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Contextually sensitive power changes across multiple frequency bands underpin cognitive control

Patrick S. Cooper^{a,b}, Álvaro Darriba^c, Frini Karayanidis^{a,b}, Francisco Barceló^{c,d,*}

^a Functional Neuroimaging Laboratory, School of Psychology, University of Newcastle, Australia

^b Priority Research Centre for Translational Neuroscience and Mental Health, University of Newcastle, Australia

^c Laboratory of Neuropsychology, University of the Balearic Islands, Mallorca, Spain

^d Asociación de Neuropsicología Balear (ANEBA), Mallorca, Spain

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ABSTRACT

Flexible control of cognition bestows a remarkable adaptability to a broad range of contexts. While cognitive control is known to rely on frontoparietal neural architecture to achieve this flexibility, the neural mechanisms that allow such adaptability to context are poorly understood. In the current study, we quantified contextual demands on the cognitive control system via *a priori* estimation of information across three tasks varying in difficulty (oddball, go/nogo, and switch tasks) and compared neural responses across these different contexts. We report evidence of the involvement of multiple frequency bands during preparation and implementation of cognitive control. Specifically, a common frontoparietal delta and a central alpha process corresponded to rule implementation and motor response respectively. Interestingly, we found evidence of a frontal theta signature that was sensitive to increasing amounts of information and a posterior parietal alpha process only seen during anticipatory rule updating. Importantly, these neural signatures of context processing match proposed frontal hierarchies of control and together provide novel evidence of a complex interplay of multiple frequency bands underpinning flexible, contextually sensitive cognition.

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Introduction

Goal-directed control of thoughts and behaviors is a hallmark of flexible human cognition. This cognitive control is typically employed to facilitate information propagation between goal/task-relevant regions of the cortex, operating over various temporal periods. For instance, Braver (2012) distinguishes between anticipatory, sustained *proactive control* processes that serve to prepare the system for an upcoming need for goal-appropriate control of behavior and stimulus-driven, *reactive control* processes that are transiently recruited on a needs basis. Information processing associated with cognitive control is known to rely on a complex, multifaceted, frontoparietal architecture linking key hubs in medial and lateral prefrontal cortex with posterior parietal and subcortical regions (Cole and Schneider, 2007; Corbetta and Shulman, 2002; Dosenbach et al., 2008).

Despite extensive evidence for the existence of this cognitive control network, the neural mechanisms that operate to achieve flexible control remain incompletely understood. In part, this is due to the fact that the functional imaging techniques (e.g., functional magnetic resonance imaging; fMRI) that have been employed to characterize the structure

E-mail address: f.barcelo@uib.es (F. Barceló).

of these frontoparietal control networks have limited temporal resolution, sampling neural processes in timescales that far exceed the subsecond time scale of many cognitive control processes. By contrast, electroencephalography (EEG) has excellent temporal resolution, making it an important tool to study the functional properties and fast temporal dynamics of cognitive and neural processes.

Event-related potentials (ERPs) are extracted from the EEG by averaging across multiple repetitions of the same trial type. A number of frontal ERP negative components have been associated with control processes. These frontal negativities are typically elicited on trials that require the implementation of reactive control, for instance, after response feedback of an incorrect response or during conflict detection (Bartholow et al., 2005; Folstein and Van Petten, 2008; Olvet and Hajcak, 2008), and are probably generated in the anterior/medial cingulate cortex (Cohen et al., 2008; Wang et al., 2005). Further, these reactive control ERP components are associated with specific frequency spectra of the EEG. In particular, low frequency theta (4–7 Hz) oscillations are typically increased in the time range of these frontal negativities (see Cavanagh and Frank, 2014), suggesting that these ERP components are part of an underlying low frequency response generated during reactive control (Luu et al., 2004; Trujillo and Allen, 2007). The ubiquitous parietal positive ERP component, the P300, is reliably elicited when the trial requires context updating (for review see Polich, 2007) and is commonly associated with delta (0.5-4 Hz) power responses







^{*} Corresponding author at: Laboratory of Neuropsychology, University of the Balearic Islands, Ctra. Valldemossa, km 7.5, E-07122 Palma de Mallorca, Spain.

during response inhibition and novelty processing (Başar-Eroglu et al., 1992; Harper et al., 2014; Knyazev et al., 2008; Prada et al., 2014; Qassim et al., 2013). These reactive control indices are invoked in standard conflict paradigms (i.e., go/no go, stop-signal, flanker tasks), which all rely on conflict resolution processes.

While ERP components and EEG frequency responses associated with reactive cognitive control are fairly well established, the corresponding mechanisms for proactive control are less well understood. The situational demands that characterize the need for proactive control are more varied, and the little work that has explored neural mechanisms of proactive processes has produced a less consistent set of results.

One paradigm that is particularly suited for examining proactive control processes is the task-cueing paradigm, where participants can utilize cue information to prepare for the required task on the upcoming target. ERPs elicited in the cue-target interval typically show a switchrelated positivity; a larger parietal positivity for cues that indicate that the target will require a switch in task rather than a repeat of the same task completed on the previous trial (e.g., Barceló et al., 2006; Jost et al., 2008; Karayanidis et al., 2003; Karayanidis et al., 2009; Nicholson et al., 2005; Periáñez and Barceló, 2009; for reviews, see Karayanidis and Jamadar, 2014; Karayanidis et al., 2010). However, the frequency signature of this anticipatory switch-positivity is not well defined. Studies have reported multiple spectral indices of proactive control during task switching, including bilateral parietal increases in alpha (8-14 Hz; Foxe et al., 2014; Mansfield et al., 2012); increased theta in frontal (Cunillera et al., 2012), centroparietal (Cooper et al., 2015a, see Supplementary Materials; Sauseng et al., 2006), and occipital (Gladwin and de Jong, 2005) sites and centroparietal increases in delta (Prada et al., 2014).

While some of these discrepancies between task-switching studies may be attributed to differences in the time-frequency extraction procedures used (e.g., frequency resolution of wavelets in Fourier transforms, "pure" vs. task-referenced baselines or reference montages used), such methodological differences do not typically impact on the pattern of effects reported in other paradigms that utilize *reactive* control processes. For instance, oddball, go/nogo, and stop-signal tasks are all associated with delta and theta frequency responses (Harper et al., 2014; Lavallee et al., 2014). Given that such paradigms all rely on common motor/inhibition processes, it is likely that common cognitive processes are associated with distinct neural signatures in the frequency domain. Therefore, the question remains: what are the specific frequency signatures of well-established anticipatory ERP components in the proactive control of task switching?

This guestion has remained elusive because anticipatory processes in task switching are contextually sensitive, which results in specific neural signatures emerging depending on the particular attributes of the paradigm used. According to Braver (2012), the particular combination of "situational factors" that are active at any given moment bias toward the implementation of proactive or reactive control. For instance, if sufficient information is provided prior to target onset regarding the demands of the upcoming goal, the control system can utilize proactive processes in an anticipatory manner and facilitate performance. These factors have been seen to affect both task-switching performance and ERPs. For instance, during task switching, the longer the cue-target interval, the greater the opportunity to prepare to switch task and the lower the switch cost (i.e., switch-repeat performance; e.g., Lavric et al., 2008; Nessler et al., 2012; Nicholson et al., 2006). However, other factors can also affect opportunity for or choice to activate control proactively; for instance, increasing the probability of switch trials also influences behavioral performance and switch-related ERPs (e.g., Monsell and Mizon, 2006). Thus, subtle differences in the context within which the paradigm is situated can substantially affect the cognitive control processes that are invoked and, as indicated in the above examples, can result in differences in neural responses and behavioral performance. Importantly, paradigms that rely purely on reactive control are probably less susceptible to these contextual influences and hence elicit more consistent neural responses than those that require proactive control.

To date, the oscillatory patterns of activity associated with such contextual influences on cognitive control in humans remain to be determined. One way to quantify contextual influences on cognitive control is by using information theory, wherein task properties including stimulus-level interference, episodic demands, and stimulus probabilities can be assigned binary digit values or bits (cf. Attneave, 1959; Koechlin and Summerfield, 2007). In its purest form, information can be measured simply by counting the number of bits in a signal. For example, in the two arrays (i) 101111 and (ii) 100010, array i has 5 bits of information whereas array ii has only 2 (i.e., counting the number of ones present in each array). These information estimates translate into the mean and joint probabilities of task events often reported in experimental paradigms. Reducing stimulus properties into bits of information has provided nuanced approaches that can account for contextual demands in tasks with remarkable success (Barceló and Knight, 2007; Koechlin and Summerfield, 2007). These approaches have been successfully applied to cognitive control paradigms (e.g., Fan et al., 2008; Mackie et al., 2013), including task switching (Barceló et al., 2008; Cooper et al., 2015b; Kopp and Lange, 2013), to highlight the fact that the greater the level of information the greater the need for cognitive control.

Likewise, Koechlin and Summerfield (2007) propose that increasingly anterior portions of the prefrontal cortex are engaged in processing information associated with more complex information, providing a framework in which to link cognitive control architecture to contextual influences on the control system. That is, according to Koechlin and Summerfield, distinct regions of the prefrontal cortex are involved in subroutines of cognitive control processes. Specifically, posterior regions of the prefrontal cortex are associated with implementing goal and behaviorally relevant responses based on stimulus-response mappings (i.e., sensorimotor control). More anterior portions of the prefrontal cortex are involved in adjustments and implementations of stimulus-response mappings due to (a) immediate situational demands (i.e., contextual control) and (b) updating due to past events or temporal contingencies (i.e., episodic control). Thus, quantifying the amount of information present during tasks can provide a common language to successfully communicate contextual demands across tasks and experiments.

Given that context is a general term applied to numerous cognitive processes, here we operationalize context as summated information across multiple levels of the cognitive control hierarchy (i.e., sensorimotor, contextual, and episodic control; Koechlin and Summerfield, 2007). By doing so, we consider context as the particular stimulus-response mappings that can vary both between conditions and across time. In the current study, we aimed to identify contextually sensitive oscillatory indices at various levels of the cognitive control hierarchy. To do so, we manipulated the context in which stimuli were presented via a priori estimates of information over three cognitive control tasks and compared EEG power during these contexts. We did this by defining three common cognitive control tasks, oddball, go/nogo, and task switching, with an identical set of stimuli. Thus, while the sensory input remained identical for all three tasks, the contextual information provided by the stimuli varied as a function of the specific task demands and the corresponding sensorimotor information transmitted between stimuli and associated responses (see Materials and Methods). Therefore, any differences in electrophysiological and behavioral measures can only be attributed to different cognitive control processes activated under the different contexts.

Based on the notion that distinct regions of the prefrontal cortex respond preferentially to particular contextually sensitive information (Koechlin and Summerfield, 2007), we expected oscillatory activity to differ within a frontal hub of electrodes with changing task and temporal contexts. Given previous evidence that EEG delta and theta power Download English Version:

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