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Review

Oscillatory multiplexing of neural population codes for interval timing and working memory

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ABSTRACT

Interval timing and working memory are critical components of cognition that are supported by neural oscillations in prefrontal–striatal–hippocampal circuits. In this review, the properties of interval timing and working memory are explored in terms of behavioral, anatomical, pharmacological, and neurophysiological findings. We then describe the various neurobiological theories that have been developed to explain these cognitive processes – largely independent of each other. Following this, a coupled excitatory – inhibitory oscillation (EIO) model of temporal processing is proposed to address the shared oscillatory properties of interval timing and working memory. Using this integrative approach, we describe a hybrid model explaining how interval timing and working memory can originate from the same oscillatory processes, but differ in terms of which dimension of the neural oscillation is utilized for the extraction of item, temporal order, and duration information. This extension of the striatal beat-frequency (SBF) model of interval timing (Matell and Meck, 2000, 2004) is based on prefrontal–striatal–hippocampal circuit dynamics and has direct relevance to the pathophysiological distortions observed in time perception and working memory in a variety of psychiatric and neurological conditions.

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1. Introduction

Neural oscillations are a fundamental property of brain function that modulate cognitive processes such as attention, memory, and decision-making as well as the duration and beat-based timing mechanisms involved in timing and time perception (Allman et al., 2014; Benchenane et al., 2011; Buhusi and Meck, 2005; Cheng et al., 2008, 2009; DeCoteau et al., 2007; Matell and Meck, 2004; Teki et al., 2011, 2012; Varela et al., 2001; Wang, 2001; Ward, 2003). For example, in the context of working memory, oscillatory processes are thought to facilitate the encoding, maintenance, and synchronization of stimulus attributes presented in specific temporal sequences (Bonnefond and Jensen, 2012). This temporal structure provides us with the ability to compare the durations of relevant events (stimuli or responses), allowing us to perceive that 'it's time' after a specific sequence of events has passed. In this sense, interval timing and working memory are intimately related and may largely be distinguished in terms of the type of information that is extracted from the underlying mechanisms, i.e., duration and temporal order information in the case of interval timing and specific auditory, visual, or semantic information in the case of working memory (see Baddeley, 2012; Lustig et al., 2005). However, it's important to note that interval timing reflects a specialized form of working memory in that an internal representation of time needs to be maintained in order to control temporal processing even in the absence of an external stimulus (Aagten-Murphy et al., 2014; Buhusi and Meck, 2000; Hälbig et al., 2002; Meck and Benson, 2002; Meck et al., 1984; Muller and Nobre, 2014; Wiener, 2014; Wiener and Coslett, 2008).

Various lines of research have examined the capacity and limitations of interval timing and working memory; however many issues remain unresolved and numerous controversies exist (Baddeley, 2003; Broadway and Engle, 2011a,b; Buhusi and Meck, 2009b; Fortin, 1999; Fortin et al., 2010; Taatgen and van Rijn, 2011; van Rijn et al., 2011). In order to get a clearer picture of the connections between interval timing and working memory, their shared features need to be viewed from multiple levels—including functional and neural mechanisms (Meck, 2003; Meck et al., 1984). Diverse evidence supporting co-variation between interval timing and working memory will be brought together so that the knowledge from each domain can inform and constrain the other. In an effort to achieve this goal, properties that are crucial to both interval timing and working memory will be selected and focused on such that the defining characteristics of each process are chosen and critically reviewed based on this overall goal.

To begin with, temporal processing occurs across different time scales ranging from sub-second intervals to hours and days and has been categorized into millisecond, interval, and circadian timing (Buhusi and Meck, 2005; Buonomano, 2007; Lewis and Miall, 2009). Millisecond timing is frequently studied in reference to speech perception and motor control (Kotz and Schwartze, 2010; Ivry et al., 2002; Schirmer, 2004), whereas interval timing (ranging from milliseconds to minutes) is known to be important for computational learning and decision-making (Gallistel and Gibbon, 2000, 2001; Gibbon, 1977; Meck et al., 2012b; Taatgen et al., 2007; van Rijn, 2014; van Rijn et al., 2014; Yin et al., in press). Multiple lines of research suggest an important cut-off dividing sub-second and supra-second timing between 500 ms and 2 s, with evidence of different properties (e.g., scalar vs. non-scalar variance, differential interaction/interference in dual-tasks, and the ability to make ordinal comparisons—see Buonomano et al., 2009; Cordes and Meck, 2014; Cordes et al., 2007; Fortin and Couture, 2002; Ivry and Spencer, 2004; Johnston et al., 2006; Michon, 1985; Rammsayer and Lima, 1991; Rammsayer and Ulrich, 2011). In addition to the sub- and supra-second distinction, Lewis and Miall (2003a,b, 2006) have considered other factors such as whether stimuli reoccur in a repeating cycle so that the temporal sequence can be predicted with relatively little (if any) attention; and whether the durations are defined by motor movement. As a consequence, they proposed two timing systems that engage different neuronal circuits—one that is automatic and another that is cognitively controlled (Lewis and Miall, 2003b). In this review, for better comparison with working memory, an emphasis will be placed on cognitively controlled temporal processing involving supra-second intervals not defined by specific movements or a continuous predictable pattern of stimulus presentation (see Matthews and Meck, 2014, in press; Matthews et al., 2014).

A "multi-component" model of working memory developed by Baddeley and colleagues (e.g., Baddeley, 1986, 2000; Baddeley and Hitch, 1974; Repovs and Baddeley, 2006) has been highly influential in the field. This model proposes that a central executive function provides attentional control over memory-storage systems that include a visuo-spatial sketch pad, phonological loop, and an episodic buffer for multimodal storage. This model, however, has been exclusively developed to account for data from human participants. Because this review includes both primate and rodent studies, a somewhat different working-memory model is preferred in order to support a more comparative perspective. Postle (2006), for example, has defined working memory as an emergent property of neural systems representing many different types of information. With evidence of diversity in the stimulus attributes maintained in working memory (e.g., egocentric and allocentric spatial information, olfactory and somatosensory cues, etc.), it seems reasonable to assume, as stated by Postle (2006, p. 29) "that if the brain can represent it, the brain can also demonstrate working memory for it". In this regard, the definition of working memory in the current review represents an emergent property of neural systems, which in other words is "the temporary retention of information that was just experienced, but no longer exists in the external environment, or was just retrieved from long-term memory" (D'Esposito, 2007) and can be actively maintained, rehearsed, and also manipulated for its use in making predictions and guiding behavior (Borst et al., 2010).

From this perspective, shared features between interval timing and working memory will be identified and physiological accounts of these processes will be explored in an attempt to specify the common underlying mechanisms. The organization of this paper includes an overview of the behavioral, neuroanatomical, and neurophysiological features of interval timing and working memory, followed by a description of current theoretical models. Finally, a novel framework incorporating the shared features of interval timing and working memory will be proposed in order to better emphasize the common oscillatory mechanisms supporting these cognitive processes. This framework highlights the role of multiplexing, whereby multiple information streams share a common neural substrate. The basic idea is that such multiplexing, implemented as a function of the relative power in different frequency bands observed in local field potentials within and between different brain structures, enables the reconfiguration of effective connectivity and the types of information stored and/or extracted from the neural network (Akam and Kullmann, 2010, 2014).