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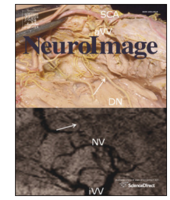

Conflict awareness dissociates theta-band neural dynamics of the medial frontal and lateral frontal cortex during trial-by-trial cognitive control

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ABSTRACT

Recent findings have refuted the common assumption that executive control functions of the prefrontal cortex exclusively operate consciously, suggesting that many, if not all, cognitive processes could potentially operate unconsciously. However, although many cognitive functions can be launched unconsciously, several theoretical models of consciousness assume that there are crucial qualitative differences between conscious and unconscious processes. We hypothesized that the potential benefit of awareness in cognitive control mechanisms might become apparent when high control has to be maintained across time and requires the interaction between a set of distant frontal brain regions. To test this, we extracted oscillatory power dynamics from electroencephalographic data recorded while participants performed a task in which conflict awareness was manipulated by masking the conflict-inducing stimulus. We observed that instantaneous conflict as well as across trial conflict adaptation mechanisms were associated with medial frontal theta-band power modulations, irrespective of conflict awareness. However, and crucially, across-trial conflict adaptation processes reflected in increased theta-band power over dorsolateral frontal cortex were observed after fully conscious conflict only. This suggests that initial conflict detection and subsequent control adaptation by the medial frontal cortex are automatic and unconscious, whereas the routing of information from the medial frontal cortex to the lateral prefrontal cortex is a unique feature of conscious cognitive control.

Introduction

Many perceptual and cognitive functions can be influenced by subliminal information and in recent years it has been shown that even "high-level" executive functions (i.e. error/conflict processing, task-set switching, response inhibition) can be launched unconsciously (for reviews, see Desender and Van Den Bussche, 2012; van Gaal and Lamme, 2012). These findings contradict the commonly held assumption that executive functions of the prefrontal cortex exclusively operate consciously (for reviews, see Badgaiyan, 2000; Dehaene and Naccache, 2001; Eimer and Schlaghecken, 2003; Hommel, 2007; Jack and Shallice, 2001; Norman and Shallice, 1986). More speculatively, these results might even suggest that all cognitive processes can potentially operate in two separate modes: a conscious one and an unconscious one.

However, although unconscious processes seem very powerful, there might be crucial differences between conscious and unconscious executive processes. We hypothesize that these become evident when increased levels of control have to be maintained for longer periods of time and conflict adaptation requires the information exchange between distant prefrontal brain regions. Previous studies have shown that subliminal information processing is fleeting (decaying within ~500 ms Greenwald et al., 1996) and restricted to local processing modules (van Gaal and Lamme, 2012). According to the global neuronal workspace theory (Dehaene and Naccache, 2001), conscious information processing, on the other hand, is associated with strong and durable neuronal firing and relies on the sharing and routing of information among several high-level inter-connected cortical regions, among which the dorsolateral prefrontal cortex (DLPFC) seems to play a crucial role (Dehaene et al., 2014).

To test the potential benefit of awareness and the role of the DLPFC in trial-by-trial executive control processes (as compared to online transient control), we extracted oscillatory neural dynamics from current-source density transformed EEG data recorded while human participants performed a typical "conflict task" in which conflict awareness was manipulated by masking (Fig. 1A). Conflict tasks (i.e. Stroop, Flanker) are often performed to study conflict monitoring/detection mechanisms on the current trial as well as trial-by-trial conflict-

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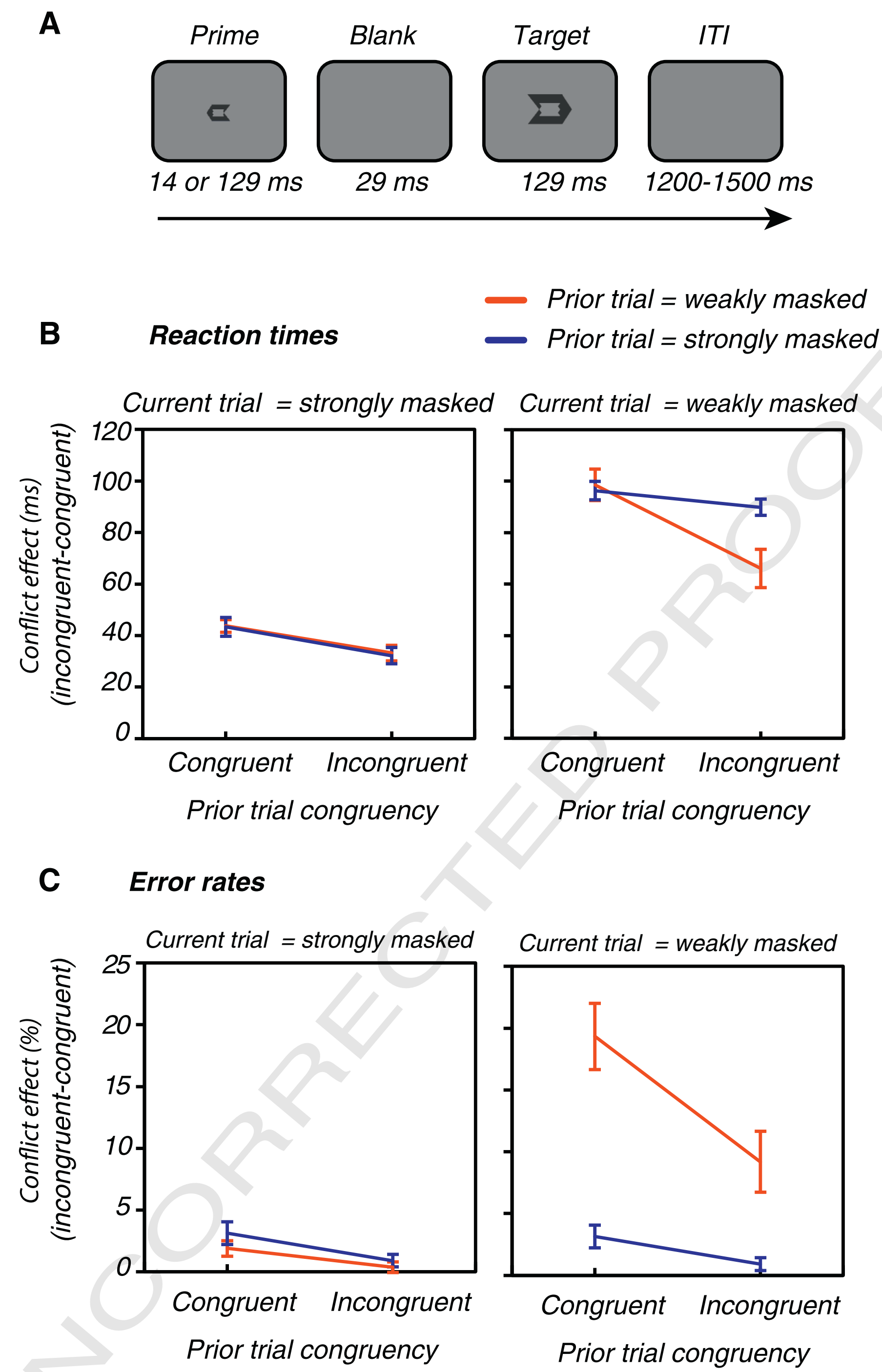

Fig. 1. Experimental design and behavioral results. (A) Schematic representation of the experimental task and the stimuli. Primes could be congruent or incongruent with the direction of the target (50/50 congruent/incongruent trials). Primes could be presented briefly (14 ms, strongly masked primes) or longer (129 ms, weakly masked primes). (B/C) Conflict adaptation effects for different levels of masking strength in the prior and current trial. Conflict effects in trial n for RTs (mean RT on incongruent trials–mean RT on congruent trials, B) and error rates (mean percentage of errors on incongruent trials–mean percentage of errors on congruent trials, C) as a function of prime-target correspondence in trial $n-1$ (congruent vs. incongruent), masking strength in trial n (weak vs. strong masking) and masking strength in trial $n-1$. Error bars reflect the standard error of the mean.

induced control adaptations on the next trial (the "Gratton" effect, Gratton et al., 1992). The underlying neural sources of conflict resolution are studied extensively and there are several models trying to explain the phenomenon (Egner, 2007). The conflict-monitoring model proposes that the medial frontal cortex (MFC) and the anterior cingulate cortex (ACC) in particular, monitor or detect the presence of conflict and then signal other regions, most prominently the DLPFC, to subsequently implement cognitive control (Botvinick et al., 2001; MacDonald et al., 2000). Others have argued for a control-implementing or "regulatory" role, in contrast to a mere "monitoring" role, of the ACC instead (Posner and DiGirolamo, 1998; Roelofs et al., 2006). Theta-band neural dynamics over midfrontal/dorsolateral frontal cortex are thought to be a candidate mechanism for the realization of cognitive control (Cavanagh and Frank, 2014). It seems that it is especially the DLPFC that has a mnemonic function in maintaining information about recently experienced conflict in order to modify the