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## Neuronal synchrony

Résumé des conférences du Collège de France (2007-2008)

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### 1. NEURONAL SYNCHRONY : METABOLIC AND WIRING COSTS OF EXCITATORY AND INHIBITORY SYSTEMS

The major part of the brain's energy budget (~ 60-80%) is devoted to its communication activities. While inhibition is critical to brain function, relatively little attention has been paid to its metabolic costs. Understanding how inhibitory interneurons contribute to brain energy consumption (brain work) is not only of interest in understanding a fundamental aspect of brain function but also in understanding functional brain imaging techniques which rely on measurements related to blood flow and metabolism. In this talk I will examine issues relevant to an assessment of the work performed by inhibitory interneurons in the service of brain function.

### 2. NEURONAL SYNCHRONY : OSCILLATORY AND NON-OSCILLATORY EMERGENCE OF CELL ASSEMBLIES

Timing of spikes within the theta cycle has been shown to reflect the spatial position of the animal ("phase precession"). The phase of spikes correlates more strongly with distance than with the time elapsed from the point the rat enters the place field. We show here that at faster running speeds place cells are active for fewer theta cycles but oscillate at a higher frequency and emit more spikes per cycle. As a result, the phase shift of spikes from cycle to cycle (i.e., temporal precession slope) is faster. Interneurons also show transient phase precession and contribute to the formation of coherently precessing assemblies. Thus, the speed-correlated increase of place cell oscillation is responsible for the phase-distance invariance of hippocampal place cells. We report that temporal spike sequences from hippocampal "place" neurons on an elevated track recur in reverse order at the end of a run but in forward order in anticipation of the run, coinciding with sharp waves. Vector distances between the place fields are reflected in the temporal structure of these sequences. This bidirectional reenactment of temporal sequences may contribute to the establishment of higher order associations in episodic memory.

### 3. NEURONAL SYNCHRONY : INTERNALLY ADVANCING ASSEMBLIES IN THE HIPPOCAMPUS

Five key topics have been reverberating in hippocampal-entorhinal cortex research over the past five decades: episodic and semantic memory, path integration ("dead reckoning") and landmark ("map") navigation, and theta oscillation. We suggest that the systematic relations between single cell discharge and the activity of neuronal ensembles reflected in local field theta oscillations, provide a useful

insight into the relationship among these terms. In rats trained to run in direction-guided (1-dimensional) tasks, hippocampal cell assemblies discharge sequentially, with different assemblies active on opposite runs, that is place cells are unidirectional. Such tasks do not require map representation and are formally identical with learning sequentially occurring items in an episode. Hebbian plasticity, acting within the temporal window of the theta cycle, converts the travel distances into synaptic strengths between the sequentially activated and unidirectionally connected assemblies. In contrast, place representations by hippocampal neurons in 2-dimensional environments are typically omnidirectional, characteristic of a map. Generation of a map requires exploration, essentially a dead reckoning behavior. I suggest that orthogonal and omnidirectional navigation through the same places (junctions) during exploration gives rise to omnidirectional place cells and, consequently, maps free of temporal context. Analogously, multiple crossings of common junction(s) of episodes convert the common junction(s) into context-free or semantic memory. Theta oscillation can hence be conceived as the navigation rhythm through both physical and mnemonic space, facilitating the formation of maps and episodic/semantic memories.

A longstanding conjecture in neuroscience is that aspects of cognition depend on the brain's ability to self-generate sequential neuronal activity. We found that reliably and continually-changing cell assemblies in the rat hippocampus appeared not only during spatial navigation but also in the absence of changing environmental or body-derived inputs. During the delay period of a memory task each moment in time was characterized by the activity of a unique assembly of neurons. Identical initial conditions triggered a similar assembly sequence, whereas different conditions gave rise, uniquely, to different sequences, thereby predicting behavioral choices, including errors. Such sequences were not formed in control, non-memory, tasks. We hypothesize that neuronal representations, evolved for encoding distance in spatial navigation, also support episodic recall and the planning of action sequences.

#### 4. NEURONAL SYNCHRONY : COUPLING OF HIPPOCAMPAL AND NEOCORTICAL SYSTEMS

Both the thalamocortical and limbic systems generate a variety of brain state-dependent rhythms but the relationship between the oscillatory families is not well understood. Transfer of information across structures can be controlled by the offset oscillations. I suggest that slow oscillation of the neocortex, temporally coordinates the self-organized oscillations in the neocortex, entorhinal cortex, subiculum and hippocampus. Transient coupling between rhythms can guide bidirectional information transfer among these structures and might serve to consolidate memory traces.

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