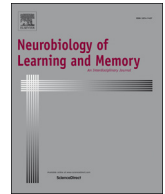




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Review

Oscillation patterns of local field potentials in the dorsal striatum and sensorimotor cortex during the encoding, maintenance, and decision stages for the ordinal comparison of sub- and supra-second signal durations

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ABSTRACT

Ordinal comparison of successively presented signal durations requires (a) the encoding of the first signal duration (standard), (b) maintenance of temporal information specific to the standard duration in memory, and (c) timing of the second signal duration (comparison) during which a comparison is made of the first and second durations. Rats were first trained to make ordinal comparisons of signal durations within three time ranges using 0.5, 1.0, and 3.0-s standard durations. Local field potentials were then recorded from the dorsal striatum and sensorimotor cortex in order to investigate the pattern of neural oscillations during each phase of the ordinal-comparison process. Increased power in delta and theta frequency ranges was observed during both the encoding and comparison stages. Active maintenance of a selected response, “shorter” or “longer” (counter-balanced across left and right levers), was represented by an increase of theta and delta oscillations in the contralateral striatum and cortex. Taken together, these data suggest that neural oscillations in the delta-theta range play an important role in the encoding, maintenance, and comparison of signal durations.

1. Introduction

Temporal processing is fundamental to many aspects of cognition and behavior; in order for behavior to be adaptive, an animal must be able to predict not only *where*, but also *when* an event is likely to occur (Matthews & Meck, 2016). The ability of animals to represent stimulus (event) duration, and to discriminate between different durations has been the focus of much research (Buhusi & Meck, 2005; Merchant, Harrington, & Meck, 2013). Cortico-striatal-thalamic circuits have been implicated as a crucial brain area for timing and time perception, especially for cognitively controlled timing processes in the msec to sec range (Allman, Teki, Griffiths, & Meck, 2014; Gu, van Rijn, & Meck, 2015; Lewis & Miall, 2003a, 2003b; MacDonald, Fortin, Sakata, & Meck, 2014). Lesion studies (Jones & Jahanshahi 2011; Meck, 2006a, 2006b), human imaging studies (Coull, Vidal, Nazarian, & Macar, 2004, 2011; Harrington, Zimbelman, Hinton, & Rao, 2010; Hinton & Meck, 2004; Lewis & Miall, 2006; Meck, Penney, & Pouthas, 2008; Wiener, Turkeltaub, & Coslett, 2010) as well as electrophysiology studies (Chiba, Oshio, & Inase, 2008; Matell, Meck, & Nicolelis, 2003; Merchant et al., 2013; Mita, Mushiake, Shima, Matsuzaka, & Tanji, 2009; Narayanan & Laubach, 2009) have supported the important role of

cortico-striatal circuits in timing behavior. Neural responses in this region showed continuous changes of spike patterns characterized by ramping up, decaying, or peak-shaped firing rates as a function of time since signal onset (Gouvêa et al., 2015; Jazayeri & Shadlen 2015; Jin, Fujii, & Graybiel, 2009; Lebedev, O’Doherty, & Nicolelis, 2008; Matell et al., 2003, 2011; Mita et al., 2009; Narayanan & Laubach, 2009; Niki & Watanabe, 1979). In addition to the investigation of neural spike patterns in timing, a small number of pioneering rodent studies have recently focused on oscillatory properties of frontal-striatal circuits and their involvement in temporal information processing (e.g., Emmons, Ruggiero, Kelley, Parker, & Narayanan, 2016, 2017; Kim et al., 2017; Parker, Chen, Kingyon, Cavanagh, & Narayanan, 2014). Specifically, these studies showed that delta and theta rhythms in frontal-striatal circuits were modulated with interval timing and these rhythms were related with the dopamine and ramping activity of spikes. In addition, reward related visual cue produced theta rhythm in visual cortex which was related to the precision of timing (Levy, Zold, Namboodiri, & Hussain Shuler, 2017), and sequential tapping behavior produced beta rhythms, especially with internally driven timing of tapping in the cortico-striatal circuit of monkey (Bartolo & Merchant, 2015).

Moreover, a limited number human studies have focused on neural

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oscillations during temporal processing (Cravo, Rohenkohl, Wyart, & Nobre, 2011; Hsieh, Ekstrom, & Ranganath, 2011; Kononowicz & van Rijn, 2015; Roberts, Hsieh, & Ranganath, 2013). Specifically, human electroencephalography (EEG) studies show that theta activity near the central midline differs across conditions with different temporal expectations (Cravo et al., 2011) and that frontal theta activity was increased when the temporal-order of multiple items is required to be maintained compared to when specific features or spatial information of items are required to be maintained (Hsieh et al., 2011; Roberts et al., 2013). In addition, repetitive motor timing in a tapping behavior produced beta rhythm increase, and the higher beta power predicted longer duration to be produced (Kononowicz & van Rijn, 2015). A slow negative waveform designated as the Contingent Negative Variation (CNV) recorded from fronto-central or parietal-central regions has been shown to be related to the duration of the timed stimulus (e.g., Macar & Vidal, 2003, 2009; Macar, Vidal, & Casini, 1999; Pouthas, Garnero, Ferrandez, & Renault, 2000; Tarantino et al., 2010; Walter, Cooper, Aldridge, McCallum, & Winter, 1964), and is thought to reflect temporal accumulation; however, there are controversies with the interpretation of the role of the CNV in timing (Kononowicz & van Rijn, 2011; Kononowicz et al., 2018; Mento, 2017; van Rijn, Kononowicz, Meck, Ng, & Penney, 2011).

The roles of neural oscillations in cognition have recently received a considerable amount of attention and are considered essential to brain operations. Especially theta rhythms, oscillations in the range of 4–12 Hz, have been extensively studied in human, non-human primate, and rodent studies in relation to various cognitive processes in multiple brain areas. In rodent studies, theta rhythms are reported in the cortex and hippocampus during working memory (Duzel, Penny, & Burgess, 2010; Fujisawa & Buzsaki, 2011; Hyman, Zilli, Paley, & Hasselmo, 2010; Jones & Wilson, 2005; Meck, Church, & Matell, 2013; Siapas, Lubenov, & Wilson, 2005), in the hippocampus during spatial information processes (Burgess & O'Keefe, 2011; Huxter, Burgess, & O'Keefe, 2003), and also in the striatum during learning, decision-making or timing (Berke, Okatan, Skurski, & Eichenbaum, 2004, 2009; DeCoteau et al., 2007a, 2007b; Emmons et al., 2016; Levy et al., 2017; Tort et al., 2008). The roles of other frequency ranges of neural oscillations are also suggested in various cognitive functions, for example, delta oscillations (1–4 Hz) have been proposed as playing a functional role in attentional selection and/or anticipatory mechanisms in human and other animals (Kim, Grabowecy, Paller, Muthu, & Suzuki, 2007; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008; Morgan, Hansen, & Hillyard, 1996; Schroeder & Lakatos, 2009; Stefanics et al., 2010).

In order to investigate the nature of neural oscillations during the temporal processing, we recorded Local field potentials (LFPs) from the cortex and striatum in rats during an ordinal-comparison task with signal duration as the relevant stimulus dimension (Cordes & Meck, 2014; Gu & Meck, 2011; Harrington et al., 2010). The ordinal-comparison procedure requires the rats initially encode a Standard signal duration that is shortly thereafter contrasted with the duration of a Comparison signal. In order to obtain reward, rats must correctly report whether the second Comparison signal is “shorter” or “longer” than the Standard signal by pressing the left lever for “shorter” and the right lever for “longer” with response mapping to duration judgments being counter-balanced across rats. Under ideal conditions, temporal ordinal comparison includes the initial timing (i.e., encoding) of the Standard signal, the maintenance of this representation in memory during the inter-stimulus interval, the timing of the Comparison signal, compared in real time with either the current trial's Standard signal or a mixture of previously timed Standards presented during the session. The comparison process involves collecting information during the Comparison signal until it ends or until the subject is able to self-terminate the timing of the signal as a result of a determination that the current clock reading exceeds the duration of the Standard signal. Taken together, these separate phases of temporal processing allow for the identification of specific neural patterns during initial timing, maintenance, and

duration comparison (cf., MacDonald et al., 2014).

Various models can explain duration comparison process, for example, drift-diffusion models explain that information is sampled from the percept to drive the decision process (e.g., Ratcliff, Gomez, & McKoon, 2004; Ratcliff & McKoon, 2008), and this sampling drives a time-continuous random walk that terminates when the accumulated evidence crosses one of two boundaries, each corresponding to a different perceptual decision, i.e., “longer” or “shorter”. The *drift rate* determines the net rate of information accumulation in favor of one response, and the features of the stimulus (e.g., the signal-to-noise ratio) can affect the drift rate for example, fast and accurate decisions with high drift rate and a slower, less accurate judgments with low drift rate and noisy evidence accumulation. The distance between the response boundaries, and the relative location of the starting point between these boundaries, correspond to the decision maker's caution and bias, respectively. Recent work has demonstrated the potential power of this approach to the analysis of decision-making in temporal bisection and temporal ordinal-comparison procedures (e.g., Akdoğan & Balci, 2016; Balci & Simen, 2014, 2016; Lusk, Petter, MacDonald, & Meck, 2016; Matthews & Meck, 2016; Simen, Vlasov, & Papadakis, 2016; Tipples, 2015).

In addition, the excitatory-inhibitory oscillator (EIO) model (Gu et al., 2015), which extends the striatal beat-frequency (SBF) model can be used to explain the mechanism of duration comparison procedures. The SBF model explains that a coincident pattern of cortical neurons can be detected by striatal medium spiny neurons (MSN) at a specific time since signal onset (Matell & Meck, 2004). EIO model extends this idea into that the cortical cells producing the coincident pattern are paced by the interference between excitatory and inhibitory oscillating inputs to neurons, and the population activity of these cortical cells will produce the pattern of theta entrained in delta rhythms. Then, two groups of decoder neurons (e.g. subgroups of MSNs) detect coincident patterns for “shorter time” or “longer time”, and connect to “shorter response” and “longer response” respectively, so that the competition between the two decoder neurons can result in a decision of response. Growing body of literature support the involvement of delta and theta rhythms with temporal processing (Emmons et al., 2016; Kim et al., 2017; Parker et al., 2014), and the current study will explore the involvement of these rhythms in relation to the EIO model.

2. Methods

Fifteen adult male Sprague-Dawley (Charles River) rats were trained on a temporal ordinal-comparison procedure. Rats were housed in a temperature-controlled room with 12 h light /12 h dark cycles and were trained during the light phase. The rats were allowed continuous access to water in their home cages and their body weights were maintained at approximately 85% of their ad lib weights (300–400 g) by restricting access to food. Of these, five (out of 15) rats with good behavioral performance contributed data to the electrophysiological studies. All studies were conducted in accordance with standard procedures approved by the Duke University Institutional Animal Care and Use Committee.

Behavioral data were collected using eight identical lever boxes that were housed in sound- and light- attenuating chambers (all equipment from MED Associates, St. Albans, VT). One of the walls contained a recessed food-cup and above the food-cup were two retractable response levers (to the left and right, respectively). Centered above the levers was a house-light (28-V, 80-ma, 2500-lx) which remained off for the majority of sessions, but whose illumination served as a warning cue for signal onset in a subset of rats. The stimulus to-be-timed was white noise presented through a speaker mounted on the opposite sidewall. Lever boxes used during electrophysiological recording were the same as those used for behavioral training, with the following exceptions: The ceiling had a hole in the center (15 cm) for the headstage cable bundle, and the food cup was not recessed in order to minimize

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