The time is "right:" Electrophysiology reveals right parietal electrode dominance in time perception

Erik M. Benau[1], Laura C. DeLoretta, Stephen T. Moelter[*]

Department of Behavioral and Social Sciences, University of the Sciences, Philadelphia, PA, USA

ABSTRACT

In the present study, healthy undergraduates were asked to identify if a visual stimulus appeared on screen for the same duration as a memorized target (2 s) while event-related potentials (ERP) were recorded. Trials consisted of very short (1.25 s), short (1.6 s), target (2 s), long (2.5 s) or very long (3.125 s) durations, and a yes or no response was required on each trial. We examined behavioral response as signal detection (d') and response bias via a Generalized Accuracy Coefficient (GAC). We examined the mean amplitude as well as the change in amplitude of the initial Contingent Negative Variation (iCNV) and overall CNV (oCNV) and P350 (a P300-like component that follows stimulus extinction) potentials in paired, lateralized posterior electrodes. Results showed a bias to identifying shorter trials as the target more than longer trials via negative GAC scores. The slope and amplitudes of the iCNV and oCNV were consistently greater in right parietal electrodes. Also in right parietal electrodes, the iCNV correlated to d' scores while greater P350 amplitudes in the short condition correlated with more negative GAC scores. The results indicate dominance in the right hemisphere in temporal processing for durations exceeding 1 s. The P350 should also be studied further.

1. Introduction

The physical phenomena that influence the subjective perception of time are well established (Einstein, 1923), yet the psychological and neurological processes influencing time perception are less understood (Zimbardo & Boyd, 1999). Time perception feels effortless and, yet it is essential for a multitude of experiences and processes, including consciousness, communication, motor performance and coordination, memory, and navigation (Grondin, 2010; Meck, 2005). Recent research has begun to reveal the neural basis for time perception. The cerebellum, supplementary motor area (SMA), basal ganglia, thalamus, insula, and striatum are central, but not exclusive, neural hubs for time perception (Grondin, 2010; Kononowicz, Van Rijn, & Meck, 2016; Merchant, Harrington, & Meck, 2013; Wittmann, 2013). Modality, task, sensory input, duration, state- and trait-level emotion, neurologic disease, and psychopathology all may influence time perception, and the extent to which neural networks are recruited (Capuano, Rivielo, Cordasco, & Esposito, 2013; Gallagher, 2012; Gan, Wang, Zhang, Li, & Luo, 2009; Gil & Droit-Volet, 2009; Ivry & Schlerf, 2008; Msetfi, Murphy, & Kornbrot, 2012; Pasinski, McAuley, & Snyder, 2016; Wittmann, 2013).

Electroencephalography (EEG) and event-related potentials (ERPs) detect neural activity associated with time perception with high temporal resolution. An ERP component known as the contingent negative variation (CNV) is an accumulation of electrical activity in the time period prior to an expected event, with or without behavioral response or even conscious recognition of these events (Praamstra, 2012; Walter, Cooper, Aldridge, McCallum, & Winter, 1964). While Walter and colleagues (1964) argued that the CNV reflected psychological, non-motoric activation of learning responses, others argued that the CNV likely reflected the activation of motor responses as the effect was enhanced when response was required (van Boxtel & Böcker, 2004). However, it soon became apparent that the motor response reflected in these early anticipatory components were discrete components (e.g., the Stimulus Preceding Negativity) and, therefore, the CNV specifically is associated with the psychological processes involved in the perception of time (Macar & Vidal, 2002, 2003; Mento, 2013; Pfeuty, Ragot, & Pouthas, 2003; Pouthas, Garneo, Ferrano, & Renault, 2000; Taatgen & van Rijn, 2011; Tarantino et al., 2010; van Boxtel & Böcker, 2004; van Rijn, Kononowicz, Meck, Ng, & Penney, 2011).

Present models of the neuropsychological representation of time include the *centralized internal clock model*. This model suggests that a *pacemaker* generates pulses, perhaps based on physiological sensations such as heartbeat (Pollatos, Laubrock, & Wittmann, 2014; Praamstra,

---

2012; Wittmann, 2013), that are then referenced by memory and attention systems to match a template of duration (Taatgen & van Rijn, 2011). The pacemaker may reflect sensory integration in the basal ganglia-thalamocortical pathways (Pollatos et al., 2014; Praamstra, 2012), which is then reflected by an *accumulator* that can be indexed by the increasing amplitude of the CNV (Casini & Vidal, 2011; Kononowicz & van Rijn, 2011; Praamstra, 2012; van Rijn et al., 2011). A source of controversy in the accumulator model is that it is difficult to interpret, inconsistently replicated, and does not account for cognitive functions employed during temporal judgments, such as memory and attention (Kononowicz & Penney, 2016; Kononowicz et al., 2016; van Rijn et al., 2011).

In addressing the function of the CNV and its relation to time perception, there is increasing evidence that the component may be better understood as several subcomponents rather than a singular entity. Three subcomponents have been identified: the initial CNV (iCNV), overall CNV (oCNV), and terminal CNV (tCNV), which is sometimes referred to as the late CNV or lCNV (Böcker, Timsit-Berthier, Schoenen, & Brunia, 1990; Kononowicz et al., 2016; Kropp, Kiewitt, Göbel, Vetter, & Gerber, 2000; Van't Ent & Apkarian, 1998). Of the three subcomponents of the CNV, the iCNV has been identified as the most reliable, and likely reflects the strongest indicator of arousal, task engagement, and time perception (Fischer, Langner, Diers, Brocke, & Birbaumer, 2010; Kononowicz et al., 2016; Kropp et al., 2012; Kropp et al., 2000; Kropp, Linstedt, Niederberger, & Gerber, 2001). The iCNV has also been found to be stronger in right hemisphere electrodes, regardless of motor-response (Van't Ent & Apkarian, 1998; Van't Ent & Apkarian, 1999). The oCNV occurs between a cue and stimulus onset, and remains engaged as a slow-wave until a second stimulus or stimulus offset. The oCNV can likely be understood as what is typically labeled the CNV (Böcker et al., 1990). The tCNV reflects motoric activation and response preparation and is observed prior to an anticipated second stimulus (Kropp et al., 2001; Wascher, Verleger, Jaskowski, & Wauschkuhn, 1996).

A final ERP component of interest is the P350 (Desmedt & Debecker, 1979a, 1979b; Sato et al., 2002). Desmedt and Debecker (1979a, 1979b) presented a stimulus and asked participants to judge its duration. They identified a large positivity following stimulus offset and suggested that this "P350" component is specific to judging the perception of time (Desmedt & Debecker, 1979b). To our knowledge, the relation of the P350 to time perception has not been assessed further.

Relatively few studies have examined the neural and psychological processes involved in the perception of time without motor response or replication. Pfeuty et al. (2003) found that, during an auditory time perception task where the target duration was 700 ms, when the probe exceeded 700 ms, the CNV increased in amplitude until the target time and then returned to baseline. Moreover, the increase in amplitude occurred primarily in right sided electrodes. There is some evidence of this phenomenon occurring in other modalities. Macar and Vidal (2003) found that the CNV increased in amplitude until the 2 s target and, for the conditions that exceeded the target, the CNV returned to baseline. Macar and Vidal argue that the CNV may reflect the accumulation of beats until the target duration. Taken together with Pfeuty et al. (2003), this process occurs regardless of the target duration itself.

Because time perception varies as a function of duration, modality, and intensity of signal (Gontier, Hasuo, Mitsudo, & Grondin, 2013; Lejeune & Wearden, 2009; Ng, Yip, Soh, & Penney, 2009; Pande & Pati, 2010; Pasinski et al., 2016), it is important to understand the neural mechanisms that underlie these differences and establish the generalizability of these processes. The goal of the present study was to better understand how the CNV and P350 change during representation of longer durations of time using a visual stimulus, and to assess the laterality of this process. To address this goal, we synthesized the work of Pfeuty et al. (2003) and Macar and Vidal (2003) by using longer-duration visual stimuli to generate a CNV. Participants were asked to identify if a visual stimulus matched the duration of a memorized target

(2 s). We hypothesized larger CNV amplitudes and slopes would occur in the right than in the left parietal electrodes. We also predicted that the P350 would correspond to response bias and accuracy. However, to our knowledge, the relation of this component to behavioral response has not yet been examined. Therefore, given the exploratory nature of these analyses, we broadly predict that the P350 amplitude, and its correlations with behavioral accuracy and response bias, would be greater in right electrodes than the left. The proposed replications and extensions of previous work will facilitate the ability to generalize previous research results.

2. Methods

2.1. Participants

Twenty-six right-handed undergraduates (18 women and two participants who did not report their gender) aged 18–21 at the University of the Sciences completed this study in exchange for course credit. Participants reported no history of traumatic brain injury or neurological disorder. Handedness was confirmed via the Edinburgh Handedness Questionnaire. Three male participants were excluded due to excessive artifact (discussed further below), thus, the final sample included 23 subjects. According to G∗power software (Faul, Erdfelder, Lang, & Buchner, 2007), this sample is large enough to power the repeated measures analyses described below and detect the medium to large effects we hypothesized $(1 - \beta = 0.88)$. The Institutional Review Board of the University of the Sciences approved the present methods and all participants completed written and verbal consent procedures before beginning the study.

2.2. Task

Participants were shown a small green dot presented above a fixation cross ("+") for the same durations as those from Macar and Vidal (2003): 1.25 s, 1.6 s, 2.0 s, 2.5 s, or 3.125 s (a 25% increase for each interval). The fixation cross remained onscreen throughout the task except during break screens. Participants began each block with a "training" condition in which they were presented the dot above a red fixation cross for five cycles (ten cycles prior to the first round) of the target duration (2 s). Participants were not informed of the duration, but were informed that the target durations were identical throughout the task. Following training, a 250 ms white screen to indicate the next trials required response (probe condition) and the color of the fixation cross changed to white. The dot was then presented for the durations mentioned above, in random order and in equal probability. Participants were asked to judge if the duration of the stimulus presentation matched the target (2 s) by pressing a green button with their right index finger if the answer was "yes," and a red button with their right middle finger if the answer was "no." Participants were instructed to respond during inter-trial intervals (1.25 s) in which there was only the fixation cross on screen preceding the appearance of the next dot. Fig. 1 presents a graphical schematic of the task.

Participants completed 60 trials of each of the five durations, totaling 300 trials. A self-paced break screen appeared every 25 trials. After each break, the participant was again presented with five trials of "training" followed by a 250 ms white screen indicating the resumption of the task. Participants were instructed to remain as still as possible and to blink as infrequently as was comfortable during the main trials. The experiment was preceded by a practice block in which participants completed 25 trials with each of the stimulus durations with an added 1 s (i.e., 2.25 s, 2.6 s, 3 s, 2.5 s, 4.125 s). If participants did not complete the practice round with at least 12 correct trials, they completed a second practice block and were given further instruction when to respond.