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Single trial beta oscillations index time estimation

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ABSTRACT

Recent work shows that putamen-originating beta power oscillations serve as a carrier for temporal information during tapping tasks, with higher beta power associated with longer temporal reproductions. However, given the nature of tapping tasks, it is difficult to determine whether beta power dynamics observed in these tasks are linked to the generation or execution of motor programs or to the internal representation of time. To assess whether recent findings in animals generalize to human studies we reanalyzed existing EEG data of participants who estimated a 2.5 s time interval with self-paced onset and offset keypresses. The results showed that the trial-to-trial beta power measured after the onset predicts the produced duration, such that higher beta power indexes longer produced durations. Moreover, although beta power measured before the first key-press also influenced the estimated interval, it did so independently from post-first-keypress beta power. These results suggest that initial motor inhibition plays an important role in interval production, and that this inhibition can be interpreted as a biased starting point of the decision processes involved in time estimation.

1. Introduction

Perceiving the passage of time is an ubiquitous experience and a building block for other cognitive processes and behaviors such as controlling movements in time (Allman et al., 2014; van Wassenhove, 2009), both in well-controlled laboratory settings (Van et al., 2014) and in tasks with higher external validity (Matthews and Meck, 2014; Van Rijn, 2014). However, the neural underpinnings of these abilities are not yet well understood. Although it has been convincingly shown that climbing neural activity (CNA, Durstewitz, 2003) is somehow linked to time estimation (e.g., Macar and Vidal, 2004; Wiener et al., 2012; Wittmann, 2013), previous studies have found that EEG-based CNA does not co-vary with trial-to-trial fluctuations in subjective timing (Kononowicz and Van Rijn, 2011; Van Rijn et al., 2011, cf., Wiener et al., 2012) whereas electrophysiological potentials evoked by the end of the interval do covary with the subjective percept Kononowicz and van Rijn (2014a). However, post-interval evoked potentials cannot be used to track or index the dynamics of subjective time (also see Van Wassenhove and Lecoutre (2014)). Typically, dynamics of subjective time has been investigated by tracking slow changes in electric potentials (Macar and Vidal, 2004) or investigated dynamics of neuronal spiking patterns such as interval tuning (Crowe et al., 2014; Merchant et al., 2013), CNA (Merchant et al., 2011) or scalable population codes (Mello et al., 2015). However, the dynamics of neural oscillations has been investigated very rarely (but see Kononowicz (2015), Parker et al. (2014)).

Interestingly, a recent synchronization-continuation tapping studies have shown that putamen-originating beta power was larger for longer durations, suggesting that beta power reflects the to-be-produced duration (Bartolo et al., 2014; Bartolo and Merchant, 2015), and thus indicating that beta power is linked to the development of subjective time or to guidance of internally driven motor sequences. If beta power dynamics is only linked to generation of motor sequences, without having any relationship to interval timing, fluctuations in beta power should not correlate with behavior on a time production task. However, if beta power is linked to internal sense of time it should covary with the length produced interval. Moreover, the nature of tapping tasks makes it impossible to attribute the observed beta power to the onset of a temporal interval, or to the offset of the previous interval, as each response is both offset and onset of an interval. Here we focus on a supra-second time production task in which the onset and the offset of an interval are separately indicated. Additionally, tapping tasks typically use intervals below one second. As timing mechanism were suggested to differ for intervals shorter and longer

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than one second, the aim of this paper is to assess whether the results presented by Bartolo et al. (2014), obtained in a tapping task with subsecond intervals, generalize to longer intervals.

Therefore, to assess whether beta power as well as other frequency bands can track or index the dynamics of subjective time, sufficiently long intervals should be used in a paradigm that allows for distinguishing the onset and offsets of temporal intervals. By assessing the power of different frequency bands of an existing data set (Kononowicz and Van Rijn, 2011) that has been previously used to investigate the relationship between temporal performance and the amplitude of contingent negative variation, we address whether trial-to-trial variability in interval timing is predicted by oscillatory power, both measured before the onset of the trial (see, e.g., De Lange., 2013), and immediately after. This setup allows us to eliminate biases coming from experimentally manipulated durations and instead focus on the naturally occurring fluctuations in timing performance.

2. Method

Detailed information on stimuli, experimental procedures and participants can be found in Kononowicz and Van Rijn (2011). Below we will provide a summary of the information relevant for the analyses reported in this work.

2.1. Stimuli, procedure and data acquisition

We investigate the role of beta power during the self-paced production of intervals of 2.5 s (participants indicated both onset and offset of the interval by a keypress) in a task setup that meets the criteria for an accurate measurement of beta power. First, the length of target interval is long enough to allow post-movement beta power after the initial keypress to fully evolve, and to reach its peak without strong contamination from upcoming movement preparation. Second, because visual feedback was provided after every trial and every trial started with a short waiting period, the experimental setup enforces a minimum inter-trial interval of 2.7 s, allowing beta power associated with the motor response to the offset of the trial to return to "baseline" before the onset of a next trial.

Although the original dataset consists of two separate experiments, these experiments are identical for the purposes of the analyses reported here. We will therefore discuss the original data as one, collapsed, dataset of 32 participants that were tested in a setup as approved by the Ethical Committee Psychology of the University of Groningen. The outline of a task is depicted in Fig. 1. The participants were asked to produce the 2.5 s interval by pressing the spacebar twice using the right hand index finger. Visual feedback was presented after each trial indicating the deviation from the standard duration. During the entire interval a small circle served as a fixation point. Before the first keypress, the circle was shown in light gray on a black background. The first keypress changed the color of the circle to white, as a visual cue that the interval had started. The second keypress removed the circle from the screen, and feedback was presented. The feedback was delivered as a row of five circles, immediately above the location of the fixation point. The middle circle turned green if the time production was between 2.4 and 2.6 s. If time production was between 1.8 and 2.4 s or between 2.6 and 3.2 s, the circle just to the left or right of the middle circle turned green. If the time production was shorter than 1.8 or longer than 3.2 s, the left or right outer circle turned red. Before each trial, participants either saw a short instruction requesting them to blink their eyes, or where just presented a blank screen, depending on the experiment. The time between the instruction to blink and the onset of the interval was at least 1.5 s.

2.2. Time-frequency analysis

We selected the 20 electrodes (AFz, F3, Fz, F4, FC3, FC1,FCz, FC2, FC4, C3, C1, Cz, C2, C4, CP3, CPz, CP4, P3, Pz, P4) that were used in both original experiments and performed an analysis of oscillatory power by comparing the 3 pseudo-experimental conditions that were previously presented by Kononowicz and Van Rijn (2011), see also Macar (1999): trials in which the response was slightly too

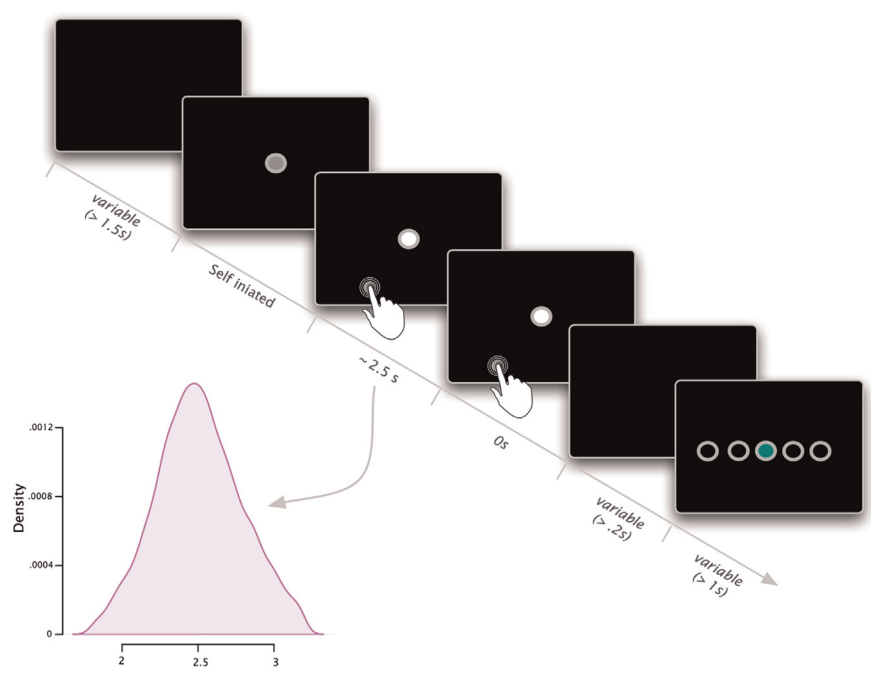

Fig. 1. Time course of an experimental trial. Intervals marked as variable differed slightly between the two experiments. The distribution shown in the lower left corner depicts the probability density function (Sheather and Jones, 1991) of observed time productions ranging from 1.8 to 3.2 for all subjects.