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Research paper

Frontoparietal theta oscillations during proactive control are associated with goal-updating and reduced behavioral variability



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ABSTRACT

Low frequency oscillations in the theta range (4–8 Hz) are increasingly recognized as having a crucial role in flexible cognition. Such evidence is typically derived from studies in the context of reactive (stimulus-driven) control processes. However, little research has explored the role of theta oscillations in preparatory control processes. In the current study, we explored the extent of theta oscillations during proactive cognitive control and determined if these oscillations were associated with behavior. Results supported a *general* role of theta oscillations during proactive cognitive control, with increased power and phase coherence during the preparatory cue interval. Further, theta oscillations across frontoparietal electrodes were also modulated by proactive control demands, with increased theta phase synchrony and power for cues signaling the need for *goal updating*. Finally, we present novel evidence of negative associations between behavioral variability and both power and phase synchrony across many of these frontoparietal electrodes that were associated with the need for goal updating. In particular, greater consistency in frontoparietal theta oscillations, indicated by increased theta phase and power during mixed-task blocks, resulted in more consistent task-switching performance. Together, these findings provide new insight into the temporal dynamics and functional relevance of theta oscillations during proactive cognitive control.

1. Introduction

Successful adaptation to our environment requires control over thoughts and behaviors. This need for control is especially important when habitual or response biases are insufficient to meet goals. In such situations, a set of processes collectively referred to as cognitive control is employed in order to prioritize processing of goal-relevant information (Braver, 2012; Mackie, Van Dam, & Fan, 2013; Miller & Cohen, 2001; Miyake et al., 2000). Such control processes rely in part on an extensive frontoparietal network that links key hubs in lateral and medial prefrontal cortices with posterior parietal cortex (Corbetta & Shulman, 2002; Dosenbach, Fair. Cohen. Schlaggar, & Petersen, 2008; Petersen & Posner, 2012). However, it

remains unclear how these frontoparietal networks implement flexible integration of goal-appropriate information.

Low frequency oscillations within the frontoparietal network play a critical role in cognitive control. In particular, cortical theta rhythms (4–8 Hz) are frequently associated with cognitive control processes (Cavanagh, Zambrano-Vazquez, & Allen, 2012; see also Cavanagh & Frank, 2014; Sauseng et al., 2010 for recent reviews). For instance, an increase in theta power over frontocentral electrodes (i.e., midline frontal theta; MFθ) is typically observed during moment-to-moment adjustments of the control system.² Intracranial human recordings suggest that MFθ is generated in the medial cingulate cortex (MCC; Cohen, Ridderinkhof, Haupt, Elger, & Fell, 2008; Wang, Ulbert, Schomer, Marinkovic, & Halgren, 2005), a key hub in cognitive control

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² Typically, MFθ is defined as a relative increase in theta amplitude along frontocentral electrodes that lasts anywhere from 1 s to more than 10 s (see Mitchell et al., 2008 Mitchell , McNaughton , Flanagan & Kirk, 2008). However, many studies report MFθ as a much briefer increase in frontocentral theta. e.g., as short as 400 ms (Hanslymayr et al., 2008). This time course is consistent with transient employment of cognitive control processes. In this paper, we define MFθ as increased theta oscillatory activity with mid-frontal topology, rather than a strictly sustained increase in mid-frontal theta activity.

networks (Dosenbach et al., 2008). MF θ power is enhanced when conflict monitoring/resolution processes are required, such as, after the elicitation of an incorrect vs. correct response (Cavanagh, Cohen, & Allen, 2009; Luu, Tucker, & Makeig, 2004; Trujillo & Allen, 2007), when the stimulus elicits response conflict e.g., Stoop task (Hanslmayr et al., 2008), flanker task (Cohen & Cavanagh, 2011; Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012) and when inhibiting a response (e.g., nogo trials during go/nogo tasks; Funderud et al., 2012; Kamarajan et al., 2004).

Frontoparietal theta (FPθ) activity has also been reported. FPθ can refer to either synchronized activity between anterior and posterior recording sites or the contemporaneous increase in theta power at frontal and posterior electrodes. Such distinctions are important to note, as synchronization is likely to reflect communication between cortical hubs whereas increases in power may reflect engagement of that cortical region. FPθ has been reported during goal-updating processes, such as when adjusting behavioral response-sets in the presence of goal-conflict (e.g., synchronization; Moore, Gale, Morris, & Forrester, 2006; Moore, Mills, Marshman, & Corr, 2012), encoding information during working memory tasks (synchronization and power increases; Sauseng, Klimesch, Schabus, & Doppelmayr, 2005; synchronization; Summerfield & Mangels, 2005; Weiss, Müller, & Rappelberger, 2000) and switching between tasks (synchronization; Cooper et al., 2015, Sauseng et al., 2006).³

Links between theta oscillations and cognitive control have typically relied on paradigms that engage reactive cognitive control processes. However, cognitive control can also be employed proactively, setting up the system in preparation for anticipated change or conflict (Braver, 2012). Recent work suggests that theta oscillations are also involved in proactive cognitive control. For instance, Cunillera et al. (2012) reported enhanced theta power over frontal electrodes during a cued-Wisconsin card sorting task when cued to shift categorization rule. Likewise, in a Simon task, van Driel, Swart, Egner, Ridderinkhof, and Cohen (2015) found increased MF0 to cues predicting a high conflict target. With a response-cueing paradigm, MF0 power was increased on trials that may have required response inhibition as compared to trials definitely required a go response (van that Noordt. Campopiano, & Segalowitz, 2016). In a related study, van Noordt, Desjardins, Gogo, Tekok-Kilic, and Segalowitz (2016) also found increased MF0 to cues that allowed preparation for an upcoming antisaccade. Finally, Rawle, Miall, and Praamstra (2012) reported shortlived increases in frontal and parietal theta power to preparatory cues during a visual/memory search task. Interestingly, all the above instances of MF0 during proactive control involve some type of response conflict anticipation, consistent with the view that MF θ serves as a signature of action monitoring (e.g., Cavanagh et al., 2012).

Proactive theta effects have also been shown in contexts that do not involve response conflict anticipation. Cooper et al. (2015) measured theta phase-locking across the scalp during a cued-trials task-switching paradigm in both cue-target interval (CTI) and post-target periods. Theta synchronization early in the CTI was sensitive to preparation to switch, corresponding temporally to the early differential event related potential (ERP) positivity typically reported between switch and repeat trials (Karayanidis et al., 2009; Nicholson, Karayanidis, Davies, & Michie, 2006). This 'switch-preparation' network was followed by a distinct frontoparietal theta network that emerged after target onset for cues that did not allow task updating during the CTI. The latter theta network corresponded temporally with conflict resolution effects typically seen during interference control in taskswitching (Jamadar, Hughes, Fulham, Michie & Karayanidis, 2010; Nicholson et al., 2006). Interestingly, while both proactive and reactive theta networks were frontoparietally distributed, conjunction analysis showed that they were in fact distinct, i.e., not comprised of identical connections. Thus, while both proactive and reactive control modes are facilitated by frontoparietal theta networks, different control demands activate distinct frontoparietal networks. Importantly, these networks are involved in more than just conflict anticipation.

Effective use of proactive and reactive control modes is a hallmark of efficient cognitive control (Braver, 2012). In well-learnt tasks, participants who can effectively engage proactive and reactive control mechanisms have more consistent performance than participants who cannot. Lower inter-trial reaction time (RT) variability has been associated with more effective goal-directed control (e.g., Bellgrove, Hester, & Garavan, 2004). Increased trial-by-trial variability in behavioral performance is also seen in psychopathologies associated with cognitive control deficits (e.g., ADHD, see Kofler et al., 2013; schizophrenia, e.g., Kaiser et al., 2008; Smyrnis et al., 2009). As such, trial-bytrial RT variability may be a good metric for assessing such cognitive control efficiency.

Relationships between theta oscillations (i.e., phase synchronization across trials) and cognitive control efficiency (i.e., trial-by-trial RT variability) have been established principally in reactive control paradigms, where behavioral adjustments are made to deal with stimulusdriven conflict or interference (e.g., flanker tasks, Cohen & Cavanagh, 2011; Simon tasks, Cohen & Donner, 2013; go/nogo tasks, Papenberg, Hämmerer, Müller, Lindenberger, & Li, 2013; stop signal tasks, Schmeidt-Fehr, Dühl, & Basar-Eroglu, 2011). These studies show that variability in cognitive control efficiency may be linked to the neural dynamics of the frontoparietal network, and in particular, that theta oscillations are strongly associated with reactive cognitive control processes. However, given recent evidence that the phase of frontoparietal theta oscillations is also important for proactive control (Cooper et al., 2015), it is possible that preparatory theta oscillations may also contribute to cognitive control efficiency.

The current study investigated the influence of proactive theta oscillations on behavioral variability using the cued-trials task-switching paradigm. We quantified theta oscillatory activity using both power and inter-trial phase clustering (ITPC) measures. ITPC is a measure of phase synchrony across trials, not between electrodes, and so provides information about phase variability *within* a network, rather than being a direct measure of network structure. ITPC determines the influence of consistent phase responses, or timing, that may be important for cognitive control. We used ITPC to derive measures of MF0 and FP0 from distinct electrodes or electrode clusters. This provides a different source of information than inter-site phase clustering, which measures phase synchronization between sites and identifies time-critical windows for communication between electrodes/brain regions (Cooper et al., 2015).

We computed theta power and ITPC during proactive control processes and examined their relationship to trial-by-trial behavioral variability. We first aimed to replicate previous work (e.g., Cooper et al., 2015; Cunillera et al., 2012; Rawle et al., 2012; van Driel et al., 2015; van Noordt, Campopiano et al., 2016; van Noordt, Desjardins et al., 2016) that theta oscillations are involved in proactive cognitive control. If modulation of theta oscillations is a general index of cognitive control, we expected increased theta power and ITPC during the CTI in the mixed-task block, which requires greater proactive control, as compared to the single-task block - a comparison corresponding to measures of general switch cost (Jamadar, Thienel & Karayanidis, 2015). Behavioral and ERP studies have shown that proactive control processes are differentially activated across switch and repeat trials in the mixed-task block, giving rise to specific switch costs. In ERPs, goal setting and task updating processes on switch trials are associated with an increased centroparietal positivity as compared to repeat trials (Karayanidis et al., 2009; Karayanidis, Whitson, Heathcote, & Michie,

³ Note that theta oscillations are not exclusively linked to cognitive control. Recently Cohen (2014a) suggested that theta oscillations could be a biological consequence of interactions between cortical layers in the prefrontal cortex. In this scenario, other cognitive processes linked to theta oscillations (e.g., encoding and rehearsal of new information; Klimesch, 1999; Klimesch, Freunberger & Sauseng, 2010) also engage similar microcircuits as cognitive control and thus produce theta rhythms (see also Cooper et al., 2016).

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