Proactive and reactive control processes involve dynamic reorganisation of alpha and theta oscillatory networks

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**Introduction**

Cognitive control processes allow us to adjust our behaviour flexibly in order to meet internal motivations or goals. Depending on contextual constraints, this control can be adopted in either proactively,pre-setting the system to be sensitive to goal-relevant features of the environment or reactively, responding to such goal-relevant features on a needs basis ([Braver, 2012](#_ENREF_2)). The implementation of these control processes is known to rely on an extensive and well-described frontoparietal communication architecture ([Corbetta & Shulman, 2002](#_ENREF_4); [Seeley et al., 2007](#_ENREF_31); [Vincent, Kahn, Snyder, Raichle, & Buckner, 2008](#_ENREF_36)) that is well-suited to promote flexible and rapid information propagation ([Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008](#_ENREF_8)). Yet, despite the increasing knowledge regarding the anatomical architecture that permits flexible control, the functional properties of this network are less well characterised.

One plausible mechanism by which information can be flexibly adjusted and rerouted in the frontoparietal network is oscillatory synchronisation. This refers to the process whereby separate populations of neurons are able to exchange information transiently by synchronising the excitability windows in which they are most sensitive to electrical influxes ([Fries, 2005](#_ENREF_10); [Womelsdorf & Fries, 2006](#_ENREF_37)). Such synchronisation produces assemblies of neurons that are functionally connected for a given period of time. The neurons in these assemblies oscillate rhythmically, allowing receiving and transmitting components to precisely time their firing rates, and thereby achieving an efficient mechanism to exchange information within the assembly that is also less sensitive to competing inputs from alternative assemblies ([Azouz & Gray, 2003](#_ENREF_1); [Engel, Fries, & Singer, 2001](#_ENREF_9)). Indeed, oscillatory synchronisation has been shown to be functionally relevant in numerous higher-order cognitive processes such as working memory ([Huang et al., 2013](#_ENREF_11); [Palva, Palva, & Kaila, 2005](#_ENREF_26); [Pesonen, Hamalainen, & Krause, 2007](#_ENREF_28); [Sauseng, Klimesch, Schabus, & Doppelmayr, 2005](#_ENREF_30); [Wu, Chen, Li, Han, & Zhang, 2007](#_ENREF_38)), selective attention ([Doesburg, Green, McDonald, & Ward, 2009](#_ENREF_6); [Doesburg & Ward, 2007](#_ENREF_7); [Kahlbrock, Butz, May, & Schnitzler, 2012](#_ENREF_13); [Maris, Womelsdorf, Desimone, & Fries, 2013](#_ENREF_20)) and inhibition ([Papenberg, Hammerer, Muller, Lindenberger, & Li, 2013](#_ENREF_27); [Serrien & Sovijarvi-Spape, 2013](#_ENREF_33); [Tallet, Barral, & Hauert, 2009](#_ENREF_34)). By transiently synchronising activity within the frontoparietal network, goal-relevant representations may be afforded an elevated processing status that permits effective cognitive control.

The evidence for the role of oscillatory synchronisation in cognitive control is currently largely restricted to slow wave, theta (4-7Hz) synchronisation in goal and response conflict resolution. For example, increase in theta synchronisation has been reported in paradigms requiring error detection and post-error correction ([Cavanagh, Cohen, & Allen, 2009](#_ENREF_3); [Luu, Tucker, & Makeig, 2004](#_ENREF_17); [Trujillo & Allen, 2007](#_ENREF_35)), goal conflict and response selection ([Moore, Gale, Morris, & Forrester, 2006](#_ENREF_22); [Moore, Mills, Marshman, & Corr, 2012](#_ENREF_23)), as well as in task switching ([Sauseng et al., 2006](#_ENREF_29)). As these goal-relevant processes are important contributors to cognitive control ([Miyake et al., 2000](#_ENREF_21)), these findings suggest thatwtheta oscillations may be a neural signature of goal-directed processes.

Interestingly, the role of theta in cognitive control has been investigated almost exclusively using paradigms that do not differentiate between proactive and reactive control. . For example, Sauseng and colleagues reported widespread frontoparietal coherence in the theta band when participants switched randomly between digit magnitude and digit classification tasks compared to repeating one of these tasks ([Sauseng et al., 2006](#_ENREF_29)). There was no advance information about whether the upcoming trial would require a switch or a repeat in task. Instead, the stimulus had to be encoded firstly decide which task needed to be implemented (e.g., repeat the same task or change to alternative task) and secondly to implement that task in the presence of competing information (e.g., respond smaller/greater than 5, ignore parity). Similarly, other studies investigating the role of theta synchronisation in cognitive control have used paradigms that do not differentiate between proactive and reactive control (e.g., Flanker tasks in Cavanagh et al., 2009).

In fact, studies that have specifically targeted proactive control, by examining electrophysiological activity in the cue-target interval, i.e., the interval between an informative cue to switch or repeat task and the subsequent target, have shown changes not in theta, but in alpha (8-13Hz) power ([Mansfield, Karayanidis, & Cohen, 2012](#_ENREF_18)) and oscillatory synchronisation ([Serrien, Pogosyan, Cassidy, & Brown, 2004](#_ENREF_32)). Together, these findings suggest that proactive and reactive cognitive control modes may involve distinct neural processes. As functionally relevant neural coupling often occurs between frequencies ([Jensen & Colgin, 2007](#_ENREF_12)), perhaps the frontoparietal control architecture dynamically shifts between theta and alpha oscillatory synchronisation depending on contextual demands.

The current study aimed to investigate dynamic shifts in frontoparietal oscillatory synchronisation with respect to both proactive and reactive control processes. To do so, we employed a previously used cued task switching paradigm that allows us to disentangle both preparatory, proactive control processes from target-driven, reactive control ([Karayanidis et al., 2009](#_ENREF_14); [Mansfield, Karayanidis, Jamadar, Heathcote, & Forstmann, 2011](#_ENREF_19)). Considering the implicated role of theta synchronisation in cognitive control, we wanted to explore whether there were differences in theta synchronisation between proactive and reactive control modes. We have previously shown switch specific event-related potential EEG components that are associated with preparation for a change in task and for target-driven implementation of a switch ([Karayanidis et al., 2009](#_ENREF_14); [Nicholson, Karayanidis, Davies, & Michie, 2006](#_ENREF_24)). If switching is associated with increased frontoparietal theta synchronisation, we expect to see distinctive frontoparietal connectivity during the early preparation for an anticipated switch and post switch trial target onset, in line with Sauseng et al. (2006) that is absent for non-switch conditions. If theta connectivity is only associated with reactive control though, frontoparietal synchronisation should be observed in those conditions in which proactive control was not sufficient (i.e. switch-away and noninformative trials, see Methods). Finally, given previous suggestions of alpha activity during switch trials, we aimed to investigate the role of alpha synchronisation during switch-specific preparation. Previous work has suggested that the lower alpha band is associated with general attentional and readiness processes whereas the upper alpha band is linked to active working memory manipulation and inhibition so we explore the role of each sub-band uniquely ([Klimesch, Sauseng, & Hanslmayr, 2007](#_ENREF_16); [Sauseng et al., 2005](#_ENREF_30)).

**Methods**

*Participants*

Twenty-nine (13 male, mean age 25.69 ± 5.64 years) young adults from the Newcastle community took part in the current study as part of the larger project (<http://www.age-ility.org.au/>) and received $20 per hour reimbursement. Participants undertook three testing sessions as part of the larger project: an initial neuropsychological testing session where participants performed an extensive neuropsychological testing battery and learnt the current task switching paradigm, an EEG recording session and a final MRI scanning session. Only data from the EEG session is reported here. All participants were asked to abstain from caffeine and alcohol prior to testing, were right-handed and had no current neurological or psychiatric disorder. The University of Newcastle Humans Ethics Research Committee approved the current study.

*Stimuli and Task*

Participants completed a cued trials task switching paradigm, described elsewhere ([Karayanidis et al., 2009](#_ENREF_14)), whilst having simultaneous EEG recorded. In brief, participants were presented with a wheel divided into six segments, with two adjacent segments representing one of three classification tasks (letter task – vowel/consonant; digit task – odd/even; colour task – hot/cold; see Figure 1a). Two adjacent segments of the wheel were bolded, serving as a cue for 1000ms prior to target onset to indicate what the upcoming task would be. The cue disappeared at target onset. The cue could highlight an entire task section, providing a fully-informative cue that facilitates preparatory, proactive control. If this cue indicated the same task as the previous trial, we deemed this a *repeat* trial, if it indicated a change we deemed this a *switch-to* trial (see Figure 1a). Alternatively, a cue could highlight two adjacent segments of the wheel that contained two possible tasks. If the cue indicated a change in task but not the identity of the upcoming task, we deemed this a *switch-away* trial. If the cue segments highlighted a previous task and an additional task we deemed this a *noninformative* trial. Participants completed 72 trials per block (plus five initial dummy trials) for 10 blocks. Fifty per cent of trials were fully-informative, 25% switch-away, 12.5% noninformative repeat and 12.5% noninformative switch. All targets contained a task relevant feature (e.g. a vowel for a cued letter task), an incongruently mapped distractor (e.g. an even digit) and a neutral feature for the third task (e.g. a grey target ‘A4’). The same target did not occur on successive trials, participants responded using push buttons built into a chair and response hand mappings were counterbalanced between participants.

*Procedure and EEG recording*

Before the EEG session participants learnt and practiced both the single blocks of each task and switching blocks over two training sessions, comprising 1320 practice trials total. At the time of the experimental session, participants performed the task switching paradigm in a dimmed testing room with simultaneous EEG recorded. EEG was recorded continuously at a sampling rate of 2048Hz from 64 scalp electrodes and eight external leads (two outer canthi of the eyes, two supraorbital, two infraorbital, and left and right mastoids) using an ActiveTwo Biosemi EEG system. Data was recorded with reference to the common mode signal (CMS) and right driven leg (DRL) electrodes. Initially participants undertook a brief two minutes eyes closed resting state scan, with an additional resting state scan after five blocks and a final resting period at the conclusion. Only task-based EEG is presented here. Participants were presented a tone after errors and had their reaction times and accuracy for each block presented as inter-block feedback alongside a brief entertaining video. These breaks were semi-self paced, with participants informing the experimenter when they were ready to proceed to the next block. This was done to minimise fatigue effects.

*Data Analysis*

For both behavioural and EEG analyses the first five trials from each block were excluded, alongside trials faster than 200ms and slower than three standard deviations above each participant’s mean RT. For EEG processing, trials following an error were also excluded.

*EEG Analysis*

EEG data was processed offline in MATLAB 2011b (MathWorks) using a custom built analysis pipeline, utilising the open source toolboxes Fieldtrip ([Oostenveld, Fries, Maris, & Schoffelen, 2011](#_ENREF_25)) and EEGLab ([Delorme & Makeig, 2004](#_ENREF_5)) as well as custom built jobs (Figure 1b). First, for each participant, continuous data was rereferenced to the common average, filtered (50Hz notch filter; 0.1Hz high pass) and visually inspected for poor channels. If needed, noisy channels were interpolated using neighbouring electrodes. Next, trials were defined relative to cue onset (-1000ms to 3500ms) and the criteria listed above. Channels with large excursions from the mean were considered noisy and removed prior to independent components analysis (ICA). A large excursion was considered any of the following three possibilities: a clear outlier based on trial variance, an absolute value of greater than 1000µv or a z-value > 4. This exclusion step was performed to increase the odds of EOG components being the strongest components in the analysis and thus easier to remove. ICA was performed on the data using the *fastica* function in Fieldtrip. EOG-related components and those that were clearly identifiable as artefactual were removed from the data. Next, we adopted a semi-automated approach to remove trials with artefacts. First, we performed a low pass 30Hz filter to remove EMG artefacts, then applied an automatic ±100uv rejection criteria to remove any trials containing additional artefacts. Trials that remained were visually inspected and removed if any additional artefacts were observed or if they still were considered an outlier based on their variance. Finally, the trial based data were transformed using a current-source-density (CSD) transformation ([Kayser & Tenke, 2006](#_ENREF_15)). As our coherency data was interpreted at the sensor-based level, it is important to control for volume conduction effects that can produce artificial correlations between electrodes. CSD transformation minimises volume conduction by eliminating the effect of reference montages across sites as the transformation is reference free and by removing signatures with a wide spatial distribution.

*Power Analysis*

References

Azouz, R., & Gray, C. M. (2003). Adaptive coincidence detection and dynamic gain control in visual cortical neurons in vivo. *Neuron, 37*, 513-523.

Braver, T. S. (2012). The variable nature of cognitive control: a dual mechanisms framework. *Trends Cogn Sci, 16*(2), 106-113. doi: 10.1016/j.tics.2011.12.010

Cavanagh, J. F., Cohen, M. X., & Allen, J. J. (2009). Prelude to and resolution of an error: EEG phase synchrony reveals cognitive control dynamics during action monitoring. *J Neurosci, 29*(1), 98-105. doi: 10.1523/JNEUROSCI.4137-08.2009

Corbetta, Maurizio, & Shulman, Gordon L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci, 3*(3), 201-215.

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics using independent component analysis. *Journal of Neuroscience Methods, 134*, 9-21.

Doesburg, S. M., Green, J. J., McDonald, J. J., & Ward, L. M. (2009). From local inhibition to long-range integration: a functional dissociation of alpha-band synchronization across cortical scales in visuospatial attention. *Brain Res, 1303*, 97-110. doi: 10.1016/j.brainres.2009.09.069

Doesburg, S. M., & Ward, L. M. (2007). Long-distance alpha-band MEG synchronization maintains selective visual attention. *International Congress Series, 1300*, 551-554. doi: 10.1016/j.ics.2006.12.072

Dosenbach, N. U., Fair, D. A., Cohen, A. L., Schlaggar, B. L., & Petersen, S. E. (2008). A dual-networks architecture of top-down control. *Trends Cogn Sci, 12*(3), 99-105. doi: 10.1016/j.tics.2008.01.001

Engel, A. K., Fries, P., & Singer, W. (2001). Dynamic predictions: Oscillations and synchrony in top-down processing. *Nature Reviews Neuroscience, 2*, 704-716.

Fries, P. (2005). A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. *Trends in Cognitive Science, 9*(10), 474-480. doi: 10.1016/j.tics.2005.08.011

Huang, L. Y., She, H. C., Chou, W. C., Chuang, M. H., Duann, J. R., & Jung, T. P. (2013). Brain oscillation and connectivity during a chemistry visual working memory task. *Int J Psychophysiol, 90*(2), 172-179. doi: 10.1016/j.ijpsycho.2013.07.001

Jensen, O., & Colgin, L. L. (2007). Cross-frequency coupling between neuronal oscillations. *Trends Cogn Sci, 11*(7), 267-269. doi: 10.1016/j.tics.2007.05.003

Kahlbrock, N., Butz, M., May, E. S., & Schnitzler, A. (2012). Sustained gamma band synchronization in early visual areas reflects the level of selective attention. *Neuroimage, 59*(1), 673-681. doi: 10.1016/j.neuroimage.2011.07.017

Karayanidis, F., Mansfield, E. L., Galloway, K. L., Smith, J. L., Provost, A., & Heathcote, A. (2009). Anticipatory reconfiguration elicited by fully and partially informative cues that validly predict a switch in task. *Cogn Affect Behav Neurosci, 9*(2), 202-215. doi: 10.3758/CABN.9.2.202

Kayser, J., & Tenke, C. E. (2006). Principal components analysis of Laplacian waveforms as a generic method for identifying ERP generator patterns: I. Evaluation with auditory oddball tasks. *Clin Neurophysiol, 117*(2), 348-368. doi: 10.1016/j.clinph.2005.08.034

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res Rev, 53*(1), 63-88. doi: 10.1016/j.brainresrev.2006.06.003

Luu, P., Tucker, D. M., & Makeig, S. (2004). Frontal midline theta and the error-related negativity: neurophysiological mechanisms of action regulation. *Clin Neurophysiol, 115*(8), 1821-1835. doi: 10.1016/j.clinph.2004.03.031

Mansfield, E. L., Karayanidis, F., & Cohen, M. X. (2012). Switch-related and general preparation processes in task-switching: evidence from multivariate pattern classification of EEG data. *J Neurosci, 32*(50), 18253-18258. doi: 10.1523/JNEUROSCI.0737-12.2012

Mansfield, E. L., Karayanidis, F., Jamadar, S., Heathcote, A., & Forstmann, B. U. (2011). Adjustments of response threshold during task switching: a model-based functional magnetic resonance imaging study. *J Neurosci, 31*(41), 14688-14692. doi: 10.1523/JNEUROSCI.2390-11.2011

Maris, E., Womelsdorf, T., Desimone, R., & Fries, P. (2013). Rhythmic neuronal synchronization in visual cortex entails spatial phase relation diversity that is modulated by stimulation and attention. *Neuroimage, 74*, 99-116. doi: 10.1016/j.neuroimage.2013.02.007

Miyake, A., Friedman, N. P., Emerson, M. J., Witzki, A. H., Howerter, A., & Wager, T. D. (2000). The unity and diversity of executive functions and their contributions to complex "Frontal Lobe" tasks: a latent variable analysis. *Cogn Psychol, 41*(1), 49-100. doi: 10.1006/cogp.1999.0734

Moore, R. A., Gale, A., Morris, P. H., & Forrester, D. (2006). Theta phase locking across the neocortex reflects cortico-hippocampal recursive communication during goal conflict resolution. *Int J Psychophysiol, 60*(3), 260-273. doi: 10.1016/j.ijpsycho.2005.06.003

Moore, R. A., Mills, M., Marshman, P., & Corr, P. J. (2012). Behavioural Inhibition System (BIS) sensitivity differentiates EEG theta responses during goal conflict in a continuous monitoring task. *Int J Psychophysiol, 85*(2), 135-144. doi: 10.1016/j.ijpsycho.2012.06.006

Nicholson, R., Karayanidis, F., Davies, A., & Michie, P. T. (2006). Components of task-set reconfiguration: differential effects of 'switch-to' and 'switch-away' cues. *Brain Res, 1121*(1), 160-176. doi: 10.1016/j.brainres.2006.08.101

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput Intell Neurosci, 2011*, 156869. doi: 10.1155/2011/156869

Palva, J. M., Palva, S., & Kaila, K. (2005). Phase synchrony among neuronal oscillations in the human cortex. *J Neurosci, 25*(15), 3962-3972. doi: 10.1523/JNEUROSCI.4250-04.2005

Papenberg, G., Hammerer, D., Muller, V., Lindenberger, U., & Li, S. C. (2013). Lower theta inter-trial phase coherence during performance monitoring is related to higher reaction time variability: A lifespan study. *Neuroimage, 83*, 912-920. doi: 10.1016/j.neuroimage.2013.07.032

Pesonen, M., Hamalainen, H., & Krause, C. M. (2007). Brain oscillatory 4-30 Hz responses during a visual n-back memory task with varying memory load. *Brain Res, 1138*, 171-177. doi: 10.1016/j.brainres.2006.12.076

Sauseng, P., Klimesch, W., Freunberger, R., Pecherstorfer, T., Hanslmayr, S., & Doppelmayr, M. (2006). Relevance of EEG alpha and theta oscillations during task switching. *Exp Brain Res, 170*(3), 295-301. doi: 10.1007/s00221-005-0211-y

Sauseng, P., Klimesch, W., Schabus, M., & Doppelmayr, M. (2005). Fronto-parietal EEG coherence in theta and upper alpha reflect central executive functions of working memory. *Int J Psychophysiol, 57*(2), 97-103. doi: 10.1016/j.ijpsycho.2005.03.018

Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., . . . Greicius, M. D. (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. *J Neurosci, 27*(9), 2349-2356. doi: 10.1523/JNEUROSCI.5587-06.2007

Serrien, D. J., Pogosyan, A. H., Cassidy, M. J., & Brown, P. (2004). Anticipatory cortico-cortical interactions: switching the task configuration between effectors. *Exp Brain Res, 154*(3), 359-367. doi: 10.1007/s00221-003-1667-2

Serrien, D. J., & Sovijarvi-Spape, M. M. (2013). Cognitive control of response inhibition and switching: hemispheric lateralization and hand preference. *Brain Cogn, 82*(3), 283-290. doi: 10.1016/j.bandc.2013.04.013

Tallet, J., Barral, J., & Hauert, C. A. (2009). Electro-cortical correlates of motor inhibition: a comparison between selective and non-selective stop tasks. *Brain Res, 1284*, 68-76. doi: 10.1016/j.brainres.2009.05.058

Trujillo, L. T., & Allen, J. J. (2007). Theta EEG dynamics of the error-related negativity. *Clin Neurophysiol, 118*(3), 645-668. doi: 10.1016/j.clinph.2006.11.009

Vincent, J. L., Kahn, I., Snyder, A. Z., Raichle, M. E., & Buckner, R. L. (2008). Evidence for a Frontoparietal Control System Revealed by Intrinsic Functional Connectivity. *J Neurophysiol, 100*(6), 3328-3342.

Womelsdorf, T., & Fries, P. (2006). Neuronal coherence during selective attentional processing and sensory-motor integration. *J Physiol Paris, 100*(4), 182-193. doi: 10.1016/j.jphysparis.2007.01.005

Wu, X., Chen, X., Li, Z., Han, S., & Zhang, D. (2007). Binding of verbal and spatial information in human working memory involves large-scale neural synchronization at theta frequency. *Neuroimage, 35*(4), 1654-1662. doi: 10.1016/j.neuroimage.2007.02.011



*Figure 1*. Schematics for a) the cued-task switching paradigm and b) EEG processing pipeline. a) Task mapping for the task switching paradigm, wherein the letter, digit and colour tasks were mapped to a major third of the wheel respectively. The current trial (trial n) was defined relative to the preceding task in trial n -1. b) EEG data was passed through a semi-automated custom-built pipeline offline, which included visual inspection stages (shown as a pair of eyes).