



The time course of temporal discrimination: An ERP study

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ARTICLE INFO

Article history:

Accepted 8 September 2009

Available online 14 November 2009

Keywords:

Contingent negative variation (CNV)

Interval timing

Reference memory

Visual time discrimination

ABSTRACT

Objective: The question of how temporal information is processed by the brain is still a matter of debate. This study aimed to elucidate the brain electrical activity associated with a visual temporal discrimination task.

Methods: For this purpose, 44 participants were required to compare pairs of sequentially presented time intervals: a fixed standard interval (1000 ms), and an equal-to-standard, longer (1200 ms) or shorter (800 ms) comparison interval. Behavioural data and event-related potentials (ERPs) were analyzed.

Results: Long intervals were more rapidly identified than short intervals. The amplitude of the contingent negative variation (CNV) found at frontocentral sites before the end of the comparison interval was significantly affected by the difference between its duration and the standard one. The amplitude and the scalp distribution of ERPs registered after the offset of the comparison interval were linearly modulated by its absolute duration.

Conclusions: ERP components associated with the offset of the comparison intervals clarified the involvement of working memory processes and different brain structures in temporal discrimination.

Significance: This study further improves our understanding of the cognitive processes and neural substrates underlying temporal discrimination in healthy subjects and lays the ground for the investigation of clinical samples with time processing deficits.

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1. Introduction

The ability to discriminate temporal intervals of stimuli in the range of hundred milliseconds is essential for many cognitive and motor processes, from basic to complex behaviours, such as encoding perceptual events or fine tuning motor actions. Recently, there has been growing interest in understanding the cognitive and neural bases of such a time processing ability; however, as yet, the mechanisms by which the brain computes time are not fully understood (Coull and Nobre, 2008; Wittmann and van Wassenhove, 2009). Questions remain, for example, regarding the existence of single or multiple specialized brain areas that act as a clock, and whether timing is an intrinsic property of neural networks (Ivry and Spencer, 2004; Ivry and Schlerf, 2008).

To date, one of the most influential models of time processing is the Scalar Expectancy Theory (SET; Gibbon et al., 1984), which proposes the existence of a common cognitive and neural mechanism

that intervenes in all timing operations. This so-called ‘internal clock’ marks out time through the activity of a pacemaker (oscillator) that emits pulses, and an accumulator that integrates such pulses. In a further extension of the model, the activity of the clock is assumed to be affected by attentional processes, especially when intervals exceeding 1 s are being processed (the attentional-gate model; Macar et al., 1994; Block and Zakay, 1996). More precisely, it has been hypothesized that attentional processes allow pulses generated by the pacemaker to be counted by the accumulator, by closing a gating mechanism (switch) at the beginning of the temporal interval. The pacemaker’s rate is thought to be influenced by the level of arousal. The higher the rate of the pacemaker, or the faster the closing of the switch, the more pulses are accumulated and the longer a temporal interval is perceived.

The internal clock models assume that the clock mechanism is the first step in a three-stage process, which subsequently involves a memory and a decision stage. In the memory stage, the pulses accumulated during the currently perceived or produced interval are counted and briefly stored in working memory in order to be compared with a previously memorized interval, stored in the reference memory. This process relies on working memory resources (Fortin and Rousseau, 1998; Ulbrich et al., 2007). A

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decision regarding the duration of a particular interval is then made on the basis of the previous comparison.

Clearly, attention and memory resources are differentially engaged depending on the task requirements as well as on the length of the interval. Intervals in the range of hundred milliseconds have been hypothesized to require automatic processing, whereas intervals in the order of seconds and minutes need higher cognitive resources (Brown and Boltz, 2002; Monfort and Pouthas, 2003; Lewis and Miall, 2006b).

Alternative models have been proposed, which partly extend but also challenge the internal clock framework. According to the multiple-oscillators theory, for example, time is represented by a set of oscillators, each with a unique period, ranging from milliseconds to days (Church and Broadbent, 1990; Miall, 1989; Matell and Meck, 2004). Because of the existence of different oscillators, with different local maxima in sensitivity across different orders of time intervals, our perception of time intervals is not linear.

The Multiple Time Scales framework (MTS; Staddon and Higa, 1999; Lewis and Miall, 2006a,b) dispenses with the pacemaker and implies that the processing of the duration of an event is based on the decay of its trace in memory. Accordingly, the information that the brain uses to measure time is derived from the ramping activity of neurons in the prefrontal cortex during the event, which is also responsible for the working memory process.

The State-Dependent Network (SDN; Karmarkar and Buonomano, 2007) proposes that there is no specific mechanism dedicated to time processing, but neural populations within each brain region intrinsically encode the temporal characteristic of sensory events through time-dependent neural changes (Ivry and Schlerf, 2008; Spencer et al., 2009; van Wassenhove et al., 2008).

Neuropsychological and neuroimaging evidence has identified several functionally integrated brain regions that subserve time processing tasks. These networks include the cerebellum, the basal ganglia, the insula, the frontal (dorsolateral prefrontal cortex and supplementary motor area) and the inferior parietal cortices (Gibbon et al., 1997; Harrington et al., 1998; Macar et al., 1999; Rao et al., 2001; Macar and Vidal, 2002; Meck and Benson, 2002; Fernandez et al., 2003; Lewis and Miall, 2003, 2006a,b; Coull et al., 2004; Ivry and Spencer, 2004; Meck and Malapani, 2004; Rubia and Smith, 2004; Buhusi and Meck, 2005; Lustig et al., 2005; Pouthas et al., 2005; Koch et al., 2007, 2009; Buetti et al., 2008; Coull et al., 2008; Coull and Nobre, 2008). By means of an independent component analysis (ICA) on fMRI data, Stevens et al. (2007) identified four main brain circuits that may represent the neural substrates of a temporal reproduction task. These brain circuits were found to encompass frontostriatal, cerebellar, frontoparietal and motor areas, respectively.

The prevalent contribution of specific structures depends on the duration of the interval to be processed, on the cognitive load, on the type of task and the stimulus modality used (Lewis and Miall, 2006a,b; Koch et al., 2009). Among these circuits, the activity of the cerebellum seems more crucial when subjects are engaged in processing sub-second intervals; on the other hand basal ganglia have been associated with the processing of intervals in the order of both milliseconds and seconds (Ivry, 1996; Rammsayer, 1999; Lewis and Miall, 2003, 2006a,b; Koch et al., 2007). The dorsolateral prefrontal and parietal regions are mostly linked to timing tasks that imply a higher cognitive level of attention and working memory (i.e. Mimura et al., 2000; Koch et al., 2002, 2003). Lewis and Miall (2006a,b) hypothesized that the firing of prefrontal neurons, especially those in the right DLPFC, during a delay in which information has to be held online, is both an index of working memory and an index of tracking the passage of time, especially for intervals longer than 1 s (cognitively controlled timing system).

Nevertheless, the functional contribution of each neural region of the network to timing tasks is still not clear cut. Deficits in the

millisecond range, for example, have been observed in patients with prefrontal lesions (Nichelli et al., 1995; Coslett et al., 2009). Furthermore, many questions remain on the time course of the activation of the different brain regions.

Measurement of event-related potentials represents the most adequate experimental technique for elucidating the time course of brain activation associated with time processing. Among electrophysiological measures, a sustained negative slow wave, which shows the characteristics of a contingent negative variation (CNV), has been hypothesized to be an online index of timing (Macar and Vidal, 2004; Meck et al., 2008). The CNV is typically observed in between two stimuli, a warning signal and a subsequent target, when a subject is expecting the occurrence of the target in the next few seconds, and usually displays the maximum amplitude at fronto-central sites. The CNV changes to a biphasic waveform, the initial and the terminal components, when the interval between the warning and the target exceeds 3–4 s (Loveless and Sanford, 1974). It is generally agreed that the initial component constitutes an index of the orienting response to the warning stimulus, while the terminal component has been linked to preparatory processes (Rohrbaugh et al., 1976). Shorter intervals, in the range of 1–2 s, do not allow sufficient time for the CNV to develop its biphasic waveform, and the CNV presents a monophasic waveform that is the consequence of the overlapping components (Rohrbaugh and Galliard, 1983). However, several lines of evidence also support the hypothesis that the monophasic waveshape of the CNV found in timing tasks, where the estimation of intervals shorter than 3 s is required, reflects a qualitatively different process, i.e. the processing of temporal duration (Macar and Vitton, 1982; Elbert et al., 1991). The CNV amplitude has been shown to be modulated in amplitude by interval length in tasks in which subjects have to explicitly or implicitly process a duration, and, more noticeably, a CNV resolution has been found before the end of a duration to be estimated, at a point in time at which an interval equal to a previously memorized standard one has elapsed (Macar and Vidal, 2003; Pouthas et al., 2000, Pouthas, 2003; Pfeuty et al., 2003, 2005; N'Diaye et al., 2004; Praamstra et al., 2006). Consequently, this ERP component has been proposed to reflect an increase in neural activity associated with the accumulation of pulses, the retrieval of reference memory, and the decision-making stage.

By combining positron emission tomography (PET) and ERP techniques in a time discrimination task, Pouthas et al. (2000) confirmed that the activity of the medial frontal cortex was related to the length of a comparison duration matched to a previously memorized standard duration. From a neural point of view, the CNV has been proposed to reflect the activity of the supplementary motor area (SMA), a major component of the frontostriatal loop, which receives input from the basal ganglia (Macar et al., 1999; Macar and Vidal, 2002, 2004; Macar et al., 2004).

Among ERP components, a Late Positive Component related to time (LPct) has been reported in frontopolar sites in visual time discrimination tasks, which increased in amplitude as a function of stimulus durations (Paul et al., 2003). This component has been hypothesized to be related to the decision-making stage of time processing.

Although the role of the CNV component, which develops during the duration to be processed, has been extensively investigated, the role of later electrophysiological correlates, which show after the duration, is still unclear. The decision process associated with temporal discrimination has been linked to both the CNV and the LPct. In fact, intervals longer than the standard may be processed before their end, but this is not the case for equal-to-standard and shorter intervals.

The aim of this study was to clarify the time course of brain activation associated with the temporal discrimination process by specifically examining the functional significance of ERP components

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