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| Abstract                       | <p>Unravelling the neural substrates of behavior has made possible to dissociate a high level representation system dedicated to the build-up and storage of a world model, and an implementation system for decision, strategic choices, and sequential behavior. In most ecological situations, particularly in the animal kingdom, a tight functional association between the two blurs their boundaries. Nevertheless, some specific situations like sleep, memory consolidation, planning, or conversely habit performance tax specifically one of the two systems.</p> <p>Within the paradigm of spatial-temporal learning and navigation are presented the contributions of the main structures of the representation system such as hippocampus, entorhinal, prefrontal and parietal cortices; and of the implementation system, the cortical-striatal loops in particular, monitoring the transition between goal-oriented controlled behavior and automatic habit. The electrophysiological and behavioral results of a continuous navigation task which taxes both systems, as well as goal-oriented and habit spatial-temporal strategies are presented.</p> |  |
| Keywords<br>(separated by “-”) | Hippocampus - Entorhinal - Prefrontal - Parietal cortices; limbic - Associative-cognitive - Sensori-motor cortico-striatal loops - Goal-oriented behavior - Habit  |  |

# Representation-Implementation Trade-Off in Cortico-Limbic Ganglio-Basal Loops

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and B. Poucet

**Abstract** Unravelling the neural substrates of behavior has made possible to dissociate a high level representation system dedicated to the build-up and storage of a world model, and an implementation system for decision, strategic choices, and sequential behavior. In most ecological situations, particularly in the animal kingdom, a tight functional association between the two blurs their boundaries. Nevertheless, some specific situations like sleep, memory consolidation, planning, or conversely habit performance tax specifically one of the two systems.

Within the paradigm of spatial-temporal learning and navigation are presented the contributions of the main structures of the representation system such as hippocampus, entorhinal, prefrontal and parietal cortices; and of the implementation system, the cortical-striatal loops in particular, monitoring the transition between goal-oriented controlled behavior and automatic habit. The electrophysiological and behavioral results of a continuous navigation task which taxes both systems, as well as goal-oriented and habit spatial-temporal strategies are presented.

**Keywords** Hippocampus • Entorhinal • Prefrontal • Parietal cortices; limbic • Associative-cognitive • Sensori-motor cortico-striatal loops • Goal-oriented behavior • Habit

Stimulus-response and Tolman cognitive theories which issued from the splitting of Behaviorism in early twentieth century, still provide surprisingly relevant accounts of behavior, as well as a useful framework for unravelling its neural bases. Indeed, cognitivist theory introduces the concepts of representation, and goal-oriented behavior, while S-R paradigm may include habits as a repetition-related end product of the previous mode.

The outstanding progresses in identifying the neural components of behaviour allow to recognize a representation system, comprising in particular medial

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prefrontal (mPFC), entorhinal (EC) and posterior parietal (PP) cortices, hippocampus (HS), and amygdala, in direct hold with an implementation system made essentially of cortical-striatal-thalamic loops and cerebellum.

Early hierarchical models of information processing make a distinction between the subcortical structures responsible for automatic behavior and the cortical structures that allow representations of event-relationship and value responsible for purposive behavior. The cortical/subcortical hierarchy is supplemented by an intra-cortical hierarchy, which dissociates the posterior sensory areas and the anterior associative areas, such as the prefrontal cortex.

After fronto-striatal loops discovery, cortico-subcortical relationships are often described as segregated, parallel networks (limbic, associative-cognitive, sensorimotor) [1]. This description, very different from the aforementioned hierarchical organization of behavioral and cognitive processes, emphasizes a tight 'vertical' relationship between cortical and subcortical components within distinct, independent, functional channels.

Nevertheless, recent evidence of "spiraling" connections between components of these loops, in particular between striatum and midbrain dopamine (DA) systems, and between thalamic relay nuclei and cortex [2], suggests that the loops are not as closed as originally thought, but also support unidirectional, antero-posterior interactions and integration, supposing oriented transfer of activation and learning between devoted channels. Whereas, in the early models, the frontal pole of the brain, at the top of the hierarchy constitutes the endpoint of the long-range forward cortical connections, the frontal-limbic-striatal system, in the fronto-striatal loop model, is at the origin of a backward-oriented spiraling connectivity, and information transfer.

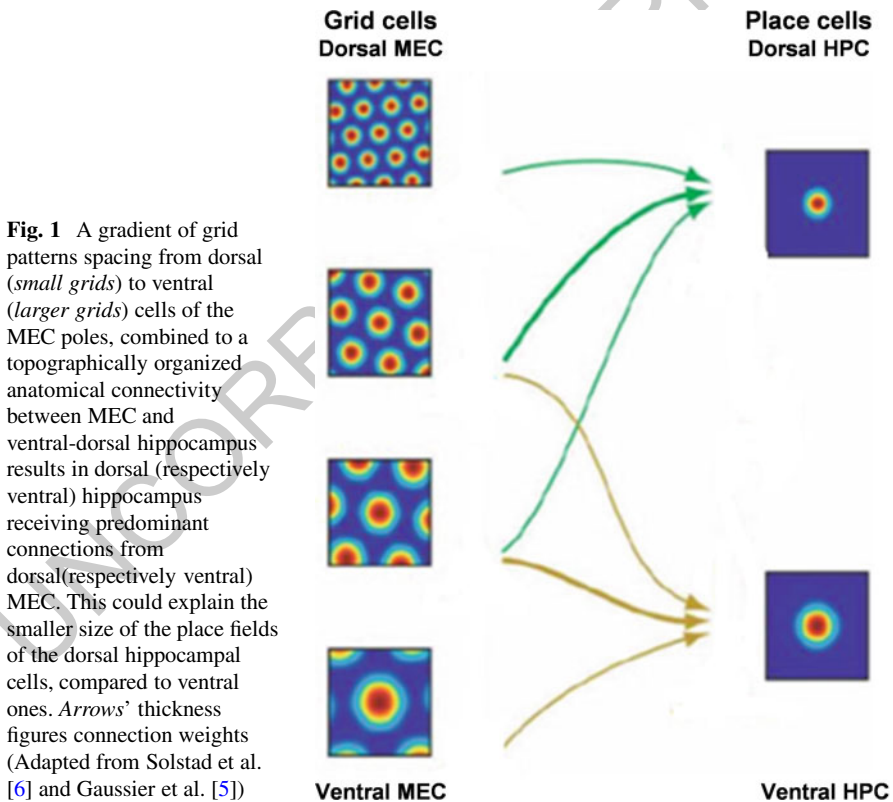
In this context, while cortico-striatal implementation systems stand at the forefront of neurobiological research, and in particular modeling, the limbic representation system is often under-considered. Indeed, in many situations, this limbic part of the representation system plays a role in the preparation-for-action and behavior. Nevertheless, there are conditions where active behavior is not the purpose of representation processes. Furthermore, in a phylogenetic perspective, it could be proposed that the degree of independence between the representation and the implementation systems stands as an index of 'encephalisation', in the animal kingdom.

We first draw a sketch of the relations of key components of the representation and implementation systems, as well as their functional articulation. Then will be presented the results of an experimental paradigm, the continuous navigation task, where typically spatial and temporal representations are directly bound to action, but also where learning deeply modulates the functional implication of the different systems involved in the task.

# 1 Representation System

As a prototypical exemplar of the representation system functions, spatio-temporal encoding within archi-, meso- and neo-cortical structures will be considered. These different levels lead to more abstract and complex representations, and eventually, to cognitive maps.

The different stages of spatial representation are relatively well known, even though their relations are not completely understood. Dorsomedial parts of the entorhinal cortex (MEC) contain cells with multiple firing fields organized in a regular grid-like structure of equilateral triangles, coextensive to the explored space (Fig. 1). Grid fields with the same triangular geometry vary across different grid cells, according to spatial frequency (field distance), orientation (tilt angle of the map), and phase (field offset relative to an external reference) [3]. Because grid cells patterns are relatively independent of the environment, and because a small number



**Fig. 1** A gradient of grid patterns spacing from dorsal (*small grids*) to ventral (*larger grids*) cells of the MEC poles, combined to a topographically organized anatomical connectivity between MEC and ventral-dorsal hippocampus results in dorsal (respectively ventral) hippocampus receiving predominant connections from dorsal(respectively ventral) MEC. This could explain the smaller size of the place fields of the dorsal hippocampal cells, compared to ventral ones. *Arrows' thickness* figures connection weights (Adapted from Solstad et al. [6] and Gaussier et al. [5])

of their firing patterns suffice to reconstruct animal's position during navigation, 83  
these EC patterns are thought to represent a universal metric of the environment, 84  
from which downstream hippocampal (Fig. 1) and cortical spatial representations 85  
are derived, even though some authors propose an alternative interpretation [4]. 86

The properties of hippocampal place fields vary according to the exact location 87  
where place cells are recorded (i.e. dentate gyrus: DG, CA3, CA1). However 88  
place cells share the spatial specificity of their strongly location-related signal, 89  
and exquisite sensitivity to the environment and context, either spatial or temporal. 90  
Different models have mechanistically demonstrated how the combination of grid 91  
cells with different spatial frequencies give rise to DG place fields of different 92  
sizes [5, 6]. Further, in a entorhinal-hippocampal loop model [5, 7, 8], spatial 93  
and temporal representations combine in CA3 and CA1 to provide a dynamic 94  
representation of the animal's navigation, under the form of *transitions* from 95  
place to place, rather than pure locations, by associating allothetic and idiothetic 96  
information. Transitions form the building blocks for sequence and trajectory 97  
encoding. 98

Indeed, beyond the hippocampal stage, and in particular in deep MEC layers, 99  
strict spatial specificity is lost, in favor of trajectory encoding. In particular, in 100  
inverted W or in alternating T maze experiments, the firing field of EC pyramidal 101  
cells expands to an entire maze arm (Fig. 2). A supra-ordinate factor, like heading 102  
direction or path context could integrate successive firing fields in cells combining 103  
place and direction or task information. 104

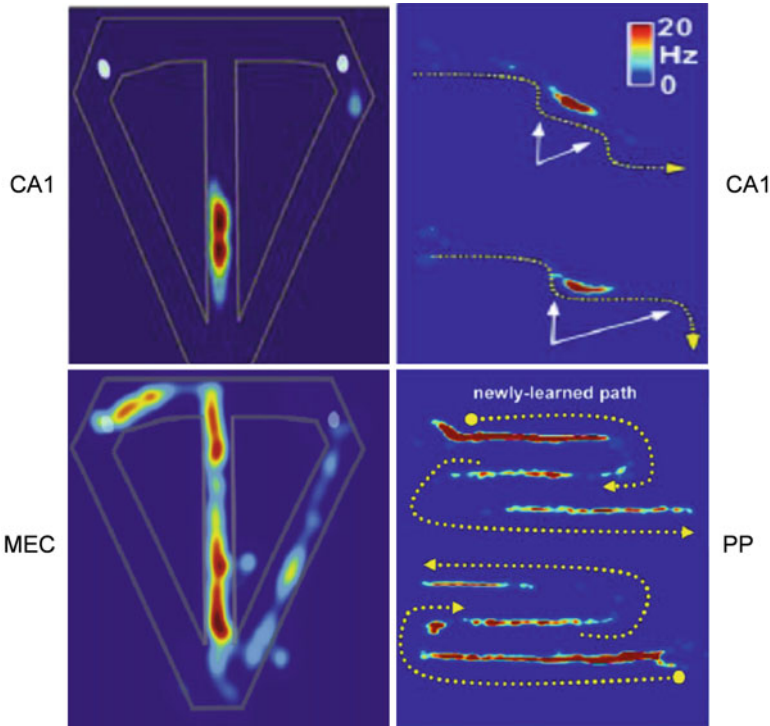
From HS, spatio-temporal information may be routed to the posterior pari- 105  
etal (PP) cortex through the retrosplenium. In PP neurons, the trajectory coding 106  
undergoes further abstraction, becoming trajectory, size and direction independent 107  
(Fig. 2); mapping the order of multiple navigational epochs in a route; integrating 108  
location and self-movement information. 109

The head direction system which pervades all these structures seems to provide 110  
coherence between allo-centric and ego-centric representations. 111

Functional dissociation between representation and implementation systems can 112  
result from at least two different rationales: the process has basically nothing to 113  
do with action, like music listening, meditation in humans . . . ; the process relates 114  
to action, but the brain is in a memory or planning mode, and implementation is 115  
not relevant, like in quiescent phases or sleep, in rodents; in this case, it seems 116  
that two opposite modulations take place: first, activation of the cortical areas 117  
where memories are recorded, and simultaneously inhibition of the subcortical 118  
implementation systems. 119

## 2 Implementation Structures 120

The phylogenetic evolution of the distinct cortical structures (archi-, paleo-, meso-, 121  
neo-cortex) takes place through the dual process of increased complexity (e.g., 122  
number of layers) and inclusion of older structures into more recent ones. The same 123



**Fig. 2** Place fields in different anatomical structures: CA1, MEC, or Posterior Parietal cortex (PP) in different maze experiments. *Left*: discharge rate-maps for CA1/MEC neurons in rats performing a T-maze alternation task for right-to-left trials, to get reward at the white hole. *Right*: same rate-maps for outbound (CA1) and outbound (*upper plots*) and inbound (*lower plot*) (PP) traversal of a newly-learned path shown by *broken yellow lines*. For each of the two traversals the PP neuron discharges along each path's entire first segment and the final half of the last segment. While the spatial specificity of the place fields of CA1 place cells remains very strong whatever the geometry of the maze, this specificity is partly lost in MEC and furthermore in PP neurons, in favor of a more functional, task-related significance (Adapted from Eichenbaum et al. [9] and Nitz [10])

type of inclusion is found within ventral and dorsal (neo)striatum, through (older) 124  
 patch and (recent) matrix compartments, such that authors suppose that cortical 125  
 evolution may have influenced striatal evolution. This could account for the tight 126  
 functional links between the two structures. Indeed, there is an anatomic, hodologic, 127  
 and functional coherence between the different compartments, limbic, associative- 128  
 cognitive and sensori-motor, at all levels of the cortico-ganglio-basal loops: cortex, 129  
 striatum, thalamus. 130

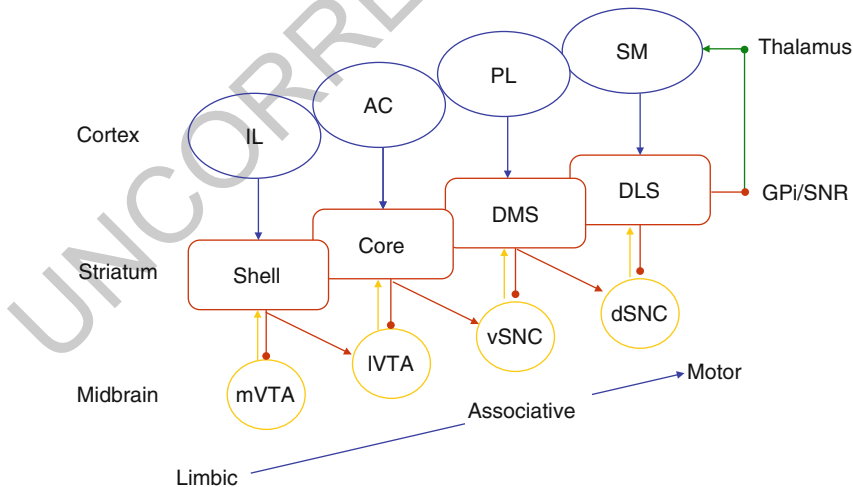
Following the characterization of cortico-striato-thalamic loops [1], the functions 131  
 of the different striatal compartments have been progressively refined, particularly 132  
 in relation to reinforcement learning, pavlovian conditioning, and instrumental 133  
 conditioning in goal oriented behavior. Thus, the nucleus accumbens (ACu) has 134  
 been more particularly associated to Pavlovian conditioning and stimulus-outcome 135

(SO) association. The core is involved in preparatory CR and anticipatory approach; core lesions impair drug-seeking behavior triggered by drug-associated reinforcers. The shell mediates consummatory CRs and hedonic URs; its lesions preserve drug-seeking acquisition.

Similarly, dorso-medial striatum (DMS), involved in instrumental conditioning, during goal-oriented actions, plays a long-lasting role in the acquisition and expression of action-outcome (AO) learning, in clear contrast with the short-lived function of the medial prefrontal cortex (mPFC) in the same conditions. It contributes to the selection and learning of situations representing valuable parts of the task. The dorsolateral striatum (DLS) transforms goal-oriented repetitive behaviors into habits and skills, and contributes to learning behavioral sequences in general.

However, this view of dedicated functions of the striatal components of the loops can only be partial if the spiraling connections between the different loops are not taken into account [2]. Striatal neurons send direct inhibition to DA neurons from which they receive projections, and also disinhibitory connections to DA neurons projecting to the distinct next striatal area, allowing unidirectional activation-propagation from limbic to associative to motor loops (Fig. 3). A learned conditioned stimulus (CS) could simultaneously suppress a ventral tegmental area (VTA) DA learning signal, and potentiate a substantia nigra compacta (SNc) DA signal in the next cognitive loop. Thus, limbic striatal loops are in a position to control learning and processing within associative and sensori-motor cortico-striatal networks.

Pavlovian Instrumental Transfer (PIT) resorts to the same principle of learning-transfer from one structure to the next: after separate learning of a classical Pavlovian SO contingency, and of an instrumental AO contingency, with the same



**Fig. 3** Spiraling connections between striatal regions and midbrain DA system. *Abbreviations:* AC Anterior cingulate, DMS(DLS) dorso-medial (lateral) striatum, IL(PL) infralimbic (prelimbic), mPFC medial prefrontal cortex, m(l)VTA medial (lateral) ventral tegmental area, v(d)SNC ventral (dorsal) substantia nigra compacta (Adapted from Yin et al. [11])

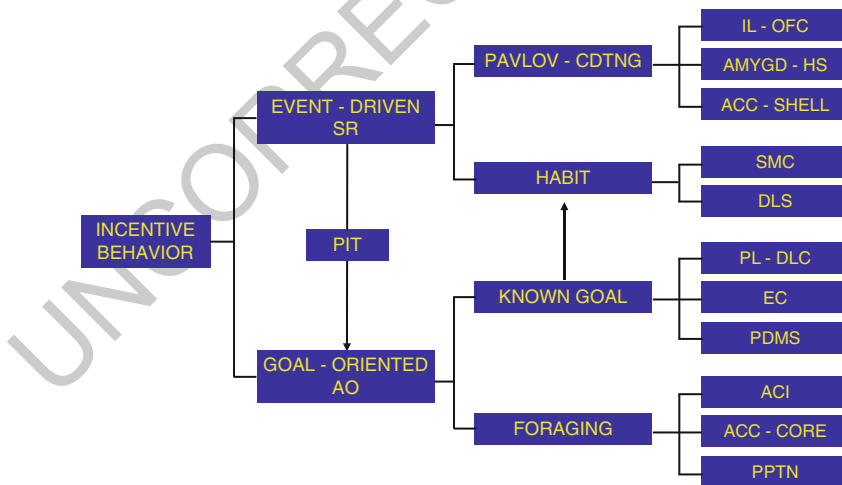


outcome, the expression of the instrumental contingency is potentiated by the concomitant presentation of the CS, but not the reverse. The integrity of both core and shell is necessary for the expression of general and specific aspects of PIT, respectively.

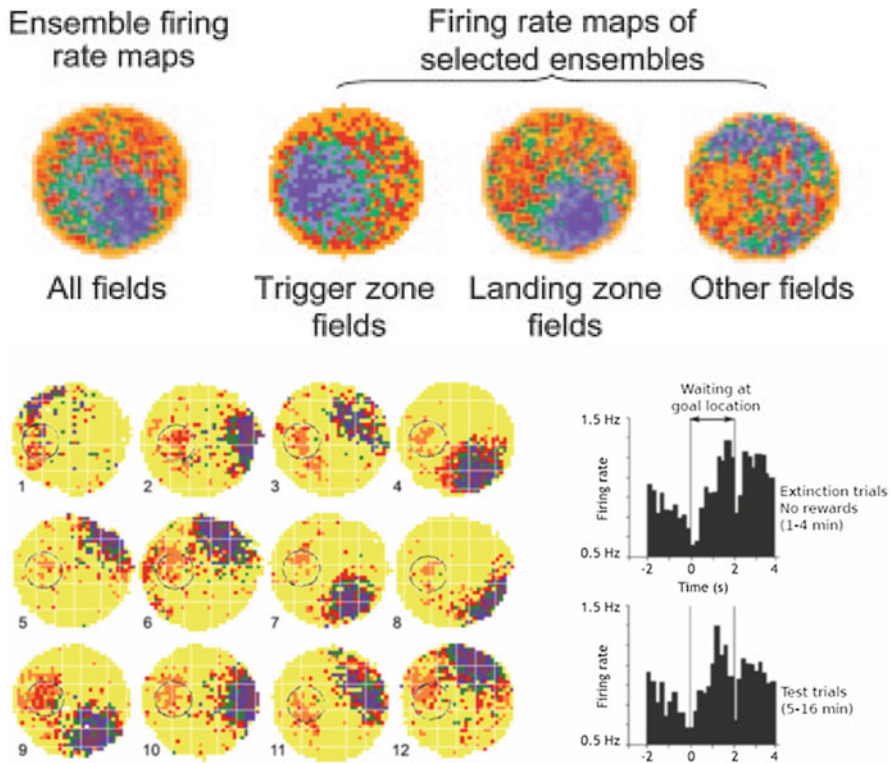
### 3 Experimental Results

In the continuous place-navigation task, the rat must reach an unmarked goal location in an open arena with a single polarizing cue card. At this goal location, it must stay immobile for a 2 s delay. A food pellet is then delivered by a food dispenser above the arena. As it bounces when hitting the ground, it can end anywhere in the arena. Therefore, the rat must explore the arena to find the food pellet.

Despite its apparent simplicity, this paradigm combines two distinct instrumental conditioning tasks: -goal-oriented navigation to the virtual goal zone, and -foraging to find the food pellet; and also two variants of Pavlovian conditioning: -classical (CS=click of food dispenser; US=food pellet); -secondary conditioning (CS=Goal zone landmark configuration; US=Click). Therefore, all cortical and subcortical areas presented in the branching tree describing learning and performance in general (Fig. 4) should be concerned, if we suppose that goal navigation becomes an habit after overtraining.



**Fig. 4** The different types of behaviors and their interrelations are associated to the structures that support them. *Abbreviations:* AO action-outcome, DLPFC dorsolateral prefrontal cortex, EC entorhinal cortex, OFC orbitofrontal cortex, PIT pavlovian-instrumental transfer, PPTN pedunculo-pontine tegmental nucleus, SMC, sensori-motor cortex, SR stimulus-response



**Fig. 5** *Upper*: place fields in PL-IL neurons of mPFC (Hok et al. [12]); *Lower left*: spatial activity of hippocampal CA1 place cells (Hok et al. [12]). *Circles* mark goal location and secondary fields; *Lower right*: cumulative PETHs for all recorded CA1 place cells at the goal

Most of these results challenge classical knowledge on navigation: First, PL/IL 179  
rather than anterior cingulate neurons of mPFC have clear spatial correlates, in 180  
particular at the goal and landing zones [12, 13] (Fig. 5). This is all the more 181  
important that no spatial correlates were found in a simple foraging task [14]. 182

In HS, place fields were not overrepresented in the goal zone, as expected. Yet, 183  
after overtraining, HS place cells presented, in addition to their location-specific 184  
main place field, a weaker secondary field at the goal location as rats were waiting 185  
for the required 2 s [13] (Fig. 5). 186

Third, HS secondary fields, as well as PL goal cell activity displayed a temporal 187  
profile reaching a maximum just prior the end of the 2 s waiting period (Fig. 5) 188

Finally, ventral HS inactivation suppressed PL place and timing activity [15], 189  
whereas mPFC inactivation did affect neither HS place cell timing activity nor 190  
secondary fields [16]. 191

These results confirm the supposed function of mPFC in combining place and 192  
valence information to define goals; yet, confirming previous results, this function 193

appears to be transient and limited to early learning stages. Indeed, inactivation of mPFC after overtraining does not affect behavioral performance [16]. These findings suggest both bottom-up and top-down information transfer between mPFC and HS, that could be expressed by the secondary fields of HS place cells. Moreover, for the first time, to the best of our knowledge, the very same HS pyramidal cells are shown to display simultaneously spatial and timing codes, which are conveyed to neocortical structures. Space and time, possibly through frequency modulation of the electrical field potentials could form a common frame for the coordination, and eventually the synchrony of distant brain structures. As a whole, these results shed new light on the role of the PF-HS circuits in goal-oriented and other types of navigation.

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**References**

1. Alexander, G.E., DeLong, M.R. & Strick, P.L. (1986) Parallel organization of functionally segregated circuits linking basal ganglia and cortex. *Annu.Rev. Neurosci.*, 9, 357–381.
2. Haber, S.N. (2003) The primate basal ganglia: parallel and integrative networks *J. Chem. Neuroanat.*, 26, 317–330.
3. Fyhn, M., Molden, S., Witter, MP, Moser, El., Moser, MB. (2004) Spatial representation in the entorhinal cortex. *Science* 305:1258–1264.
4. Poucet, B, Sargolini, F., Song, E. Y., Hangya, B., Fox, S. E., Muller, R. (2013) Independence of landmark and self-motion guided navigation: a different role for grid cells. Submitted to *Phil. Trans.R. Soc. B-Issue*.
5. Gaussier, P., Banquet, JP, Sargolini, F., Giovannangeli, C., Save, E., Poucet, B. (2007) A model of grid cells involving extrahippocampal path integration and the hippocampal loop. *J of Integrative Neuroscience*, 6(3), 447–476.
6. Solstad, T., Moser, E.I., and Einevoll, G.T. (2006) From grid cells to place cells: A mathematical model. *Hippocampus* 16:1026–1031.
7. Banquet, J. P., Gaussier, P., Quoy, M., Revel, A., Bur nod, Y. (2005). A hierarchy of associations in hippocampo-cortical systems: cognitive maps and navigation strategies. *Neural Comput.*, 17(6):1339–1384.
8. Hirel, J., Gaussier, P., Quoy, M., Banquet, J.P., Save, E. & Poucet, B. (2013) The hippocampocortical loop : Spatio-temporal learning and goal-oriented planning in navigation. *Neural Netw.*, 43:8–21.
9. Eichenbaum, H., Sauvage, M., Fortin, N., Komorowski, R., Lipton, P. (2012). Towards a functional organization of episodic memory in the medial temporal lobe. *Neuroscience and Biobehavioral Reviews* 36: 1597–1608.
10. Nitz, D.A. (2006) Tracking Route Progression in the Posterior Parietal Cortex. *Neuron* 49: 747–756.
11. Yin, H.H., Ostlund, S.B. & Balleine, B.W (2008). Reward-guided learning beyond dopamine in the nucleus accumbens: the integrative functions of cortico-basal ganglia networks. *European J. of Neurosci* 28:1437–1448.
12. Hok V, Save E, Lenck-Santini PP, Poucet B (2005) Coding for spatial goals in the prelimbic/infralimbic area of the rat frontal cortex. *Proc Natl Acad Sci U S A* 102:4602–4607.

13. Hok V, Lenck-Santini PP, Roux S, Save E, Muller RU, Poucet B (2007) Goal-related activity in hippocampal place cells. *J Neurosci* 27: 472–482. 239  
240
14. Poucet, B. (1997). Searching for the spatial correlates of unit firing in the prelimbic area of the rat medial frontal cortex. *Behav. Brain Res.*, 84:151–159. 241  
242
15. Burton BG, Hok V, Save E, Poucet B (2009) Lesion of the ventral and intermediate hippocampus abolishes anticipatory activity in the medial prefrontal cortex of the rat. *Behav Brain Res* 199:222–234. 243  
244  
245
16. Hok, V., Chah, E., Save, E., & Poucet, B. (2013). Prefrontal cortex focally modulates hippocampal place cell firing patterns. *J Neurosci* 33:3443–3451. 246  
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