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## Review

## Multifaceted roles for low-frequency oscillations in bottom-up and top-down processing during navigation and memory

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## ABSTRACT

A prominent and replicated finding is the correlation between running speed and increases in low-frequency oscillatory activity in the hippocampal local field potential. A more recent finding concerns low-frequency oscillations that increase in coherence between the hippocampus and neocortical brain areas such as prefrontal cortex during memory-related behaviors (i.e., remembering the correct location to visit). In this review, we tie together movement-related and memory-related low-frequency oscillations in the rodent with similar findings in humans. We argue that although movement-related low-frequency oscillations, in particular, may have slightly different characteristics in humans than rodents, placing important constraints on our thinking about this issue, both phenomena have similar functional foundations. We review four prominent theoretical models that provide partially conflicting accounts of movement-related low-frequency oscillations. We attempt to tie together these theoretical proposals, and existing data in rodents and humans, with memory-related low-frequency oscillations. We propose that movement-related low-frequency oscillations and memory-related low-frequency oscillatory activity, both of which show significant coherence with oscillations in other brain regions, represent different facets of “spectral fingerprints,” or different resonant frequencies within the same brain networks underlying different cognitive processes. Together, movement-related and memory-related low-frequency oscillatory coupling may be linked by their distinct contributions to bottom-up, sensorimotor driven processing and top-down, controlled processing characterizing aspects of memory encoding and retrieval.

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## Introduction

Research on navigation and memory-related low frequency oscillations suggest two distinct functional characterizations. Extensive empirical and theoretical work in the rodent has helped to characterize a movement-related 3–12 Hz oscillation in the hippocampus. This low-frequency oscillation, also referred to as the “theta” oscillation, increases with movement speed (McFarland et al., 1975) and has a distinct relationship with the activity of “place cells,” which code spatial location (O’Keefe and Recce, 1993). We refer to these oscillations as “movement-related low-frequency oscillations”. Comparison of changes in oscillatory coherence for correct vs. incorrect retrieval of which arm is baited on a maze alternation task has also identified a potentially separate phenomenon of coherent and/or phase synchronized low-frequency oscillations (Benchenane et al., 2010; Fujisawa and Buzsaki, 2011; Jones and Wilson, 2005b). These oscillations increase in coherence between hippocampus and prefrontal cortex (PFC) during correct alternations on a maze or correct utilization of a recently learned rule but do not appear to be driven by movement-speed alone (Benchenane et al., 2010; Fujisawa and Buzsaki, 2011; Jones and Wilson, 2005b). We refer to these oscillations, and oscillatory changes driven by memory processing in general (for a review, see: Nyhus and Curran, 2010), as “memory-related low-frequency oscillations.”

Recordings in the human brain have also identified low-frequency oscillations, although with slightly different characteristics, providing an important extension to the rodent work. Humans display movement-related hippocampal low-frequency oscillations (Ekstrom et al., 2005; Watrous et al., 2011, *in press*) although some of their properties – specifically, their peak frequency and mean cycle length – may differ somewhat from those characterized in rodents (Lega et al., 2012; Watrous et al., 2011, *in press*). Recordings in humans from multiple cortical sites and the medial temporal lobe, similar to the rodent, have demonstrated the presence of low-frequency oscillations that increase in coherence during correct memory retrieval (Anderson et al., 2009; Watrous et al., 2013b). These results thus provide an important extension to similar findings in rodents by relating these increased oscillations specifically to successful memory encoding and retrieval (Rutishauser et al., 2010; Sederberg et al., 2003) and coding of different contexts (Watrous et al., 2013b).

Given the literature suggesting differences between movement and memory-related low-frequency oscillations, as well as the need to tie together these oscillations in rodents with humans, the purpose of this review is two-fold. First, we wish to provide a characterization of movement-related oscillations in both rodents and humans and discuss possible reasons why low-frequency oscillations in the two species may manifest differently. We will also discuss several theoretical frameworks that account for movement-related low-frequency oscillations and provide explanations for their functional relevance. We will then discuss evidence in rodents and humans that suggests that these movement-related oscillations are not just a local phenomenon within the hippocampus but interact in a coherent fashion with similar low-frequency oscillations in areas such as parietal cortex (Ekstrom et al., 2005; Sirota et al., 2008).

Second, we will discuss memory-related low-frequency coherent oscillations between hippocampus, prefrontal cortex, and other cortical and subcortical areas, and possible differences in their functional characteristics compared to movement-related oscillations. Finally, we will attempt to tie together movement-related and memory-related oscillations to provide a unitary account of their function. We suggest that movement-related oscillations represent the down-stream result of sensorimotor entrained signals (Schroeder et al., 2010) – specifically, increases in power and frequency locked to increases in optic flow and motor movements (Chen et al., 2013). In contrast, we suggest that memory-related oscillations manifest as the result of long-range synchronization underlying recruitment and cooperation of different brain regions important for decisions, including retrieval. As such, we argue that these manifest as largely top-down, internally driven signals

(e.g., Buschman and Miller, 2007). While many aspects of our model remain to be validated, we believe that it represents a first step in trying to tie together disparate findings on low-frequency oscillations across mammalian species.

## Rodent hippocampal low-frequency oscillations and correlation with movement

Vanderwolf first identified rhythmic low-frequency oscillations occurring between 8 and 8.3 cycles/second during walking and rearing (“voluntary movements”) in the local field potential (LFP) of the rodent hippocampus. This activity was distinct from lower frequency activity (6.6–7 Hz) that emerged during handling food, licking, or grooming. Extending Vanderwolf’s findings relating theta oscillations to voluntary movements, McFarland et al. (1975), testing rats running on a treadmill at various speeds, concluded that oscillatory amplitude varied monotonically with running speed (McFarland et al., 1975). Several studies have since replicated this finding in both rats and other species, including mice, guinea pigs, rabbits, cats, and dogs (Arnolds et al., 1979; Chen et al., 2011, 2013; Czurko et al., 1999; Ekstrom et al., 2001; Geisler et al., 2007; Li et al., 2012; Shen et al., 1997). A similar and related finding is that oscillatory frequency also increases with running speed; this frequency shift is fairly slight (<1 Hz in some cases) (Geisler et al., 2007) although consistently observed in several reports (Chen et al., 2011; Geisler et al., 2007; Li et al., 2012; Oddie et al., 1996; Recce, 1994; Shen et al., 1997; Woodnorth and McNaughton, 2005). The increases in theta power and frequency with running speed are often considered benchmark findings on low-frequency oscillations and have had a significant influence on theories detailing the functional significance of theta during both navigation and memory (Bland and Oddie, 2001; Buzsaki, 2006; Hasselmo et al., 2002).

Rodent movement-related oscillations also have a fairly precise link with the phase at which hippocampal pyramidal cell spikes occur. During navigation, pyramidal cells often fire at specific spatial locations. Within the place field of these “place cells” (O’Keefe and Dostrovsky, 1971), spikes tend to occur at earlier phases of on-going theta oscillation as the rat traverses the place field (O’Keefe and Recce, 1993), termed “phase precession.” The increase in power and frequency is central to allowing phase precession; increases in power with movement provide sufficient oscillatory signal for phase precession to occur in the first place. The increase in frequency with running speed is also important; because neural firing rate also increases with running speed (McNaughton et al., 1983), increases in theta frequency allow for a critical offset between the activity of place cells and the period of theta (Geisler et al., 2007). The simultaneous offset, yet coupled activity of theta oscillations and firing rate, is one explanation of how phase precession might emerge mechanistically within the hippocampus (Geisler et al., 2007; O’Keefe and Recce, 1993).

Phase precession also provides a critical link between oscillations, neural activity, and behavior. Including phase in reconstruction of a rat’s location during navigation in addition to firing rate conveys more information about the rat’s spatial position than firing rate alone (Jensen and Lisman, 2000). Phase coding may also provide a critical timing mechanism for controlling what types of information the activity of single neurons in the hippocampus provides compared with rate coding (Huxter et al., 2003). Another interesting proposal relates phase precession to the binding of memories via phase offsets between different place fields (Dragoi and Buzsaki, 2006). Additionally, several *in vivo* and *in vitro* studies have linked theta oscillations to states of increased and decreased synaptic plasticity. Long-term potentiation (LTP), a measure of synaptic plasticity in the hippocampus and elsewhere, is modulated by the theta oscillation (Holscher et al., 1997; Huerta and Lisman, 1995), such that LTP is easier to induce at the peak compared to the trough of theta. This in turn has provided an important link between low-frequency oscillations as a modulator of neural activity and information coding generally (Seager et al., 2002). Together, these studies

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