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# Theta frontoparietal connectivity associated with proactive and reactive cognitive control processes

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## Abstract

Cognitive control involves both proactive and reactive processes. Paradigms that rely on reactive control have shown that frontoparietal oscillatory synchronization in the theta frequency band is associated with interference control. This study examines whether proactive control is also associated with connectivity in the same frontoparietal theta network or involves a distinct neural signature. A task-switching paradigm was used to differentiate between proactive and reactive control processes, involved in preparing to switch or repeat a task and resolving post-target interference, respectively. We confirm that reactive control is also associated with frontoparietal theta connectivity. Importantly, we show that proactive control is also associated with theta band oscillatory synchronization but in a different frontoparietal network. These findings support the existence of distinct proactive and reactive cognitive control processes that activate different theta frontoparietal oscillatory networks.

## 1. Introduction

Cognitive control processes enable flexible adjustment of intentions and actions in order to guide goaldirected behavior. Imaging studies have shown that the implementation of these control processes relies on an extensive frontoparietal network (Corbetta and Shulman, 2002; Seeley et al., 2007; Vincent et al., 2008) that is well-suited to promoting flexible and rapid information propagation (Dosenbach et al., 2008). One mechanism by which information can be flexibly adjusted and rerouted in the frontoparietal network is oscillatory synchronization of electrical activity (Fries, 2005;Womelsdorf and Fries, 2006). Oscillatory synchronization allows neuronal assemblies to exchange information transiently by synchronizing or rhythmically oscillating their firing rate. This process both promotes efficient exchange of information within that assembly and protects against competing inputs from neighboring assemblies (Azouz and Gray, 2003; Engel et al., 2001).

Cognitive control and related top-down processes have often been linked to oscillatory synchronization in the slow wave, theta (4–7 Hz) frequency band. For example, top-down maintenance and manipulation of items in working memory is typically accompanied by synchronized theta activity (e.g. Klimesch et al., 2006; Jacobs et al., 2006; Jensen and Tesche, 2002; Onton et al., 2005; Raghavachari et al., 2006), and successful encoding and recollection of items are linked to current theta wave phases (Rizzuto et al., 2006). Increased need for allocation of mental resources is also associated with greater interregional theta synchronization or coherence, particularly between distributed frontal and parietal sites (Mizuhara and Yamaguchi, 2007; Sauseng et al., 2005, 2006). Furthermore, increased theta synchronization has been associated with conflict-related processes, such as error detection and post-error correction (Cavanagh et al., 2009; Luu et al., 2004; Trujillo and Allen, 2007), goal conflict and response selection (Moore et al., 2006, 2012). This evidence supports a unique role of theta oscillations in gating neural assemblies in order to promote integration of information and enable goal-directed control processes (see <u>Sauseng et al., 2010</u>). Thus, low frequency EEG oscillations appear to be intimately tied to key cognitive control processes (e.g., information prioritization and transfer) that promote widespread integration across cortical regions.

Models of cognitive control differentiate between distinct modes of control. For instance, Braver (2012) differentiates between reactive control processes, that are required to resolve conflict and overcome interference, and proactive control processes, that are involved in pre-setting or preparing the system to be sensitive to future goal-relevant features of the environment. Reactive control is seen in moment-to-moment adjustment of neural activity. For example, in event-related potentials (ERPs), reactive control may be linked to adjustment of processing to deal with target-level conflict (e.g., the N2 component linked to conflict control, Folstein and Van Petten, 2008) or response feedback (e.g., the post-error negativity associated with response feedback, Gehring et al., 1993). Proactive or preparatory control is typically assumed to promote sustained attention towards upcoming goals, as indicated by sustained prefrontal activity in fMRI (Braver et al., 2009; Marklund and Persson, 2012), and pre-stimulus activity in

ERPs (<u>Bekker et al., 2004; Bickel et al., 2012</u>). However, proactive control processes can also be transiently adjusted when using cues to selectively prepare in anticipation of target onset (<u>Karayanidis et al., 2009;</u> <u>Mansfield et al., 2011</u>). Despite converging evidence for a key role of theta oscillations in cognitive control (<u>Cavanagh and Frank, 2014</u>), the role of theta synchronization in proactive control has received little attention.

Task-switching paradigms that differentiate between proactive and reactive control processes can be used to define the nature of theta oscillations during cognitive control. In cued-trial paradigms, the cue provides valid information regarding the upcoming goal (e.g., to repeat or switch tasks). This allows temporal differentiation between proactive control processes activated during the cue–target interval (e.g., preparing to switch or repeat task) and reactive control processes activated after target onset (e.g., goal implementation and interference control). In cue-locked ERPs, proactive control processes are represented in an early, transient, positive component for switch vs. repeat cues (typically between 200 and 400 ms post-cue; e.g. Karayanidis et al., 2003; 2009; Miniussi et al., 2005; Nicholson et al., 2005; Periáñez and Barceló, 2009) and a later, sustained negativity peaking prior to target onset (Astle et al., 2008; Karayanidis et al., 2009; Mueller et al., 2007). In addition, when the cue identifies the task to be performed, the early switch-positivity is followed by a second sustained switch-positivity and the pre-target negativity varies as a function of task information (e.g., <u>Karayanidis et al., 2009</u>). In target-locked ERPs, reactive control processes are represented in modulation of the N2 and P3 as a function of differential carry-over and target-driven interference for switch and repeat trials (e.g., Karayanidis et al., 2003; <u>Nicholson et al., 2005;</u> see for review Karayanidis et al., 2010 and Karayanidis and Jamadar, 2014).

The timing of ERP components linked to proactive and reactive control processes in task-switching may inform time windows where oscillatory networks would be expected to exhibit proactive and reactive control activity. Despite the utility of the task-switching paradigm, there are few studies examining the role of oscillatory activity during task-switching (Gladwin et al., 2006; Mansfield et al., 2012; Sauseng et al., 2006). For example, using a task-switching paradigm that did not differentiate between proactive and reactive control processes, Sauseng et al. (2006) reported that switching tasks was associated with a reduction in upper alpha (10–13 Hz) power as well as a large increase in theta, but not alpha, coherence across fronto-posterior networks. This is consistent with findings from other paradigms that rely primarily on reactive control processes. In a cued-Wisconsin Card Sorting task, cues associated with a rule switch led to sustained theta band activity across frontal and parietal sites, as well as a decrease in centro-parietal alpha band power (Cunillera et al., 2012). However, using a cued-trial paradigm, Mansfield et al., (2012) found differences in low-mid frequency oscillations between switch and repeat cues, relative to a noninformative cue baseline, over right frontal and bilateral parietal sites in time windows corresponding the early switch positivity and pre-target negativity, respectively. In sum, these studies suggest a role for low frequency oscillations in task-switching, with differentiable effects at timelines consistent with proactive and reactive control.

The present study examines the role of theta band oscillations under proactive and reactive control conditions using a cued-trial task switching paradigm. If proactive and reactive control processes both rely on theta synchronization, switch-related frontoparietal theta oscillation networks will be evident both in the cue–target interval, i.e., when preparing to switch or repeat tasks, and after target onset, i.e., when controlling interference. Given neuroimaging evidence that preparation to switch and implementation of a switch response involve distinct networks (for review see <u>Ruge et al., 2013</u>), theta oscillatory synchronization for proactive and reactive control may be expected to involve distinct networks. Additionally, as previous work with this paradigm has shown increased alpha power when preparing to switch (<u>Mansfield et al., 2012</u>; see also Sauseng et al., 2006), we examine whether alpha oscillatory networks are also evident during switch preparation and/or implementation.

#### 2. Methods

#### 2.1. Participants

Twenty nine adults with no current neurological or psychiatric disorder (13 males, mean age 25.69  $\pm$  5.64 years, 27 right-handed) gave written, informed consent and were reimbursed \$20/h for participating in this study. Participants were asked to abstain from caffeine and alcohol at least 2 h prior to testing. 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

Participants viewed a circle (5° of visual angle) divided into six wedges with pairs of adjacent wedges grouped by thicker lines demarcating three task sections: digit, letter, and color (see Fig. 1A; see Karayanidis et al., 2009). 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 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 right hand response) and one that was neutral (e.g., letter and digit presented in gray that was not mapped to any response). The target remained on the screen until a response was emitted or for 5000 ms. The same target could not appear on successive trials.

Each trial consisted of a cue-target sequence. Four cue types were defined by cue location and presented with equal probability in a pseudo-random sequence so that the same cue type was not repeated on more than four consecutive trials (Fig. 1B). The target always appeared in one of the two adjacent segments highlighted by the cue. Repeat cues highlighted the two segments associated with the task that was completed on the preceding trial, indicating that the same task would be repeated. Switch-to cues highlighted segments associated with one of the tasks not completed on the previous trial, both indicating that the task would change and identifying the new task. Switchaway cues highlighted one segment associated with each of the tasks not completed on the previous trial, indicating that the task would change, but not specifying which of the other two tasks would be relevant. Finally, non-informative

cues highlighted one segment associated with the task completed on the preceding trial and another adjacent segment associated with one of the other two tasks, indicating that a switch or a repeat trial was equally likely. For both switch-away and non-informative cues, only the location of the target defined which task would be performed. Non-informative cues resulted equiprobably in a switch or a repeat trial. Thus, trials differed in whether the cues afforded the opportunity for proactive control and in the need for reactive control. Specifically, switch-to and switch-away cues validly predicted a task change, allowing participants to disengage the previously relevant task set. Switch-to cues also specified the relevant task, allowing uploading of the new task rules before target onset. In contrast, non-informative cues allowed no preparation, and like switch-away cues required task uploading after target onset. Participants used their left and right index fingers to respond and the hand assigned to each response was counterbalanced across participants. Participants were instructed to respond as quickly and as accurately as possible. Incorrect responses were followed by an auditory feedback tone. At the end of each block, reaction times and accuracy for that block were presented and a brief humorous video was shown (5–10 s) to provide a brief rest. A longer break was offered mid-way through testing to minimize fatigue. The response–target interval was 1400 ms and included a 1000 ms cue–target interval (CTI).

#### 2.3. Procedure and EEG recording

In order to examine behavioral and EEG data for switching between well-learnt cue–target and target–response associations, participants completed two training sessions scheduled no more than 14 days apart, first on each task alone (single-task blocks) and then on switching between tasks (mixed-task blocks, total of 1320 practice trials). 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 (48 trials/block, one block per task). Each block included an additional five warm-up trials. Only mixed-task block data are presented here.

EEG was recorded continuously (2048 Hz, bandpass filter of DC-400 Hz, 64 scalp electrodes plus bilateral mastoid, outer canthi, supraorbital, and infraorbital ocular sites) using an ActiveTwo Biosemi EEG system. Common mode sense (CMS) and driven right leg (DRL) electrodes for the Biosemi active electrode system were positioned inferior to P1 and P2 respectively. EEG data were recorded relative to an amplifier reference voltage, and then re-referenced to the Cz electrode to remove common-mode signals.

## 2.4. Data analysis

The five warm-up trials, as well as trials with responses faster than 200 ms, slower than three standard deviations from each individual's mean RT or associated with incorrect responses were excluded from analyses (mean 7.4% of trials ± 6.2 SD). Trials with unsuitable noise levels (see below) were also excluded from EEG analyses.

### 2.5. EEG analysis

EEG data were processed using MATLAB 2011b through a pipeline utilizing Fieldtrip (<u>Oostenveld et</u> al., 2011), EEGLab (Delorme and Makeig, 2004), CSD Toolbox (Kayser and Tenke, 2006), and in-house

functions (see Fig. 2). EEG data were initially read into Fieldtrip and re-referenced to electrode Cz, then downsampled from 2048 Hz to 512 Hz using a zero-phase anti-aliasing filter with a low-pass cutoff frequency of 245 Hz and filtered (high pass: 0.1 Hz, forward phase; 50 Hz notch: zero phase). Bad channels (maximum of 2 per participant) were identified by visual inspection and excluded from processing. Trial epochs (repeat, switch-to, switch-away, non-informative) were extracted from -1000 ms to +3500 ms with respect to cue onset. To remove blink and vertical eye-movement artifact, independent component analysis (ICA) was performed using the fastica algorithm (Hyvärinen and Oja, 2000). This produces a set of components, equal to the number of available electrodes, from which one or two components corresponding to ocular artifact were identified by visual inspection and deleted. The remaining components were then projected back into sensor (electrode) space. The data were low pass filtered (30 Hz, zero-phase) to remove high frequency noise including muscular artifacts. Trials that contained residual artifact larger than ±100 µV were deleted, after which an average of 135.3 (±33.9 SD) repeat, 130 (±32.5 SD) switchto, 128.7 (±35.1 SD) switch-away and 132.4 (±31.4 SD) non-informative trials remained for analysis.

EEG data were transformed into estimates of scalp current density (SCD) at each electrode site by computing the spatial laplacian of the spherical-spline interpolated scalp topography. SCD reduces volume conduction effects in EEG sensor space and is independent of the choice of reference electrode. SCD acts as a high pass spatial filter, enhancing sensitivity to focal activity in the cortical mantel, while suppressing wide-spread EEG signals originating deeper within the brain (Kayser and Tenke, 2006). Thus it reduces the extent to which coherence between electrodes is inflated by volume conduction and provides a more sensitive measure of the underlying connectivity between cortical regions. After SCD, channels that were deemed bad were reintroduced by interpolating data between neighboring electrodes.

## 2.6. Coherence analysis

We used imaginary coherence as a measure of oscillatory synchronization in order to minimize artificial interactions at sensor space (<u>Stam et al., 2007</u>). Coherence refers to the normalized cross-spectral correlation between two time series, and contains information relating to both the absolute magnitude of the relationship and the complex component representing phase information. The complex component isolates phase coupling between two time series.

First, the power from each condition was obtained through the average of all decomposed singletrial time-frequency representation. In order to obtain a time-frequency decomposition of single-trial data P (Eq. (2)), for each EEG signal Xj, at electrode j (where  $j \in 1, ..., 64$ ), a product between the power spectrum (Fast Fourier Transform, FFT) of the EEG and the power spectrum of complex Morlet wavelets (Eq. (1)) was calculated.

$$\varphi(t,f) = e^{i2\pi f} e^{\frac{-t^2}{2\delta^2}}$$

Equation 1

Equation 2 
$$P_i(t, f) = iFFT (FFT(x_i) * FFT(\varphi(t, f)))$$

where *f* is the current frequency (80 logarithmically scaled intervals ranging from 2Hz to 50Hz), *t* is the time (400ms pre-cue to 2200ms post cue), and  $\delta$  is the width of each frequency band  $\frac{n}{2\pi f}$  (where *n* increases logarithmically from 3 to 14 with respect to *f*). An inverse FFT (*iFFT*) was performed on the output of the above steps to convolve signals together.

 $P_j(t,f)$  was then normalized with a decibel (dB) transformation (Eq. (3)),

Equation 3 
$$dB_{P_j(t,f)} = 10 \log_{10} \left( \frac{|P_j(t,f)|^2}{baseline} \right)$$

where  $|P_j(t,f)|^2$  is the magnitude of power at electrode *j*, and *baseline* activity was the average magnitude of power from 200ms pre-cue to cue onset. This process was repeated for all electrodes.

Next, imaginary coherence was calculated by first computing the cross-spectrum,  $S_{jk}(t,f)$  between each exhaustive but non-repetitive permutation of electrodes ( $j,k \in 1, ..., 64$ ), for each time point across the 80 frequency intervals (Eq. (4)),

Equation 4 
$$S_{jk}(t,f) = P_j(t,f) * \overline{P_k}(t,f)$$

where  $\overline{P_k}(t, f)$  denotes the complex conjugate of the power at electrode *k*.

As coherence is a measure based on auto and cross-spectral properties, we divided the derived cross-spectrum by the root of the power for each respective electrode in order to compute coherence (Eq. (5)),

Equation 5 
$$C_{jk}(t,f) = \frac{S_{jk}(t,f)}{\sqrt{S_{jj}(t,f)S_{kk}(t,f)}}$$

Imaginary coherence for each permutation of *j* and *k* was obtained by extracting the complex component of  $C_{ik}(t,f)$ .

## 2.7 Connectivity Analysis

To establish that any effects of cognitive control were specific to the hypothesized frequency band, we defined a connectivity matrix for five frequency bands (i.e., delta:  $\delta \in 2-4$  Hz, theta:  $\theta \in 4-7$  Hz, lower alpha:  $\alpha_1 \in 8-10$  Hz, upper alpha:  $\alpha_2 \in 10-13$  Hz, beta:  $\beta \in 13-30$  Hz) by averaging the imaginary coherence output for that frequency band across partially overlapping 200 ms windows using a 100 ms sliding step from cue onset to 600 ms post target. This resulted in 15 time ranges for each frequency band (5), for each trial type (4). As SCD correction can produce artifacts at edge electrodes, our final connectivity matrices included only non-peripheral electrode sites (i.e., AF3, F1, F3, F5, FC5, FC3, FC1, C1, C3, C5, CP5, CP3, CP1, P1, P3, P5, P7, P07, P03, O1, AFz, Fz, FCz, Cz, CPz, Pz, P0z, Oz, AF4, F2, F4, F6, FC6, FC4, FC2, C2, C4, C6, CP6, CP4, CP2, P2, P4, P6, P8, P08, P04, O2).

The repeat trial type was used as the baseline condition because it requires the least proactive control (task updating) and the least reactive control (resolution of interference). For each participant, the connectivity matrices for switch-to, switch-away and non-informative trial types were converted into a difference matrix by subtracting the connectivity matrix from repeat trials. As the imaginary coherence value for each pair of electrodes in these connectivity matrices contains phase information that captures both the lagging and the leading electrodes in a pair, and is dependent on the order with which the electrodes are organized in the connectivity matrix, statistical analyses examine differences in strength of connectivity, irrespective of direction.

#### 2.8 Statistical Analyses

Statistics on coherence results were performed using map-wise t-tests, with a false-discovery rate (FDR) of p < 0.005 (Benjamini and Yekutieli, 2001) and following the multiple comparison correction guidelines of Nolte et al. (2004). Connectivity matrices for each 200 ms window from cue onset to 400 ms post-target for switch-to, switch-away and non-informative vs. repeat trial types were examined (see Supplementary materials).We present results from windows that produced the strongest results for intervals associated with proactive control (early cue-to-target interval, CTI: 100–300 ms and mid-CTI: 400–600 ms) and reactive control (post-target: 200–400 ms). These time courses also corresponded to transient processes of cognitive control seen in previous ERP results with this paradigm, i.e. large preparation effects within a 150–400 ms post-cue range for switch-to and switch-away trials, and largest task implementation differences around 200–500 ms post-target (Karayanidis et al., 2009; Nicholson et al., 2006). The entire time course for each condition is presented in SM1 in Supplementary materials. Synchronization effects were specific to the hypothesized theta and alpha bands and hence, we only report networks in these frequencies.

### 3. Results

## **3.1 Behavioral Results**

Behavioral data were analyzed using a 5 (TRIAL TYPE) x 3 (TASK) repeated-measures ANOVA in SPSS. For RT, Mauchly's sphericity test indicated a violation of sphericity for the TRIAL TYPE main effect  $(\chi^2(9) = 70.4 \text{ p} < .001)$  and this was corrected using Greenhouse-Geisser correction ( $\varepsilon = .42$ ). Significant main effects for TRIAL TYPE,  $F_{(4,112)} = 73.6$ , p < 0.001,  $\eta^2 = .73$ , and TASK,  $F_{(3,56)} = 20.6$ , p < 0.001,  $\eta^2 = .42$ , were found. There was also a small but statistically significant TRIAL TYPE \* TASK interaction  $F_{(8,224)} = 2.6 p =$ .009,  $\eta^2 = .09$ . Overall, RT was faster for the color than the letter and number tasks, and this task was greater for *repeat* and *switch-to* trials which allowed task updating prior to target onset. As shown in Table 1, RT was faster for *repeat* trials than for *switch-to* ( $t_{(28)} = -6.8$ , p < 0.001), *switch-away* ( $t_{(28)} = -12.2$ , p <0.001) and *non-informative repeat* ( $t_{(28)} = -12.3$ , p < 0.001). *Switch-to* trials were faster than both *switch-away* ( $t_{(28)} = -11.1$ , p < 0.001) and *non-informative switch* trials ( $t_{(28)} = -9.2$ , p < 0.001) but *non-informative switch* trials were not significantly different than *switch-away*; see Table 1).

Overall responding was very accurate, with a significant main effect for TRIAL TYPE  $F_{(4,112)} = 13.2$ , p < 00.1,  $\eta^2 = .32$  but not for TASK. The TRIAL \* TASK interaction also reached significance  $F_{(8,224)} = 4.2 p < 0.001$ ,  $\eta^2 = .13$ . Post-hoc t-tests showed that *repeat* trials were significantly more accurate than *switch-to*  $(t_{(28)} = 2.7, p = .012)$  and *switch-away*  $(t_{(28)} = 4.8, p < 0.001)$ . *Switch-to* trials were significantly more accurate than *switch-away*  $(t_{(28)} = 2.3, p = 0.027)$  while *non-informative switch* trials were no more accurate than *switch-away*.

### 3.2 Coherence Analyses

Figs. 3 and 4 present imaginary coherence differences for each of the three trial types (*switch-to*, *switch-away*, *non-informative*) relative to the *repeat* baseline for theta and upper alpha frequency bands, respectively. Early post-cue (100-300 ms), mid post-cue (400-600 ms), and post-target (1200-1400 ms after cue onset) windows are presented in each figure. As this paper is focused on identifying whether proactive and reactive control processes involve the same or distinct networks, the figures depict significant differences in phase synchrony between each trial type and the *repeat* baseline irrespective of the direction of the difference (i.e., *switch-to* greater or less than *repeat*)<sup>1</sup>.

## 3.2.1 Theta Coherence

In the early CTI window (100-300 ms post-cue), theta connectivity for *switch-to* and *switch-away* trial types differed from *repeat* trials across a broad network linking frontocentral, parietal and occipital sites (Fig. 3A). Left occipital/parietal sites (PO3, PO7, O1, P7, P5, P3, P1) showed strong connectivity with centro-parietal sites as well as with frontal sites. Both these switch trial types showed major centroparietal hubs (e.g. CP2, CP4, CP1, CP3) that had extensive long-range connectivity. This extensive theta band connectivity subsided midway along the CTI (400-600 ms; Fig. 3B), which showed only a less extensive

<sup>&</sup>lt;sup>1</sup> For all measures, phase synchrony was predominantly greater for the repeat baseline than the respective trial type. However, this was reversed for the early theta coherence window, for which phase synchrony was predominantly

centroparietal network between CP6, CP4 CP2 and left parietal sites when comparing *switch-away* and *repeat* trials. In contrast, the comparison between *non-informative* and *repeat* trials showed only minimal theta connectivity in a different network linking right and left posterior sites (e.g. CP6, PO7, P5) in the early preparation interval. Thus, differences from the *repeat* baseline were predominantly evident for the two trial types that provided switch certainty and were most extensive early in the preparation interval.

The pattern of theta connectivity was very different after target onset (200-400 ms post-target, Fig. 3C). There was no consistent pattern of differential theta connectivity for *switch-to* relative to *repeat* trials. In contrast, both *switch-away* and *non-informative* trial types, for which target onset provided information about task identity, showed a very strong and similar pattern of theta connectivity. This included long range connections between frontal/central (C1, Cz, FC4, FC2) and centroparietal/parietal/occipital sites (CP2, CP4, P8, PO8, O2, Oz, O1, PO7, P7, PO4, POz), as well as short range connections between left and right occipital and parietal sites.

Overall, this pattern of results indicates two prominent sets of networks in the theta band. A strong, switch-related preparation network extensively connected frontocentral and parietoccipital sites only for *switch-to* and *switch-away* cues that validly informed of an upcoming task switch (i.e., Fig. 3A). A distinct task-related network was evident after target onset and extensively connected anterior-posterior connections on trials where task identity was only evident after target onset (i.e., Fig. 3B).

#### 3.2.2 Alpha Coherence

Connectivity was only evident in the upper alpha band. During the preparation interval, there was no consistent pattern of frontoparietal connections for any of the three trial types in either early or middle CTI window (Figs 4A and B). After target onset, two sets of networks emerged (Fig. 4C). Both *switch-to* and *switch-away* trials that reliably predicted a task switch showed differential phase synchrony compared to the *repeat* baseline in a broad network of cross-hemispheric frontal/frontocentral connections (left and right F/FC sites). This network was most extensive for *switch-to* trials, in which the cue also identified the task to perform, thereby allowing both goal and task-set updating prior to target onset. *Switch-away* and *non-informative* trial types in which the identity of the task was not revealed until target onset showed differences in phase synchrony from the repeat baseline in a distinct pattern of connections linking parieto-occipital sites (e.g. PO8, P6) with centroparietal sites (CPz, P1, C5).

#### 4. Discussion

The key finding of this study is that distinct frontoparietal theta (4–7 Hz) networks are associated with switch-related, proactive control processes and interference-related, reactive control processes, consistent with dissociable control networks (Braver, 2012). Specifically, early in the preparation interval, both switch-to and switch-away contrasts in which the cue validly predicted a change in task showed extensive anterior–posterior theta oscillatory networks. Importantly, these networks were not elicited by

non-informative cues, which were equally likely to result in a switch or repeat trial. After target onset, theta connectivity was sparse on switch-to trials for which task-specific preparation could be completed in the cue–target interval. In contrast, switch-away and non-informative trials, for which task identity was not revealed until target onset, showed differential theta band connectivity in frontoparietal networks that was distinct from those seen during preparation. Proactive and reactive control networks are more clearly differentiated in Fig. 5 which presents conjunction analysis derived by extracting common pairs of electrodes that were significantly connected for switch-to and switch-away contrasts in the preparation interval and the switch-away and non-informative contrasts in the post-target interval. To our knowledge, this is the first evidence that both proactive and reactive control processes involve modulation of theta oscillatory activity, but in different anterior–posterior networks.

This finding fits well with prior evidence of frequency-specific neural synchronization for higher order cognitive processes such as working memory (Huang et al., 2013; Palva et al., 2005; Pesonen et al., 2007; Sauseng et al., 2005; Wu et al., 2007), selective attention (Doesburg et al., 2009; Doesburg and Ward, 2007; Kahlbrock et al., 2012; Maris et al., 2013) and inhibition (Papenberg et al., 2013; Tallet et al., 2009). It is also consistent with increasing evidence that theta oscillations are a neural correlate of the need for cognitive control (see Cavanagh and Frank, 2014; Sauseng et al., 2010).

#### 4.1. Proactive control and theta connectivity

Event-related potential (ERP) studies have differentiated between ERP components associated with advance preparation and interference control. The cued trials paradigm used here produces a large positive ERP deflection during the preparation interval for switch-to and switch-away trials, but not for repeat and non-informative trials, peaking within the latency range of the fronto-parietal theta network i.e. circa 250 ms (Karayanidis et al., 2009; Nicholson et al., 2006). The amplitude of this early switch-positivity is associated with both response time and response threshold — a measure of cautiousness in decisionmaking (Karayanidis et al., 2009). Using multivariate pattern classification analyses, Mansfield et al. (2012) showed activity in a right frontal source for switch relative to non-switch trials within the same latency range (see also Lavric et al., 2008). These studies also showed later activation in parietal sources for trials that permit task-specific preparation, irrespective of whether the task switches or repeats (Lavric et al., 2008; Mansfield et al., 2012). These ERP findings have been interpreted as indicating at least two preparation processes: an early switch-specific process that is activated when there is switch certainty and prepares for an upcoming change in task, and a later general preparation process that is activated when the identity of the task to be performed to the upcoming target is known in advance and may represent task or response readiness (see Karayanidis et al., 2010; Karayanidis and Jamadar, 2014). The early component is consistent with the frontoparietal theta connectivity seen here for the same two trial types.

Both switch-away and switch-to trials provide reliable information that the upcoming target will require a change in task, although in the former trials, the task is not specified until target onset. There is converging evidence from cognitive model parameters and ERPs (Karayanidis et al., 2009), multivariate EEG

pattern analyses (Mansfield et al., 2012) and now theta connectivity data that, on both these trial types, processes related to switch preparation are activated early in the preparation interval. These processes are not activated on non-informative trials where the cue equiprobably leads to a task switch or task repeat. The processes activated for both switch-to and switch-away trials are likely to be involved in goal resetting (e.g., inhibition of the irrelevant task-set, adjusting response threshold), as these cues provide certainty that the upcoming target will not require task repetition<sup>2</sup>. Note that unlike the theta oscillations associated with maintaining information in working memory during a retention interval (Jensen and Tesche, 2002; Jacobs et al., 2006; Khader et al., 2010), in the current context, it is the intention to switch that is updated and maintained on switch-away trials, rather than a test item or a task-set. Hence, as switch-away cues do not define the relevant task, this process is not consistent with reloading of the relevant task-set into working memory (e.g., Karayanidis and Jamadar, 2014; Koch et al., 2010; Monsell, 2003). The topography of the strong frontoparieto-occipital theta connectivity for cues that provide valid information that the task will change is compatible with fMRI evidence for switch-related proactive activation in frontoparietal networks (e.g. Badre and Wagner, 2006; Braver et al., 2003; see Ruge et al., 2013). In this study, we focused on transient changes in proactive control in preparation for different trial types within the same mixed-task block. Future work could look at networks activated during the preparation interval for repeat trials in single-task versus mixed-task blocks (i.e., mixing cost) to examine whether this same network is involved in sustained proactive control.

## 4.2. Reactive control and theta connectivity

There is considerable electrophysiological evidence for a unique role of theta in control and attentional processes that typically rely on reactive control (i.e. overriding a prepotent response or resolving goal/response conflict). For example, midline frontal EEG theta power is increased in response to error detection and correction (Cavanagh et al., 2009; Luu et al., 2004; Trujillo and Allen, 2007), as well as other types of conflict (HansImayr et al., 2008; Nigbur et al., 2011). Additionally, coherence and phase-locking measures suggest the presence of long-range communication between frontal, temporal and parietal sites when manipulating information in working memory (e.g., Sauseng et al., 2006). The present data are consistent with the role of theta connectivity in reactive control.

On both switch-away and non-informative trials, it is not possible to update the relevant task-set during the preparation interval. Increased theta synchronization after target onset on these trials may represent task-set updating, as previously seen with working memory tasks (e.g. Jensen and Tesche, 2002; Khader et al., 2010). In the current task, the position of the target reveals the task-rules that need to be applied on that trial, and this information must be extracted before the relevant feature of the target can be selected for further processing and response selection. This is especially critical in this paradigm, as the target is bivalent (i.e., contains features from both relevant and irrelevant tasks) and incongruent (i.e., task-

<sup>&</sup>lt;sup>2</sup> As the direction of theta phase synchrony differed between *switch-to* and *switch-away* vs. *repeat* contrasts (see Footnote 1), further work is needed to characterize the nature of the underlying processes.

relevant and task-irrelevant features are mapped to different responses). This post-stimulus interference is likely to require reactive control, especially when task-set updating cannot be completed during the preparation interval, as is the case for switchaway and non-informative trials. The extensive long-range theta connectivity network found for both these contrasts is consistent with top down control at the level of stimulus processing (Fig. 3B; Fig. 5B). The time course of these networks also overlaps with the conflictrelated N2 component found in ERPs (see Folstein and Van Petten, 2008), suggestive of control processes related to conflict control process. Similar connectivity patterns have also been reported previously under conflict conditions. For example, in a working memory task, <u>Moore et al. (2006)</u> reported extensive frontoparietal theta connectivity on trials where conflict was detected and needed to be overcome. Interference control can also account for the <u>Sauseng et al. (2006)</u> findings, as their task switching paradigm did not differentiate between preparation (cuelocked) and interference (post-target) processes.

## 4.3. Alpha connectivity

While alpha networks were not as extensive as the theta networks, transient upper alpha connectivity was also evident during both preparation and post-target intervals. Conjunction analysis on these networks did not produce any shared set of connections in either case, suggesting that these networks are either not as robust as the theta networks or are more strongly linked with general task performance rather than specific, distinguishable control processes. It is possible that alpha and theta connectivity are associated with sustained and transient aspects of cognitive control, respectively. Examining coherence using a different baseline condition, such as a single task block, may highlight sustained cognitive control processes and their related networks. For example, Czernochowski (2014) reported differences in sustained right-frontal preparatory ERP components for informative and non-informative trial types.

### 4.4. Conclusions

Our findings confirm a role of frontoparietal theta oscillatory networks in cognitive control and importantly, indicate that distinct anterior–posterior theta oscillatory networks are activated for different types of control. Proactive control processes related to preparation to switch were associated with a centroparietal hub with strong frontal and posterior connections. This network was evident in the latency range of the early switch-positivity, an ERP component shown to be associated with higher response threshold setting in anticipation of a switch in task (Karayanidis et al., 2009). Reactive control processes related to task-set updating and interference control were associated with an extended anterior–posterior network. This network was evident in the latency range of the frontocentral N2 component which is associated with conflict resolution and interference control in both task-switching and other interference paradigms (for review see Karayanidis and Jamadar, 2014). These findings suggest that effective transient cognitive control processes, important for flexible interactions with our environment, are intimately entwined with transient theta oscillatory networks.

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## Appendix A. Supplementary data

Supplementary data to this article can be found at http://dx.doi.org/10.1016/j.neuroimage.2014.12.028.

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Trial Type	RT(ms) ± (SEM)	Accuracy (%correct) ± (SEM)
Repeat	682.8 ± 21.7	98.1 ± 0.2
Switch-To	817.4 ± 36.2	96.9 ± 0.4
Switch-Away	921.7 ± 34.2	96.1 ±0.4
Non-Informative: Repeat	785.4 ± 19.6	97.7 ± 0.3
Non-Informative: Switch	920.2 ± 32.5	95.4 ±0.5

Table 1. Reaction time and percent correct for the four task switching trial types. Note that for noninformative cues, we present separate results depending on whether the target resulted in a switch or a repeat trial.



Figure 1. Cued-trial task switching paradigm. A) Each major segment of the wheel is consistently mapped to one of the three tasks: letter, digit and color. The table shows the eight exemplars used for each task and an example of stimulus-response mappings. B) Timeline of a specific trial. Response-cue interval (RCI) and cue-target interval are fixed at 400ms and 1000ms, respectively. On each trial, the cue highlights two of the six segments of the circle and indicates that the target will appear in one of these two segments. In this instance, the cue covers both 'letter task' segments, and the participant can prepare to apply the 'letter' task rules on the upcoming target. When the target (e.g., A4) appears in a letter task segment, participants must respond to the task-relevant feature of the target (e.g., the letter A is a vowel, respond with left hand), and ignore the task-irrelevant feature of the target (e.g., the number 4). C) The progression from trial N-1 to trial N defines the trial type. i) If, having completed the letter task on trial N-1, the same segment is highlighted on trial N, it is a repeat trial and the participant will repeat the letter task. ii) If the cue highlights both segments of one of the other tasks, it is a *switch-to* trial. The target will appear in one of the two highlighted segments, and the participant can use the CTI to update the new task rules (e.g., digit task, in this example). iii) If the cue highlights adjoining segments of the two tasks not completed on trial N-1 (e.g., digit and color), it is a switch-away trial. The target is equally likely to appear in the digit and color segments and the participant can prepare to switch task (e.g., not repeat the letter task), but does not know which task to upload until the target appears. The position of the target indicates which task to complete. iv) If the cue highlights one segment from the task completed on trial N-1 (e.g., letter task) and one from another task (e.g., digit task), it is a non-informative trial. The target is equally likely to appear in the letter or the digit segment, and require either a repeat (non-informative repeat) or a switch (non-informative switch) in task.



**Figure 2.** Processing pipeline for EEG analysis. EEG data were processed using an in-house developed, semi-automated pipeline utilizing Fieldtrip (blue), EEGLab (green) and custom (brown) routines. For details, refer to *Methods*.



**Figure 3.** Theta (4-7Hz) coherence. Connecting lines between electrodes represent phase synchrony values that had a *t*-value significant at a< 0.05 after correcting for multiple comparisons. Electrode size is proportional to node degree (number of connections involving respective electrode). A lateral transverse view of electrode configuration is shown in order to depict cross-hemispheric effects (see head model reference to right). A) Early CTI (100-300ms): An extensive theta frontoparietal connectivity network is seen for *switch-to* and *switch-away* trials relative to the repeat baseline, extending from centroparietal sites to right frontal and both ipsilateral and contralateral parietoccipital sites early in the preparatory interval. Non-informative trials show minimal theta connectivity restricted to centroparietal sites. B) Mid CTI (400-600ms). C) Post-target (1200-1400ms after cue onset): Extensive frontoparietal theta connectivity is seen for *switch-away* and *non-informative* trials but not for *switch-to* trials. R: *repeat*; ST: *switch-to*; SA: *switch-away*; NI: *non-informative*.



**Figure 4.** Upper alpha (10-13Hz) coherence. Significant *t*-values after correcting for multiple comparisons are depicted. Electrode size is proportional to node degree (number of connections involving respective electrode). A lateral transverse view of electrode configuration is shown in order to depict cross-hemispheric effects (see head model reference to right). A) Early CTI (100-300ms). B) Mid CTI (400-600ms). C) Post-target (1200-1400ms after cue onset): Note bilateral connectivity across frontal sites for *switch-to* trials, and extending between posterior and central sites for *non-informative* trials. *Switch-away* trials showed a combination of these two networks. R: *repeat*; ST: *switch-to*; SA: *switch-away*; NI: *non-informative*.



**Figure 5.** Conjunction analyses showing common theta (4-7Hz) connectivity for A) *switch-to and switch-away* trials during the early preparation period (100-300ms) and B) *switch-away* and *non-informative* trials after target onset (1200-1400ms). Only connections that were significant for both contrasts are shown.