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

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Highlights

- Theta activity was present across a frontoparietal network during proactive control
- Parietal theta emerged prior to frontal theta during cue period
- This frontoparietal anticipatory theta was linked goal-updating
- Enhanced power and phase were associated with lower behavioral variability
- Preparatory oscillatory activity is predictive of cognitive control efficiency

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.

Keywords: cognitive control; executive function; proactive control; task switching; theta; EEG; power; inter-trial phase-coherence

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 et al., 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, Griesmayr, Freunberger & Klimesch, 2010 for recent reviews). For instance, an increase in theta power over frontocentral electrodes (i.e., midline frontal theta; MF θ) is typically observed during moment-to-moment adjustments of the control system¹. Intracranial human recordings suggest that MF θ 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 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

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

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 (FP θ) activity has also been reported. FP θ 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. FP θ 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 et al., 2005; synchronization; Summerfield & Mangels, 2005; Weiss, Müller, & Rappelberger, 2000) and switching between tasks (synchronization; Cooper et al., 2015, Sauseng et al., 2006)².

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 MF θ to cues predicting a high conflict target. With a response-cueing paradigm, MF θ power was increased on trials that may have required response inhibition as compared to trials that definitely required a go response (van Noordt,

² 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, Darriba, Karayanidis & Barceló, 2016).

Campopiano, & Segalowitz, 2016). In a related study, van Noordt, Desjardins, Gogo, Tekok-Kilic and Segalowitz (2016) also found increased MF θ to cues that allowed preparation for an upcoming anti-saccade. Finally, Rawle, Miall and Praamstra (2012) reported short-lived increases in frontal and parietal theta power to preparatory cues during a visual/memory search task. Interestingly, all the above instances of MF θ 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 et al., 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 task-switching (Jamadar, Hughes, Fulham, Michie & Karayanidis, 2010; Nicholson et al., 2005). 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-learned 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-by-trial 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 stimulus-driven 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 MF θ and FP θ 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 et al., 2016a; 2016b) 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; 2011). Therefore, we expected that theta effects would be strongest for cues that encourage preparation to switch than for repeat cues, especially within the first half of the CTI. After establishing that theta oscillations are involved during proactive control, we expected that enhanced theta power and ITPC would be associated with improved cognitive control efficiency (i.e., lower trial-by-trial RT variability). We expected these relationships to be most pronounced for switch trials and early in the cue-target interval (CTI) when switch-specific preparation processes occur.

Although cognitive control processes are most consistently linked to oscillatory activity in the theta band, activity in other frequency bands has also been reported, especially during task-switching. In particular, switch trials show increased alpha (8-13 Hz) oscillations compared to repeat trials (e.g., Foxe et al., 2014; Mansfield, Karayanidis & Cohen, 2012; Serrien, Pogossyan, Cassidy & Brown, 2004; but see Sauseng et al., 2006). Such alpha effects are usually present at posterior electrodes and may reflect selective attention/inhibition processes involved in changing task sets (Foxe et al., 2011; Rihs,

Michel & Thut, 2007; Sauseng et al., 2005b). Furthermore, recent studies exploring the role of theta oscillations during proactive control also report accompanying posterior alpha processes (e.g., van Driel et al., 2015; van Noordt, Desjardins, Gogo, Tekok-Kilic & Segalowitz, 2016; see also Cooper et al., 2016). These findings suggest that attention/inhibition processes may facilitate preparatory control using alpha oscillations. Therefore, while the current study focuses primarily on the role of midfrontal and frontoparietal theta oscillations, we present time-frequency results for a broad range of frequencies, including alpha, for completeness where appropriate.

2. Methods

2.1. Participants

Two hundred and fifteen participants aged from 15 to 35 from the wider Newcastle area provided written, informed consent (participants under 18 years of age also provided parental consent prior to testing) and were reimbursed \$20 per hour for participating in the current EEG experiment as part of a larger project (Karayanidis et al., 2016; <http://www.age-ility.org.au/>). Participants were asked to abstain from caffeine and alcohol at least two hours prior to testing. Data from three participants were excluded: two participants had very fast responses and very high error rates (i.e., participants were simply responding to the presence of a target rather than performing the task) and EEG data from one participant was incorrectly recorded. As measures of variability are sensitive to the number of trials contributing to the EEG analysis, 27 participants with fewer than 80 trials for at least one condition in the mixed task block after EEG preprocessing were also excluded. This resulted in a final sample of 185 participants, including 29 participants aged 15-17 years (see Table 1 for demographic information). The current protocol complies with the Declaration of Helsinki and was approved by the University of Newcastle Human Research Ethics Committee (HREC: H-2012-0157).

2.2. Task and stimuli

A gray circle (visual angle = 5°) was continuously presented onscreen and divided into six segments. Pairs of adjacent segments were marked with thicker lines denoting three task sections: letter, digit, and color (see Fig. 1A). The target was a pair of characters consisting of combinations of a letter, a digit, or a non-alphanumeric symbol and was presented either in gray or in color. Each target (e.g., gray A4) consisted of three dimensions: one relevant to the currently cued task (e.g., the letter A mapped to a left-hand response), one selected randomly from one of the two alternative tasks and incongruently mapped with the relevant task (e.g., the digit 4 mapped to a right-hand response) and one that was neutral (e.g., letter and digit presented in gray that was not mapped to any response). The same target could not appear on consecutive trials. Targets remained onscreen until response or for 5000 ms.

Note: $n=185$, no significant differences between the number of males and females. Matrix reasoning measured with the Wechsler Abbreviated Scale of Intelligence (Wechsler, 1999), span length = number of items recalled during digit span task (Wechsler, 1999).

Each trial consisted of a cue-target sequence with a 1000 ms cue-target interval (CTI) and a 400 ms response-cue interval (RCI; Figure 1B). Four cue types were defined according to their location on the circle and were presented with equal probability in a pseudo-random sequence so that the same cue type was not repeated on more than four consecutive trials. Targets were always presented in one of the two cued segments. *Repeat* cues (25 % of cues) highlighted the two segments associated with the same task as that completed on the preceding trial, indicating the task would be repeated. Note, to differentiate between repeat trials happening in a single-task block (i.e., where all trials are repeat trials) and repeat trials in a mixed-task block, we refer to them as *all-repeat* and *repeat trials*, respectively. *Switch-to* cues (25 % of cues) highlighted segments associated with a task not completed on the previous trial, indicating both that the task would switch and the identity of the upcoming task. *Switch-away* cues (25 % of cues) highlighted a segment from each of the tasks not completed on the previous trial, indicating a change in task but not specifying which of the other two tasks would be completed. Finally, *non-informative* cues (25 % of cues) highlighted one segment associated with the

task completed on the preceding trial and an adjacent segment associated with one of the other two tasks, indicating that a repeat or switch trial was equally likely. *Non-informative* cues were therefore not entirely uninformative (as this would introduce an additional confound into the experimental design). Like *switch-away* cues, they indicated which two of the three tasks would be relevant on the upcoming target but were uninformative with respect to whether the upcoming target would require a task repeat or switch.

Figure 1. Cued-trial task-switching paradigm (c.f. Karayanidis et al., 2009). A) Major segments of the gray circle are associated with one of three classification tasks. Exemplars used for each task with an example of stimulus-response mappings are shown in the table. B) Timeline of a specific trial, comprised of a cue-target pair. C) Progression from trial N-1 to trial N defines the trial type. See 2. Methods for further details.

These four cue types placed different demands on proactive and reactive control processes. Both *repeat* and *switch-to* cues allowed task identification to be completed during the CTI, whereas for *switch-away* and *non-informative* trials, task identification could only occur after target onset. However, *switch-away* cues were partly informative, in that they indicated that the task would definitely change. Thus, during the CTI, both *switch-to* and *switch-away* cues allowed switch preparation, but *switch-to* cues also allowed task preparation, i.e., reloading of task-set and updating of stimulus-response (S-R) mappings. As task identification could only occur after target onset on *switch-away* and *non-informative* trials, reactive control was necessary for updating of task-set and S-R mappings.

Participants responded with button presses using their left and right index fingers, with the hand assigned to each response counterbalanced across participants. Participants were instructed to respond as quickly and as accurately as possible. Incorrect responses were paired with an auditory feedback tone. After each block, average accuracy and RT for that block were presented so participants could monitor their performance. A short, humorous video (5-10 s) was presented after each block to foster an inter-block rest and participants were offered a longer rest halfway through the experiment to minimize fatigue.

2.3. Procedure and EEG recording

To examine behavioral and EEG data for switching between well learned cue-target and target-response associations, participants completed two training sessions scheduled no more than 14 days apart. Training included practice first on each task alone (single-task blocks) and then on switching between tasks (mixed-task blocks, total of 1320 practice trials; training sessions ran for approximately 1 hour in total). The second training session was followed by the EEG recording during which participants performed ten mixed-task blocks (72 trials/block) and three single-task blocks (*all-repeat*; 48 trials/block, one block per task). Each block included an additional five warm-up trials, resulting in a total of 929 trials. Three brief 2.5 minutes resting-EEG periods were also recorded: one

before commencing the experiment, another halfway through and a final resting period at the conclusion of all blocks. In total, the EEG experiment ran for approximately 1 hour.

EEG was recorded continuously using an ActiveTwo Biosemi EEG system (2048 Hz, bandpass filter of DC-400 Hz) from 64 scalp electrodes (arranged according to the 10-20 layout system) plus bilateral mastoid, outer canthi-, supraorbital-, and infraorbital-ocular sites. The Biosemi system uses active electrodes with common mode sense (CMS) and driven right leg (DRL) electrodes providing a reference relative to the amplifier reference voltage.

2.4. Data analysis

Only valid trials were entered into RT and EEG analyses. Trials were excluded if they i) had RT faster than 200 ms or slower than three standard deviations (SD) above the individual's mean RT, ii) were associated with an incorrect response or followed an error, or iii) were warm-up trials. On average, $17.4\% \pm 6.68$ SD were thus excluded ($\sim 1\text{-}2\%$ too fast/too slow, $\sim 5\%$ incorrect, $\sim 5\%$ post-error and 7% warm-up). Trials with high EEG noise levels were also excluded from EEG analyses (see below).

2.5. EEG Analysis

EEG data were processed using MATLAB (Mathworks, Natick, MA) through a pipeline utilizing Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011), EEGLab (Delorme & Makeig, 2004), CSD Toolbox (Kayser & Tenke, 2006a), and in-house functions (written by authors AW and PC). Preprocessing was performed using Fieldtrip as follows. First, EEG data were re-referenced offline to electrode Cz to remove common-mode signals (a step critical for data acquired using the Biosemi system), downsampled from 2048 Hz to 512 Hz using a zero-phase anti-aliasing filter with a low-pass cut-off frequency of 245 Hz and then filtered to remove low-frequency drift and line noise (high pass: 0.1 Hz, forward phase; 50 Hz notch: zero phase, respectively). Excessively noisy channels were identified with visual inspection and excluded (mean bad channels = 0.72 ± 1.31 SD, range = 0 - 8).

Epochs for each condition (*all-repeat*, *repeat*, *switch-to*, *switch-away*, and *non-informative*) were extracted from -1000 ms to +3500 ms with respect to cue onset. Note epoch length was extensive to facilitate time-frequency analyses sensitive to lower frequencies (such as theta). Next, blink and eye-movement artifact were removed using independent component analysis (ICA; *fastica* algorithm; Hyvärinen & Oja, 2000). ICA produced a set of components, one less than the number of available electrodes, from which 1 - 4 components corresponding to ocular artifact were identified by visual inspection and deleted (mean components = $1.32 \pm .65$ SD). Remaining components were back projected and low-pass filtered (30 Hz, zero-phase) to remove high-frequency noise including muscular artifacts. Trials that contained residual artifact larger than $\pm 120 \mu\text{V}$ were deleted, resulting in an average of 113.42 (± 21.79 SD) *all-repeat*, 137.54 (± 21.4 SD) *repeat*, 132.54 (± 23.26 SD) *switch-to*, 131.75 (± 22.39 SD) *switch-away* and 133.9 (± 22.09 SD) *non-informative* trials for further analysis. Channels that were previously deemed bad were reintroduced by interpolating data between neighboring electrodes, using a weighted average of neighboring electrodes (*ft_channelrepair* function; Fieldtrip). Finally, EEG data were transformed using a surface Laplacian filter (smoothing = 10^{-5} , number of iterations = 50, spherical spline order = 4) to reduce volume conduction effects in EEG sensor space and enhance the spatial resolution of EEG signals (CSD Toolbox; Kayser & Tenke, 2006).

2.6. Behavioral analyses

All behavioral analyses were run in SPSS 24 (IBM). Main effects of Cue Type are reported if they remained significant after Greenhouse-Geisser correction to control for violation of the assumption of sphericity (Vasey & Thayer, 1987), but non-corrected degrees of freedom are reported. For behavioral analyses, we report mean RT, accuracy and behavioral variability for all cue types (i.e., *all-repeat*, *repeat*, *switch-to*, *switch-away*, *non-informative repeat* and *non-informative switch*). Behavioral variability was quantified using the coefficient of variation (CV; *standard deviation/mean RT*, a measure of trial-by-trial RT variability). We selected CV as a measure of within-subject variability because standard deviation may reflect an increase in mean RT rather than RT variability *per se*, given

that standard deviation and mean RT correlate highly (Wagenmakers & Brown, 2007). For each behavioral measure (i.e., RT, accuracy and CV), six planned comparisons were used to measure: switch cost under (1) prepared (*repeat* vs. *switch-to*) and (2) unprepared (*non-informative repeat* vs. *non-informative switch*) conditions; (3) the effect of preparation on repetition benefit (*repeat* vs. *non-informative repeat*); (4) the benefit of updating task-set on switch trials (*switch-to* vs. *switch-away*); (5) the benefit of preparing to switch, even when unable to update task-set (*switch-away* vs. *non-informative switch*) trials and (6) the mixing cost (*all-repeat* vs. *repeat*). Family-wise Bonferroni correction was applied to correct for multiple comparisons ($\alpha = .008 [.05/6]$).

2.7. ERSP and ITPC analysis

We used inter-trial phase clustering (ITPC; also known as phase-locking factor; Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996) as a measure of phase-locking synchrony across trials. ITPC captures the extent of event-related phase similarity across trials so that, within each frequency, time points with aligned phases have high ITPC values (i.e., approaching 1) whereas time points that have unaligned phases have low ITPC values (i.e., approaching 0) and are deemed out of phase. As ITPC is a measure of coherence across *trials* at a single site, we are not measuring functional connectivity *between electrodes*. In addition to phase-locking, we extracted the event-related spectral perturbation (ERSP; Makeig, 1993), which captures all event-related changes of power in the frequency domain (i.e., both phase and non-phase amplitude changes). Considering both ITPC and ERSP allows us to examine the influence of both phase-specific and combined phase and non-phase oscillatory activity on cognitive control, respectively.

To extract ERSP and ITPC values, time-frequency analyses were performed on the surface Laplacian filtered data (cf. Cooper et al., 2015). For each cue type (*all-repeat*, *repeat*, *switch-to*, *switch-away* and *non-informative*) single-trial time-frequency representations were extracted via complex Morlet wavelet convolution (via 80 logarithmically spaced frequency bins from 2 to 30 Hz

with logarithmically spaced tapers ranging from 3 to 14 cycles). ERSP and ITPC values were obtained from the average of these single-trial time-frequency representations.

ERSP was converted to normalized decibel values ($10\log_{10}[\text{power}/\text{baseline}]$), measured as magnitude change in time-frequency activity from a baseline period. ITPC values were extracted from baseline corrected power data ($\text{power}-\text{baseline}$) taking the absolute value of the mean of each trial's exponent of complex angles (i.e., imaginary component) from the time-frequency data. Baseline was defined as the average power over a 100-300 ms interval before cue onset. We offset the end of the baseline period by 100 ms to limit any post-cue time-frequency activity bleeding into the baseline period (see Cohen, 2014b).

We used these baseline-corrected time-frequency data to perform two sets of analyses. First, task-general analyses were performed to assess the role of theta oscillations during cognitive control. Here all data were contrasted against the *all-repeat* trials (i.e., single task block). Second, ERSP and ITPC for each cue type in the mixed task block were assessed by contrasting between these mixed-task block cue types (cue-specific analyses). Details of these analyses are presented below.

2.7.1. Task-general modulations of ERSP and ITPC

First, we sought to identify theta oscillations (ERSP and ITPC) associated with task switching in broad frontal (average of F1, Fz, F2, FC1, FCz, FC2) and parietal (average of CP1, CPz, CP2, P1, Pz, P2) regions of interest (ROIs). For ERSP and ITPC, in each ROI, we averaged activity across all cue types in the mixed-task block and subtracted the single-task baseline condition – a contrast corresponding to a general switch cost in the task-switching literature. To identify statistically significant pixels across the time-frequency map from frontal and parietal ROIs, we performed one-sample *t*-tests at each time*frequency pixel. For ERSP data, we used a threshold of $\alpha < .001$ with FDR-correction control for Type I errors (Benjamini, Krieger & Yekutieli, 2006). As ITPC values have a restricted range, a one-sample *t*-test is not appropriate. Instead, we estimated the critical *value* of ITPC that would correspond to a significance level of $\alpha < .001$ and compared ITPC values against this (for further

discussion regarding statistical assessment of ITPC, see Cohen, 2014b). Critical ITPC was calculated using the following equation at each pixel separately:

$$ITPC_{crit} = \sqrt{\frac{-\ln(p)}{n}}$$

where p = desired significance level (i.e., .001) and n = number of time*frequency points within each ROI time-frequency map.

To examine the scalp topography of these task-general theta ERSP and ITPC time*frequency effects at frontal and parietal ROIs, we extracted peak activity from hotspots within each significant time*frequency cluster. Significant time*frequency clusters were extracted using the MATLAB *bwconncomp* function on binarized versions of the time-frequency significance maps at frontal and parietal ROIs separately. We created a hotspot for topographical analyses within each time*frequency cluster by identifying peak ERSP and ITPC activity and extracting values from a small window around it (window width = 60 time bins, window height = 6 frequency bins, centered around the peak t -statistic within the cluster). We only quantified activity from hotspots that comprised at least 360 contiguous pixels (i.e., the height and width of the window) and restricted analyses to hypothesized theta and alpha bands. This measure was used to plot topographies and test for statistical significance at each electrode, using one-sample t -tests for ERSP (FDR-corrected at $\alpha < .001$) and $ITPC_{crit}$ for ITPC.

2.7.2. Cue-specific modulations of ERSP and ITPC

To examine ERSP and ITPC differences between cue types within the mixed-task block, we computed the time-frequency space at the frontal (F1, Fz, F2, FC1, FCz, FC2) and parietal (CP1, CPz, CP2, P1, Pz, P2) ROI for each cue type in the mixed-task block. We performed one-way, repeated-measures ANOVAs with 5 levels of the Cue Type factor (*all-repeat*, *repeat*, *switch-to*, *switch-away*, and *non-informative*) at each time*frequency pixel within each ROI for ERSP and ITPC measures separately. This produced F -maps (FDR-corrected, $\alpha < .001$) depicting clusters of time*frequency pixels of the main effect of Cue Type. As in task-general analyses above, we assessed the spatial

distribution of these clusters across the scalp by extracting ERSP/ITPC hotspots from a 60 time bins*6 frequency bins window centered at the peak F -statistic within the cluster, using the *bwconncomp* MATLAB function. These hotspot values were entered into separate one-way, repeated-measures ANOVAs at each electrode to determine the scalp distribution of the main effect of Cue Type (FDR-corrected, $\alpha < .001$).

2.8. Brain-behavior correlations

We examined the relationship between theta ERSP and ITPC measures and the coefficient of variation (CV) using simple linear regression (i.e., Pearson's linear correlation coefficient) at each electrode (64) and for each cue type (5). To limit the number of correlations performed, we focused correlations on those hotspot regions identified in the cue-specific analyses performed above. That is, ERSP and ITPC were related to CV at key time*frequency periods identified in the previous step. Both uncorrected significant ($p < .05$) and corrected (FDR $\alpha < .05$) associations are presented.

3. Results

3.1. Behavioral Results

Mean RT (Figure 2A) showed a significant main effect of trial type, $F_{(5,920)} = 391.60$, $p < .001$, $\eta^2 = .680$. Bonferroni-corrected comparisons revealed a significant mixing cost (RT: *all-repeat* < *repeat*, $t_{(184)} = 15.21$, $p < .001$). There were significant prepared and unprepared switch costs (RT: *repeat* < *switch-to*, $t_{(184)} = 13.25$, $p < .001$; *non-informative repeat* < *non-informative switch*, $t_{(184)} = 14.97$, $p < .001$). Task preparation resulted in faster RT for both repeat (*repeat* < *non-informative repeat*, $t_{(184)} = 23.56$, $p < .001$) and switch trials (*switch-to* < *switch-away*, $t_{(184)} = 24.75$, $p < .001$).

Mean accuracy scores (Figure 2B) also showed a significant main effect of trial type ($F_{(5,920)} = 54.61$, $p < .001$, $\eta^2 = .229$). *Repeat* trials were performed more accurately than *switch-to* ($t_{(184)} = 9.20$, $p < .001$) and *non-informative repeat* ($t_{(184)} = 5.38$, $p < .001$). *Non-informative repeat* trials had higher accuracy compared to *non-informative switch* ($t_{(184)} = 7.16$, $p < .001$).

Finally, trial-by-trial variability (CV) produced a significant main effect for trial type ($F_{(5,920)} = 170.86, p < .001, \eta^2 = .481$). As shown in Figure 2C, CV produced a significant mixing cost (*all-repeat* < *repeat* trials: $t_{(184)} = 16.41, p < .001$) and prepared switch cost (CV: *repeat* < *switch-to*, $t_{(184)} = 3.77, p < .001$). *Non-informative repeat* trials had higher CV compared to *non-informative switch* trials ($t_{(184)} = 8.98, p < .001$). There was a significant effect of task preparation with higher CV for both repeat (*repeat* vs. *non-informative repeat*; $t_{(184)} = 6.07, p < .001$) and switch trials (*switch-to* vs. *switch-away*; $t_{(184)} = 25.23, p < .001$). Finally, *switch-away* trials had significantly higher CV compared to *non-informative switch* trials ($t_{(184)} = 3.15, p = .002$).

Figure 2. A) RT, B) accuracy and C) coefficient of variation (CV) during task-switching. Solid lines indicate significant differences, with ** indicating $p = .002$ and *** $p < .001$. Error bars depict confidence intervals calculated for a within-subjects design (c.f., Loftus & Masson, 1994). RA, *all-repeat*; R; *repeat*, ST; *switch-to*, SA; *switch-away*; RN; *non-informative repeat*, SN; *non-informative switch*.

3.2. Task-general effects

Figure 3 depicts time-frequency plots for the task-general ERSP (left panel) and ITPC (right panel) time-frequency space at frontal and parietal ROIs. Black outlines depict clusters of significant differences in activity for the mixed-task compared to the single-task block (FDR-corrected at $\alpha < .001$). Scalp distribution of ERSP and ITPC associated with the hotspot within significant clusters are depicted in head maps adjacent to the time-frequency maps. Note, these clusters and hotspots are

equivalent to the *general switch cost* in task-switching (i.e., the difference between performing in a mixed-task block vs. single-task block).

3.2.1. ERSP

At both frontal and parietal ROIs, significant ERSP was evident across a broad spectral range spanning from cue onset to approximately 750 ms post-cue (Figure 3, left panel). ERSP peaked in the theta band for both ROIs (frontal: 6.87 Hz, parietal: 5.99 Hz), and 101 ms earlier in the parietal as compared to the frontal ROI. The parietal ROI also showed transient alpha and beta (14-30 Hz) ERSP activity in the first half of the CTI. Topographical ERSP head maps show that the theta ERSP hotspots measured at both frontal and parietal ROIs were broadly distributed across the scalp with a midfrontal peak.

Figure 3. Task-general effects. Differences between mixed-task and single-task blocks for event-related spectral perturbation (ERSP, left) and inter-trial phase clustering (ITPC, right) at frontal and parietal ROIs (baseline: 100-300 ms before cue). Black outlines indicate significant clusters of time*frequency pixels. Head plots depict the spatial distribution of significant activity from the time*frequency hotspot derived from the corresponding ROI (blue stars represent electrodes showing significant differences). The positive range of each scale represents the general switch cost (mixed-task > single-task block).

3.2.2. ITPC

ITPC time-frequency plots (Figure 3, right panel) show weak but significant ITPC effects in alpha and theta bands within the same time interval as the ERSP effects reported above and at both frontal and parietal ROIs (~100-400 ms post-cue). At the frontal ROI, ITPC peaked in the alpha range (9.35 Hz) and showed a strong bilateral posterior topography. At the parietal ROI, a stronger ITPC theta effect (7.61 Hz) was also posteriorly distributed with maxima at midline centro-parietal and bilateral parieto-occipital sites, peaking 48 ms earlier than the frontal ITPC effect.

In summary, ERSP and ITPC showed significant theta band modulation with distinct temporal and scalp distributions, consistent with involvement in proactive cognitive control.

3.3. Cue-specific effects

We next examined modulation of ERSP and ITPC as a function of distinct proactive control processes activated by different cue types.

3.3.1. ERSP

Figure 4 shows ERSP time-frequency plots of the *F*-statistic for the main effect of cue type at frontal (top panel) and parietal (bottom panel) ROIs. At both ROIs, ERSP produced strong significant main effects of cue type across delta and theta bands, with effects extending into alpha and beta bands, especially in early CTI.

Within the frontal ROI, the main effect of cue type was significant across the early CTI, but was stronger after 200ms, peaking at 361 ms at the theta/alpha border (7.88 Hz) and this was used to define a frontal ERSP hotspot (F1-ERSP: Figure 4; top panel). The F1-ERSP headmap shows the spatial distribution of the *F*-statistic for the above F1-ERSP hotspot. The effect of cue type in ERSP was widely distributed across the scalp, but strongest at midfrontal sites.

The parietal ROI produced a strong main effect of cue type starting earlier than the effect measured at the frontal ROI and spreading across the first half of the CTI. A parietal hotspot (P1-

ERSP) was defined in theta band (5.99 Hz) centred at 307 ms post-cue, i.e., roughly 50 ms earlier than F1-ERSP (Figure 4, bottom panel). The P1-ERSP hotspot was also stronger at midline, though somewhat more posteriorly and with significant bilateral posterior activity.

The bar plots depict ERSP activity for each cue type at F1-ERSP and P1-ERSP measured at the frontal and parietal ROI, respectively. The pattern of ERSP activation differences across cue types was similar at these two hotspots, although the actual values vary (Table 2). Specifically, ERSP values showed a progressive and significant increase from *all-repeat* to *repeat*, *switch-to* and *switch-away* cues, but a sharp reduction for *non-informative* cues.

Figure 4. Cue-specific ERSP effects. *F*-statistic maps of cue main effect for event-related spectral perturbation (ERSP) at frontal and parietal ROIs (black outlines indicate significant clusters of time*frequency pixels). Head plots depict the spatial distribution of the *F*-statistic at each electrode for the time*frequency hotspot derived from the corresponding ROI – F1-ERSP and P1-ERSP (blue stars represent electrodes displaying a significant main effect of cue type). Bar plots show ERSP activity for each cue type at F1-ERSP and P1-ERSP derived from that ROI. RA, *all-repeat*; R, *repeat*; ST, *switch-to*; SA, *switch-away*; NI, *non-informative*.

Note: RA, *all-repeat*; R, *repeat*; ST, *switch-to*; SA, *switch-away*; NI, *non-informative*. * = $p < .05$ adjusted for Bonferroni correction; ** $p < .01$; *** = $p < .001$.

3.3.2. ITPC

Figure 5 shows ITPC time-frequency plots of the F -statistic for the main effect of cue type at frontal (top panel) and parietal (bottom panel) ROIs. At the frontal ROI, the main effect of cue type produced was significant in an early theta-alpha-beta cluster that peaked at 314 ms post-cue in the alpha/theta border (8.4 Hz). This was used to define a frontal ITPC hotspot (F1-ITPC; Figure 5: top panel). This F1-ITPC hotspot showed a significant main effect of cue type most electrodes, but was stronger across a bilateral posterior band of electrodes (Figure 5; F1-ITPC headmap). This was followed by a low theta band cluster peaking around 600 ms in lower theta band (4.25 Hz). This F2-ITPC hotspot had a strong midfrontal topography (Figure 5; F2-ITPC headmap) with weaker effects at bilateral frontal and centroparietal sites.

The parietal ROI also produced a significant early effect of cue type in the theta-alpha band that spanned the first half of the CTI. A P1-ITPC hotspot was measured around a strong theta peak (5.99 Hz) at 240 ms, 74 ms earlier than the F1-ITPC hotspot. This P1-ITPC hotspot produced significant effects of cue type across most of the scalp, with strongest effects at centroparietal midline and posterior lateral sites. A later small theta cluster also produced a significant cue type effect. The P2-ITPC hotspot was defined in theta band (6.4 Hz) at 594 ms, roughly in the same timeframe as F2-ITPC with a sparse distribution of significant electrodes.

Bar graphs depicting individual trial types indicate that the F1-ITPC and P1-ITPC hotspots showed a pattern similar to the corresponding ERSP hotspots. Specifically, for both hotspots, ITPC increased from *all-repeat* to *repeat*, *switch-to* and *switch-away* trials, but dropped sharply for *non-informative* cues (see Table 3). The later hotspots (i.e., F2-ITPC, P2-ITPC) showed a different but

common pattern characterized by higher ITPC for *all-repeat* cues than other types (see Table 3).

Figure 5. Cue-specific ITPC effects. Accompanying topographical head plots depict the spatial distribution of the hotspot derived from the F -statistic presented, with arrows depicting the hotspot for each cluster. For the frontal and parietal clusters, bar plots adjacent to the topographical maps show condition-specific ITPC for the respective time*frequency hotspot. Black outlines indicate significant time*frequency pixels and blue stars on the topographical head plots represent significant electrodes associated with the F -statistic activity. *RA*, *all-repeat*; *R*, repeat; *ST*, switch-to; *SA*, switch-away; *NI*, non-informative.

In sum, both ERSP and ITPC show strong activity in first half of CTI peaking earlier at parietal than at frontal ROIs and predominantly in theta or theta/alpha border. This activity was largest over midline mid-frontal/central scalp and increased with increasing contextual ambiguity, with the exception of the non-informative cues. In ITPC only, this was followed by weaker frontal and parietal theta hotspots that were strongest for *all-repeat* compared to all other cue types.

It is worth noting that the frontal ERSP and ITPC hotspots peaked in roughly the same frequency band (7.9 and 8.4Hz, respectively) and the same for the parietal ERSP and ITPC hotspots (5.99Hz for both), although in both cases, ITPC values peaked roughly 50ms before the corresponding ERSP values. Additionally, the parietal hotspots peaked roughly 50-60 ms earlier than the corresponding frontal hotspots and all four showed a similar pattern of cue effects. This suggests that these ERSP and ITPC hotspots are tapping into similar underlying processes that emerge earlier over

parietal than frontal cortex. In the following section, we focus on how activity in these hotspots is associated with behavioral variability (CV).

Note: Cluster number refers to significant clusters found within each ROI. * = $p < .05$ adjusted for Bonferroni correction; ** $p < .01$; *** = $p < .001$. *RA*, *all-repeat*; *R*, *repeat*; *ST*, *switch-to*; *SA*, *switch-away*; *NI*, *non-informative*.

3.4. Brain-behavior correlations

Figure 6 depicts topographical maps of r -values from regression analyses comparing behavior variability (CV) for each cue type and at frontal (F1-ERSP, F1-ITPC) and parietal (P1-ERSP, P1-ITPC) hotspots identified during the early CTI period (i.e., in Figures 4 and 5, respectively). All significant correlations were negative, indicating that higher ERSP/ITPC activity was associated with lower behavioral variability (CV).

Increased power in the F1-ERSP hotspot was associated with decreased CV across a mid-frontal, central and parietal electrodes for all cue types except *all-repeat* (Figure 6; top row), but the effect was significant after FDR correction only at sporadic electrodes. A similar pattern can be seen for the F1-ITPC hotspot.

Stronger correlations between behavioral variability and ERSP/ITPC activity were found at the hotspots defined from the parietal ROIs. Again, there was no correlation between CV and ERSP/ITPC activity for *all-repeat* cues. Increased activity in P1-ERSP was significantly associated correlated with reduced CV across clusters of electrodes over midfrontal, right centroparietal and right central scalp. After FDR correction, the midfrontal cluster was significant only for *repeat* cues, whereas the right centroparietal cluster remained significant for all cue types in the mixed-task block. P1-ITPC showed a similar pattern of effects. All mixed-block cue types were associated with CV across a broad set of midline and right electrodes across central and posterior scalp. P1-ITPC at centroparietal midline and centro-parietal-occipital sites was associated with reduced CV for all cue types, with a more posterior shift for the three cues that have greater ambiguity (*switch-to*, *switch-away* and *non-informative*).

In sum, enhanced ERSP/ITPC activity during the early CTI period was associated with reduced behavioral variability (i.e., reduced CV) across midline fronto-central and right-lateralized centroparietal networks. These effects are only evident in the mixed-task blocks, but do not show any clear pattern of differentiation between repeat and switch cues in that block.

Figure 6. Correlations between behavioral variability and event-related spectral perturbation (ERSP, top) / inter-trial phase clustering (ITPC, bottom) at frontal and parietal cluster hotspots evident in the early CTI. Blue stars on topographical head plots represent significant electrodes that survived FDR correction at $\alpha < .05$. RA, *all-repeat*; R, *repeat*; ST, *switch-to*; SA, *switch-away*; NI, *non-informative*.

4. Discussion

In this study, we contribute to recent evidence that theta oscillatory activity is involved in proactive cognitive control processes (e.g., Rawle et al., 2012; van Driel et al., 2015). In addition, we extend current understanding of the role of theta oscillatory activity, by showing that it is not related exclusively to the anticipation of (proactive) or the resolution of (reactive) conflict. Finally, we report novel evidence that the strength of theta oscillations during proactive cognitive control is associated with efficiency of cognitive control, as indicated by trial-by-trial performance variability.

Before discussing the implications of these findings, it is important to comment on the overall pattern of effects in this dataset. As we stressed earlier, ERSP and ITPC do not measure a network *per*

se (i.e., they measure activity at a single electrode/cluster rather than the relationship between electrode/clusters). Nevertheless, we argue that these findings can be interpreted as indexing activity generated within a common frontoparietal network. In the first half of the CTI, the pattern of ERSP and ITPC effects is highly consistent within the frontal ROI, as well as within the parietal ROI. More importantly, within each measure, the frontal and parietal ROIs produce consistent clusters of significant activity largely centered within the theta (or sometimes lower alpha) band. The hotspots defined within each of these clusters show a similar central scalp distribution of this activity – centered around a midline centroparietal set of electrodes, with additional lateral activity more posteriorly. This pattern is common for ERSP and ITPC hotspots defined from both frontal and parietal clusters (Figures 4 & 5). In addition, cue type differences within these four measures show a highly similar pattern of variability – activity increasing from *all-repeat*, to *repeat*, to *switch-to* and *switch-away*, but falling off sharply for *non-informative* cues. All these findings point to a high likelihood that we are sampling the same frontoparietal network mechanisms, at time points when a stronger frontal vs. parietal weighting is taking place. However, importantly, there is one difference between frontal and parietal activity: within each measure, the parietal activity peaks around 50-60ms earlier than the corresponding frontal activity. Temporal lags such as this are consistent with the notion that information is being propagated through a network (we discuss the direction of this temporal lag below; Stam, Nolte & Daffertshofer, 2007). Therefore, we interpret the ERSP and ITPC findings derived from frontal and parietal ROIs as snapshots that provide converging evidence for a dynamic frontoparietal theta proactive control network that shows maximal activity over midline scalp, consistent with what is often referred to as mid-frontal theta in reactive control contexts. This conclusion is consistent with increasing evidence that cognitive control relies on a broad frontoparietal network that employs theta oscillations to facilitate information integration (e.g., Cavanagh & Frank, 2014).

This frontoparietal theta activity (FP θ) was modulated by general switch cost (i.e., single-task vs. mixed-task block; Figure 3) that was sustained for most of the cue period but peaked around 300-

400 ms, consistent with increased proactive control under increased task demands. FP θ was also sensitive to differential information provided by the cue within the mixed-task block, again especially during the first half of the CTI (Figures 4 & 5). Together, these findings indicate that this theta oscillatory activity was sensitive not only to the need for a sustained increase in proactive control (i.e., on the more difficult mixed-task as compared to the easier single-task conditions), but also to transient changes in need for proactive control across different cue types in the mixed-task block. Specifically, FP θ was sensitive to mixing cost (*all-repeat* vs. *repeat*) and switch cost (*repeat* vs. *switch-to*), and was even larger for *switch-away* cues, which validly predicted the need to switch but did not define the new task. At first glance, it appears surprisingly that the *non-informative* cues, which provided neither switch nor task information, showed a sharp drop in both ERSP and ITPC and at both frontal and parietal hotspots, resembling more the activity for the *all-repeat* cues in the single-task block. However, this pattern is consistent with previous findings with this paradigm: cues that provide certainty of an upcoming change in task (i.e., *switch-to*, *switch-away*) produce a larger early switch-positivity (Karayanidis et al., 2009), an increase in response caution (Karayanidis et al., 2009), changes in activation in frontal and striatal regions (Mansfield, Karayanidis, Jamadar, Heathcote & Forstmann, 2011), and activation of a frontoparietal theta network (Cooper et al., 2015), effects that are not evident for *repeat* or *non-informative* cues. These effects are consistent with increased proactive control under conditions that validly forewarn of that task goals will change on the upcoming trial.

Finally, FP θ activity was associated with variability in behavioral performance, especially at the parietal hotspot (i.e., P1-ERSP, P1-ITPC; Figure 6). This relationship between theta modulation and behavioral variability was absent for *all-repeat* cues (i.e., the single-task block), but significant for all four cues in the mixed-task block, even the *non-informative* cues that showed a significant dip in activity relative to other mixed-task block cues. Reduced behavioral variability under high demand task conditions is believed to be an index of cognitive control efficiency (West, Murphy, Armilio, Craik, & Stuss, 2002). Thus, these results suggest that individuals who elicited greater FP θ oscillations to cues in the mixed-task block showed greater cognitive control. Together, these data suggest that,

under high-demand task conditions, increased frontoparietal theta oscillations during the CTI are indicative of more effective proactive control processes, which in turn, results in more efficient behavior.

As discussed earlier, FP θ modulation is typically reported in contexts that require reactive resolution of conflict (e.g., Moore, Gale, Morris, & Forrester, 2006; Moore, Mills, Marshman, & Corr, 2012). The few studies that have reported FP θ modulation in the context of proactive control have interpreted it as reflecting *conflict anticipation* (Rawle et al., 2012; van Driel et al., 2015; van Noordt et al., 2016a; 2016b). However, two recent studies have shown that FP θ modulation may also be related with the need for goal-updating mechanisms (Cooper et al., 2015; Cunillera et al., 2012). Cooper et al. (2015) showed activation of an early frontoparietal network early in the preparation interval that was activated when the cues validly indicated that the task would change. Cunillera and colleagues found increased theta power at frontal, central and parietal sites only for cues that indicated a change in task rules during a cued Wisconsin Card Sorting Task. The present pattern of FP θ oscillatory activity across the different cue types is consistent with such a goal-updating mechanism. *All-repeat* trials do not need goal updating, as the task remains the same across the entire single-task block. In the mixed-task block, *repeat* cues must be processed to decide to maintain the same task goal. Although there is no need to update the goal, there is evidence that goal-updating may occur on some trials (e.g., de Jong, 2000) or by some people (e.g., older adults tend to update task-goals for both switch and repeat cues, Karayanidis, Whitson, Heathcote & Michie., 2011). Both *switch-to* and *switch-away* cues require task-goal updating – i.e., they indicate that the previous task rules are not relevant (and the former also allows loading of the new task rules). However, anticipatory goal-updating is not possible for *non-informative* cues, which are equally likely to result in a repeat or a switch trial. The fact that these cues, like *all-repeat* trials, elicit low FP θ activity (current results) and do not elicit parietal ERP activity (e.g., Karayanidis et al., 2009) is consistent with FP θ early in CTI representing the need for proactive control processes related to goal-updating.

Rawle and colleagues (2012) reported increased theta power over parietal and midfrontal electrodes when cues indicated that the target would require conflict resolution (i.e., cues for 2 or 4 target features). Interestingly, the parietal theta activity peaked approximately 80 ms earlier than the frontal theta (Figure 5; Rawle et al., 2012), providing a tentative time course for neural dynamics within frontoparietal networks. This is consistent with the FP θ activity reported here which peaked earlier at parietal than frontal ROIs. Such a feed-forward model (where parietal theta occurs prior to frontal theta) is consistent with evidence from source modeling of selective attention mechanisms (Green, Doesburg, Ward & McDonald, 2011; Green & McDonald, 2008). In two separate studies, Green and colleagues found that, within a frontoparietal network, theta activity was first enhanced over parietal cortex before emerging frontally. A second wave of activity occurred later, peaking again parietally and then across sensory-specific cortical regions (i.e., occipital vs. temporal cortices for their visual vs. auditory attention tasks respectively). Interestingly, this spatiotemporal pattern of theta occurred during a cueing interval, where participants were cued to the upcoming spatial location of a target. Together these findings provide convergent evidence that theta oscillations may facilitate the dynamic interactions between frontal, parietal and sensory areas, implementing top-down control over attentional mechanisms.

Traditional models of frontoparietal network dynamics using fMRI suggest that the frontal cortex biases parietal cortex in top-down, feed-back mechanism. Using effective connectivity measures, Wang et al. (2009) showed directional dependency of connections between parietal and frontal cortices based on surprising vs. conflicting information. The findings discussed above are consistent with such complex interactions between simple association and higher-order association cortices, which is enabled by a dynamic interplay of feed-forward and feed-back operations. Proactive (anticipation/goal-updating) vs. reactive (conflict detection) control processes might differentially engage feed-forward vs. feed-back mechanisms. Such predictions could be assessed

with network-based measures of phase-lag differences between frontal and parietal cortices (Polanía, Nitsche, Korman, Batsikadze, & Paulus, 2012).

4.1. Conclusion

The current study provides evidence consistent with a role of theta oscillations in cognitive control. A common frontoparietal theta network manifested in both power and phase measures and was associated with the need for *goal-updating*. Activation of this FP θ network was associated with cognitive control efficiency, consistent with engagement of proactive control. Interestingly, we also showed that theta oscillations within this frontoparietal network peaked earlier over parietal vs. frontal regions. These findings support the notion of a feed-forward mechanism where goal-relevant information is transmitted from parietal to frontal regions in order to engage in effective anticipatory processes. Together, these findings support a broader view that theta is associated with the *need for control* (Cavanagh & Frank, 2014), beyond simple conflict detection/resolution and that theta oscillations within cognitive control neural networks play a key role in individual differences in cognitive goal-setting and strategy.

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Table 1. Summary data of participants

Measure	Mean	SD
Age (years)	21.66	4.96
Matrix Reasoning	54.1	9.57
Span Length (Forwards)	6.97	1.25
Span Length (Backwards)	5.12	1.23
Span Length (Sequencing)	6.68	1.26
Sex	Female N (%)	Male N (%)
	98 (53%)	87 (47%)
Handedness	Left-handed N (%)	Right-handed N (%)
	15 (8.1%)	170 (91.9%)

Table 2. Cue-specific comparisons for ERSP hotspots at frontal and parietal ROIs. Values represent *t*-test scores.

ERSP		Contrast						
ROI		RA vs. R	R vs. ST	R vs. SA	R vs. NI	ST vs. SA	ST vs. NI	SA vs. NI
	Frontal	8.19***	3.12**	5.44***	4.36***	2.46*	6.83***	9.68***
	Parietal	16.8***	2.13*	2.37***	12.67***	4.14***	13.56***	16.18***

Table 3. ITPC *t*-tests at frontal and parietal ROIs.

ITPC		Contrast						
ROI (Cluster)		RA vs. R	R vs. ST	R vs. SA	R vs. NI	ST vs. SA	ST vs. NI	SA vs. NI
	Frontal (1)	1.38	3.75***	4.85***	1.48	2.53*	4.55***	5.75***
	Frontal (2)	4.31***	0.93	1.29	1.58	2.02*	2.54*	0.22
	Parietal (1)	7.69***	2.07*	5.56***	8.32***	4.66***	8.52***	11.54***
	Parietal (2)	4.47***	0.59	2.27*	1.26	1.46	0.58	0.80