robotic experiment. The combination of these overlapping activities builds a potential landscape, with a potential vector, proper to every location. (B) After learning four place-action associations around the goal (filled circles with arrows), the robot could navigate to the goal from an unlearned place (empty squares) along a path materialized by a sequence of arrows (learning generalization). As in the previous figure, the $x_i y$ plane represents the space of the experimental room, in arbitrary coordinates, partitioned by four place fields. The *z*-axis represents the levels of the behavioral attractor. This figure illustrates the navigation strategy associated with the potential landscape of part A of the figure. Any unlearned location in the environment was associated with the action(s) related to the closest learned place(s). Therefore the movement (or the weighted combination of movements for a population code with smooth trajectory) associated with these places was performed. This strategy amounted to implementing in the behavior of the agent a gradient descent toward the goal. The exploration phase was not represented on this figure, just the navigation to the goal. The associated behavioral attractor basin illustrated in this figure resulted from sensorimotor learning.



learning purely temporal or spatiotemporal sequences, as well as learning by imitation (Banquet, Gaussier, Revel, et al., 2001; Gaussier, Joulain, & Banquet, 1998). Thus, the model contributes to bridging the gap between the two main hippocampal theories—cognitive map versus episodic memory. Experiments with rats and robots were conducted in parallel (Paz-Villagran et al., 2003, 2004).

The observed properties are emergent characteristics of the model and its inputs, and not direct consequences of a specific network architecture. The three levels of association jointly provided the foundations of higher cortical functions such as sequence learning and planning. Multimodal PR-PH units performed a product to give rise to landmarks by object-location association (Rolls & Treves, 1998). The activity of PR-PH units reflected, by its location and activation, the characteristics of "What" and "Where" input layers. Landmark constellations formed local views, transformed into entorhinal place codes (Frank et al., 2000; Mizumori et al., 1992; Quirk et al., 1992). The monotonical decrease of place recognition as a function of distance to a learned place in superficial EC reflected the continuity of space. As a population, these diffuse place cells in EC supported a context-independent universal map, in agreement with PC patterns in EC and SUB relatively independent of context (Sharp, 1999). Conversely, spatiotemporal learning in CA3-CA1 (Gilbert et al., 2001) computed transitions between places, which were associated with corresponding movement vectors. The model solutions showed several interesting properties.

Figure 8: (A) Cognitive map built by exploration of a simulated environment, with artificial landmarks. The landmarks are the crosses on the border. Each dot is a subgoal. The links indicate that the corresponding two subgoals have been successively activated. The subgoals and the learned connections formed the cognitive map. Each learned place represented by a dot is surrounded by an area of graded decay of activity (not represented), such that the robot entering this zone performed the learned movement associated with the transition. Thus, the trajectory of the robot toward the goal (dotted line) took advantage of the map but was not constrained by the learned trajectories. Further, simulation of the inertia of the robot provided for smooth trajectories. (B) Results of an experiment where the latent learning of an environment by the robot provided a graph-map that was subsequently used during goal-oriented navigation. The curved lines delineate the real robot trajectory. The straight lines represent the ideal trajectories derived from path integration between two adjacent locations and associated with the transitions between these locations. In spite of the absence of direct connections between nodes coding transition BC and CE (not experienced during exploration), the combination of the priming or prediction of the possible transitions by CA1 and of the diffusion of activation from the goal in prefrontal cortex network (maximal for the shortest trajectory) allowed selecting this shortcut.



4.1 Generalization. Two interactive levels of generalization were demonstrated. Locally, the PC coding for a location A fired not only when the robot was in A, but to a lesser degree for a significant area around each location, in particular for EC place cells. The generalization related to the diffuse activity of the EC place cells depended on the large size of their place fields (different from hippocampal place fields), as well as on the open environment. In the frame of a universal map, the robot learned but a few places around the goal and was able to generalize to the whole room the local learning of the capture of the goal, without the need to learn every location-action association, as in other similar models. Indeed, the movement to perform in order to reach the goal from a new place was computed as a weighted sum of the movement vectors associated with the learned neighboring places.

The local generalization was also found to be essential for a simple, straightforward use of the contextual maps during navigation. The same graded decay around peak location-specific activity made the trajectories during performance of graph-map navigation, not necessarily superposed on the learned ones. This topological interpretation of the ability of an animal to generalize an incomplete learning to novel parts of an environment is an alternative to the hypothesis of a Euclidean metric map encountered in some vectorial models of space representations (O'Keefe, 1991; Burgess et al., 1994; Arleo & Gerstner, 2000), which, however, provides a better account of novel path finding by animals. Nevertheless, the large EC place fields of our model provide a generalization capacity that allows choosing a correct place-action association in order to solve the Morris water maze from a novel starting location (cf. Figure 7).

4.2 Parahippocampal Cortical Networks and Spatial Maps. Properties of single neurons and populations closely resembling those of neurons in the parahippocampal cortices and the hippocampus in both rat and monkey were given mechanistic interpretations in terms of network operations; functional and behavioral significance in terms of spatial versus contextual maps could be associated with distinct locale navigation strategies (O'Keefe, 1991). The associations performed by the modules of the parahippocampal cortices, through proximal recurrent collaterals, without hippocampal mediation, were essentially local and induced a fusion of complementary features such as pattern and location into complex monolithic entities such as landmarks. Distinct object-location associations were encoded by different neural populations in a "What"-to-"Where" network. Yet these structures were more than simple relay stations forwarding cortical inputs to HS. They were responsible for the computation of landmarks in PR-PH and a weak spatial code in EC. Functional models have already attributed complementary roles to the spatial representation in EC-SUB versus HS (Sharp, 1999); yet our model gives a precise mathematical

formulation and a mechanistic interpretation of the two types of spatial codes in the frame of hippocampo-cortical interactions. In particular, the weak EC spatial information supports a context-independent universal map; it is also at the origin of a refined spatial code in DG and of spatiotemporal sequence learning in CA1 and downstream structures.

The navigation strategy associated with the EC spatial map implied more than a simple stimulus-response mechanism in which hippocampal spatial signals and discrete locomotor responses served, respectively, as the stimulus and the response (Sharp et al., 1996). Indeed, no direct perception of the goal or of a cue pointing to the goal was necessary. Therefore, the strategy was better characterized as a route navigation. But no links were learned between successive places (at variance with graphs), only associations between a few places and the corresponding motions to the goal, as in Burgess (Burgess et al., 1994). Yet in the graph-map, we associated transitions to sensory representations of the corresponding actions; that provided several nice properties, in particular path desambiguation, without dramatically taxing the neural memory set (about four times more transitions than simple locations). Obvious limitation, such a universal map was inappropriate for planning a trajectory to the goal (at variance with the graph-map), but was sufficient to account for simple reactive strategies according to Sharp (Sharp et al., 1996).

4.3 Hippocampal Networks, Temporal Processing, and Context-Dependent Maps. Several functional or mathematical models used the associative capacities of the CA3 network for spatial computations. McNaughton (1989) postulated linked sets of local views associated with movements in order to carry the rat from one place field to the next, without a global map-like representation of the environment. One aspect of our model comes close to a mechanistic implementation of this idea. CA3 association of two successively visited places created a transition that, through selfmotion information and path integration, was naturally and uniquely associated with the movement vector involved in the transition. Learned links between transitions during exploration formed sequence building blocks that could correspond to the elongated place fields recorded in deep EC (Frank et al., 2000). These chains generalized into graphs that supported, at the population level, contextual maps. Yet recent experimental results performed in parallel with robots and rats (Paz-Villagran et al., 2003, 2004) suggest that the hippocampal representations are only fragmentary and under the grip of current sensory information. The global, stable maps more independent of current sensory information could be stored in cortical structures such as posterior parietal (PP) or prefrontal (PF) cortices. The buildup of a map (see Figure 8A) and the existence of a graded decay of activity around each learned place avoided the combinatorial problems faced by stimulus-response and list-learning strategies.

A topological theory of spatial representation (Muller et al., 1991) and the related goal-oriented cognitive graph models (Trullier & Meyer, 2000) proposed that an interconnected CA3 population globally reflected the topological connectivity of the environment in a context-dependent manner. For both theories (McNaughton, 1989; Muller et al., 1991), some form of cognitive mapping can be viewed as a sequence learning and prediction problem. We further showed that dynamic sequence codes and stable place codes could coexist in different structures and collaborate for navigation. However, both theories (McNaughton, 1989; Muller et al., 1991) faced the difficulty of covering a continuous space by discontinuous trajectories. Attractor networks avoided this difficulty (Redish & Touretzky, 1997, 1998; Redish, 1999; Samsonovich & McNaughton, 1997). Yet it must be noticed that a sparse connectivity in a CA3 asymmetric recurrent network (Rolls & Treves, 1998) is more appropriate for learning temporal sequences (Levy, 1996), than for the generation of attractor states. This type of sequence learning by CA3 is compatible with the learning of transitions by this structure in our model, which form the building blocks of our sensorimotor sequences. In different implementations of our model, we also used neural fields and chaotic attractors (Tsuda, 2001) in order to learn and control temporospatial sequences in robotic experiments (Quoy, Banquet, & Dauce, 2001; Dauce et al., 2002). Yet the model presented here is not strictly an attractor model; in particular, just CA3 heteroassociations and not recurrent connections were implemented. Some of these attractor models (Redish, 1999) emphasized the existence of multiple maps and reference frames (reference point, orientation, and distance metric) of an environment (according to reward location in particular) as a way of coding both spatial and nonspatial context. In our model, the transitions occurred between the place fields of a same map, not between reference frames or maps as in Redish. Finally, we acknowledged the possibility of multiple maps within a single environment. Beyond that, we hypothesized that two or several complementary maps of a different nature could independently coexist in the hippocampal system and, if needed, support vicarious navigation strategies, even though there should be some stage of fusion between the two maps for the sake of spatial coherence. For the fusion of spatial view and self-motion information, Stringer (Stringer, Rolls, Trappenberg, & de Araujo, 2002) proposed appropriate connections for performing the idiothetic (self-motion) update of a continuous attractor. In our model, the transition views are associated with their corresponding movement vector. And navigation implies the whole hippocampo-cortical network. Therefore, we make a distinction between multimodal (e.g., visual and idiothetic) representations of transition-action associations hypothesized to take place in CA3 and/or SUB, and the context-dependent selection and implementation of actions in relation to these transitions that have been shown to reside in the striatum (including the nucleus accumbens) (Banquet et al., 2004). The inclusion of recurrent connections in our CA3 network would be straightforward if

they were used for pattern completion (Hopfield network) rather than for temporal diffusion of the activity (Levy, 1996). There is complementarity rather than incompatibility between the processing and learning performed by these connections and the processing currently implemented essentially based on heteroassociative connections. CA3-recurrent NMDA-knockout mice or NMDA receptor blockade (Kentros et al., 1998; McHugh et al., 1996, Rotenberg et al., 1996) essentially prevented the long-term stabilization of newly established firing fields.

Once learned, our contextual maps were used in a reactive or a planning mode that could manage several simultaneously active drives or goals (Banquet, Gaussier, Revel, et al., 2001; Gaussier et al., 2002; Banquet, Gaussier, Quoy, et al., 2001). Remarkably, navigation based on this type of map made of transitions and involving planning presented several behavioral advantages and overcame typical limitations of map-based navigation:

- Path disambiguation occurred at choice points in the graph, when several trajectories were possible.
- Due to the existence of a graded decay of activity around learned place fields, the system was not compelled to follow precisely the learned trajectories.
- The diffusion of activation from the goal location made possible creating shortcuts that had not been previously learned.
- Deadlock situations encountered during planning with place cell graphs could be solved.
- Chaining of transitions into temporospatial sequences became straightforward.

The process of remapping confirms that PCs do not just encode locations; rather, collectively, they provide a signature of the environment and context. A cue rotation during a constant task induces an angular rotation of the place fields within a stable PC population (O'Keefe & Speakman, 1987; McNaughton, 1989; Quirk, Muller, & Kubie, 1990; Markus et al., 1995; Save, Nerad, & Poucet, 2000); only a change in the geometry of the environment or in the behavioral task (Markus et al., 1995) induces a remapping (substantial shift in angular and radial position of the place fields of a PC population), implying at least a partial renewal of the CA3-CA1 population coding the space. The geometrical remapping takes place only for environments that have been previously learned (Lever et al., 2002); if not, CA3-CA1 cells undergo a topological adaptation to the shape of the new environment comparable to that of the EC place cells. This result could be accounted for by our model if two different learning dynamics were introduced: a rapid learning of path integration and/or landmark-based spatial features, and its diffusion through the hippocampal system; a slower tuning of HS neurons to the more subtle geometrical and contextual characteristics of the environment.

Movement-related information served in the model for the path integration between two place fields that was associated with transitions and also to reset views after a robot motion. This model was expanded to incorporate a detailed model of path integration (Banquet et al., 2004). In this version, the model has similarities with others (Guazzelli, Bota, & Arbib, 2001) but differs in that visual and proprioceptive information are not artificially provided to perceptual and feature detector layers; rather, it comes from real data extracted from the environment or robot movement. Both independent and merged place codes exist in distinct structures.

The computation of transition fields and their association with their corresponding direction-motion vector through path integration in the SUB implemented in the model a basic transition-action association. This essential feature of the model, beyond requiring the computation of path integration, extended the associative capacities of the CA3 network to the temporal domain (Levy, 1996) and supported the learning of temporospatial sequences in downstream structures such as the nucleus accumbens and the prefrontal cortex (Banquet et al., 2004; Poucet et al., 2004). The prediction of a temporospatial dimension in hippocampal processing was recently confirmed by the double dissociation between DG and CA1 functions in spatial and spatiotemporal (sequence) pattern discrimination (Gilbert et al., 2001). The second prediction of a basic association of a transition with the representation of the corresponding movement vector, within a purely sensory modality (and not at an interface between sensory and motor systems), was implemented by the association of a transition with its corresponding path-integration vector, coding direction, and displacement; it was based on the convergence of place information and path integration on SU and/or EC (Redish & Touretzky, 1997; Sharp, 1999). Further, whole body motion cells have been recorded in monkey CA3 field (O'Mara, Rolls, Berthoz, & Kesner, 1994). This combination of transition and action representation is also supported by path equivalence found in deep EC pyramidal cells (Frank et al., 2000), which reflects behavioral similarities between spatially close but distinct trajectories. Motion-related information and path integration could be responsible for this path equivalence. Exteroceptive, mostly visual, information would serve not only to periodically recalibrate the path-integration system, but also to transform a trajectory-dependent map in deep EC into a purely spatial map in superficial EC that could be recycled into and refined by the hippocampal system. The longer place fields recorded in deep EC neurons (Frank et al., 2000) could relate positions over longer distances and capture behavioral regularities that may support the animal's ability to generalize across experiences. The eventuality that basic transition action-representation associations do not take place at an interface between sensory and motor systems, but in a multimodal system like the hippocampus, thanks to the proprioceptive and idiothetic component of

the movement related modality, is one of the unexpected predictions of the model.

5 Conclusion .

The model makes several original contributions. First, it takes into account and gives functional significance to the existence of at least two types of PCs: diffuse EC place cells that adapt to task and geometrical context rather than change their code, and DG-CA3-CA1 well-delimited PCs that depend on task context and therefore change their code if the context is changed. Both types of PCs seem to be under the control of head direction cells, since a rotation of the landmarks induces a commensurate rotation of the place fields. The EC PCs would encode the spatial layout of the environment independent of task and context constraints on the basis of purely spatial, dominant, movement-related information used for path integration. Conversely, CA3-CA1 transition cells would encode temporospatial sequences dependent on the task context in particular. In this contextual encoding, the temporal, or at least sequential, aspect of learning during task performance would prevail on the purely spatial aspect. Both types of maps are complementary. Distinct navigation strategies in order to capture a goal have been associated with each of them.

Second, the encoding of transitions in CA3-CA1 (instead of simple locations as in other models) was inspired by the memory properties of these structures. They allowed an unambiguous and straightforward link between spatial representation and implementation into temporospatial sequences during navigation and planning. Path integration computed the ideal trajectory between two locations, whatever the exploration path in between. This was not the case when simple locations were associated with many possible displacements.

Third, these high-level functional properties derived from basic distinctions between the local associations performed by the different cortices, with a limited (even if increasing with the hierarchies of associations) scope and the global all-inclusive associations performed by the CA3 system.

Fourth, the submission of the model to the test of robotic paradigms of navigation in environments different in shape or complexity provided a functional-behavioral validation of the model and made possible the straightforward integration of two originally distinct models of hippocampal function: PC computation and timing-sequence learning. In further developments, animal and robotic experiments are conducted in parallel, during identical tasks; complex paradigms like navigation are considered to implicate, beyond the hippocampus, a network of systems, including in particular prefrontal cortex and the ventral basal ganglia. In this network, spatial as well as temporal dimensions serve as a common framework and a functional link between anatomically distant or functionally distinct systems.

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