Theta and Gamma Oscillations as the Clocking System for a Neural Code used by Cortex and Hippocampus

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Theta oscillations occur in many brain regions. In many cases it is clear that theta and gamma occur together. Moreover, the two oscillations interact ---gamma amplitude is modulated at theta frequency---- suggesting that they are part of a common functional system (Bragin et al., 1995). I will argue that theta and gamma oscillations are a clocking system for a neural code that allows multiple items to be stored in working memory. In this code, individual items are represented by the group of cells that fire in a given gamma cycle (a period of about 20msec). Note that the temporal synchrony postulated to encode an item is not precise, unlike the coding schemes of Singer in which millisecond differences in firing are deemed important. In the theta/gamma scheme, different items are encoded in different gamma subcycles of theta, i.e. with different discrete theta phase. Importantly, such coding provides an absolute phase reference that can be used to record the order of items.

The term “working memory” includes both the process of “short-term memory” in which incoming sensory information is kept on-line in cortex and the process by which information stored in long-term memory (i.e. in synaptic weights) is brought back on-line during recall. What follows is a brief review of the evidence that both types of working memory involve theta/gamma coding.

Hippocampal Recall Process: The phase precession of hippocampal place cells provides the clearest evidence to date of the importance of theta phase (O'Keefe and Recce, 1993). Reconstruction of the animal’s position is greatly improved by taking theta phase into consideration, but phase distinctions finer than a gamma cycle do not improve reconstruction accuracy (Jensen and Lisman, 2000). The correlation of cell firing with field gamma oscillations is established (Bragin et al., 1995), providing support for a discrete phase code clocked by gamma. The phase precession has been interpreted as a recall process: during each theta cycle, a spatial cue produces the recall from long-term memory of the next 5-6 places along a well known track (Jensen and Lisman, 1996; Tsodyks et al., 1996). Moreover, the circuitry of the hippocampus appears well suited to perform such sequence recall (Lisman, 1999) (see also Raffone et al, this meeting)

Multi-item short-term memory: The gating of human cortical theta oscillations precisely during the period of short-term memory (Raghavachari et al., 2001) provides the clearest evidence for the involvement of theta in short-term memory. Gamma oscillations are also observed, but the interdependence of the oscillations is not yet established. The theta/gamma coding scheme may explain fundamental behavioral findings regarding short-term memory (Lisman and Idiart, 1995); the fact that there are about 7 gamma cycles within a theta cycle could account for the 7+-2 capacity limit on short-term memory and the period of a gamma cycle could explain the 20-30msec temporal separation of items during memory scanning. With the recent discovery of single unit activity in sensory cortex that is theta modulated during short-term memory (Lee et al., 2003), it will become possible to test a critical prediction of the theta/gamma model: during a multi-item short-term memory task cells encoding different items should fire with different theta phase and preserve the order of item of presentation.

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