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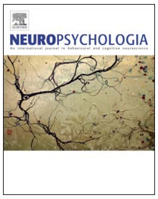

The role of the P3 and CNV components in voluntary and automatic temporal orienting: A high spatial-resolution ERP study

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ABSTRACT

A main distinction has been proposed between voluntary and automatic mechanisms underlying temporal orienting (TO) of selective attention. Voluntary TO implies the endogenous directing of attention induced by symbolic cues. Conversely, automatic TO is exogenously instantiated by the physical properties of stimuli. A well-known example of automatic TO is sequential effects (SEs), which refer to the adjustments in participants' behavioral performance as a function of the trial-by-trial sequential distribution of the foreperiod between two stimuli. In this study a group of healthy adults underwent a cued reaction time task purposely designed to assess both voluntary and automatic TO. During the task, both post-cue and post-target event-related potentials (ERPs) were recorded by means of a high spatial resolution EEG system. In the results of the post-cue analysis, the P3a and P3b were identified as two distinct ERP markers showing distinguishable spatiotemporal features and reflecting automatic and voluntary a priori expectancy generation, respectively. The brain source reconstruction further revealed that distinct cortical circuits supported these two temporally dissociable components. Namely, the voluntary P3b was supported by a left sensorimotor network, while the automatic P3a was generated by a more distributed frontoparietal circuit. Additionally, post-cue contingent negative variation (CNV) and post-target P3 modulations were observed as common markers of voluntary and automatic expectancy implementation and response selection, although partially dissociable neural networks subserved these two mechanisms. Overall, these results provide new electrophysiological evidence suggesting that distinct neural substrates can be recruited depending on the voluntary or automatic cognitive nature of the cognitive mechanisms subserving TO.

1. Introduction

As do all living organisms, human beings must cope with the essential fact that their behaving in the world is unavoidably constrained by time. In fact, our cognition and behavior are inextricably founded on the capacity to compute the precise temporal metrics that regulate the dynamic flux of sensory events. As a consequence, the prioritizing of sensory information that is temporally relevant for our goals is an essential cognitive mechanism for proactively regulating our behavior (Nobre, 2001). Within this framework, the ability to direct attention in specific moments in time, known as temporal orienting (TO), stands as a fundamental attentional mechanism biasing our cognitive resources in order to optimize our behavior (Correa, 2010; Coull et al., 2000; Coull and Nobre, 1998).

In the last two decades, an increasing number of studies have shed light on the nature of the cognitive processes involved in TO as well as on their neural underpinnings (Correa, 2010; Coull and Nobre, 1998; Coull et al., 2011; Coull, 2010). Overall, a main distinction has been proposed between voluntary and automatic mechanisms as two distinct sources of TO (Barnes and Jones, 2000; Correa, 2010). Voluntary TO calls into play the explicit encoding of the association between the physical properties of a given stimulus and its temporal meaning. A classic, real-life example implying the use of voluntary TO is the yellow light signaling the impending stop signal that allows us to adjust driving behavior accordingly. Conversely, automatic TO mechanisms do not require voluntary efforts to create stimulus-duration associations as these are exogenously instantiated by the temporal properties of stimuli (Coull and Nobre, 2008; Rohenkohl et al., 2011). An experimental phenomenon that well describes the automatic orienting of temporal attention consists in sequential effects (SEs). SEs are adjustments in participants' behavioral performance as a function of sequential changes (i.e., trial-by-trial) in the temporal structure of a repetitive stream of events, such as the foreperiod (FP) interval between successive stimuli delivered in a trial. In the experimental context of the

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variable FP paradigm, SEs refers to the fact that the reaction time (RT) to an imperative stimulus depends not only on the current FP (FP_n) but also on the FP of the immediately preceding trial (FP_{n-1}) (Baumeister and Joubert, 1969; Drazin, 1961; Los and Heslenfeld, 2005; Steinborn et al., 2008; Vallesi et al., 2007b; Van Der Lubbe et al., 2004; Woodrow, 1914). For example, a short FP_{n-1} will lead to the automatic prediction of a short waiting time in the following FP_n trial, resulting in a clear behavioral advantage (i.e., RT speeding up). Several lines of research provided consistent evidence in favor of the automaticity of SEs. In particular, there is evidence that SEs (1) are not interfered with by a concurrent working memory task (Capizzi et al., 2013, 2012; Vallesi et al., 2014); (2) are already present in four-year-old children (Vallesi and Shallice, 2007); (3) follow a stable, adult-like developmental trajectory until adult age (Mento and Tarantino, 2015); and (4) are ubiquitously present in children engaged in spatiotemporal orienting tasks (Johnson et al., 2016, 2015).

Neuroimaging studies individuated a distributed frontoparietal cortical network as the main neural substrate of voluntary TO (Cotti et al., 2011; Coull et al., 2013, 2000; Coull and Nobre, 1998). In particular, there is converging evidence that the left inferior parietal sulcus (l-IPS) may play a central role in both generation and implementation of fixed temporal expectancy, which are two computational steps at the basis of voluntary TO (Coull et al., 2016; Coull, 2011; Mento and Vallesi, 2016). However, the neural bases of SEs have been much less studied. Overall, the existing literature suggests a possible neural locus of SEs in the cortical premotor and parietal areas as well as in subcortical structures (Correa et al., 2014; Triviño et al., 2016, 2010; Vallesi et al., 2007a).

In parallel to neuroimaging research, event-related potential (ERP) studies have shed light on the neural dynamics underlying TO. Specifically, the contingent negative variation, or CNV (Mento, 2013; Walter et al., 1964), preceding the imperative stimulus has been consistently reported as a marker of temporal expectancy voluntarily induced by the informativeness of the cue (Capizzi et al., 2013; Correa et al., 2006a; Griffin et al., 2002; Griffin and Nobre, 203; Mento, 2013; Mento et al., 2015; Mento and Vallesi, 2016; Miniussi et al., 1999). Nonetheless, other studies have demonstrated that the CNV is also sensitive to SEs, as its amplitude in a given trial *n* is significantly affected by the FP experienced in the preceding trial (Capizzi et al., 2013; Los and Heslenfeld, 2005; Mento, 2013; Trillenberg et al., 2000; Van Der Lubbe et al., 2004). This finding suggests that the CNV is a common ERP marker of voluntary and automatic TO, in line with the account of this component's multicomponential cognitive significance (Mento, 2013; Mento et al., 2013; Mento and Valenza, 2016). Other studies have reported larger ERP effects following the task-relevant stimulus, including a modulation of the post-target evoked electrophysiological activity (for a review, see Nobre, 2010). Likewise the CNV, post-stimulus ERP effects have been observed in response to either voluntarily or automatically expected stimuli (Correa et al., 2006a; Correa and Nobre, 2008; Lange, 2013; Miniussi et al., 1999). In other words, the existing ERP studies have shown that either pre-target CNV or post-target evoked responses are similarly modulated by voluntary and automatic TO, leaving unsolved the question whether different attentional mechanisms may operate through spatially and/or temporally overlapping neural mechanisms. In summary, while neuroimaging studies suggest that voluntary and automatic TO may be based upon partially distinct and dissociable neurocognitive mechanisms, current electrophysiological evidence does not allow for their neat and definitive dissociation.

To address this issue, in the present study, current knowledge of the electrophysiological activity underlying TO was, for the first time, extended upon analysis of early post-cue ERP activity. The choice to focus on this computational time window is justified by the assumption that TO may operate via a feed-forward process in which temporal expectancy of forthcoming stimuli is established a priori in an early time window and then implemented/updated over time as a function of sensory evidence (Coull et al., 2016; Coull, 2011; Mento and Vallesi, 2016). The working assumption of this study was that the allocation of attentional resources can be established as soon as the task-relevant information provided by the cue is made available, resulting in spatiotemporally dissociable ERP activity for voluntary and automatic TO. To substantiate this hypothesis, high spatial resolution EEG activity was collected from healthy participants underlying an experimental task in which the symbolic value of the cue was manipulated in order to provide or not provide valid temporal information about the onset of a subsequent target.

2. Materials and methods

2.1. Participants

Data were collected from sixteen healthy, right-handed adults (mean age, 24.5 years [SD, 2.05]; range, 22–27 years; 8 males). Visual acuity was normal or corrected to normal. All experimental methods had ethical approval from the Research Ethics Committee of the School of Psychology at the University of Padua (prot. N. 1179).

2.2. Stimuli and task

Participants were seated comfortably in a chair at a viewing distance of ~ 60 cm from the monitor. Stimuli were presented on a 17-in. monitor at a resolution of 1280 × 1024 pixels. All participants performed a simple reaction time task already employed by Mento and Tarantino (2015) and Mento and Vallesi (2016), which included either cued (temporal) or uncued (neutral) blocks (Fig. 1).

Each trial began with the display of a visual cue (500 ms) at the center of the screen, followed by the presentation of a target stimulus,

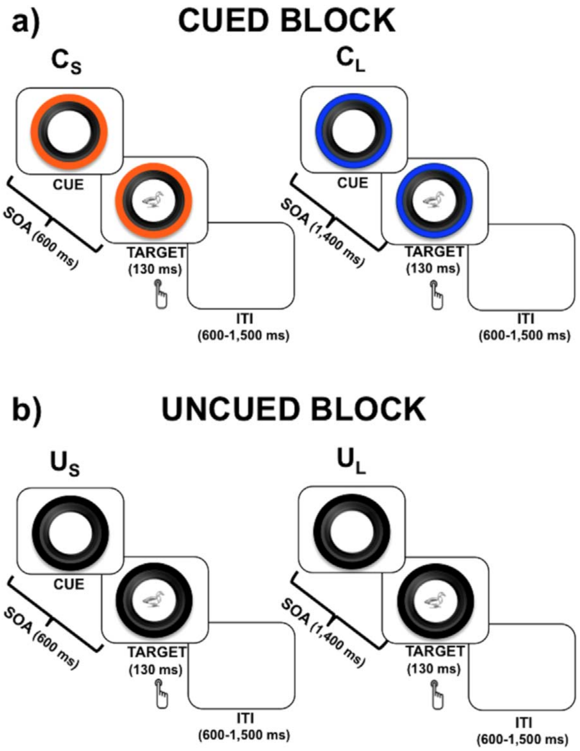

Fig. 1. Experimental paradigm. In the cued block (a) the visual cue provided fixed temporal information concerning the stimulus-onset asynchrony (SOA) duration, which could be short (left panel) or long (right panel), according to the color of the cue (counterbalanced across subjects). By contrast, in the uncued block (b) participants never knew in advance the duration of the SOA, which could nevertheless have the same short or long duration as in the temporal cueing task. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).