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Repetition enhancement and memory effects for duration

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ABSTRACT

A remarkable aspect of conscious perception is that moments carryover from one to the next, also known as temporal continuity. This ability is thus crucial for detecting regularities, such as in speech and music, and may rely on an accurate perception of time. Investigations of human time perception have detailed two electroencephalographic (EEG) components associated with timing, the contingent negative variation (CNV) and late positive component of timing (LPCt); however, the precise roles of these components in timing remain elusive. Recently, we demonstrated that the perception of duration is influenced by durations presented on prior trials, which we explained by the creation of an implicit memory standard that adapts to local changes in sequence presentation. Here, we turn to the neural basis of this effect. Human participants performed a temporal bisection task in which they were required to classify the duration of auditory stimuli into short and long duration categories; crucially, the presentation order was first-order counterbalanced, allowing us to measure the effect of each presented duration on the next. EEG recordings revealed that the CNV and LPCt signals both covaried with the duration presented on the current trial, with CNV predicting reaction time and LPCt predicting choice. Additionally, both signals covaried with the duration presented in the prior trial but in different ways, with the CNV amplitude reflecting the change in the memory standard and the LPCt reflecting decision uncertainty. Furthermore, we observed a repetition enhancement effect of duration only for the CNV, suggesting that this signal additionally indexes the similarity of successive durations. These findings demonstrate dissociable roles for the CNV and LPCt, and demonstrate that both signals are continuously updated on a trial-by-trial basis that reflects shifts in temporal decisions.

Introduction

One of the hallmarks of conscious experience is temporal continuity from one moment to the next (Pöppel, 1997). Indeed, James (1890) noted that temporal continuity was a necessary requirement for consciousness to flow. A critical feature of this continuity is that we can make predictions about upcoming events based on the statistics of prior experience, allowing for perceptual stability (Kiebel et al., 2008). Learning the rhythm of a song, or adjusting to the speed at which a person is speaking to better understand them are both examples of this remarkable ability. The ability to adapt to changes in temporal context depends on our perception of time (Ossmy et al., 2013; Rohenkohl et al., 2012). However, the neural mechanisms governing contextual effects in time perception are currently unknown.

Currently, our understanding of temporal processing within the human brain has been limited to a large number of neuroimaging studies exploring the localization of timing abilities to particular regions. Perhaps unsurprisingly, these studies have revealed a wide diversity of areas that may be implicated. In a recent series of quantitative, voxel-wise meta-analyses, we (Wiener et al., 2010) demonstrated that the neural regions responsible for timing could be fractionated on the basis of task context, including (but not limited to) the range of intervals employed, the motor requirements of the task and the attentional state of the subject. These findings suggested that separate yet overlapping neural circuits are flexibly recruited, depending on the nature of the timing task at hand. Crucially, our findings also demonstrated that the bilateral supplementary motor area (SMA) and right inferior frontal gyrus (rIFG) were activated across all task variations. Although these studies provide some insight to *where* timing functions may reside, they do nothing to answer *how* these regions are involved, a step that is necessary for a truly comprehensive understanding of timing functions and the potential impact of disruption from neural pathology.

A second area of recent interest in neuroscience is how sensory-based timing is processed within a larger temporal context. The temporal context refers to the separation between stimuli in time, as well as the distribution of experienced intervals in memory. Two common influences of temporal context are central tendency and carryover effects, both of which may rely on Bayesian integration (Shi et al., 2013). Central tendency, also known as Vierodt's Law, refers to a gravitation of timed responses to the mean of presented intervals (Jazayeri and Shadlen, 2010), whereas carryover effects refer to the influence of recently experienced intervals on a presently perceived one (Hellström, 1985).

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However, the neural bases of both effects for temporal perception have never been explored. Recently, we demonstrated that the perception of time is susceptible to carryover effects, such that the perception of duration on a given trial is influenced by the duration presented on the preceding one (Wiener et al., 2014). This influence depended on the difference between the present and prior interval, and was contrastive in nature, with longer prior intervals leading to shorter perceived durations, and vice versa. In order to explain these effects, we devised an implicit memory model that continuously updated an internal standard that was weighted by more recently presented intervals. Previous research has similarly demonstrated behavioral effects resulting from the order of presented intervals on time perception and memory mixing (Gu and Meck, 2011; Jones and McAuley, 2005; Taatgen and van Rijn, 2011; Dyjas et al., 2012). These findings are additionally consistent with a model of population-coding for duration, in which individual neurons are tuned to specific duration lengths (Ivry, 1996; Heron et al., 2012; Merchant et al., 2013a; Wiener et al., 2014). Such a mechanism would be expected to be susceptible to adaptive changes to repeated stimulus durations, resulting in repetition suppression (Grill-Spector et al., 2006) or enhancement (Segaert et al., 2013).

Recent experimental evidence suggests that the SMA interfaces with the basal ganglia and thalamus as an integrated circuit for predicting and measuring temporal intervals (Merchant et al., 2013a; Wiener et al., 2011), which exhibits duration-tuning properties (Mita et al., 2009; Merchant et al., 2013b). Activity in this circuit may also be probed in humans by frontocentral scalp EEG measurements of slow cortical potentials, such as the contingent negative variation (CNV) (Nagai et al., 2004; Fan et al., 2007; Scheibe et al., 2010). The amplitude of the CNV component has been hypothesized to relate to the output of an accumulator mechanism for time (Casini and Vidal, 2011); accordingly, pacemaker pulses are summated into an accumulator mechanism while subjects attend to duration (Gibbon et al., 1984). As such, longer durations are characterized by relatively greater accumulation and hence relatively larger amplitude CNV events (Wiener et al., 2012). However, the involvement of the CNV in temporal accumulation is complicated by recent findings suggesting that the CNV is additionally involved in memory (Macar and Vidal, 2003), decision making (Ng et al., 2011; Kononowicz and van Rijn, 2014; Mento et al., 2013) and response caution (Boehm et al., 2014). Among these findings is evidence demonstrating that the CNV amplitude, under certain task conditions, peaks when the standard interval in memory has elapsed (Macar and Vidal, 2003; Pfeuty et al., 2003; Ng et al., 2011), thus placing the CNV within the context of evidence accumulation accounts of decision-making (Balci and Simen, 2014).

A separate line of research has revealed that signal offset-related EEG activity may also index perceived duration and decision-making mechanisms (Kononowicz and van Rijn, 2014; Paul et al., 2011; Tarantino et al., 2010; Lindbergh and Kieffaber, 2013; Gibbons and Stahl, 2008). For example, Kononowicz and van Rijn (2014) demonstrated that sensory-evoked potentials associated with a stimulus marking the end of an interval were better predictors of perceived duration than the preceding CNV, suggesting that the CNV amplitude does not index the temporal accumulator, but rather preparatory processes. Similarly, Paul and colleagues (Paul et al., 2003, 2011; Gontier et al., 2009) have demonstrated a post-offset component, termed the late positive component of timing (LPCt), that is associated with decision-making and difficulty in temporal discrimination. Notably, the LPCt signal is similar to other positive components associated with decision making, such as the P3 (Polich, 2011; San Martin et al., 2013) and late positive deflection (Itthipuripat et al., 2014; Kelly and O'Connell, 2013; Hilyard et al., 1971).

In the context of the above ambiguities, carryover effects can serve as a means to disentangle the roles of the CNV and LPCt in time perception processes. If, for example, the CNV signal indexes the output of an accumulator, then it should not be influenced by preceding intervals, and should only reflect the output of the present interval (van Wassenhove and Lecoutre, 2015). However, if the CNV instead indexes memory mechanisms, then changes in the CNV amplitude should fluctuate on a trial-by-trial basis with the current value of the memory standard, which will be a product of recently experienced intervals. The same may hold true for the LPCt signal. Moreover, if the LPCt indexes decision-making, then it should covary with both the current choice and the influence of prior choices. In order to measure carryover, we adopted a continuous carryover design (Aguirre, 2007), wherein the presentation sequence of stimuli was first-order counterbalanced, allowing us to independently measure the effect of every duration in our stimulus set on the current trial and prior one. Continuous carryover designs with serially balanced stimulus sequences are suited to the characterization of "similarity spaces" in which the perceptual similarity of stimuli is related to the structure of neural representation (Fig. 1; Kriegeskorte et al., 2008). In our case, the similarity space is the stimulus duration, rather than any other stimulus property that may affect perceived duration (Matthews, 2015). As such, we may also index the neural effect of similarity between successive durations.

Materials and methods

Participants

A total of 15, right-handed participants (8 female; 18–33 years old) participated in the experiment. Participants were recruited from the population at George Mason University. Written informed consent was obtained from all participants, and the Institutional Review Board of George Mason University approved the study protocol. One subject was removed due to excessive noise in the recorded EEG signals, reducing the sample size to $N = 14$.

Task design

Participants performed a temporal bisection task, (partition variant; Wearden and Ferrara, 1995), of a similar design to our previous study (Wiener et al., 2014). All participants sat in front of a Dell LCD monitor. On a given trial, participants heard a series of stimuli, one-at-a-time, that persisted for one of seven logarithmically spaced intervals of time, between 300 and 900 ms [300, 360, 433, 520, 624, 749, 900 ms]. On each trial, participants were required to judge whether the stimulus presented was "long" or "short", based on their own subjective feeling, and press one of two response keys for each choice; left and right-hand responses for short and long were counterbalanced between subjects. Participants were instructed to make each response as quickly, yet as accurately as possible, and not to over-think their responses. At the beginning of each run, participants were presented with three stimuli at the geometric mean of the stimulus set (520 ms) as an example of the average stimulus duration and for comparison purposes for the first few trials. Auditory stimuli were generated using Audacity, version 2.0 (http://audacity.sourceforge.net/), and consisted of a white noise burst (0.5 amplitude, 44,100 Hz digitization) presented via two speakers situated on either side of the monitor at a comfortable volume, individually adjusted for each participant (loudness range: [69–73 dB). Only one white noise burst was used for the entire experiment, differing only in duration. Stimulus timing and control were carried out using the Python programming environment with extensions provided by Psychopy, version 1.78 (Peirce, 2008). Each trial consisted of the presentation of a central fixation point for 500 ms, which then extinguished and was followed by the auditory stimulus of variable duration, followed by a blank screen that was terminated by a choice response.

The order of stimulus presentation was determined by a path-guided de Bruijn sequence (https://cfn.upenn.edu/aguirre/wiki/public:de_bruijn). de Bruijn sequences are modified Hamiltonian cycles through a stimulus set, such that every possible order combination of stimuli is presented (Aguirre et al., 2011). The path-guided process of the de Bruijn sequence allows the Hamiltonian cycle to be modified by