

Contextually sensitive power changes across multiple frequency bands underpin cognitive control



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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

of these frontoparietal control networks have limited temporal resolution, sampling neural processes in timescales that far exceed the sub-second 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

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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 switch-related 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; Periañez 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; Lavalée 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 question 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

increases during conflict or uncertain trials in oddball, go/nogo, and task-switching paradigms when studied independently, we predicted that “target” stimuli that carry similar amounts of sensorimotor information would be associated with a similar pattern of increased power in these frequency bands, regardless of their task context. That is, targets conveying similar sensorimotor information for response selection in oddball, go, and switch tasks would be associated with common neural frequency responses, regardless of their precise task context. By contrast, stimuli whose sensorimotor information content varied as a function of their temporal context (whether they are targets, distracters, or cueing events) would have distinct oscillatory power signatures. That is, identical stimuli holding different temporal contingencies with contextually related goal-directed actions would have corresponding differences in EEG power. We computed transmitted sensorimotor information between stimuli and responses (i.e., the inter-dependence of a stimulus–response pair or “input–output correlations”; Miller, 1956) as a metric to estimate even subtle differences in cognitive demands under changing task and temporal contexts. For instance, grey Gabor patches differed in processing requirements as a function of their task context and thus were susceptible to such contextually sensitive changes in power. In particular, grey Gabor patches could serve as an irrelevant non-target distractor (*oddball*), a nogo, withhold signal (*go/nogo*) relying on reactive cognitive control or as an anticipatory cue (*switch*) utilizing proactive control processes. Given the extensive literature on low frequency oscillations in cognitive control, we expected these context-sensitive power changes to occur in the delta and theta ranges (i.e., Arnal and Giraud, 2012; Harper et al., 2014; Prada et al., 2014).

Materials and methods

Participants

Thirty-one participants (25 female, 21.8 ± 2.7 years) took part in the current study and received course credit for their participation. All participants were graduate or postgraduate students at the University of the Balearic Islands with normal or corrected-to-normal vision and reported no history of neurological or psychiatric disorders. Informed consent was obtained from all participants and experimental procedures and behavioral testing was undertaken in accordance with the Declaration of Helsinki and with the approval by the ethics committee of the university.

Stimuli and procedures

Participants were seated in a dimly lit, sound attenuated, and electrically shielded room at a viewing distance of 150 cm from a 27-in. video LCD monitor (800×600 at 75 Hz). Stimuli were presented against a grey background (2.85 cd/m^2) at a visual angle of 6.5° to the left or right of a central fixation cross with $0.5^\circ \times 0.5^\circ$ of visual angle.¹ The central fixation cross remained continuously present throughout the experiment. Stimuli consisted of four equally probable ($p = 0.21$) colored Gabor patches (red or blue) with 4 or 10 cpd horizontal gratings (25% contrast, 1° visual angle, 3.5 cd/m^2) and two infrequent ($p = 0.08$) grey Gabor patches (oriented vertically or horizontally, 2 cpd, 25% contrast, 1° visual angle, 3.5 cd/m^2). Participants responded via a hand-held response pad with their left or right index finger.

A test sequence including 976 trials of colored and grey Gabor patches was semi-randomly generated offline, with the constraint that consecutive grey Gabor patches were separated by four to eight colored patches. This test sequence was divided into eight blocks to allow for

brief self-paced breaks approximately every five minutes. Each trial consisted of a Gabor patch presented for 100 ms in the left or the right visual hemifield. On designated target trials, participants had to respond within a maximum of 1200 ms after stimulus onset. Participants were instructed to fixate their gaze on the central cross and avoid shifting their eye gaze to the lateralized Gabor patches. Instructions emphasized both response speed and accuracy. All error trials (i.e., incorrect, late responses, and false alarms, i.e., button presses to non-target grey gratings) were followed by visual feedback (“incorrect” or “too late” displayed in Spanish), and the following trial was delayed by 500 ms to help subjects keep track of the correct rule. As a consequence, stimulus onset asynchrony (SOA) was 1900 and 2400 ms on correct and error trials, respectively. Analyses were based on trials that formed a correct sequence (i.e., grey Gabor and subsequent three color Gabor targets were all correct). The stimulus display and behavioral response recording were carried out using Presentation® software (Neurobehavioral Systems Inc., Albany, CA).

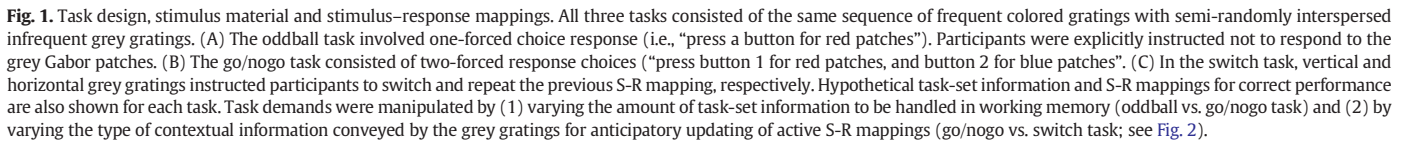
Each participant was presented with a pseudorandomly generated test sequence that was repeated three times with three different task instructions, which defined the oddball, go/nogo, and switch tasks. Thus, the three tasks were yoked for stimuli and trial runs but involved different cognitive and response demands (Fig. 1). These tasks were administered in counterbalanced order between participants to control for inadvertent order effects.

The *oddball task* (Fig. 1A) served as a “control” for both switch and go/nogo tasks, having an identical stimulus context and equivalent perceptual demands, but with different response demands. Specifically, a response was required only to red Gabor stimuli, which were defined as oddball targets. All other stimuli did not require a response. The *go/nogo task* (Fig. 1B) served as a “control” condition for the switch task. It involved an identical stimulus sequence and again participants responded only to the colored Gabors. However, importantly, here the grey Gabors had no predictive significance regarding the task to be performed. Rather, they were defined as nogo stimuli and participants were asked to withhold their response. Participants completed color classification across the entire sequence. In essence, this task is very similar to a single-task block, except that the intermittent “cues” are not mapped to any task. The task involved responding to the same targets, an identical stimulus sequence, and similar response demands as the switching task. These S–R mappings were the same as the color condition in the switch task. The *switch task* (Fig. 1C) was a variant of the intermittent-instruction paradigm (Monsell, 2003; Rushworth et al., 2002). The grey Gabor stimuli were the cues, indicating whether to switch or repeat task. The colored Gabor stimuli were the targets and required a left or right hand response based on either the color (blue or red grating) or the grating spatial frequency (thick or thin grating). Hence, in this task, the direction of the grating in the grey Gabor (cue) instructed participants whether to switch task or repeat the task they had been completing on the previous set of trials. The relation between grey grating orientation and instruction was counterbalanced between participants. Before the switch task, a short block of 74 test trials was administered to ensure that participants understood task instructions. Together, all stimuli, in all contexts, relied on reactive control processes. However, in the switch task, the grey Gabor afforded the opportunity for task preparation and thus specifically relied on proactive cognitive control.

Electrophysiological recordings

Continuous EEG data (0.05–100 Hz band-pass) were collected using SynAmps RT amplifiers (NeuroScan, TX, USA) from 60 scalp sites using tin electrodes mounted on an elastic cap (Synamp2 Quikcap, Compumedics, TX) at a sampling rate of 500 Hz. EEG electrodes were placed following the extended 10–20 position system (Fp1, Fp2, AF7, AF3, AFz, AF4, AF8, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCz, FC2, FC4, FC6, FT8, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3,

¹ Stimuli were presented to the left or right of the fixation cross in order to assess hemispatial attentional deficits in unilateral lesion patients (cf., Barceló and Knight, 2007). Pilot data suggested this peripheral display did not significantly modulate electrophysiological indices of task switching when compared to a traditional, central display.



² In order to confirm that differences in the number of trials contributing to different trial types did not inadvertently affect our findings, we examined whether observed power was correlated with trial counts. No significant effects were found, indicating that differences between conditions are not due to differences in trial number.

grey, target 1, and target 3 Gabor for each of the three tasks (*oddball*, *go/nogo*, and *switch*) by averaging all decomposed single-trial time-frequency representations for each Gabor patch. Single-trial time-frequency representations were obtained via complex Morlet wavelet convolution for 80 logarithmically spaced frequencies ranging from 2 to 30 Hz with logarithmically spaced tapers ranging from 3 to 14 cycles. Resulting power values were normalized with a decibel (dB) transformation ($10 \log_{10}(\text{power}/\text{baseline})$), where the baseline was defined as the average power over a 500 to 100 ms interval pre-stimulus onset.

Information theory estimations

We used an information theoretical approach to quantify contextual information, whereby *a priori* estimations of the mutual information among sensory events, motor responses, and intermediate sensorimotor operations were used to guide interpretation of EEG power results (cf. Barceló et al., 2008). For example, across all tasks, the same stimuli were used and thus stimulus-specific information is constant across contexts. By contrast, the oddball task set only contained a single stimulus–response mapping (i.e., button press to red targets) and thus had lower sensorimotor information than *go/switch* tasks that required two stimulus–response mappings based on the color of the target Gabor. In doing so, we followed the original recommendations by Miller (1956) for estimating the amount of information transmitted between contextually related stimuli and responses (or *input–output correlations*) along a putative hierarchy of sensorimotor control processes (Miller and Cohen, 2001). While stimuli were identical, context was quantified in terms of overall stimulus and response information entropies and information transmitted between contextually related visual targets, non-targets, and motor responses along a hypothesized hierarchy of sensorimotor control processes (Koechlin and Summerfield, 2007). For instance, while grey Gabors were visually identical in all tasks and appeared with identical presentation probability, the type of information provided varied. Oddball grey Gabors transmitted the lowest sensorimotor information for response selection, and no episodic information given that the same task rule was used for all oddball targets and non-target distractors. Alternatively, increased sensorimotor information was conveyed by *nogo* grey Gabors as these stimuli were associated with less frequent *nogo* responses (r_0) compared to the oddball task. Again, no episodic information can be assumed for *nogo* grey Gabors given that the same task rule was consistently used across all trials. Finally, similar sensorimotor information was transmitted by all grey Gabors in the *switch* task, plus an additional amount of episodic information was transmitted only by “switch” grey Gabors, as these served as anticipatory cues requiring access to episodic task

rules. Note that these information estimates can be seen as a more formal and accurate way to translate into bits the mean and joint probabilities of task events, as is common practice in most experimental psychology studies. For instance, instead of saying that a grey Gabor distractor occurs with an overall mean probability of $p = 0.08$ throughout our oddball task, we chose to quantify this in bits by saying that the sensory entropy of this distractor is $H(s_1) = -0.08 \cdot \log_2 0.08 = 0.29$ bits. A similar formalism was used to quantify in bits the relative probabilities of specific s_i – r_j mappings using the concept of transmitted information: $I(s_i, r_j) = \log_2 p(s_i, r_j) - \log_2 p(s_i) - \log_2 p(r_j)$. Fig. 2 presents a summary of these information-theoretic estimations; for a technical description see the Supplementary materials.

Data analyses

EEG power and behavioral analyses were performed on targets 1 and 3 for each task (*oddball*, *go/nogo*, and *switch*) and grey Gabor patches, which served as distractors, *nogo*, or repeat/switch cues for *oddball*, *go/nogo*, and *switch* tasks respectively. Note, for *go/nogo* and *switch* tasks, red and blue Gabor patches were always targets. For the oddball task, blue Gabor patches were non-target distractors that did not require a response and so their separation in power analyses was deliberate to distinguish between colored Gabor patches that were associated with a motor response and those that were not. RT and accuracy behavioral data were analyzed for targets that generated a response (i.e., target 1 and target 3 for all except non-target distractors in the oddball task). Behavioral analyses were undertaken via a 4 (TARGET TYPE; *oddball*, *go*, repeat, *switch*) \times 2 (POSITION; target 1, target 3) repeated-measures ANOVA in SPSS 23 (IBM). Bonferroni correction was applied to planned comparisons between target types (i.e., oddball vs. *go*, repeat and *switch*; *go* vs. repeat and *switch* and repeat vs. *switch*) to control for Type I errors (.05/6 = .008).

For EEG power analyses, we report condition-averaged time-frequency results for grey Gabors, target 1, and target 3 separately at a representative midfrontal electrode cluster (i.e., FC1, FCz, and FC2). This cluster was chosen based on previous work, suggesting delta and theta responses have a frontal topology in cognitive control paradigms (see Cavanagh and Frank, 2014; Cohen, 2014) and this cluster's key position along the predicted contextually sensitive frontal hierarchy (Koechlin and Summerfield, 2007). Although the model in Fig. 2 does not predict target trial effects, the position factor examined a prediction substantiated in the task-switching literature and on preliminary ERP evidence that proactive interference from the highly informative “switch” grey Gabors will be maximal on target trial 1 and minimal on

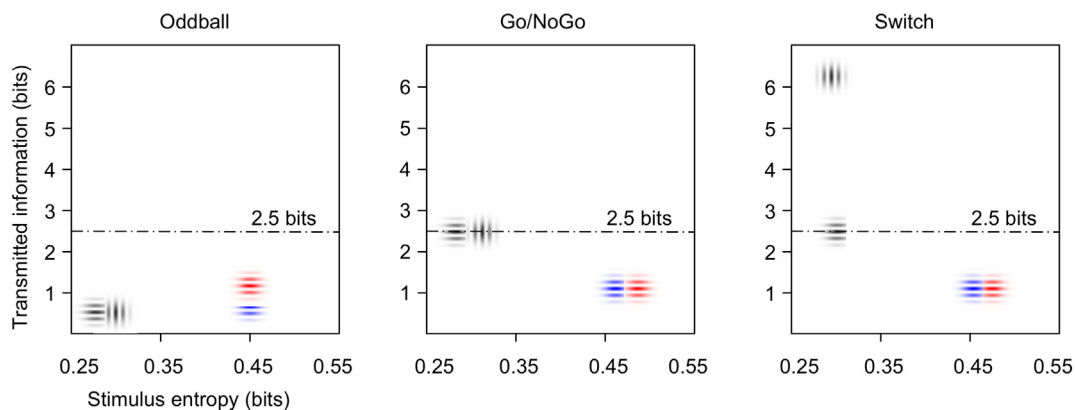


Fig. 2. *A priori* estimations of transmitted information, $I(s_i, r_j)$, between stimuli and responses as a function of the sensory entropy, $H(s_i) = -p(s_i) \cdot \log_2 p(s_i)$, of grey and colored gratings in the three tasks (or *input–output correlations*, after Miller, 1956). The dotted line marks the theoretical human capacity for holding information in working memory: 2.5 bits. According to the model's predictions, targets conveyed the same information for response selection across all tasks. In turn, grey gratings carried varying amounts of information for response selection in the oddball, *go/nogo*, and *switch* tasks. The information transmitted from stimuli to responses is derived from the notion of mutual information, $I(S; R)$, between the sets of stimuli, $S = \{s_1, s_2, s_3, s_5, s_6\}$, and associated responses, $R = \{r_0, r_1, r_2\}$, in our three tasks (cf., Attneave, 1959; Koechlin and Summerfield, 2007; see details in the Supplementary materials).

target trial 3, with target 2 reflecting a mixed intermediate stage (e.g., Barceló et al., 2014). To identify significant and common changes in power from baseline, we performed one-sample *t*-tests at each frequency \times time point for the midfrontal cluster, with multiple comparison correction applied (false discovery rate, FDR $p < .001$; Benjamini and Yekutieli, 2001). Based on this analysis, we were able to identify common power processes associated with the context of interest (i.e., grey Gabor, target 1, or target 3). Next, we used these significant frequency \times time clusters as masks and extracted average power for each of the four frequencies of interest (i.e., delta, theta, alpha, and beta) for each condition (oddball, go/nogo, repeat, and switch) separately across the scalp. Preliminary analyses suggested central and posterior power changes were also observed, alongside our hypothesized frontal power effects and so to characterize the data more completely, we extracted frequency power at frontal (F1, Fz, F2), frontocentral (FC1, FCz, FC2), central (C3, Cz, C4), parietal (P1, Pz, P2), and parietoccipital (PO3, POz, PO4) clusters. Finally, we performed separate 4 (TARGET TYPE; oddball, go/nogo, repeat, switch) \times 5 (SITE; frontal, frontocentral, central, parietal, parietoccipital) \times 4 (FREQUENCY; delta \in 2–4 Hz, theta \in 4–7 Hz, alpha \in 8–13 Hz, beta \in 14–30 Hz) repeated-measures ANOVAs for the grey, target 1, and target 3 contexts. To visualize the spatial dimension of time-frequency components, and the results of the ANOVAs, we provide representative topographical plots.

Results

Behavioral results

Greenhouse–Geisser correction was applied where necessary to control for violations of sphericity (Vasey and Thayer, 1987) but non-corrected degrees of freedom are reported for readability. For RT, the assumption of sphericity was not met for the main effect of TASK ($\chi^2(5) = 32, p < .001$). Significant main effects for TARGET TYPE ($F(3,90) = 174, p < .001$; partial $\eta^2 = .85$), POSITION ($F(1,30) = 37.1, p < .001$; partial $\eta^2 = .55$) and the TARGET TYPE \times POSITION interaction ($F(3,90) = 11.9, p < .001$; partial $\eta^2 = .28$) were found. RT was significantly faster for oddball targets than go ($t(30) = 11.7, p < .0001$), repeat ($t(30) = 15.7, p < .0001$), and switch ($t(30) = 14.7, p < .0001$) targets. Likewise, responses were faster for go targets than either repeat ($t(30) = 11.1, p < .0001$) or switch targets ($t(30) = 9.2, p < .0001$). However, a typical switch cost was not found; overall switch targets were performed *faster* than repeat targets ($t(30) = 4.8, p < .0001$). RT reduced with target position (i.e., 1 to 3) for go/nogo and switch tasks, but not for the oddball task.

For accuracy, the assumption of sphericity was not met for the main effect of TARGET TYPE ($\chi^2(5) = 16, p = .007$) and the TARGET TYPE \times POSITION interaction ($\chi^2(5) = 43.1, p < .001$). The main effects for TARGET TYPE ($F(3,90) = 55.1, p < .001$; partial $\eta^2 = .65$) and POSITION ($F(2,60) = 6.6, p = .016$; partial $\eta^2 = .18$) were significant, but not their interaction. Response accuracy increased with target position. As with RT, responses were more accurate for oddball targets than go ($t(30) = 8.2, p < .0001$), repeat ($t(30) = 7.7, p < .0001$), and switch ($t(30) = 12.2, p < .0001$) targets and for go targets than either repeat ($t(30) = 3.9, p = .001$) or switch ($t(30) = 5.7, p < .0001$) targets. There was no significant difference between repeat and switch targets (see Table 1).

In sum, behavioral performance is partly consistent with the predictions of the information theory estimates of each trial (see Fig. 2). While all target stimuli had identical stimulus entropy (see Supplementary Materials), oddball targets that were associated with lower response entropy had faster and more accurate responses than go and repeat/switch targets (see Supplementary Materials). Likewise, first position targets in the switch task which were preceded by grey gratings that required larger sensorimotor control and access to episodic information than in the other tasks had slower RT and poorer accuracy compared

Table 1

Mean RT (ms) and error rate for each trial type and target position.

	RT (ms) \pm SE			Accuracy (% error rate) \pm SE		
	Target 1	Target 3	Mean	Target 1	Target 3	Mean
Oddball	344 \pm 7.8	343 \pm 8.4	344 \pm 8.1	0.9 \pm 0.2	0.9 \pm 0.2	0.9 \pm 0.2
Go	448 \pm 12.4	410 \pm 9.3	429 \pm 10.7	6.1 \pm 0.7	4.9 \pm 0.6	5.5 \pm 0.6
Repeat	541 \pm 14.4	503 \pm 13.1	522 \pm 13.3	9.0 \pm 1.2	6.9 \pm 0.8	8.0 \pm 1.0
Switch	510 \pm 14.5	489 \pm 13.6	499 \pm 13.4	9.5 \pm 1.0	8.4 \pm 0.9	9.0 \pm 0.7

with go and oddball targets in the same position. These results appear to reflect global differences in task-set information (i.e., the sum of switch sensorimotor s_i-r_j information vs. sum of all go/oddball s_i-r_j pathways), as well as specific trial-by-trial differences in information and corresponding behavior, since the comparatively more informative grey gratings in go/nogo and switch tasks overshoot memory capacity and thus can explain residual restart costs (i.e., slower performance on first target after a switch cue) to first targets in these two tasks relative to the oddball tasks.

Power results

Grey Gabor

Fig. 3 depicts the average time-frequency responses associated with all grey Gabor at the frontocentral representative cluster, i.e., the condition-average power across electrodes (FC1, FCz, and FC2). Dark outlines indicate significant changes in power. Grey Gabors were associated with a broad increase in delta/theta power for the duration of the stimulus, peaking around 400 ms after stimulus onset. Additionally, transient decreases in alpha and beta power were also observed. As shown in the accompanying bar plot (Fig. 3B), increasing information associated with the grey Gabor was associated with increased power responses in all frequency bands.

To explore these power changes further, significant time \times frequency clusters (i.e., outlined areas seen in Fig. 3A) were extracted from each grey Gabor type (i.e., oddball, nogo, repeat, and switch cues) across multiple clusters along the head. These data were then subjected to a 4 (TARGET TYPE; oddball, nogo, repeat, and switch) \times 5 (SITE; frontal, frontocentral, central, parietal, parietoccipital) \times 4 (FREQUENCY; delta, theta, alpha, and beta) repeated-measures ANOVA, with Greenhouse–Geisser correction applied for violations of sphericity. Significant main effects were found for TARGET TYPE ($F(3,90) = 6.5, p = .003$; partial $\eta^2 = .17$); SITE ($F(4,120) = 22.9, p < .001$; partial $\eta^2 = .43$) and FREQUENCY ($F(3,90) = 157.2, p < .001$; partial $\eta^2 = .84$). Simple effects showed a significant linear trend across TARGET TYPE ($F(1,30) = 9.3, p = .005$, partial $\eta^2 = .24$), with oddball having the highest power, followed by nogo, repeat, and switch cues. By contrast, both SITE and FREQUENCY had significant quadratic trends (SITE: $F(1,30) = 31.5, p < .001$, partial $\eta^2 = .51$; FREQUENCY: $F(1,30) = 14.5, p = .001$, partial $\eta^2 = .33$), with frontal sites associated with strong increases in power and posterior sites with strong decreases and lower frequency bands (i.e., delta and theta) having increases in power and higher bands (alpha and beta) decreases. Next significant two-way interactions were found for TARGET TYPE \times SITE, $F(12,360) = 5.5, p < .001$; partial $\eta^2 = .16$; TARGET TYPE \times FREQUENCY, $F(9,270) = 30.1, p < .001$; partial $\eta^2 = .5$ and SITE \times FREQUENCY, $F(12,360) = 8.9, p < .001$; partial $\eta^2 = .23$). Finally, a significant three-way TARGET TYPE \times SITE \times FREQUENCY interaction was also present ($F(36,1080) = 4.8, p < .001$; partial $\eta^2 = .14$) reflecting the TARGET TYPE \times FREQUENCY differences in magnitude were most prominent at particular topographical locations.

To assist in detailing the above interactions, Fig. 4 depicts each Gabor's topography associated with the four frequency bands. Visual inspection highlights the relative increase in lower frequency delta and theta band power for repeat and switch Gabors compared to oddball and nogo Gabors in line with the above TARGET TYPE \times FREQUENCY and TARGET TYPE \times SITE \times FREQUENCY interactions. Indeed, contrasts

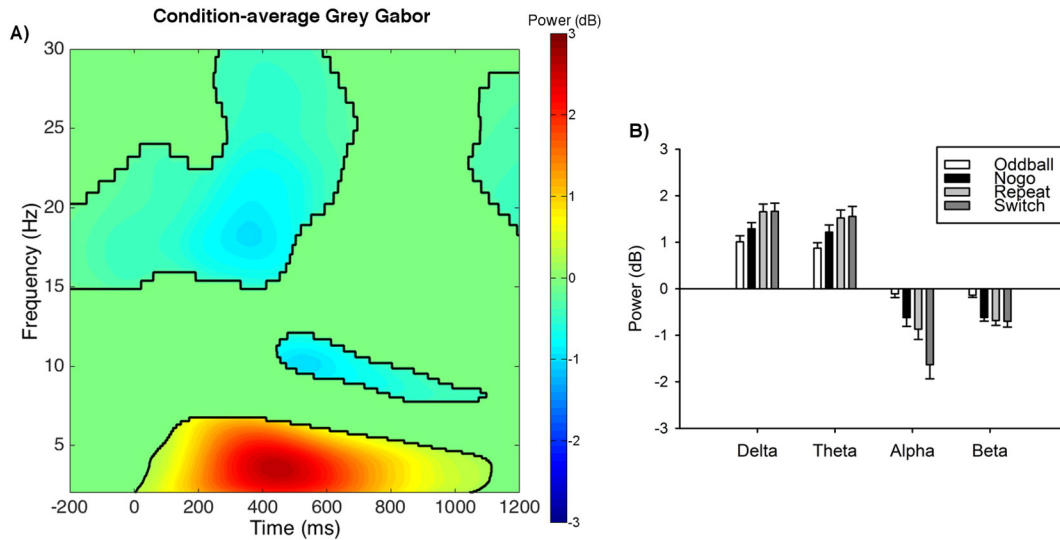


Fig. 3. Condition-average time-frequency plots for grey Gabors at the frontocentral cluster (i.e., FC1, FCz, FC2). (A) As seen in the time-frequency plot, grey Gabors were typically associated with an increase in lower frequency delta/theta power and decreases in alpha and beta power. Dark outlines indicate significant time × frequency clusters, corrected for multiple comparisons (false discovery rate; FDR $p < .001$). (B) Bar plots depicting average of frequency band clusters (shown in Fig. 3A) for each condition's grey Gabor. Delta, theta, and alpha show information-specific modulations of power levels, with highest information transmitted by repeat and switch grey Gabors leading to larger power responses.

revealed that these differences were significant, with **increased repeat/switch Gabor delta power at the frontal clusters** compared to oddball (frontocentral: repeat, $t(30) = 3.7, p = .001$; switch, $t(30) = 3.4, p = .002$) and nogo (frontal: repeat, $t(30) = 2.5, p = .019$; switch, $t(30) = 2.4, p = .024$; frontocentral: repeat, $t(30) = 2.5, p = .019$; switch, $t(30) = 2.4, p = .024$) Gabors. Likewise, theta for repeat and switch Gabors was strongest at frontal (repeat vs. oddball, $t(30) = 3.2, p = .003$; repeat vs. nogo, $t(30) = 2.1, p = .04$; switch vs. oddball, $t(30) = 3.2, p = .003$; switch vs. nogo, $t(30) = 2.7, p = .031$) and frontocentral sites (repeat vs. oddball, $t(30) = 4.3, p < .001$; repeat vs. nogo, $t(30) = 2.3, p = .03$; switch vs. oddball, $t(30) = 3.2, p = .003$). In addition, a **broad posterior decrease in alpha** was observed, strongest for the repeat/switch Gabor, present for both the parietal (repeat vs. oddball, $t(30) = 3.5, p = .001$; switch vs. oddball, $t(30) = 6.7, p < .001$; switch vs. nogo, $t(30) = 5.9, p < .001$) and parietoccipital (repeat vs. oddball, $t(30) = 3.8, p = .001$; repeat vs. nogo, $t(30) =$

$2.9, p = .007$; switch vs. oddball, $t(30) = 6.7, p < .001$; switch vs. nogo, $t(30) = 6.5, p < .001$) clusters. Additionally, repeat and switch cues significantly differed in posterior alpha power (parietal cluster; repeat vs. switch, $t(30) = 4.1, p < .001$; parietoccipital cluster; repeat vs. switch, $t(30) = 4.4, p < .001$), but not in any further frequencies. Finally, a weaker, less consistent, parietal decrease in beta was observed alongside the alpha process (parietal; nogo vs. oddball, $t(30) = 5.8, p < .001$; repeat vs. oddball, $t(30) = 4.4, p < .001$; switch vs. oddball, $t(30) = 6.7, p < .001$; switch vs. nogo, $t(30) = 4.6, p < .001$; parietoccipital; nogo vs. oddball, $t(30) = 4.1, p < .001$; repeat vs. oddball, $t(30) = 2.8, p = .009$; switch vs. oddball, $t(30) = 3.1, p = .004$). Thus together, the unexpected reduced power for repeat and switch cues seen in the main effect of TARGET TYPE above was ultimately a consequence of stronger power at frontal sites and larger decreases in power at posterior sites for Gabors with greater information. That is, while frontal delta and theta was strongest for repeat and switch cues, a large posterior decrease for alpha and beta was also present at the same time leading to an overall lower power value for these cues. Further, this posterior process was significantly different between cues indicating an upcoming need to repeat or switch tasks.

In sum, while grey Gabors are identical stimuli that occur with equal likelihood in each task, their conveyed meaning differs between contexts (and thus are associated with changes in information values). These corresponding changes in information were tied to changes in power responses, particularly with frontal delta/theta and posterior alpha/beta. That is, repeat and switch grey Gabors, which serve as proactive cues, have higher sensorimotor and episodic information values than the corresponding Gabor in the oddball/nogo contexts and in turn had power changes in line with these information values.

Target 1

Fig. 5 depicts the average time-frequency responses associated with all target 1 Gabors at the frontocentral representative cluster. As with grey Gabors, a strong, common increase in delta and theta was seen for all target 1 stimuli, peaking around 400 ms after target onset. In addition, a decrease in alpha power is seen across all targets alongside transient increases and decreases in beta. To ensure we accounted for these transient beta changes, we again ran a repeated-measures ANOVA but with the inclusion of a beta positive (beta+) and a beta negative (beta-) cluster: i.e., a 4 (TARGET TYPE; oddball, nogo, repeat and switch) × 5 (SITE; frontal, frontocentral, central,

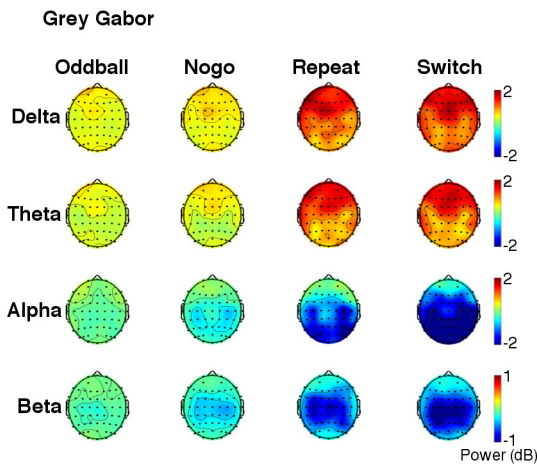


Fig. 4. Topology plots depicting the spatial dimension of each frequency cluster (seen in Fig. 3A) for each condition's grey Gabor. For delta and theta power, similar topologies are seen across all Gabor, with strongest frontal power observed for higher levels of information (i.e., repeat and switch cues). Additionally, a broad, posterior decrease in alpha power is observed specifically for repeat and switch grey Gabors, which provide the opportunity for proactive control processes to be employed. Note beta has a reduced color scale magnitude relative to the other bands.

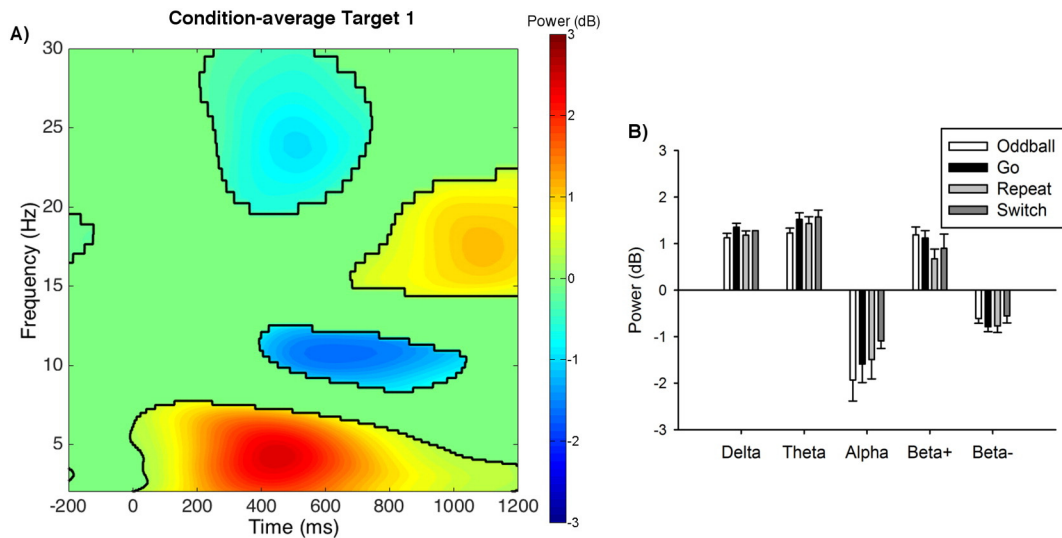


Fig. 5. Condition-average time-frequency plots for *target 1* at the frontocentral cluster (i.e., FC1, FCz, FC2). (A) Like with grey Gabors, all target 1 stimuli were associated with increases in lower frequency delta/theta power and decreases in alpha/beta power. Additionally, later transient increases in beta power were observed. Dark outlines indicate significant time × frequency clusters, corrected for multiple comparisons (false discovery rate; FDR $p < .001$). (B) Bar plots depicting average of frequency band clusters (shown in Fig. 5A) for each condition's target. Compared to the grey Gabors, relatively smaller differences are seen between conditions across the frequency bands, consistent with similar amounts of sensorimotor information present for these targets.

parietal, parietoccipital) × 5 (FREQUENCY; delta, theta, alpha, beta + and beta −) ANOVA. Across the scalp, and as before, we see significant differences of overall power between the conditions TARGET TYPE ($F(3,90) = 4.7, p = .015$; partial $\eta^2 = .14$), with switch targets associated with the strongest overall power, followed by go, repeat and oddball (simple contrasts linear trend: $F(1,30) = 5.1, p = .032$; partial $\eta^2 = .15$). Further, there were expected differences in power across the sites (SITE; $F(4,120) = 13.4, p < .001$; partial $\eta^2 = .31$) and frequencies (FREQUENCY; $F(4,120) = 87.9, p < .001$; partial $\eta^2 = .75$). As with the grey Gabors, there was a significant quadratic trend of SITE, with both frontal and posterior sites associated with increases in power, coupled with a strong decrease in power over central sites ($F(1,30) = 27.3, p < .001$; partial $\eta^2 = .47$). Likewise, a quadratic trend for FREQUENCY was observed, with strongest increases in power for delta and theta, a prominent decrease in alpha power and reduced power for beta ($F(1,30) = 13.1, p = .001$; partial $\eta^2 = .3$). A significant TARGET TYPE × SITE interaction was seen ($F(12,360) = 5.9, p < .001$; partial $\eta^2 = .16$), whereby little difference in power was seen between targets at frontal sites but differences emerged at central and posterior sites (see below; Fig. 6). Likewise, targets tended to differ in overall alpha and theta power rather than delta or beta (TARGET TYPE × FREQUENCY; $F(12,360) = 5.8, p < .001$; partial $\eta^2 = .16$). Finally, frequency bands tended to have different spatial topologies (SITE × FREQUENCY; $F(16,480) = 22.6, p < .001$; partial $\eta^2 = .43$), with broad spatial distributions for delta and beta power, a frontocentral topology for theta and a central topology for alpha (see Fig. 6). Finally, a significant TARGET TYPE × SITE × FREQUENCY interaction was also observed ($F(48,1440) = 2.1, p = .017$; partial $\eta^2 = .07$).

As seen in the topology plots shown in Fig. 6, all target types had similar spatial distributions of frequency power, with broad frontoparietal delta topologies, frontocentral theta and bilateral, central alpha. However, as suggested by the main effect of TARGET TYPE and inspection of the topology plots shown in Fig. 6, these power responses appeared strongest in the switch targets. Indeed, little difference was seen between targets in overall delta or theta power, while for alpha (go vs. oddball, $t(30) = 3.9, p < .001$; repeat vs. oddball, $t(30) = 3, p = .006$; switch vs. oddball, $t(30) = 3.6, p = .001$; go vs. switch, $t(30) = 2.3, p = .027$; repeat vs. switch, $t(30) = 2.7, p = .012$) and beta clusters (beta +; go vs. repeat, $t(30) = 2.2, p = .034$; repeat vs. switch, $t(30) = 2.1, p = .047$; beta −; switch vs. oddball, $t(30) = 2.3,$

$p = .032$; go vs. repeat, $t(30) = 3.1, p = .004$; repeat vs. switch, $t(30) = 3.4, p = .002$), targets were significantly different in power (also see Fig. 6). While for the grey Gabor repeat and switch trials had strong, posterior decreases in alpha, for target 1 all trials had central bilateral alpha changes, suggestive of common motor/response-related processes. Indeed, the blue oddball distractors, which required no motor response, had no bilateral alpha processes (blue vs. red oddball, $t(30) = 5.6, p < .001$; blue vs. go, $t(30) = 5.1, p < .001$; blue vs. repeat, $t(30) = 4.8, p < .001$; blue vs. switch, $t(30) = 3.5, p = .002$). Thus, only targets that require an overt motor response are associated with bilateral central alpha processes. Finally, for go, repeat, and switch

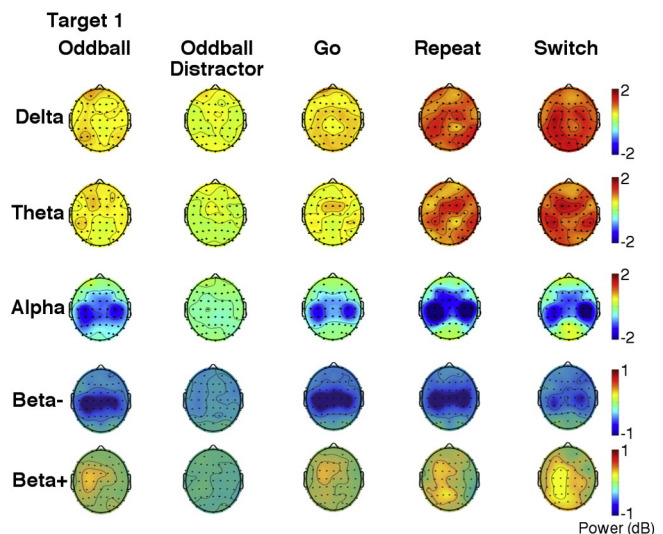


Fig. 6. Topology plots depicting the spatial dimension of each frequency cluster (seen in Fig. 5A) for each condition's target 1. A common frontoparietal delta process is seen for all targets, appearing strongest for repeat/switch targets. Next, a common frontocentral theta process is seen for all targets (albeit less focused in the oddball targets). Finally, for all targets requiring a motor response (i.e., oddball, go, repeat, and switch), a central, bilateral decrease in alpha power is seen, together with two chronologically distinct clusters of desynchronized (beta −; early occurring) and synchronized (beta +; late occurring) activity. Note that beta has a reduced color scale magnitude relative to the other bands.

targets, there appeared to be an alpha rebound in posterior power, which was significantly different than the oddball target 1 (parietal cluster for alpha: oddball vs. go, $t(30) = 3.3$, $p = .002$; oddball vs. repeat, $t(30) = 3$, $p = .005$; oddball vs. switch, $t(30) = 3.9$, $p = .001$; parietoccipital cluster for alpha: oddball vs. go, $t(30) = 5.5$, $p < .001$; oddball vs. repeat, $t(30) = 3.3$, $p = .002$; oddball vs. switch, $t(30) = 3.2$, $p = .003$). Although not explicitly predicted by our information theory estimates, these differences do correspond to those targets that followed a stimulus with high information value (i.e., the grey Gabors). Thus, it is plausible these posterior processes reflect carryover effects in line with the behavioral restart costs observed for target 1.

In sum, for target 1 stimuli, with similar levels of sensorimotor control we observed similar levels of power. Switch targets overall had greater power (regardless of frequency), while displaying similar spatial distributions of power as the other targets. In addition, for any target requiring a motor response, we saw a bilateral central decrease in alpha power, suggestive of common motor cortex activity.

Target 3

Common target 3 time-frequency activity is depicted in Fig. 7. As with both grey and target 1 Gabors, a common delta/theta process is seen, accompanied by alpha decreases and transient beta bursts. As with target 1, both beta+ and beta- are included in the FREQUENCY factor. Overall, there was a significant main effect of SITE ($F(4,120) = 12.7$, $p < .001$; partial $\eta^2 = .3$) and FREQUENCY ($F(4,120) = 102$, $p < .001$; partial $\eta^2 = .77$). Simple contrasts revealed significant quadratic trends for SITE ($F(1,30) = 32.2$, $p < .001$; partial $\eta^2 = .52$) and FREQUENCY ($F(1,30) = 23.9$, $p < .001$; partial $\eta^2 = .44$). Interestingly, no significant main effect of TARGET TYPE was found, suggesting similar oscillatory processes are occurring by the time the third target appears. Further, a significant TARGET TYPE \times FREQUENCY interaction was present ($F(12,360) = 4.8$, $p < .001$; partial $\eta^2 = .14$), with differences between the target types restricted largely to the alpha band (go vs. oddball, $t(30) = 3.5$, $p = .001$; repeat vs. oddball, $t(30) = 3.2$, $p = .003$; repeat vs. switch, $t(30) = 2.1$, $p = .044$). Additionally, a SITE \times FREQUENCY interaction was again observed ($F(16,480) = 20.7$, $p < .001$; partial $\eta^2 = .41$), with broad spatial distributions for delta and beta power, like those seen in target 1, frontocentral theta, and a central alpha topology (see Fig. 8). However, no TASK \times SITE interaction

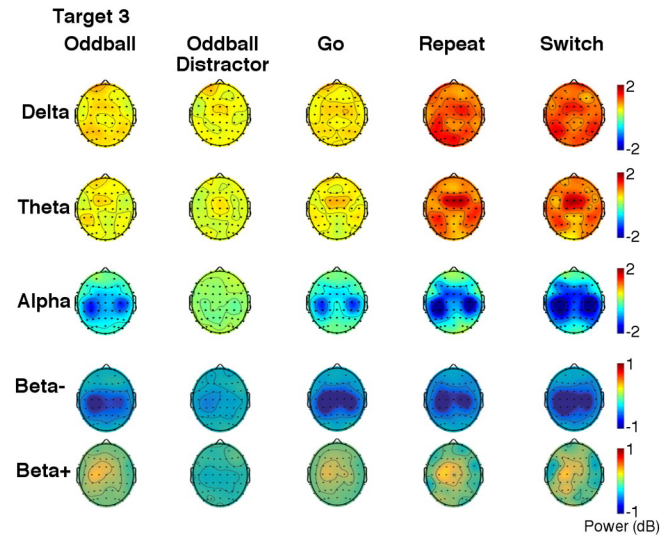


Fig. 8. Topology plots depicting the spatial dimension of each frequency cluster (seen in Fig. 7A) for each condition's target 3. As with target 1, common frontoparietal delta processes are seen for all targets, appearing strongest for repeat/switch targets. Again, a common frontocentral theta processes is seen for all targets. For all targets requiring a motor response (i.e., oddball, go, repeat, and switch), a central, bilateral decrease in alpha power is seen. Lastly, central beta desynchronization (beta-) is also seen to accompany the alpha process in targets requiring a motor response, followed by a distinct beta synchronization (beta+) mostly following motor responses. Note beta has a reduced color scale magnitude relative to the other bands.

was found, suggesting similar topographical activity for all conditions by the time target 3 appears. Fig. 8 shows a similar topographical distribution as that seen in target 1; with broad frontoparietal delta activity, frontocentral theta, and bilateral, central alpha. As before, only targets requiring a motor response were associated with the central alpha decrease. Lastly, a marginal TARGET TYPE \times SITE \times FREQUENCY interaction was observed also for target 3 ($F(48,1440) = 1.8$, $p = .046$; partial $\eta^2 = .06$).

Finally, while all three temporal contexts had similar processes evident (e.g., strong delta/theta power combined with alpha and beta

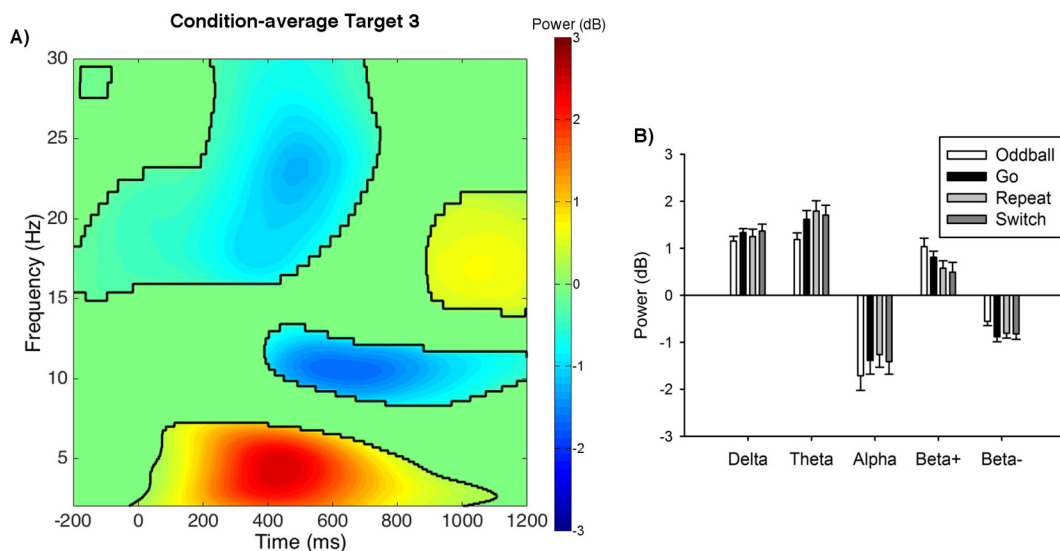


Fig. 7. Condition-average time-frequency plots for target 3 at the frontocentral cluster (i.e., FC1, FCz, FC2). (A) As seen in the time-frequency plot, all target 3 stimuli were associated with an increase in lower frequency delta/theta power and decreases in alpha power. Additionally, transient changes in beta power were observed. Dark outlines indicate significant time \times frequency clusters, corrected for multiple comparisons (false discovery rate; FDR $p < .001$). (B) Bar plots depicting average of frequency band clusters (shown in Fig. 7A) for each condition's target. Little difference is seen between conditions across the frequency bands, with the exception of oddball target 3, which had lower theta, higher alpha, and lower beta power than the other targets.

activity), visual comparison of the topology plots suggests strong frontal delta and theta components were present for grey Gabor compared to frontoparietal and frontocentral delta and theta in subsequent targets (see Figs. 4, 6 and 8). To determine if indeed there were distinct components emerging over time, we ran the above ANOVA structure (i.e., TARGET TYPE \times SITE \times FREQUENCY) with the inclusion of POSITION (i.e., grey Gabor, target 1, target 3). Note, as the grey Gabor did not have a positive beta cluster, we restricted the beta frequency to only negative clusters (i.e., beta $-$) to permit comparisons. As before, we saw main effects of SITE ($F(4,120) = 19.4, p < .001$; partial $\eta^2 = .39$) and FREQUENCY ($F(3,90) = 164.6, p < .001$; partial $\eta^2 = .85$). These main effects were associated with quadratic trends as seen in the previous sets of analyses (SITE: $F(1,30) = 52.1, p < .001$; partial $\eta^2 = .64$, FREQUENCY: $F(1,30) = 11.5, p = .002$; partial $\eta^2 = .28$). Likewise, as before, there were significant SITE \times FREQUENCY ($F(12,360) = 21, p < .001$; partial $\eta^2 = .41$) and TARGET TYPE \times FREQUENCY ($F(9,270) = 6, p = .001$; partial $\eta^2 = .17$) interactions. Interestingly, no significant main effect of TARGET TYPE or POSITION was found, suggesting that overall across all temporal contingencies stimuli rely on similar oscillatory processes. However, as seen in the previous analyses, within temporal contingencies, there are power differences, dependent on information content. Confirming this, we saw significant TARGET TYPE \times POSITION ($F(6,180) = 9.4, p < .001$; partial $\eta^2 = .24$), TARGET TYPE \times FREQUENCY \times POSITION ($F(18,540) = 21.1, p < .001$; partial $\eta^2 = .41$), TARGET TYPE \times SITE \times POSITION ($F(24,720) = 7.2, p < .001$; partial $\eta^2 = .19$), and TARGET TYPE \times FREQUENCY \times SITE \times POSITION ($F(72,2160) = 2.9, p = .001$; partial $\eta^2 = .09$) interactions.

Exploring these interactions further revealed that overall there are significant differences in power between the task-switching cues and the other grey Gabor (oddball vs. switch, $t(30) = 3.2, p = .003$; nogo vs. switch, $t(30) = 3.1, p = .004$; repeat vs. switch, $t(30) = 2.7, p = .013$). These differences are present in all frequency bands: delta (oddball vs. repeat, $t(30) = 2.5, p = .019$; oddball vs. switch, $t(30) = 3.1, p = .004$; nogo vs. switch, $t(30) = 2.4, p = .024$), theta (oddball vs. repeat, $t(30) = 3.1, p = .004$; oddball vs. switch, $t(30) = 2.7, p = .01$; nogo vs. repeat, $t(30) = 3.3, p = .002$; nogo vs. switch, $t(30) = 2.7, p = .011$), alpha (oddball vs. repeat, $t(30) = 4.5, p < .001$; oddball vs. switch, $t(30) = 7.3, p < .001$; nogo vs. repeat, $t(30) = 2.1, p = .045$; nogo vs. switch, $t(30) = 6.4, p < .001$; repeat vs. switch, $t(30) = 4.4, p < .001$), and beta $-$ (oddball vs. repeat, $t(30) = 6.5, p < .001$; oddball vs. switch, $t(30) = 8.6, p < .001$; nogo vs. switch, $t(30) = 3.7, p = .001$). By contrast, little difference is seen between power across the targets, with the exception of switch target 1 vs. target 3 ($t(30) = 3.7, p = .001$). These differences were driven by stronger alpha and beta $-$ power present at target 1 vs. target 3 (alpha, $t(30) = 3.5, p = .002$; beta, $t(30) = 5.2, p < .001$).

In sum, differences in information loaded most heavily on the grey Gabor patches which differed more explicitly in meaning across the three tasks. These differences in information were linked with changes in frontal delta and theta power. First, a common set of delta processes was present for all three tasks and all three temporal positions (i.e., cue, target 1, and target 3). Second, a frontal theta component appeared intimately related to information and was particularly associated with

temporal context. This frontal theta component was strongest for stimuli that provided the highest amount of information and required higher-order cognitive control operations (i.e., switch cues). In addition, theta appears to encompass a midfrontal component that was present for all stimuli, particularly evident in response to the targets. Finally, two alpha power changes were seen. One decrease in alpha was located bilaterally over central scalp sites for all stimuli that were linked to a response. The other centroparietal decrease in alpha was switch-specific, emerging only to the cue indicating the need to update higher-order task rules. These differences are summarized in Table 2.

Discussion

According to dual modes of cognitive control models, differences in situational factors or context influence the use of anticipatory, proactive control vs. stimulus-driven reactive control (Braver, 2012). In this study, we quantified such contextual influences using information theory (cf. Barceló et al., 2008; Koechlin and Summerfield, 2007) to explore the neural signatures of quantifiable contextual adjustments of the cognitive control system. We found that cognitive control arises from a sophisticated frequency landscape, with common context-independent and specific context-sensitive processes relying on multiple frequency bands. In particular, we identified common stimulus resolution and response generation processes associated with transient bursts of beta, frontoparietal delta, and frontocentral theta increases in power and central alpha desynchronization. These common processes likely reflect common “input” (i.e., stimulus processing; frontoparietal delta) and “output” (i.e., response-related processes; central alpha) mechanisms of the cognitive control system. Additionally, we identified context-sensitive adjustments of the cognitive control system: frontal delta power was sensitive to increasing sensorimotor control, frontal theta power was sensitive to both increasing sensorimotor and episodic control processes (i.e., temporal context), and posterior alpha desynchronization was sensitive to proactive rule updating (and their associated carryover effects).

Together, these data suggest that the cognitive control system utilizes a range of oscillatory bands depending on temporal and task contexts to achieve flexible control of thoughts and actions. While most research in frontoparietal oscillatory signatures of control focus on theta band dynamics (Cavanagh and Frank, 2014; Cooper et al., 2015a; Cunillera et al., 2012; Gladwin and de Jong, 2005; Luu et al., 2004; Moore et al., 2012; Sauseng et al., 2006; Trujillo and Allen, 2007), our findings provide novel insight into a richer and more dynamic environment comprised of multiple frequency bands that underlie cognitive control. Such multiband dynamics of cognitive processes are being increasingly recognized. For instance, Dipoppa and Gutkin (2013) recently proposed an interplay between alpha, theta, and beta/gamma bands in relation to memory trace clearing/blocking, maintenance, and loading/updating processes during working memory. Together, these findings suggest that cognitive control is achieved via a multifaceted frontoparietal functional architecture that relies on multiple frequency bands to deal with information processing associated with

Table 2

Summary of prominent frequency and spatial features for each context. Hypothesized information sensitivity is proposed beneath each finding.

	Grey Gabor (Information loading)	Target 1 (Information loading)	Target 3 (Information loading)
Delta	Frontal topology, stronger for nogo, repeat and switch vs. oddball (sensorimotor control)	Frontoparietal topology, similar across all targets (sensorimotor control)	Frontoparietal topology, similar across all targets (sensorimotor control)
Theta	Frontal topology, strongest for switch and repeat cues (sensorimotor + episodic control)	Frontocentral topology, similar across all targets, albeit weakest for oddball (sensorimotor control)	Frontocentral topology, similar across all targets (sensorimotor control)
Alpha	Posterior decrease for switch and repeat cues only (episodic control)	Bilateral central process for all targets requiring motor response (response processes)	Bilateral central process for all targets requiring motor response (response processes)
Beta	Centroparietal decrease for repeat and switch cues specifically, as per alpha (episodic control)	Posterior increase for beta, strongest for go, repeat and switch targets (carryover effects/restart costs)	Similar to central alpha process, albeit weakest for oddball targets (response processes)

Note: where targets have no hypothesized differences in information loading, we suggest a cognitive/motor mechanism.

changing contextual demands, working memory updating, and response generation.

Frequency signatures of “fractionated control”

Koechlin and Summerfield (2007) proposed that cognitive control could be fractionated into specific sub-processes based on a temporal gradient between past events and present or future actions. These ideas integrate well with dual modes of control models (Braver, 2012), wherein increasingly future-oriented processes rely on anticipatory or proactive control modes. Indeed, proactive and reactive control modes appear to utilize distinct aspects of the prefrontal cortex (Braver et al., 2009; Gilbert et al., 2010; Krug and Carter, 2012; Marklund and Persson, 2012). Recent evidence is emerging of oscillatory mechanisms corresponding with such differences (Cooper et al., 2015a; Jiang et al., 2015; Van Driel et al., 2015). In the current paradigm, future-oriented control processes were associated with information transmission between current grey gratings and the ensuing goal-directed actions required to sort color gratings under conditions of increasing task complexity. In line with Koechlin and Summerfield (2007), these grey gratings were associated with delta and theta power in anterior regions of the prefrontal cortex consistent with proactive control operations. Specifically, both repeat and switch cues that afforded opportunity for proactive control had increased delta and theta frontal power compared to identical grey gratings in the other two tasks that did not afford any preparation. Thus, **the current study provides evidence toward one potential mechanism by which neural signatures of cognitive control can be fractionated.**

In addition to informing the proactive vs. reactive control distinction, our use of information theory allowed a more nuanced dissection of contextual influences on cognitive control. We present evidence that Koechlin and Summerfield's hierarchical model of cognitive control has a corresponding frequency hierarchy, with lower control processes – i.e., sensorimotor control – associated with slower frequencies and higher episodic control processes associated with faster frequencies. Frontal delta appeared particularly sensitive to sensorimotor information, so that differences between grey and target Gabor patches within a task matched the amount of sensorimotor information predicted (i.e., the differences between red targets and grey distractors in the oddball task; see Fig. 2 and Supplementary Materials). Likewise, **corresponding targets between tasks had similar frontoparietal delta power, mapping partially to similar amounts of sensorimotor control required to implement identical stimulus–response pathways in all tasks (i.e., press a button to all red patches).** Interestingly, this distinction between rostral and frontoparietal delta for cues and targets, respectively, is reminiscent of frontal vs. centroparietal topologies of the novelty-related P3a and target-related P3b (Polich, 2007). Indeed, as delta has been linked to P300 processes (e.g., Başar-Eroglu et al., 1992), it is possible that these delta differences, that are sensitive to sensorimotor information, may be spectral indices of frontoparietal network activity that manifests as P300 components (cf. Barceló et al., 2006). However, while this hypothesis is promising, the current study did not examine ERPs and thus additional work is warranted to explore this link.

By contrast, frontal theta did differ between corresponding targets across conditions, suggesting sensitivity to more than just low-level sensorimotor control. Indeed, as frontal theta effects differed between grey and target stimuli, theta likely indexes temporal context captured in the accumulation of both sensorimotor and episodic control processes. Increasing information was associated with stronger and broader frontal theta. Recently, Cohen (2014) proposed that theta oscillations in the prefrontal cortex are a manifestation of a general processing principle of functional modules residing there, which are exploited to monitor and respond to conflict (i.e., contextually sensitive information). While EEG lacks the spatial resolution to ensure that the theta effect observed here was indeed generated from such functional modules, given the

robustness of association between frontal theta and prefrontal cortex generators (Cavanagh and Frank, 2014), it is practical to consider our results from this perspective. As such, temporal contextual demands (i.e., sensorimotor + episodic information) require additional anterior regions of the prefrontal cortex to be brought online proactively (Koechlin and Summerfield, 2007), resulting in increasing frontal theta power as more frontal generators are engaged.

This study fits well with other recent work relating low frequency oscillations to sensorimotor control (Arnal and Giraud, 2012; Arnal et al., 2015; Nacher et al., 2013; Zavala et al., 2015). For instance, Arnal and Giraud (2012) suggested that low frequency oscillations can modulate sensory processing and influence behavior through phase alignment of cortical rhythms. Specifically, delta–theta oscillations are reset in response to sensory events, which can then be used as an anticipatory mechanism during attention. **While our results support the notion of anticipatory processes relying on these frequencies, differences between tasks and context suggest that a more general link to task uncertainty, or sensorimotor information, is better suited to explain delta and theta roles in cognition.** Indeed, Nacher et al. (2013) showed that during a tactile discrimination task, long-range delta oscillations were associated with primate decision making. Here a macaque (*Macaca mulatta*) was required to integrate contextually sensitive sensorimotor information, similar to the sensorimotor information-related delta oscillations seen in the current study.

Finally, a broad parietal decrease in alpha power was only seen in response to task switching (i.e., repeat and switch) cues. This pattern of activation follows that seen previously in anticipatory task-switching studies (Foxe et al., 2014; Mansfield et al., 2012; Sauseng et al., 2006) and likely indexes a working memory/rule updating process required in task-cueing paradigms. Indeed, we saw differences within this alpha process between repeat and switch cues, which according to our information theoretical estimates differed primarily in higher episodic control processes (like rule retrieval and rule updating). Recent work has suggested that alpha synchronization/desynchronization reflects a gating mechanism that permits information to enter a “global workspace,” wherein task appropriate information is processed expediently (Palva and Palva, 2007). For example, Buschman et al. (2012) reported desynchronization or suppression of alpha oscillations at task-relevant regions of the cortex that facilitated attentional processes. In this sense, when a cue indicates an upcoming need to maintain or change rules, the global workspace is updated to reflect current task demands prior to target onset, with desynchronization occurring over visual cortices relevant for processing the color and/or spatial frequencies of the upcoming target. Such an updating process is captured in this posterior desynchronization that is distinct from the motor-related activity seen for targets. Interestingly, this updating process seen in the alpha desynchronization over posterior cortices may therefore be another neural signature of switch costs, in line with typical preparatory switch positivities seen in cue-locked ERPs (see Karayanidis et al., 2010).

As outlined above, specific components of Koechlin and Summerfield's hierarchy of cognitive control seem to correspond with specific frequency signatures. Interestingly, the inputs and outputs of the cognitive control system rely on many of the same frequencies as the contextual processing. For instance, common target processing across all targets was seen in a frontoparietal delta response and targets that required motor responding had systematic decreases in alpha power over the motor cortex. As would be predicted from reactive control literature, there was also a common frontocentral or midfrontal theta process for all targets. This supports the notion that target-driven conflict or uncertainty resolution processes rely on common midfrontal theta activity (see Cavanagh and Frank, 2014). However, only by disentangling input, cognitive control, and output processes using information theory were we able to provide such a fine-grained account of the functional mechanisms of cognitive control. Such evidence shows the remarkable flexibility of frontoparietal control networks in

facilitating goal-directed behavior and the utility of adopting computational over merely notional models of cognition.

Together, these findings indicate that the frontoparietal control network relies on multiple frequencies to meet current information processing demands. Rule implementation and response generation are achieved by appropriate regions of the cortex utilizing delta and alpha frequency bands. With increasing information, contextual demands are raised resulting in recruitment of theta generating prefrontal regions. Finally, proactive rule updating needs rely on broad posterior decreases in alpha, at least in visuomotor tasks involving simple stimulus discrimination based on color and spatial frequency.

Final words of caution should be offered with respect to these interpretations. First, while the observed broad frontal/parietal changes in power are indicative of the frontoparietal architecture that cognitive control is known to rely on, topographic changes in power do not strictly reflect a functional network. Our power analyses allowed us to interpret increasing theta power by assuming the recruitment of increasing number of prefrontal modules. However, to ascertain that these changes correspond to interactions *within* a frontoparietal network, alternative neuroimaging methodologies need to be employed. Further studies are needed which target functional connectivity (see Cohen and Gulbinaite, 2014). For example, **an appropriate next step would be to explore within-frequency and cross-frequency coupling between electrodes using inter-site clustering measures (e.g., coherence or phase-lag indices) during tasks with quantifiable contextual demands.**

Lastly, although Koechlin and Summerfield's model of fractionated cognitive control appears sufficient to dissociate proactive and reactive control processes, our implementation of this model is unable to predict some important differences between targets we observed. For instance, although local switch costs (i.e., poorer performance on switch trials vs. repeat trials) are expected from traditional task switching, we did not observe a significant switch cost behaviourally in the current paradigm. Given that we used a 1900 ms SOA, and ERP studies have suggested that task reconfiguration is a fast, short-lived process that can be completed in 800 ms for simple rules (Barceló et al., 2008; Karayanidis et al., 2011), it is likely the behavioural switch cost was eliminated due to sufficient preparation. However, we still found evidence of a neural signature of such switch costs in posterior alpha at cues and target 1. While information theory suggests that, for the cue, this alpha process likely stems from differences in episodic control demands, it is less clear why a difference in task-switching targets following the cue was present. That is, according to information theory, these behavioral restart costs and their accompanying alpha/beta changes should not occur if all targets have identical information values (as predicted here). Such differences hint at trial-by-trial, swift temporal dynamics that are not easily captured by our task-averaged information estimates, nor indeed by those derived from Koechlin and Summerfield's model. This is likely because information theory provides only a single value for each condition's representative Gabor across the whole experiment, and thus is unable to inform fast or slow time scale of neural operations involved in processing those information values. Therefore, information theory may be sufficient for characterising a stable process (whether cognitive or neural) that does not vary much over time. However, alternative models (e.g., Bayesian) might be better suited for capturing some dynamic processes that change rapidly from trial to trial. Thus, additional work confirming these unexpected effects would facilitate an eventual update of this model.

Conclusion

The regions of the cortex that promote flexible control are increasingly well recognized, but the functional mechanisms that promote such control are still poorly understood. Here, we have shown evidence that multiple frequencies are associated with particular aspects of cognitive control in a contextually sensitive fashion. Theta oscillations, increasingly considered the language of control, appear to play just one

part of a broad spectral response to information processing. In particular, *temporally* contextual information was intimately tied to frontal theta power, whereas *task* context was linked with delta oscillations. Further rule updating and response processes were shown to rely on alpha rhythms. Thus, considering multiple frequency responses together facilitates a more thorough understanding of the dynamic interplay of control networks underpinning human cognition.

Finally, only by utilizing objective measures of context were we able to highlight these signatures of cognitive control. This approach allowed insight into not only typically reported task-specific differences in electrophysiology but also relationships between temporal and task contexts that underpin cognitive control. We have thus begun to probe subtle, functional mechanisms within well-established frontal processing systems that may ultimately result in effective cognitive control.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2016.03.010>.

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Supplementary data

Information theoretic estimations of sensory, motor, and sensorimotor control at two levels of a putative hierarchy of cognitive control for the switch, go/nogo and oddball tasks (cf., Attneave, 1959; Barceló et al., 2008; Koechlin & Summerfield, 2007; Miller, 1956).

Stimulus Entropy: $H(s_i) = -\sum_{i=1}^6 p(s_i) \cdot \log_2 p(s_i)$

Table s1. All tasks. The same set and sequence of stimuli were used in all three tasks, and therefore, the same stimulus entropy can be assumed for all tasks:

<i>Gabors</i>	S^1	$H(s)$	$p(s)$	$-\log_2 p(s)$
	s_1	0.29	0.08	3.64
	s_2	0.29	0.08	3.64
	s_3	0.47	0.21	2.25
	s_4	0.47	0.21	2.25
	s_5	0.47	0.21	2.25
	s_6	0.47	0.21	2.25
$\Sigma H(s_i) =$		2.46		

Response Entropy: $H(r_j) = -\sum_0^j p(r_j) \cdot \log_2 p(r_j)$

Table s2. Oddball task. This task required one-button responses (r_1) and the absence of response (r_0) to all non-targets. The response set can be defined as $\mathbf{R} = \{r_0, r_1\}$

R	$H(r)$	$p(r)$	$-\log_2 p(r)$
r_0	0.45	0.58	0.78
r_1	0.53	0.42	1.26
$\Sigma H(r_i) =$	0.98		

Table s3. Go/nogo and switch tasks. These two tasks required two-button responses (r_1, r_2) and the absence of response (r_0) to the grey gratings. Hence, the response set is $\mathbf{R} = \{r_0, r_1, r_2\}$

R	$H(r)$	$p(r)$	$-\log_2 p(r)$
r_0	0.43	0.16	2.60
r_1	0.53	0.42	1.26
r_2	0.53	0.42	1.26
$\Sigma H(r_i) =$	1.49		

Sensorimotor Information: $I(s_i, r_j) = \log_2 p(s_i, r_j) - \log_2 p(s_i) - \log_2 p(r_j)$

¹ For simplicity, these estimates assume a stimulus set $\{S\}$ with only six stimuli, regardless of the fact that each Gabor grating was randomly displayed either to the left or the right visual hemifields.

The information transmitted from stimuli to responses, $I(s_i, r_j)$, is derived from the notion of mutual information between sets of stimuli $\{S\}$ and responses $\{R\}$ (Attneave, 1959):

$$I(S; R) = \sum_i \sum_j p(s_i, r_j) \log \frac{p(s_i, r_j)}{p(s_i)p(r_j)}$$

Table s4. Oddball task. This task required one-button responses (r_1) only to the red Gabor gratings (s_5, s_6), and hence, low-level sensorimotor control for the relevant task-set units (s_i-r_j) in the oddball task can be estimated as follows:

$S-R$	$p(s_i)$	$p(r_j)$	$p(s_i, r_j)$	$I(s_i, r_j)$
s_1-r_0	0.08	0.58	0.08	0.78
s_2-r_0	0.08	0.58	0.08	0.78
s_3-r_0	0.21	0.58	0.21	0.78
s_4-r_0	0.21	0.58	0.21	0.78
s_5-r_1	0.21	0.42	0.21	1.26
s_6-r_1	0.21	0.42	0.21	1.26
$\Sigma(s_i r_j) = 5.64$				

Table s5. Go/nogo and switch² tasks. These two tasks required two-button responses (r_1, r_2) to classify blue and red Gabor gratings (s_3, s_4, s_5, s_6), and hence, low-level sensorimotor control for the relevant task-set units (s_i-r_j) when sorting by color can be estimated as follows:

$S-R$	$p(s_i)$	$p(r_j)$	$p(s_i, r_j)$	$I(s_i, r_j)$
s_1-r_0	0.08	0.16	0.08	2.61
s_2-r_0	0.08	0.16	0.08	2.61
s_3-r_1	0.21	0.42	0.21	1.26
s_4-r_1	0.21	0.42	0.21	1.26
s_5-r_2	0.21	0.42	0.21	1.26
s_6-r_2	0.21	0.42	0.21	1.26
$\Sigma(s_i r_j) = 10.26$				

Episodic Information: $I(s_i, ts_k) = \log_2 p(s_i, ts_k) - \log_2 p(s_i) - \log_2 p(ts_k)$

Table s6. Switch task. Only the Switch task required access to episodic task-set (ts_1) information on just 8% of all trials (s_1-ts_1), while no task-set access (ts_0) was required in the

² Sensorimotor information in the switch task was slightly (~ 1 bit) larger for those color gratings that afforded bivalent responses (i.e., different buttons for either rule). For simplicity this additional source of contextual information was not included here.

remaining trials. The transmitted information between sensory stimuli and access to episodic memories in this task can be estimated as follows:

$S-TS$	$p(s_i)$	$p(ts_k)$	$p(s_i, ts_k)$	$I(s_i, ts_k)$
s_1-ts_1	0.08	0.08	0.08	3.61
s_2-ts_0	0.21	0.92	0.21	0.12
s_3-ts_0	0.21	0.92	0.21	0.12
s_4-ts_0	0.21	0.92	0.21	0.12
s_5-ts_0	0.21	0.92	0.21	0.12
s_6-ts_0	0.21	0.92	0.21	0.12
				$\Sigma(s_i, ts_k) = 4.21$

Table s7. Summary of numerical values plotted in Figure 2. Transmitted information for each task stimulus was estimated as the addition of information across two levels in the putative hierarchy of sensorimotor control processes (i.e., s_1 in the switch task= 2.61 + 3.61= 6.22 bits; s_1 in the NoGo task= 2.61 + 0= 2.61 bits, and in the Oddball task= 0.78 + 0= 0.78 bits).

	s_1	s_2	s_3	s_4	s_5	s_6
Switch	6.22	2.73	1.38	1.38	1.38	1.38
Go/NoGo	2.61	2.61	1.26	1.26	1.26	1.26
Oddball	0.78	0.78	0.78	0.78	1.26	1.26

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