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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 (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

Jean-Paul Banquet, Ph. Gaussier, M. Quoy, E. Save, F. Sargolini, 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, sensori-motor) [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

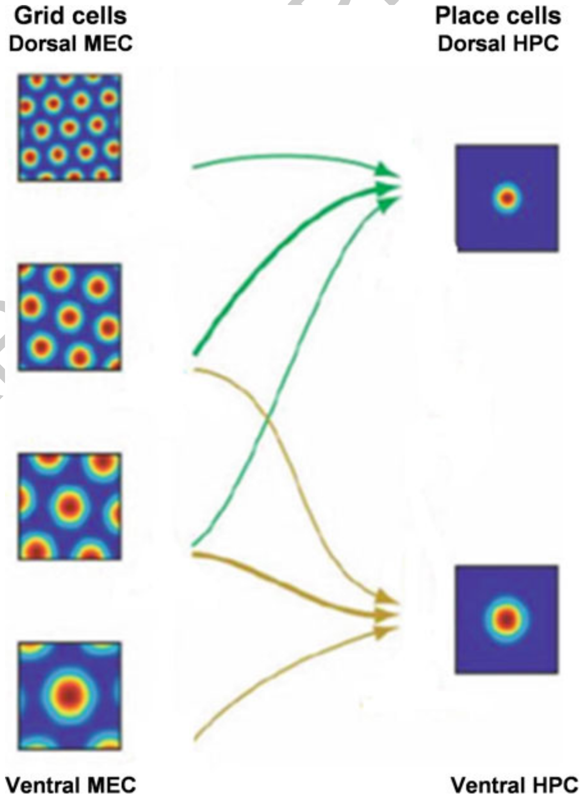

Fig. 1 A gradient of grid patterns spacing from dorsal (*small grids*) to ventral (*larger grids*) cells of the MEC poles, combined to a topographically organized anatomical connectivity between MEC and ventral-dorsal hippocampus results in dorsal (respectively ventral) hippocampus receiving predominant 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, these EC patterns are thought to represent a universal metric of the environment, from which downstream hippocampal (Fig. 1) and cortical spatial representations are derived, even though some authors propose an alternative interpretation [4].

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

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

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

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

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

2 Implementation Structures

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

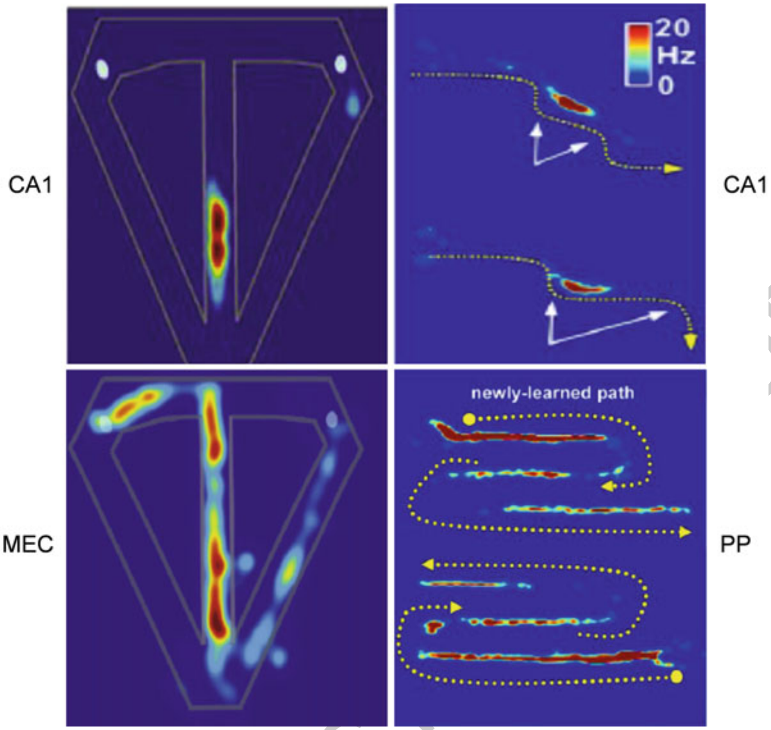

Fig. 2 Place fields in different anatomical structures: CA1, MEC, or Posterior Parietal cortex (PP) in different maze experiments. *Left*: discharge rate-maps for CA1/MEC neurons in rats performing a T-maze alternation task for right-to-left trials, to get reward at the white hole. *Right*: same rate-maps 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) patch and (recent) matrix compartments, such that authors suppose that cortical evolution may have influenced striatal evolution. This could account for the tight functional links between the two structures. Indeed, there is an anatomic, hodologic, and functional coherence between the different compartments, limbic, associative-cognitive and sensori-motor, at all levels of the cortico-ganglio-basal loops: cortex, striatum, thalamus.

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

(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

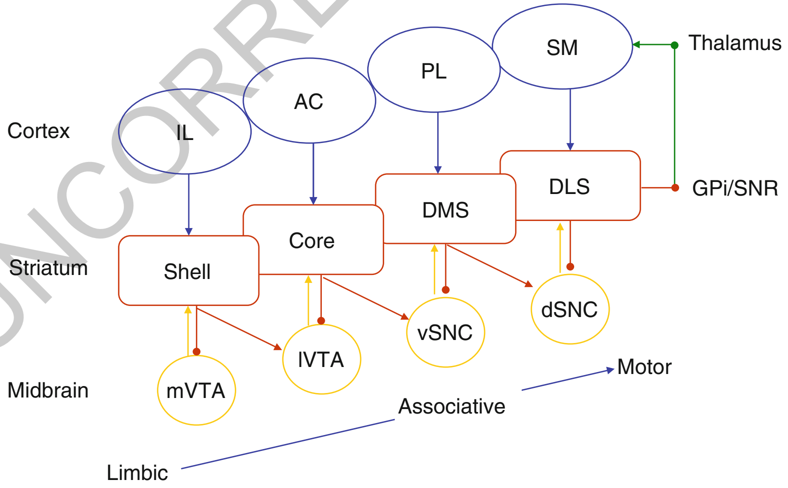

Fig. 3 Spiraling connections between striatal regions and midbrain DA system. *Abbreviations*: *AC* Anterior cingulate, *DMS(DLS)* dorso-median (lateral) striatum, *IL(PL)* infralimbic (prelimbic), *mPFC* medial prefrontal cortex, *m(l)VTA* medial (lateral) ventral tegmental area, *v(d)SNC* ventral (dorsal) 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.

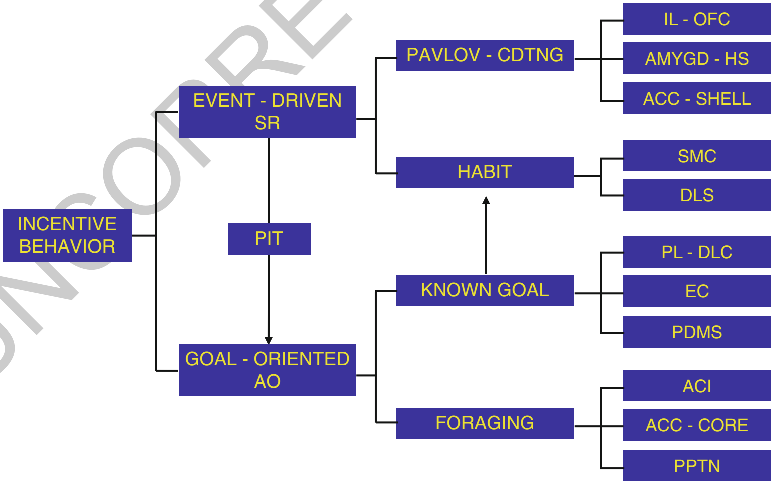

Fig. 4 The different types of behaviors and their interrelations are associated to the structures that support them. *Abbreviations: AO* action-outcome, *DLPFC* dorsolateral prefrontal cortex, *EC* entorhinal cortex, *OFC* orbitofrontal cortex, *PIT* pavlovian-instrumental transfer, *PPTN* pedonculo-pontine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

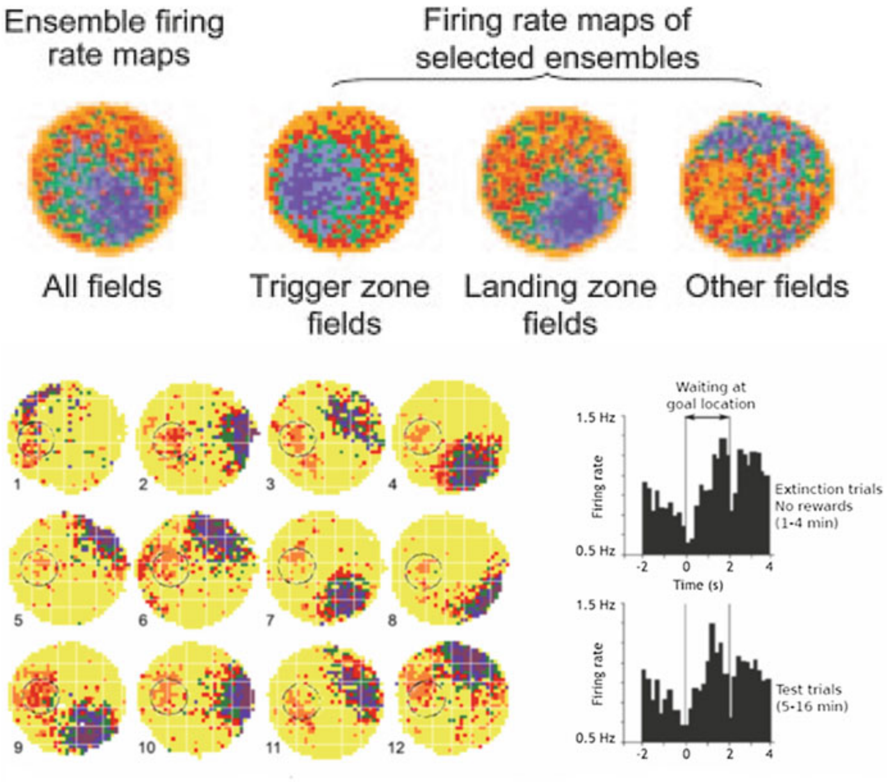

Fig. 5 *Upper*: place fields in PL-IL neurons of mPFC (Hok et al. [12]); -*Lower left*: spatial activity of hippocampal CA1 place cells (Hok et al. [12]). *Circles* mark goal location and secondary fields; *Lower right*: cumulative PETHs for all recorded CA1 place cells at the goal

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

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

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

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

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