

CONTEXT-ORIENTED PERFORMANCE BIASES IN COGNITIVE CONTROL

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Cognitive control, the ability to guide goal-directed behavior, is comprised of a variety of cognitive components functioning in a dynamic balance. Control adjustments are commonly cast as temporally local adaptations reflecting recently encountered task conflict; however, global control processes representing broad task expectancies are relatively unexplored. In an electroencephalographic (EEG) study of a prepotent response inhibition task, we tested whether the congruency effect, where performance tends to be worse for trials involving controlled processes, would be impacted by the overall task context as defined by trial-type proportions. As the proportion of high-control trials increased, we observed that accuracy improved in a more demanding, high-control condition while worsening in the less demanding, low-control condition. More interestingly, this tradeoff resulted in a reversed congruency effect in accuracy for task contexts dominated by high control trials. Furthermore, delay period EEG spectral power in the alpha-frequency band (i.e., 9-13 Hz)—a putative inhibitory mechanism (Klimesch, 2012)—was found to modulate with the task. A significant trial condition by task context interaction revealed a positive monotonic association between accuracy and induced alpha synchrony in low control task contexts with a negative monotonic association in the high control context. Our behavioral results are consistent with cognitive control adjustments occurring through an ‘adaptation-by-binding’ which posits that the continuous arousal resulting from a high conflict context strengthens active task and sensory representations even if disadvantageous to automatic processes (Verguts & Notebaert, 2009). Further, ongoing synchronous cortical

alpha-band oscillations could serve as a potential neural mechanism by which this binding effect is achieved.

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PREFACE

In honor of this work, I would like to thank my committee members, Bea Luna, Avniel Ghuman, and most notably, Raymond Cho, for their support and guidance through this project. I would also like to thank Nicola R. Polizzotto, Thomas Wozny, and Kübra Kömek for their intellectual and methodological contributions, and the many hours of brainstorming and advice they contributed. Finally, and most significantly, I would like to thank my family—my parents, Jane and Jim Walker, and my brother, Rusty Walker—whose support, encouragement, guidance, and reassurance has been immeasurable over the last several years.

1.0 INTRODUCTION

Recruitment of cognitive control capacities depends on context to inform the allocation of attentional resources on a moment-by-moment basis. Historically, most studies scrutinized the intricacies of temporally local, trial carryover effects. Post-error slowing (Laming, 1968; Rabbitt, 1966), conflict carryover effects (Gratton, Coles, & Donchin, 1992), and task-switch cost (Li, Wang, Zhao, & Fogelson, 2012; Van Loy, Liefoghe, & Vandierendonck, 2010) all suggests that our control of attention is largely guided and constrained by the most recent trial history. However, we know that control behaviors also reflect long-term history of trial expectancies, and transient adjustments of control operate in the context of sustained goal-maintenance (Braver, Reynolds, & Donaldson, 2003). Less well understood is how longer time course shifts in behavior, oftentimes thought to reflect practice (Jonides, 2004), can reflect a learned optimization of cognitive resources (Verguts & Notebaert, 2009).

1.1 CONTEXT PROCESSING

Context processing, a specialized mechanism of cognitive control, is the ability to develop an internal representation of task rules and structure in the absence of explicit instruction (see Henderson et al., 2012 for a review). Experimentally, context is determined by the relative proportions of various trial types within a specific task or environment. As a participant learns

the statistics of his or her environment, he or she may develop expectancies that serve as temporary heuristics to bias responding toward the most likely event. Two dimensions of context representation have yet to be explored. First, if context-related biasing serves to minimize mental effort, similar behavioral biases should be observable in context neutral (i.e., unpredictable) scenarios where a tonic, but elevated control state may be more advantageous. Second, as forming a context representation involves implicit learning, the associated neural mechanisms or signals should be represented in tonic baseline functioning dissociable from phasic, event related activity. This investigation seeks to address these two points.

1.1.1 Behavioral evidence

Perhaps the most commonly employed measure of context processing, the AX variant of the continuous performance test (AX-CPT) has most thoroughly characterized context processing in cognitive and clinical domains (Bickel, Dias, Epstein, & Javitt, 2012; Braver, Cohen, & Barch, 2002; Henderson et al., 2012; Thoma, Zoppelt, Wiebel, & Daum, 2007). In this task, participants are instructed to respond to specific target pairs of letters presented in a continuous fashion. In a healthy individual, the prevalence of a particular cue-target pairing affects the anticipatory processing of upcoming stimulus. Individuals with greater context processing make more errors and demonstrate increased reaction times for target violations of an expected cue-target pairing compared to when the target appears under a non-response cue. The dissociable shifts in behavior observed in tasks like the AX-CPT highlight the brain's ability to learn and adapt to environmental probabilities. Moreover, behavioral optimization does not occur globally, but rather serves to minimize effort where it is most advantageous to do so.

Similar performance patterns indexing shifts in cognitive control have been observed in the absence of context learning. When implicitly primed with goal reinforcing cues emphasizing speed, inhibition of Stroop interference effects improved with no impact on facilitation effects (Parris, Bate, Brown, & Hodgson, 2012). Interestingly, not only did performance improve for incongruent trials, but performance declined for congruent and neutral trials. When primed for speed, advance activation of inhibitory mechanisms may improve or optimize performance of the more difficult trial type. However, those same mechanisms interfered with simpler automatic processes resulting in slower responding for congruent trials. This particular pattern argues for a domain general influence of cognitive control where unnecessary application of controlled processing equalizes attentional allocation and stimulus evaluation leading to a decreased reliance on automatic processes.

1.1.2 Current theory

Within-session, block effects are oftentimes viewed as practice related improvements, improvements in neural efficiency, or the summed effect of local adjustments over time (Jonides, 2004). An example of the latter stance can be found in the conflict monitoring hypothesis which posits that long term adjustments can be explained by temporally local fine-tuning of top-down signal biasing geared toward minimizing conflict (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Miller & Cohen, 2001). Control is augmented upon encountering situations of prepotent response inhibition, error commission, and underdetermined responses where the optimal task response is not appropriately activated. In these cases current trial behavior can be predicted by an appropriate weighting of the conflict in preceding trials, suggesting conflict-induced cognitive

control should reach a steady-state relatively quickly assuming a consistent degree of conflict (Cho et al., 2002; Jones, Cho, Nystrom, Cohen, & Braver, 2002). However, the conflict monitoring hypothesis does not per se argue for the discussed behavioral impairments in automatic processing; rather, adaptation-by-binding—an extension of the conflict monitoring account which argues conflict adjustments are achieved by strengthening all active task representations—argues that experimental contexts eliciting higher arousal result in behavioral biasing by overlearning a particular task operation (Verguts & Notebaert, 2009).

1.2 CORTICAL OSCILLATIONS

While the mechanisms underlying these behavioral patterns are unclear, cognitive neuroscience methods have provided a means for elucidating them. Electro- and magnetoencephalographic (EEG and MEG, respectively) recordings and spectral analytic approaches provide a useful summary measure of cortical neural computation by quantifying the rhythmic fluctuations of electro-magnetic fields generated by the coordinated activity of pyramidal neurons. While not as ideal for spatial localization as other approaches (e.g. fMRI), EEG and MEG offer a chance to index the temporal characteristics of neural activity in a non-invasive manner. In particular, spectral analyses have allowed researchers to characterize the ongoing rhythmic fluctuation of these fields by their component frequencies in order to build upon more traditional event related potential analyses (Tallon-Baudry & Bertrand, 1999).

Cortical oscillatory activity appears to be organized into specific frequency bands, namely, theta (4-8 Hz), alpha (9-13 Hz), beta (14-29 Hz), and gamma (30-80 Hz), which also maps to differentially to different cognitive functions. For example, oscillations in the alpha

frequency band are purported to relate to ongoing inhibitory processing (Klimesch, Sauseng, & Hanslmayr, 2007). Event related synchronization (ERS) in the alpha band are considered to reflect active inhibition of task-irrelevant regions while event related desynchronization (ERD) is hypothesized to reflect a release of inhibition on task-relevant regions. Thus, increases and decreases in alpha power are thought to indirectly and inversely reflect cognitive load, especially in cases where focused attention and active inhibition of distracting information are required. In contrast, beta band oscillations are considered to be a default feature of the motor cortex and ERDs are observed during anticipatory motor planning and control (Engel & Fries, 2010; Siegel, Donner, & Engel, 2012). By contrast, gamma band oscillations have been implicated as an important network mechanisms indexing local cortical processing and ERSs has been observed in studies of visual feature binding (Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998), working memory maintenance (Howard et al., 2003), and cognitive control (Cho, Konecky, & Carter, 2006; Kieffaber & Cho, 2010; Minzenberg et al., 2010).

1.3 HYPOTHESES

Given that cortical synchrony can be sensitive to phasic control demands, it is feasible that ongoing rhythms, often subsumed into some measure of a baseline, will index a more continuous cognitive state reflecting the predictability of the task environment. To investigate this question, we examined the extent to which trial proportions, and by extension the predictability of a given trial type, biases behavioral performance of a proactive control task. As an ancillary research question, we sought to determine observed differences could be attributed to the prevalence of high control events or to the predictability of a given trial type. Further, we asked whether

ongoing EEG synchrony differences could explain such biasing. We hypothesized two possibilities. First, according to the conflict monitoring framework (Botvinick et al., 2001), with increasing ongoing control demands, the congruency effect observed in a cognitive control task would reduce (i.e., behavioral measures converge) as continuous conflict signals would reinforce controlled action. Second, if cognitive control is instantiated according to the adaptation-by-binding hypothesis (Verguts & Notebaert, 2009), the increased continuous demand would result in impaired performance of more automatic behaviors.

2.0 METHODS

2.1 PARTICIPANTS

Sixty undergraduate students at the University of Pittsburgh enrolled an introductory psychology course were recruited for this study. Informed consent was obtained in accordance with the University of Pittsburgh Institutional Review Board. Participants received course credit for their participation. Three participants were removed from the final analyses—two for being behavioral outliers (Cook’s $D > .05$), and one for poor EEG data quality. As such, the final sample consisted of 57 participants of predominantly young adults males ($M = 19.5$ years, $s = 2.5$; 20 F/37 M) (See Table 1 for group demographic breakdown).

Table 1: Group demographic information.

Demographics	Context (Proportion Incongruent)		
	30%	50%	70%
Count ($N = 57$)	20	18	19
Age (years; M (s))	19.5 (2.0)	19.1 (1.3)	19.9 (3.7)
Female	6	6	8
Left Handed	1	1	1

2.2 TASK PARADIGM

Participants completed variants of a proactive control task known as the preparing to overcome prepotency task (POP; Cho et al., 2006; Minzenberg et al., 2010; Snitz et al., 2005). The task taps into prepotent response inhibition capabilities by capitalizing on the Simon compatibility effect for lateralized response mappings (Simon, 1969). In the cued, preparatory phase, the participant is presented with a green or red square for 500 ms indicating the response mapping for the current trial. A 750 ms delay follows during which participants view a central fixation cross. Finally in the stimulus-response phase, a right or left pointing arrow appears for 500 ms to which the participant is instructed to provide a speeded response with a button press of either index finger. The color to instruction mapping was counterbalanced across participants. In the low control mapping (i.e., Congruent), an ipsilateral button press was required; in the high control mapping (i.e., Incongruent), a contralateral button press was required.

To address the core prediction of this study, control context was manipulated by adjusting the relative trial-type proportions. Participants either completed a version with 30% incongruent trials (i.e., 30% context), 70% incongruent trials (i.e., 70% context), or a 50% split of low and high control trials (i.e., 50% context). Regardless of trial-type proportion, participants completed six task blocks of 88 total trials. Within each block, trial order was pseudo-randomized and uniformly distributed with the relative proportionality being the only restraint. Trial-type proportions and color-instruction mappings were assigned to participants in a between-subjects fashion using a Latin-square assignment to conditions.

2.3 EEG RECORDING AND PREPROCESSING

High-density electroencephalography data were collected with 129-channel Geodesic Sensor Net (GSN-200; EGI, Inc., Eugene, OR). Impedances were kept under 60 k Ω . Data were digitized at 500 Hz with an elliptical passband of 0.01 to 100 Hz. Preprocessing and analyses were conducted in Matlab (MathWorks, Inc., Natick, MA). Continuous EEG data were filtered offline with an ideal 60 Hz-notch filter prior to a 0.2 to 100 Hz bandpass. Data were segmented into 2600 ms epochs beginning 700 ms prior to cue onset then entered a preprocessing pipeline in order to confine analyze to artifact free EEG. Briefly, each segment distribution and spectral properties were assessed. Values were z-score transformed in reference to ideal EEG distributions and accordingly labelled as poor quality segments if exceeding 3 standard deviations. A principal components analysis based approach was also run in order to capture temporal and spatial deviations in the correlation structure of the data. This dual approach aimed to remove local, non-stereotypical artifacts while retaining clean EEG together with artifacts that could better be modeled and removed through independent components analysis (ICA).

Viable segments were then submitted to a two stage ICA for artifact removal. First, a FastICA decomposition generated an initial component weight matrix for use with an extended Infomax ICA algorithm. This two stage approach was found to yield faster and more stable decompositions of EEG data. Furthermore, surrogate electrooculogram (EOG) channels were pre-computed and included in the training data to facilitate identification of ocular artifacts (Hassler, Trujillo, & Gruber, 2011; Keren, Yuval-Greenberg, & Deouell, 2010). Finally, the resulting unmixing matrix was applied to all data (including marked 'poor' data), and components capturing blink, electrocardiographic (ECG), saccade, and muscle artifacts were removed if matching the spectral properties of such artifacts. Reconstructed data were

reevaluated for poor quality segments which were removed and data was interpolated. In cases of removed segments mapping to adjacent channels interpolation would provide a poor estimate for missing data; accordingly in such cases, data were removed from averaging and further analyses. Data were then re-referenced to the global average and entered time-frequency analysis.

2.4 DATA ANALYSES

2.4.1 Spectral analyses

Spectral amplitude estimates were derived using complex Morlet transformations. To assess the frequency content of the data, wavelet transformations of whole epochs were computed over the range of 4 to 50 Hz in 1 Hz linear steps with $c = 5$. As per Tallon-Baudry and Bertrand (1999), cue-locked (i.e., evoked) frequency activity was derived by computing wavelet transforms of the averaged event related potentials (ERPs) for each condition. Non-cue-locked (i.e., induced) activity was assessed by computing wavelet transformations on individual epochs prior to condition averaging. Since this approach includes both phase- and non-phase locked components of the underlying signal, evoked activity was subtracted from the mean of the transformed time series. However, observation revealed the difference in segment counts contributing to the ERPs resulted in noisier time series averages for conditions with fewer trials which in turn increased estimates of evoked amplitudes. Consequently, induced averages were computed by subtracting evoked averages generated from trial-matched ERPs. Induced means were then summarized in time, frequency, and scalp location to reduce the impact of multiple statistical tests on type 1 error. Thus, data were averaged according to five frequency bands (i.e., theta, 4-8 Hz; alpha, 9-

13 Hz; low beta, 14-18 Hz; high beta, 19-30 Hz; and gamma, 31-49 Hz), four time bins aligned with trial phases (i.e., baseline: -500-0; cue: 0-500; delay: 500-1250; and probe: 1250-1750) and fifteen scalp regions (left, midline, and right clusters of electrodes corresponding to approximate 10-20 designations of frontopolar, frontal, central, parietal, and occipital electrodes; see Figure 1). Finally, spectral amplitudes were natural log transformed to normalize distributions.

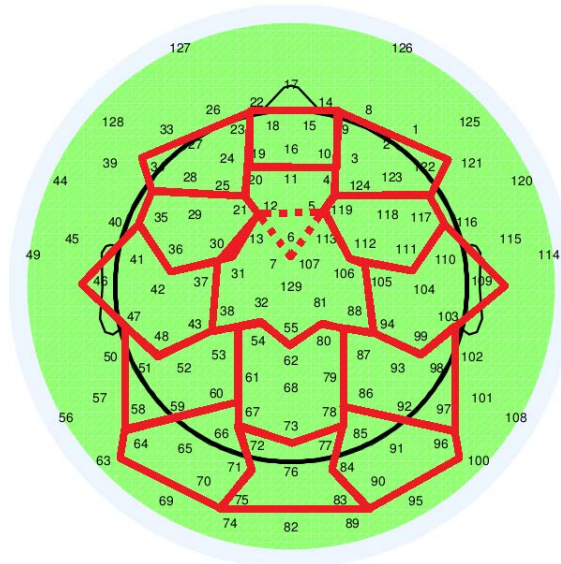


Figure 1: Scalp region used for EEG analyses. Electrodes were divided into left, right, and midline sets of electrodes approximating frontopolar (top), frontal, central/temporal, parietal, and occipital (bottom) activities. Numbers correspond to electrode locations and number designations on a 129 channel Geodesic Sensor Net (GSN-200; EGI, Inc., Eugene, OR). Note, electrode 6 contributed to both frontal and central midline region means.

2.4.2 Statistical Analyses

To assess behavioral differences across contexts, 3 x 2 repeated measures analyses of covariance (RM-ANCOVA) of reaction times (RT) and accuracy (ACC) were conducted in SPSS (IBM, inc., Armonk, NY) with context (30%, 50% and 70% incongruent trials) and condition (high- and low-control) as factors. To control for individual and group differences in trial-to-trial conflict adjustment, summary Gratton measures (i.e., cI-iI+iC-cC) were included as covariates.

Analyses of EEG spectral amplitudes were analogous to behavioral measures with the caveats that tests were conducted in Matlab to iterate across the set of regions, frequency bands, and time bins. Since RTs, ACCs, and EEG spectra were non-normally distributed, ANCOVA results were computed using log (RT and EEG) and arcsine (ACC) transformed values. For behavioral measures, an $\alpha = .05$ was used to determine statistical significance; however, a false discovery rate (FDR) corrected $\alpha = .0051$ was used to address the type 1 error inflation from iterating tests across frequency bands, time bins, and scalp regions. Only correct trials contributed to RT and EEG spectral amplitude means. Corresponding figures show raw data and variances.

For both behavioral and EEG analyses, post-hoc paired t-tests were conducted to confirm the strength and direction of within group condition differences. Post-hoc t-tests were Bonferroni corrected for nine condition comparisons (i.e., three contexts by three representative regions; $\alpha = .0055$). To assess a potential functional relationship between EEG and behavioral measures, Spearman correlation coefficients were calculated between RT and ACC measures and time/frequency bins identified as having a significant Context x Condition interaction. Separate correlations were calculated for each group and condition (i.e., 30% context, incongruent EEG X 30% context, incongruent ACC) As the Spearman rank correlation is a nonparametric test, raw data were used for these tests. For correlations, FDR and Bonferroni corrections were determined to be too conservative as the sample size for each group is relatively low for robust correlation analyses. Thus, correlation results were interpreted with critical $\alpha = .05$, and an informal approach outlined below was used to identify reliable estimates. Finally, Spearman coefficients were Fisher transformed and compared across groups with Welch-Satterthwaite t-tests to determine significant difference in coefficient estimates between contexts (Fieller, Hartley, & Pearson, 1957).

3.0 RESULTS

3.1 BEHAVIORAL MEASURES

Two-way ANCOVA of ACC measures revealed a strongly significant Context x Condition interaction, $F(2, 53) = 11.78, p < .001, \eta_p^2 = 0.31$, (Figure 2A). Post hoc analyses revealed that the interaction reflected an inverse relationship between condition ACC and proportion within each context (see Table 2 for means and standard deviations). As expected and consistent with previous studies, in the 30% context, ACC for incongruent trials ($M = 95.25, s = 3.51$) was worse than for congruent trials ($M = 96.65, s = 2.36$), $t(19) = -2.50, p = .022, 95\% \text{ CI } [-0.13 -0.01]$ (Note: Confidence intervals represent transformed data, not raw values). By contrast, this pattern was completely reversed in the 70% context where incongruent trial ACC ($M = 96.70, s = 2.45$) was better than congruent trial ACC ($M = 94.21, s = 4.07$), $t(18) = 4.09, p = .001, 95\% \text{ CI } [0.06 0.17]$. When trial-type proportions were equal, ACC was near identical between conditions ($M_{Inc} = 95.58, s_{Inc} = 3.64; M_{Con} = 95.57, s_{Con} = 3.12$), $t(17) = -0.40, p = .692, 95\% \text{ CI } [-0.03 0.04]$. Since the relationship between context and condition was inverse and symmetrical, neither the context, $F(2, 53) = .04, p = .963, \eta_p^2 = 0.00$, nor the condition, $F(1, 53) = 0.02, p = .895, \eta_p^2 = 0.00$, main effects reached significance.

Reaction times revealed a different pattern (Figure 2B; Table 2). While the 50% context appeared to have overall slower RTs ($M_{Inc} = 447, s_{Inc} = 180; M_{Con} = 426, s_{Con} = 185$) than both

the 30% context ($M_{Inc} = 414, s_{Inc} = 105; M_{Con} = 385, s_{Con} = 90$) and the 70% context ($M_{Inc} = 404, s_{Inc} = 90; M_{Con} = 361, s_{Con} = 76$), this effect was not found to be significant, $F(2, 53) = 0.48, p = .623, \eta_p^2 = 0.02$, likely due to the comparatively higher variability in the 50% context group. Nor was the Context x Condition interaction significant, $F(2, 53) = 1.81, p = .173, \eta_p^2 = 0.06$. Regardless of context, a strongly significant main effect of condition reflected the consistency of condition differences across contexts, $F(1, 53) = 35.85, p < .001, \eta_p^2 = 0.40$, such that the RT for incongruent trials was slower than congruent trials, $t_{30\%}(19) = 6.20, p_{30\%} < .001, 95\% CI_{30\%} [0.19, 0.37]; t_{50\%}(17) = 3.11, p_{50\%} = .006, 95\% CI_{50\%} [0.14, 0.75]; t_{70\%}(18) = 3.55, p_{70\%} = .002, 95\% CI_{70\%} [0.25, 0.96]$.

Table 2: Behavioral means and standard deviations across groups.

Measure	Condition	Context Means (M (s))		
		30%	50%	70%
Accuracy (%)	Incongruent	95.25 (3.51)	95.58 (3.64)	96.70 (2.45)
	Congruent	96.65 (2.36)	95.57 (3.13)	94.21 (4.07)
Reaction Time (ms)	Incongruent	414.36 (105.34)	447.16 (180.26)	404.48 (90.17)
	Congruent	385.06 (90.28)	425.81 (184.98)	361.22 (75.57)

As a potential control for conflict adjustment differences across context, summary measures were included as covariates for the primary behavioral analyses. Additionally, Gratton condition means for ACC (Figure 2A inlays) and RT (Figure 2B inlays) were analyzed to test for context related differences as well. For both measures, an expected Previous Trial x Current Trial Congruency interaction was observed, ACC: $F(1, 54) = 136.29, p < .001, \eta_p^2 = 0.72$; RT: $F(1, 54) = 12.64, p = .001, \eta_p^2 = 0.19$. An additional previous trial main effect was observed for ACC, $F(1, 54) = 11.18, p = .002, \eta_p^2 = 0.17$ while no other significant effects were found (all F s < 1). However, for RTs, significant differences were observed for previous trial condition, $F(1, 54) =$

17.52, $p < .001$, $\eta_p^2 = 0.25$, and current trial condition, $F(1, 54) = 50.62$, $p < .001$, $\eta_p^2 = 0.48$. The group main effect and all other interactions were not significant (all F s < 2.6).

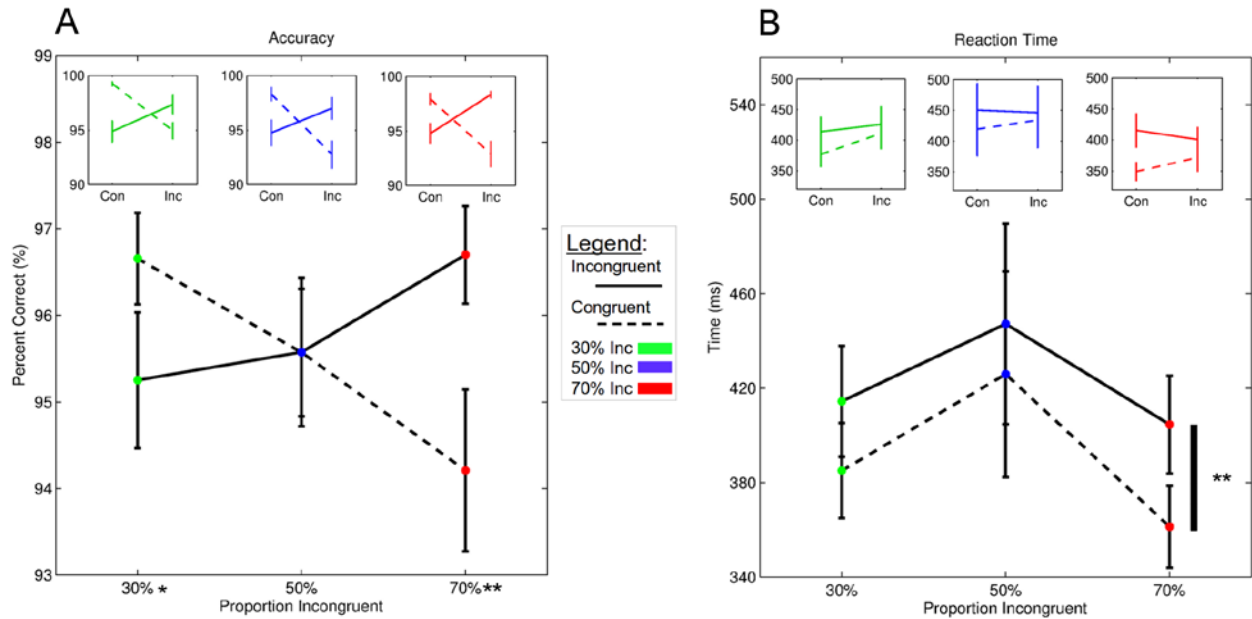


Figure 2: Behavioral means for accuracy (A) and reaction time (B) \pm standard error for the mean (*SEM*). Controlling for Gratton effects, participants are less accurate for conditions that occur less frequently while reaction time differences remain relatively consistent across proportions. Inlays depict Gratton-based averages within each context (labeled by color). Gratton patterns in accuracy did not significantly differ across contexts; however, when divided into Gratton conditions, significant reactions differences were observed for current trial condition by context, and previous trial condition by context separately. * $p < .05$, ** $p < .005$.

3.2 EEG SPECTRAL MEASURES

3.2.1 General patterns

Though no region, time, or frequency band met significance for a context main effect, a broad overview of synchronous oscillations demonstrate several global and local condition and Context x Condition effects (see Table 4 in Appendix A for the full set of ANOVA results). In the pre-

cue baseline, a significant alpha condition effect was observed across all regions save for the right frontopolar, frontal, and central (i.e., right temporal; Figure 3) regions with a Context x Condition interaction in the left frontal baseline (Figure 4). During the cue phase, a midline frontal and broad posterior condition effect was observed for theta-band synchrony where greater theta amplitudes were observed for incongruent trials. Additionally, a left frontal alpha and low beta interaction effect was complemented by wider spread midline central, parietal, and occipital, and right parietal/occipital effects ranging alpha- to high beta-band.

During the delay period, condition main effects were observed in midline central high beta- and right parietal gamma-bands. The interaction maps revealed significant condition differences near globally across the scalp for the alpha- through high beta-bands. These patterns will be detailed further below. Finally, during the probe phase, broad alpha-, beta-, and gamma-band differences were observed in the midline central region and across the span of posterior regions with a low beta band difference in midline frontopolar. The interaction effects were less focal. Alpha to high-beta differences were prominent across what appeared to be a diagonal axis from left frontopolar to right parietal/occipital regions with no effects seen in the right and midline frontopolar and left occipital. Given the prominence of alpha and beta effects across both time and region, further detailed analyses were carried out within these regions of interest.

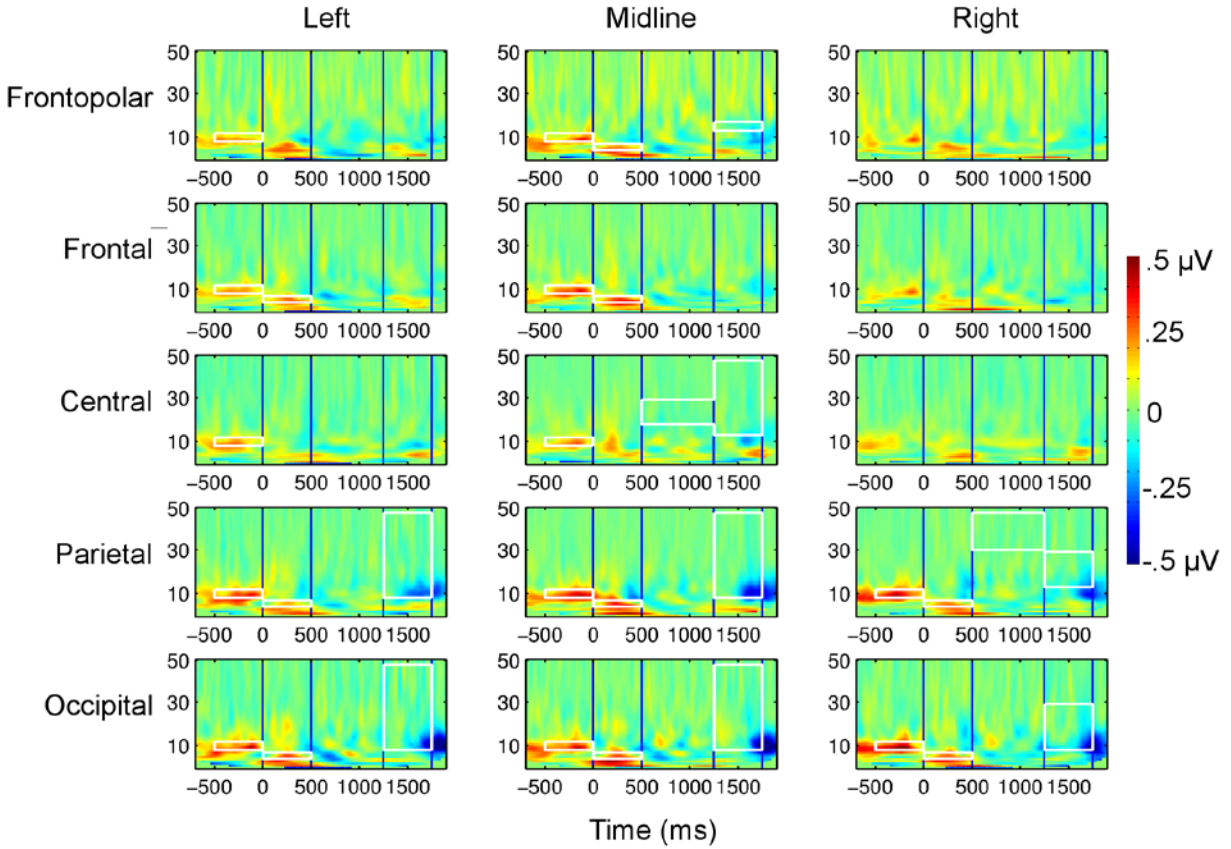


Figure 3: Incongruent-Congruent spectral mean differences collapsed across context. Frequency bands and time bins showing significant condition differences are outlined by white boxes. Most notably, a significant condition main effect reveals greater alpha synchrony in the baseline of correct incongruent trials compared to congruent trials. Vertical bars mark cue onset, delay start, and probe onset/offset.

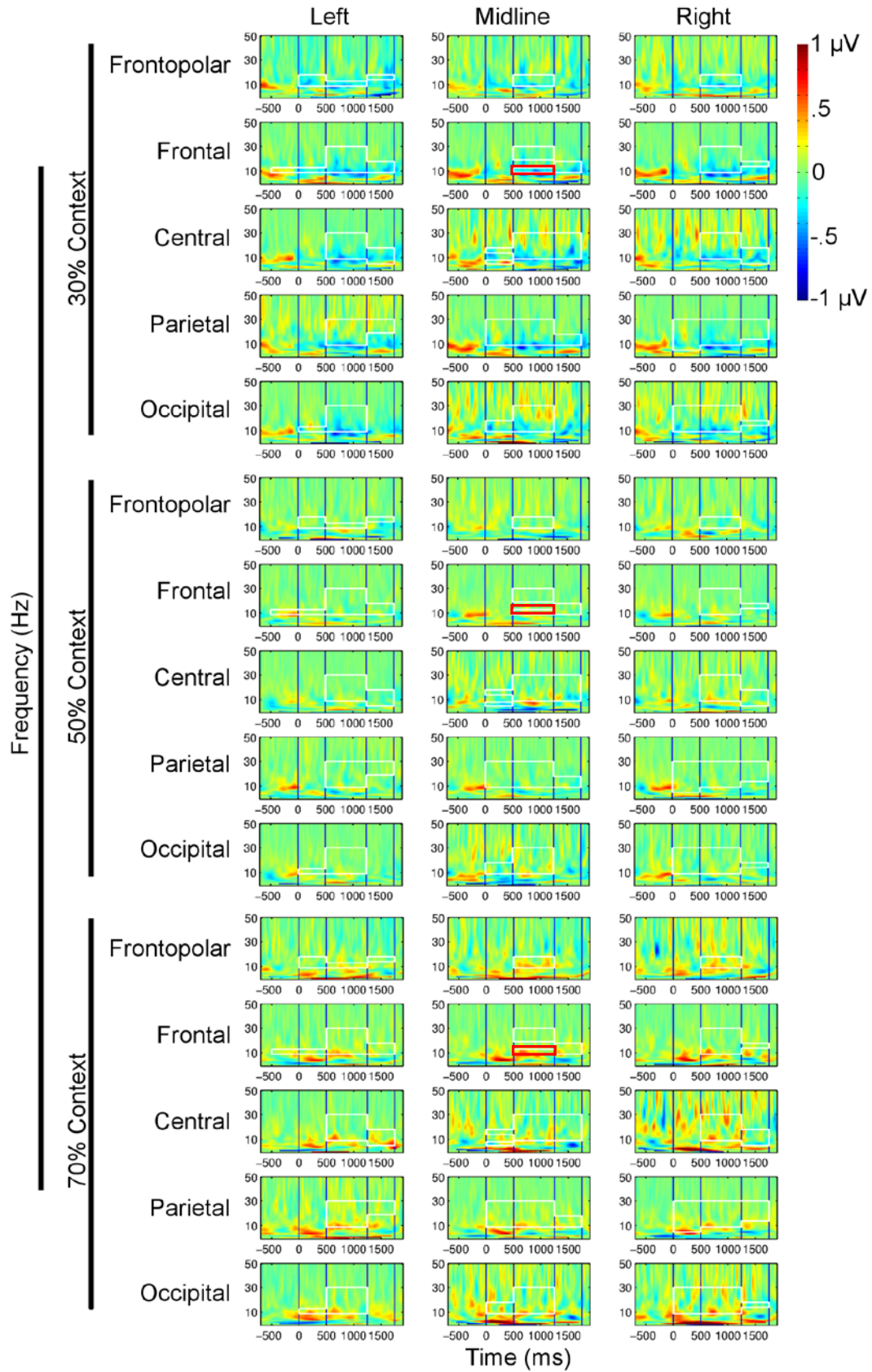


Figure 4: Incongruent-Congruent spectral mean differences across contexts. White boxes indicate significant interaction effects. Correlation effects discussed reflect activity in the region marked in red. Broadly speaking, interaction patterns tend to follow the trend of congruent > incongruent for the 30% context and incongruent > congruent for the 70% context, with synchrony being mostly equal between conditions for the 50% context. Vertical bars mark cue onset, delay start, and probe onset/offset.

3.2.2 Alpha band

Analyses of alpha band amplitudes revealed two broad patterns. First, a significant condition main effect was observed in all scalp regions save for the right frontopolar, frontal, and central locations (Figure 3). Taking the midline frontal (F), $F(1,54) = 18.97, p < .001, \eta_p^2 = 0.26$, central (C), $F(1,54) = 8.89, p = .004, \eta_p^2 = 0.14$, and parietal (P), $F(1,54) = 11.52, p = .001, \eta_p^2 = 0.18$, regions as representative, the effect is driven by greater pre-stimulus activity for incongruent trials ($M_F = 7.97, s_F = 2.97; M_C = 7.68, s_C = 3.15; M_P = 10.52, s_P = 4.74$) than for congruent trials ($M_F = 7.60, s_F = 2.71; M_C = 7.39, s_C = 2.89; M_P = 10.16, s_P = 4.56$) in the 30% context, $t_F(19) = 3.68, p_F = .002, 95\% CI_F [0.16, 0.57]; t_C(17) = 2.81, p_C = .011, 95\% CI_C [0.07, 0.50]; t_P(18) = 2.37, p_P = .029, 95\% CI_P [0.04, 0.67]$. A similar pattern emerged within the parietal region in the 70% context ($M_{PInc} = 9.91, s_{PInc} = 3.28; M_{PCon} = 9.62, s_{PCon} = 3.49$), $t(17) = 2.12, p_P = .050, 95\% CI_P [0.00, 0.58]$, (Figure 5A) though the effect does not meet the adjusted threshold for significance. No other significant condition differences were observed across the 50% and 70% contexts (see Table 3 for additional means and standard deviations).

A significant Context x Condition interaction in the delay trial phase mirrored the ACC interaction across all scalp regions, Frontal: $F(2,54) = 11.60, p < .001, \eta_p^2 = 0.30$; Central: $F(2,54) = 11.30, p < .001, \eta_p^2 = 0.30$; and Parietal: $F(2,54) = 15.91, p < .001, \eta_p^2 = 0.37$, (Figure 4). Similar to ACC means, in the 30% context, incongruent amplitudes ($M_F = 6.18, s_F = 2.07; M_C = 5.95, s_C = 2.16; M_P = 7.30, s_P = 2.84$) were lower than for congruent trials ($M_F = 6.52, s_F = 2.36; M_C = 6.26, s_C = 2.39; M_P = 8.00, s_P = 3.37$), $t_F(19) = -3.13, p_F = .006, 95\% CI_F [-0.56, -0.11]$;

$t_{C(19)} = -3.80$, $p_C = .001$, 95% CI_C [-0.47, -0.13]; $t_{P(19)} = -4.06$, $p_P < .001$, 95% CI_P [-1.06, -0.34]. No alpha synchrony differences were observed in the 50% context (all $p_s > .70$). An opposite directionality was found in the 70% context. Delay period amplitudes were greater for incongruent trials ($M_F = 5.84$, $s_F = 2.17$; $M_C = 6.15$, $s_C = 2.06$; $M_P = 7.69$, $s_P = 2.54$) compared to congruent trials ($M_F = 5.63$, $s_F = 2.04$; $M_C = 5.84$, $s_C = 1.88$; $M_P = 7.11$, $s_P = 2.26$), $t_{F(18)} = 3.27$, $p_F = .004$, 95% CI_F [0.08, 0.35]; $t_{C(18)} = 3.36$, $p_C = .003$, 95% CI_C [0.12, 0.51]; $t_{P(18)} = 4.07$, $p_P < .001$, 95% CI_P [0.28, 0.88] (Figure 5B; Table 3). Additionally, significant interactions were observed during the baseline in the right frontal region; during the cue period for right and midline frontopolar, right frontal, midline and left parietal, and all occipital regions; and during the probe period for right and midline frontal, all central, and midline parietal regions (See Table 4 for full set of all significant ANOVA results).

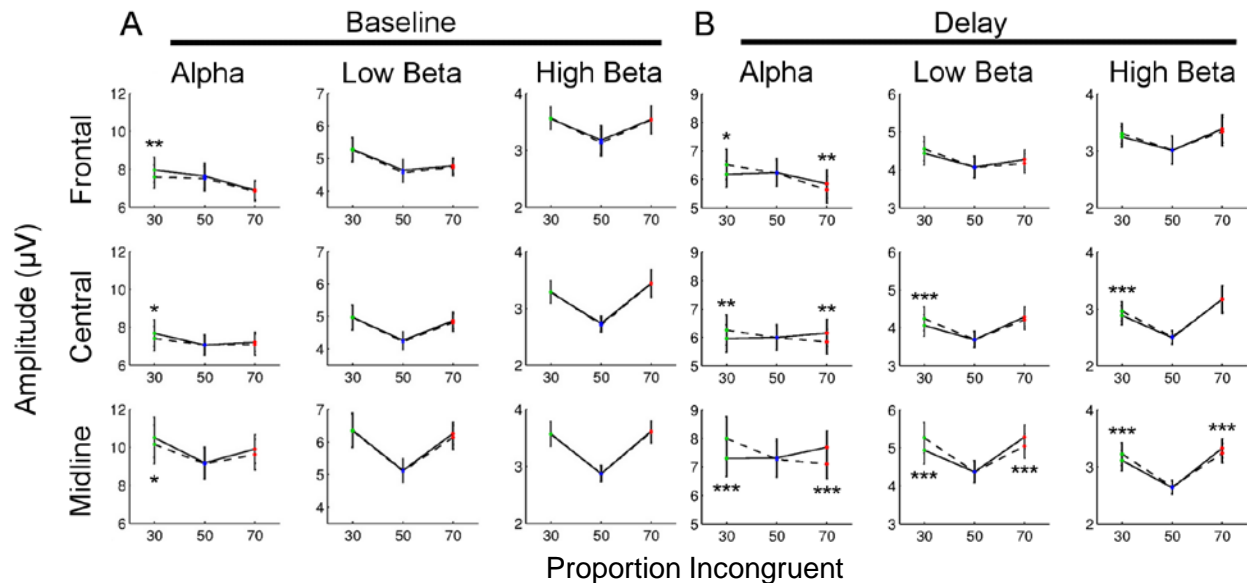


Figure 5: Summary plots for the baseline (A) and delay (B) periods. Context by condition means \pm SEM for alpha-, low beta-, and high beta-band amplitudes. (A) Alpha synchrony is somewhat equal in the baseline period with a primary incongruent $>$ congruent relationship in the 30% context baseline. (B) During the delay, alpha shows a complete reversal in the ordinal relationship between the 30% and 70% contexts. Generally speaking, the low and high beta patterns resemble a weaker version of the alpha-band patterns. * $p < .05$, ** $p < .005$. *** $p < .001$.

Table 3: Spectral means and standard deviations across groups.

Measure	Condition	Context Means (<i>M</i> (s))		
		30%	50%	70%
Baseline Synchrony (μV) [†]				
Frontal Alpha	Incongruent	7.97 (2.97)	7.64 (2.84)	6.9 (2.16)
	Congruent	7.60 (2.71)	7.52 (2.74)	6.85 (2.31)
Central Alpha	Incongruent	7.68 (3.15)	7.05 (2.22)	7.22 (2.19)
	Congruent	7.39 (2.89)	7.07 (2.23)	7.08 (2.38)
Parietal Alpha	Incongruent	10.52 (4.74)	9.18 (3.55)	9.91 (3.28)
	Congruent	10.16 (4.56)	9.14 (3.49)	9.62 (3.49)
Delay Synchrony (μV) [†]				
Frontal Alpha	Incongruent	6.18 (2.07)	6.24 (2.04)	5.84 (2.17)
	Congruent	6.52 (2.36)	6.22 (1.93)	5.63 (2.04)
Central Alpha	Incongruent	5.95 (2.16)	6.00 (1.91)	6.15 (2.06)
	Congruent	6.26 (2.39)	5.98 (1.80)	5.84 (1.88)
Parietal Alpha	Incongruent	7.30 (2.84)	7.32 (2.85)	7.69 (2.54)
	Congruent	8.00 (3.37)	7.27 (2.69)	7.11 (2.26)
Frontal Low Beta	Incongruent	4.44 (1.37)	4.07 (1.21)	4.27 (1.12)
	Congruent	4.55 (1.42)	4.07 (1.20)	4.17 (1.09)
Central Low Beta	Incongruent	4.06 (1.29)	3.68 (0.88)	4.29 (1.13)
	Congruent	4.24 (1.40)	3.70 (0.89)	4.21 (1.10)
Parietal Low Beta	Incongruent	4.94 (1.63)	4.37 (1.22)	5.29 (1.35)
	Congruent	5.26 (1.80)	4.37 (1.21)	5.05 (1.38)
Frontal High Beta	Incongruent	3.25 (0.80)	3.01 (1.06)	3.39 (1.08)
	Congruent	3.30 (0.79)	3.02 (1.02)	3.34 (1.08)
Central High Beta	Incongruent	2.89 (0.75)	2.49 (0.50)	3.17 (1.00)
	Congruent	2.96 (0.77)	2.51 (0.49)	3.17 (1.06)
Parietal High Beta	Incongruent	3.11 (0.80)	2.64 (0.50)	3.33 (0.73)
	Congruent	3.22 (0.88)	2.65 (0.50)	3.24 (0.74)

[†] Means presented are in μV ; however, statistical tests were conducted with natural log transformed values.

3.2.3 Beta bands

Closer inspection of beta-band differences revealed high beta interactions in midline frontal, $F(2,54) = 9.32, p < .001, \eta_p^2 = 0.26$, central, $F(2,54) = 7.32, p = .002, \eta_p^2 = 0.21$, and parietal, $F(2,54) = 28.07, p < .001, \eta_p^2 = 0.51$, regions, whereas low beta differences were only observed in central, $F(2,54) = 8.24, p = .001, \eta_p^2 = 0.23$, and parietal, $F(2,54) = 21.82, p < .001, \eta_p^2 = 0.45$, regions during the delay period. Post hoc analyses of the low beta results, found the

interaction to highlight significantly greater low beta amplitudes for congruent trials in the 30% context, $t_C(19) = -3.94$, $p_C < .001$, 95% CI_C [-0.27, -0.08]; $t_P(19) = -5.25$, $p_P < .001$, 95% CI_P [-0.46, -0.20] (see Table 3 for means and standard deviations). Only the parietal location showed a significant, and directionally opposite effect in the 70% context, $t_P(19) = 4.27$, $p_P < .001$, 95% CI_P [0.12, 0.36]. A similar direction of findings (30%: incongruent < congruent; 70%: incongruent > congruent) was observed across the full set of high beta results. Congruent means were greater for the 30% context, $t_C(19) = -5.06$, $p_C < .001$, 95% CI_C [-0.11, -0.04]; $t_P(19) = -4.84$, $p_P < .001$, 95% CI_P [-0.16, -0.06], and incongruent means were greater for the 70% context only for the parietal region, $t_P(18) = 4.97$, $p_P < .001$, 95% CI_P [0.05, 0.13]. Interestingly, no post hoc condition comparison of midline frontal high beta amplitudes met threshold for significance suggesting the interaction is due to specific condition differences between groups that did not meet threshold for a significant context main effect. Though considered as a whole, the effects observed in the beta ranges mirror the direction of effects in the alpha-band.

3.2.4 Correlational analyses

Given the similarities between the alpha band and the ACC interactions, correlation analyses were conducted within context and condition to address a potential functional relationship. To avoid overly conservative multiple comparison corrections, an ad hoc intersection approach was taken to identify points of reliable association. Thus, correlation analyses were limited to those regions within the set of regions and times with significant interactions. Only those points with a significant relationship in at least two group/condition sets were considered for further analysis. From this approach, the frontal midline regions was found to correlate significantly with incongruent ACC in the 30% and 70% contexts (Figure 4, red outline). Closer inspection

revealed the general direction of Spearman coefficients to be opposite for the 30% and 70% contexts. Where alpha-band activity displayed a positive monotonic association with ACC in the 30% context, $r_{s30\%}(18) = 0.51$, $p_{30\%} = .025$, 95% CI_{30%} [0.08, 0.77], a negative monotonic relationship was found with ACC in the 70% context, $r_{s70\%}(17) = -0.51$, $p_{70\%} = .028$, 95% CI_{70%} [-0.78, -0.07], (Figure 6). A direct comparison of these two coefficients indicated a significant difference between the positive relationship in the 30% context and the negative relationship in the 70% context, $t(31.21) = 3.00$, $p = .006$, 95% CI [0.33, 1.89]. Taken together, this set of patterns reveals an inverted-U relationship between alpha-band synchrony and incongruent ACC as the proportion of incongruent trials increases.

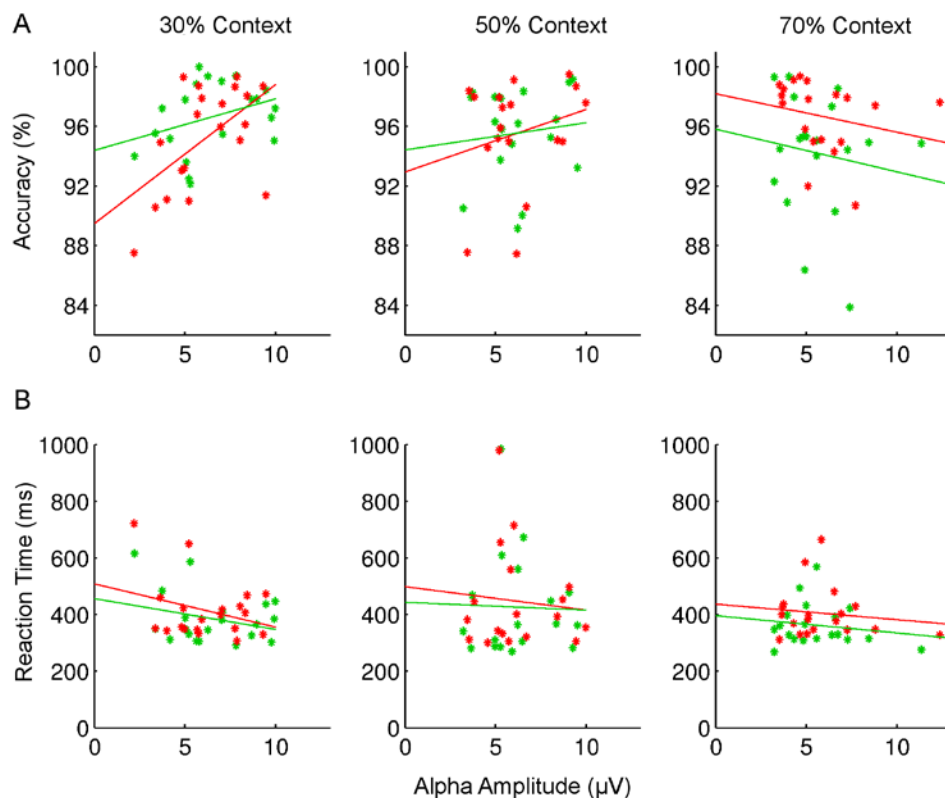


Figure 6: Scatter plots of the relationship between alpha synchrony in the midline frontal region and accuracy (A). For incongruent, a context dependent positive monotonic association was found in the 30% context, whereas a negative monotonic relationship was found in the 70% context. (B) No significant relationships were found within reaction time.

4.0 DISCUSSION

4.1 SUMMARY

The current study sought to investigate the effect of the tonic influences of task expectation on cognitive control processes. We presented participants with one of three possible experimental contexts. The 30% and 70% contexts were matched for overall predictability—differing only in difficulty in the dominant trial type. The 50% case, the even split, is context-neutral and hence the least predictable task environment. We hypothesized two potential patterns of behavior. By the conflict monitoring hypothesis, an increasing degree of higher conflict events would result in low control trial performance resembling high control performance as behavior becomes more controlled overall (Botvinick et al., 2001; Cho et al., 2002; Jones et al., 2002). We did not observe this effect. Rather our findings appeared more consistent with the adaptation-by-binding hypothesis, which posits that one's tonic control state should reflect the expectation to encounter more events requiring controlled processing. The resulting task set reinforcement would cause a behavioral tradeoff wherein performance of low controlled behaviors would suffer (Verguts, Notebaert, Kunde, & Wühr, 2011; Verguts & Notebaert, 2009). Both the behavioral tradeoff in ACC and related EEG synchrony difference support this latter interpretation. Since this effect was parametric with increasing incongruent proportion, the dominant task demand, rather than the likelihood of condition switch, appears to underlie this effect.

Taken as a whole, three broad patterns emerge. First, across contexts, RT differences maintained an expected congruency effect (i.e., incongruent > congruent). Second, the observed interactions between task context and condition for ACC and delay period alpha-band synchrony followed the predicted pattern—ACC and alpha synchrony were overall highest for the most common trial type within any given context. While ACC for incongruent trials improved as the proportion of incongruent trials increased, congruent trial performance, which taps more automatic response pathways, was impaired. This finding was intriguing considering the current task taps preparatory control. One might expect automatic behaviors to remain more stable considering prior warning; however, previous studies employing the POP task reliably find ACC to be the more sensitive behavioral measure at detecting group differences (Cho et al., 2006; Kieffaber & Cho, 2010; Minzenberg et al., 2010). Moreover, a consistent RT congruency effect may be an indicator that the cognitive decision time remains the same across contexts, and the differences in ACC are related to a failure in motor execution (e.g., Kieffaber, Kruschke, Cho, Walker, & Hetrick, 2013). Finally and unexpectedly, increased delay alpha was associated with increased ACC in the 30% context; however, the same alpha increase in the 70% context was associated with a decrease in ACC. Despite the similarity between ACC and alpha delay synchrony, the inverse direction of association suggests a differing functional role of alpha synchrony during delay period preparation.

Additionally, significant condition differences were identified in the pre-trial baseline such that alpha synchrony was greater prior to correct incongruent trials than to correct congruent trials. One common reason for such a finding as a spurious result is the mismatch of trial numbers across the conditions being compared, possibly leading to spurious differences that arise from differences in the SNR of the respective averages. However, trial numbers were

carefully matched in our analyses to address this potential concern. Closer inspection revealed this effect to likely be driven by participants in the 30% context. While the implications of this result are unclear, one potential interpretation is that the cognitive or perceptual state reflected in alpha synchrony in which a person enters a trial is predictive of downstream successful execution of that trial demand (Doppelmayr, Klimesch, Pachinger, & Ripper, 1998; Klimesch, Sauseng, & Hanslmayr, 2007; Lou, Li, Philiastides, & Sajda, 2014; Spaak, de Lange, & Jensen, 2014). Thus by analyzing only correct trials, there may have been a selection bias in the particular trials entering the respective averages, resulting in different baseline activity despite the participant not being able to anticipate the upcoming trial type. Presumably, these prestimulus differences impact trial performance by affecting early perceptual fidelity and top-down versus bottom-up integration (Lou et al., 2014; Mazaheri, DiQuattro, Bengson, & Geng, 2011). Thus, one potential explanation for a baseline difference is that errors may occur when baseline conditions are suboptimal. In such cases, the baseline prior to incongruent error trials may resemble the congruent correct trial baseline assuming the cognitive processing leading to an incongruent error reflects an unprepared state. The current task design resulted in too few error trials, and so future testing of this idea would require a similar cognitive task design optimized to maximize error variability.

4.2 CONNECTIONS WITH PREVIOUS LITERATURE

4.2.1 Context influence on cognitive control behaviors

Differential patterns in RT and ACC may not be surprising considering the dissociable nature of the processes those measures index. Indeed, a cognitive process may take similar computational time, but different instantiations of that calculation can be differentially susceptible to interference, possibly resulting in errors. A study with a similar manipulation of trial-type proportions on Stroop task behaviors found a similar dissociation of control effects (Blais, Harris, Guerrero, & Bunge, 2012). This study found congruent RTs were sensitive to incongruent proportion (i.e., congruent RTs were slower when congruent trials were uncommon), but congruent ACC remained constant across proportion condition. By contrast, incongruent ACC improved when incongruent trials were more common. However, explicit cueing of conflict can also attenuate endogenous sequential conflict effects by reducing the latency of neural correlates of conflict (Correa, Rao, & Nobre, 2009). Taken together, improvements in cognitive control may come at the detriment of more automatic processes suggesting that such processes are linked to the strength and integrity of a particular goal representation. Hence, the enhancement of an intention is sufficient to induce response biasing that simultaneously improves controlled performance while impairing automatic performance.

While we did not observe a parametric slowing of congruent RTs, we did find a similar parametric increase in ACC for incongruent trials. Interestingly, our data diverges from the pattern identified by Blais and colleagues (2012). The complementary decrease in congruent ACC observed in our own data suggests automatic motor responses are less robust to context manipulation than a more automatic and reactive process such as reading. By this logic,

consistency in RT congruency effect indicates stimulus processing and controlled motor responding is consistent across context. Yet, ACC is a function of the novelty of a stimulus, regardless of the probability of switching (e.g., 50% context) or the specific requirement of controlled action (e.g., 70% context). Although this reduction in the congruency effect has been observed in several studies manipulating trial-type proportions (Jiang, van Gaal, Bailey, Chen, & Zhang, 2013; King, Donkin, Korb, & Egner, 2012; Tzelgov, Henik, & Berger, 1992). Though to our knowledge, only one other study has demonstrated a similar behavioral tradeoff, albeit for a reactive control task (Lungu, Liu, Waechter, Willingham, & Ashe, 2007). Such a finding would not be well explained by the conflict monitoring hypothesis where increasing instances of high conflict events should enhance controlled processing overall.

Assuming a well-tuned control system, the control adjustment that improves incongruent performance may impair congruent trial performance, but not beyond incongruent trial performance. Rather, our findings are consistent with an emerging framework highlighting similarities between error and novelty evaluation (Wessel, Danielmeier, Morton, & Ullsperger, 2012). In an ERP and functional magnetic resonance imaging (fMRI) study, investigators tested a proposal of the adaptation-by-binding hypothesis—that errors and novel events are related due to their similar functional outcomes. Wessel and colleagues (2012) co-localized two well documented ERP phenomena to common neural architecture. The event related negativity (ERN), a large negative deflection in error-locked ERPs, and the novelty-related frontocentral N2 (novelty-N2b), a similarly negative deflection occurring soon after encountering an unexpected stimulus, were both isolated to the same latent component in a blind source separation analysis. A follow-up fMRI study revealed both event types resulted in functional activation of the posterior medial frontal cortex. This combined theoretical and empirical

impetus offers a potential framework to explain the decreased accuracy in—by traditional accounts—what should be an easy task condition.

4.2.2 Alpha-band oscillations

More traditionally, studies of alpha-band oscillations focus on event related synchronization (ERS) and desynchronization (ERD) from a prestimulus baseline reflecting a cortical default operational state (Pfurtscheller & Lopes da Silva, 1999). However, recent years have seen keen interest in refining our interpretation of alpha oscillations. Most notably, the inhibition-timing hypothesis (Klimesch et al., 2007; Klimesch, 2012), argues that alpha ERS reflect the execution of top-down control via active inhibition of task-irrelevant processes. Alpha ERD thus reflect a release of cortical inhibition and are considered indirect evidence of attention orienting and response preparation (Bastiaansen & Brunia, 2001; Capotosto, Babiloni, Romani, & Corbetta, 2009; Kelly, Lalor, Reilly, & Foxe, 2006; Rajagovindan & Ding, 2011; Sauseng et al., 2005). The current analytical approach takes the intentional step measuring non-baselined synchrony, and thus more directly indexes such top-down inhibitory processes. Therefore, the presence of an alpha ERD can be inferred from baseline and delay period means; however, the interpretation of the current alpha synchrony results should be considered as indexing such inhibitory processing.

Phrased in this manner, alpha-band synchrony during the delay likely represents the degree to which active inhibitory processes are adjusted in preparation for a particular action. A similar pattern can be observed during AX-CPT performance (Bickel et al., 2012). This task involves sequentially presented letters with X's being the primary target, but only when presented after an A. All other letter combinations are responded to as non-targets. In performing this task, healthy individuals develop a prepotency toward responding to the dominant trial

type—typically the AX pairing (Braver et al., 2002; Henderson et al., 2012). Bickel and colleagues (2012) found when a no-go cue (B-cue; any non-A cue) was presented in a mostly go (70% AX) context, greater alpha ERS was found prior to the second stimulus. Though when a potential response was required in a context of mostly no-go trials (70% BX; an X presented after a non-A cue), alpha ERD was greater for trial cues signaling a potential go trial (AX).

In the current study, the lower alpha synchrony for incongruent trials observed in the 30% context versus congruent trials follows the interpretation that ERD reflect the engagement of attention (Capotosto et al., 2009; Rajagovindan & Ding, 2011; Sauseng et al., 2005). However, the positive association between alpha synchrony and ACC implies that variability in alpha synchrony may represent active withholding of a motor command as the greater demand is in withholding an improper response. Consequently, this variability, which would be masked by common ERS/ERD methods, may be a computational mechanism by which controlled action is executed—by the intentional suppression of an uncontrolled action. Comparatively, in the 70% context, both the mean condition difference and association direction are reversed. Lower mean alpha synchrony for the congruent condition indicates this to be the more cognitively demanding trial type. This is broadly consistent with a similar study of task conflict where higher alpha-synchrony was observed for trial-type repetitions versus switches (Tang, Hu, & Chen, 2013). Yet, the positive relationship with automatic response inhibition in the 30% context disappears in the 70% context. Rather, the negative association implies that the continuous motor control required by this context serves a functionally different role of alpha. Thus, alpha synchrony increases when the controlled action is withholding a responds; and decreases when the controlled action is preparing a response.

4.3 STRENGTHS AND LIMITATIONS

The present study possesses notable strengths. First, on a theoretical level, the use of a proactive control task provides a stronger foundation to the binding account of cognitive control by reducing the immediate impact of reactive control mechanism, thus emphasizing intentioned control (Correa et al., 2009). Furthermore, the relatively large sample size provided increased statistical power to detect relatively subtle within-subject differences across groups. Additionally, traditional cognitive neuroimaging techniques and analyses typically rely on baseline corrections to better compare cognitive conditions. This approach is necessary for ERP-based analyses as the absolute magnitudes of EEG potentials are typically not easily interpretable and preclude the indexing of non-phase-locked activity. However, spectral analytic approaches facilitate indexing of nonphase-locked activity while also not necessitating baseline correction, which can be useful as the measured prestimulus baseline electrophysiologic activity can be informative. Thus, the technique allows for probing into ongoing cognitive processes throughout all phases of the trial, including more tonic cognitive states. In contrast with many studies that focus on incremental changes from baseline, the current study shows that baseline patterns are functionally important and reflect continuous, state-based cognitive processing. As such, unique patterns of activity were identified that may have otherwise been obscured.

The current study also has some limitations. One primary difficulty resulting from our non-baselined approach lies with our inability to interpret scalp topography in any meaningful way. In this case, the topographical profile of observed frequency effects is largely global. This feature makes predictions regarding potential sources much more difficult, though not at the cost of invalidating the observed effects. Consequently, further research will be required to replicate and hopefully characterize the contributions of such global spectral activity patterns. Current

source localization techniques may need to be refined to capture such global effects within modality. However, a multimodal imaging approach incorporating fMRI, or considering the similar neural architecture underlying error and novelty processing, targeted electrophysiological studies of the medial frontal cortex would offer a promising constraint to the current broad result.

Likewise, in spite of the relatively large sample size, the group sample size was modest ($n = 18 \sim 20$) to detect subtle effects. A between subjects approach was adopted in order to collect a sufficient number of trials for the less frequent condition within each context. Considering the small effect sizes for the observed interactions, a within subject design may elucidate context differences which were masked by intersubject variability (e.g., higher overall RTs for 50% context). In addition to reduced power for between group differences, the smaller sample sizes reduced the ability to infer a functional role of EEG synchrony patterns. Indeed, FDR corrections of nonparametric correlations were found to be too conservative and the adjusted α was determined to be zero. In the absence of a formal statistical adjustment of significance thresholds, the researchers attempted to reduce the impact of type 1 error ad hoc by only interpreting effects meeting traditional significance criteria in multiple groups. Alternative analytical techniques, such as Bayesian modeling or linear ballistic accumulator models, could address the limitations of frequentist and parametric statistical approaches and help to draw more direct inferences of the role of ongoing alpha synchrony to cognitive control behaviors (Brown & Heathcote, 2008; Donkin, Averell, Brown, & Heathcote, 2009; King et al., 2012).

4.4 FUTURE DIRECTIONS

In addition to design and analytical improvements, remaining questions raised by the current study may be addressed in further experiments. One important direction would be further investigation of the inverse relationship between accurate performance and delay period alpha-band synchrony, which raises several potential interpretations. One possibility is that the midline alpha patterns observed are the result of two unique generators with overlapping scalp distributions. If this is the case, higher alpha-band synchrony in one region facilitates accurate responding in low control contexts, whereas increasing synchrony in a second region impairs accurate responding in high control contexts. However, if both alpha patterns result from the same generator with different operating characteristics depending on context, it is likely that a secondary region is mediating the relationship between context and the influence of alpha synchrony on ACC.

Another implication that warrants further investigation of the observed associations between alpha synchrony and behavior is that alpha synchrony may serve a mediating role between other neural processes and behavior. Recently, cross-frequency coupling (CFC)—modulation of a higher frequency amplitude by the phase of a lower frequency (typically, theta to gamma and alpha to gamma)—has been proposed to play an important role in the dynamics and hierarchical organization of a variety of sensory and association cortices (Canolty & Knight, 2010; Park et al., 2011; Tort et al., 2008). In a visual discrimination task, Cohen and van Gaal (2013) found functional specification in CFC patterns in medial frontal (MF) and occipital (OCC) regions with MF favoring theta-alpha coupling while OCC favors alpha-gamma. Specifically, the authors argue that this coupling mechanism serves to integrate signals across functional networks—in this case facilitating adjustments after errors—by translating a

‘foreign’ frequency into a preferred frequency. One prediction made by the adaptation-by-binding account is that cognitive control is exerted by strengthening all active representations. As the POP task is primarily a visuo-spatial control task, the observed alpha may index this strengthening of communication between visual and control regions.

Assuming a relatively superficial cortical locus of alpha activity, transcranial magnetic stimulation (TMS) may be used to induce a temporary lesion to elucidate the causal influence of such synchrony on behavior. Such an approach would also address the question of a single versus multiple generators if performance is impaired in differentially across contexts. Additionally, if alpha synchrony reflects a mediating process, an alternative stimulation technique known as transcranial alternating current stimulation (tACS) may be used to evoke greater neural synchrony in the alpha band which would magnify the impact of context on behavior (Ali, Sellers, & Fröhlich, 2013).

4.5 CONCLUSIONS

In summary, two possible routes toward influencing baseline processes were tested—a more continuous controlled state may arise when one cannot rely on consistent trial-type expectations (i.e., 50% context) or when there is a reasonable expectation that most trials will require controlled behavior (i.e., 70% context). We demonstrated that patterns in ACC are consistent with a binding hypothesis of behavioral adaptation where increasing the proportion of high-control trials results in a performance tradeoff favoring the high-control representation at the behavioral cost of low-control trial performance. Moreover, synchronous cortical alpha-band oscillation demonstrated an inverse association with ACC for low control contexts versus high

control contexts. Taken together, our findings indicate that alpha-band synchrony may be a mechanism for either representational binding or the action biasing resulting from such binding.

APPENDIX A

SIGNIFICANT SPECTRAL ANALYTIC RESULTS

Table 4: Significant differences between task conditions across context groups

CONDITION Main Effect					
Frequency Band	Trial Phase	Region	$F(1, 54)$	p	η_p^2
Theta	Cue	Midline Frontopolar	13.48	0.001	0.20
		Left Frontal	11.29	0.001	0.17
		Midline Fronal	12.07	0.001	0.18
		Left Temporoparietal	10.63	0.002	0.16
		Midline Parietal	11.17	0.002	0.17
		Right Temporoparietal	8.53	0.005	0.14
		Left Occipital	8.55	0.005	0.14
		Midline Occipital	11.49	0.001	0.18
		Right Occipital	9.25	0.004	0.15
Alpha	Baseline	Left Frontopolar	11.71	0.001	0.18
		Midline Frontopolar	14.48	<.0005	0.21
		Left Frontal	16.66	<.0005	0.24
		Midline Fronal	18.97	<.0005	0.26
		Left Temporal	15.64	<.0005	0.22
		Midline Central	8.89	0.004	0.14
		Left Temporoparietal	15.47	<.0005	0.22
		Midline Parietal	11.52	0.001	0.18
		Right Temporoparietal	15.51	<.0005	0.22
		Left Occipital	9.19	0.004	0.15
		Midline Occipital	15.94	<.0005	0.23
		Right Occipital	24.22	<.0005	0.31

CONDITION Main Effect					
Frequency Band	Trial Phase	Region	$F(1, 54)$	p	η_p^2
Alpha	Probe	Left Temporoparietal	9.83	0.003	0.15
		Midline Parietal	15.37	<.0005	0.22
		Left Occipital	13.33	0.001	0.20
		Midline Occipital	16.64	<.0005	0.24
		Right Occipital	11.60	0.001	0.18
Low Beta	Probe	Midline Frontopolar	9.21	0.004	0.15
		Midline Central	9.43	0.003	0.15
		Left Temporoparietal	16.58	<.0005	0.23
		Midline Parietal	24.67	<.0005	0.31
		Right Temporoparietal	13.38	0.001	0.20
		Left Occipital	16.95	<.0005	0.24
		Midline Occipital	15.22	<.0005	0.22
		Right Occipital	12.6	0.001	0.19
High Beta	Delay	Midline Central	8.54	0.005	0.14
	Probe	Midline Central	19.19	<.0005	0.26
		Left Temporoparietal	21.02	<.0005	0.28
		Midline Parietal	18.74	<.0005	0.26
		Right Temporoparietal	16.31	<.0005	0.23
		Left Occipital	13.16	0.001	0.20
		Midline Occipital	8.75	0.005	0.14
		Right Occipital	14.54	<.0005	0.21
Gamma	Delay	Right Temporoparietal	9.08	0.004	0.14
	Probe	Midline Central	19.44	<.0005	0.26
		Left Temporoparietal	15.65	<.0005	0.22
		Midline Parietal	18.01	<.0005	0.25
		Left Occipital	8.63	0.005	0.14
		Midline Occipital	9.44	0.003	0.15
CONTEXT x CONDITION Interaction Effect					
Frequency Band	Trial Phase	Region	$F(2, 54)$	p	η_p^2
Theta	Cue	Midline Central	6.06	0.004	0.18
		Right Temporoparietal	9.52	<.0005	0.26
	Probe	Left Temporal	6.16	0.004	0.19
		Right Temporal	9.60	<.0005	0.26
Alpha	Baseline	Left Frontal	8.01	0.001	0.23
	Cue	Left Frontopolar	8.13	0.001	0.23
		Left Frontal	8.78	0.001	0.25

CONTEXT x CONDITION Interaction Effect

Frequency Band	Trial Phase	Region	$F(2, 54)$	p	η_p^2
Alpha	Cue	Midline Parietal	10.08	<.0005	0.27
		Right Temporoparietal	13.67	<.0005	0.34
		Left Occipital	8.11	0.001	0.23
		Midline Occipital	13.81	<.0005	0.34
		Right Occipital	13.74	<.0005	0.34
	Delay	Left Frontopolar	6.35	0.003	0.19
		Midline Frontopolar	9.33	<.0005	0.26
		Right Frontopolar	9.16	<.0005	0.25
		Left Frontal	9.99	<.0005	0.27
		Midline Fronal	11.60	<.0005	0.30
		Right Frontal	7.34	0.002	0.21
		Left Temporal	7.80	0.001	0.22
		Midline Central	11.30	<.0005	0.30
		Right Temporal	6.33	0.003	0.19
		Left Temporoparietal	7.07	0.002	0.21
		Midline Parietal	15.91	<.0005	0.37
		Right Temporoparietal	11.31	<.0005	0.30
		Left Occipital	6.04	0.004	0.18
		Midline Occipital	11.76	<.0005	0.30
	Right Occipital	13.92	<.0005	0.34	
	Probe	Left Frontal	8.06	0.001	0.23
		Midline Fronal	6.62	0.003	0.20
		Left Temporal	8.03	0.001	0.23
		Midline Central	8.78	0.001	0.25
Right Temporal		7.71	0.001	0.22	
Low Beta	Cue	Midline Parietal	8.58	0.001	0.24
		Left Frontopolar	12.17	<.0005	0.31
		Midline Central	6.38	0.003	0.19
		Midline Parietal	12.82	<.0005	0.32
		Right Temporoparietal	14.55	<.0005	0.35
	Delay	Midline Occipital	10.61	<.0005	0.28
		Right Occipital	22.57	<.0005	0.46
		Midline Frontopolar	7.47	0.001	0.22
		Right Frontopolar	8.56	0.001	0.24
		Left Frontal	8.77	0.001	0.25
Delay	Right Frontal	10.88	<.0005	0.29	
	Left Temporal	10.69	<.0005	0.28	
	Midline Central	8.24	0.001	0.23	
		Right Temporal	11.75	<.0005	0.30

CONTEXT x CONDITION Interaction Effect					
Frequency Band	Trial Phase	Region	$F(2, 54)$	p	η_p^2
Low Beta	Delay	Left Temporoparietal	9.97	<.0005	0.27
		Midline Parietal	21.82	<.0005	0.45
		Right Temporoparietal	15.17	<.0005	0.36
		Left Occipital	7.70	0.001	0.22
		Midline Occipital	13.73	<.0005	0.34
		Right Occipital	13.75	<.0005	0.34
	Probe	Left Frontopolar	6.30	0.003	0.19
		Left Frontal	12.06	<.0005	0.31
		Midline Fronal	8.31	0.001	0.24
		Right Frontal	6.81	0.002	0.20
		Left Temporal	9.34	<.0005	0.26
		Midline Central	7.37	0.001	0.21
		Right Temporal	10.76	<.0005	0.28
		Midline Parietal	9.77	<.0005	0.27
High Beta	Cue	Right Temporoparietal	6.74	0.002	0.20
		Right Occipital	8.63	0.001	0.24
		Right Occipital	8.63	0.001	0.24
High Beta	Delay	Left Frontal	10.04	<.0005	0.27
		Midline Fronal	9.32	<.0005	0.26
		Right Frontal	6.31	0.003	0.19
		Left Temporal	7.11	0.002	0.21
		Midline Central	7.32	0.002	0.21
		Right Temporal	7.37	0.001	0.21
High Beta	Delay	Left Temporoparietal	8.07	0.001	0.23
		Midline Parietal	28.07	<.0005	0.51
		Right Temporoparietal	10.65	<.0005	0.28
		Left Occipital	9.42	<.0005	0.26
		Midline Occipital	17.34	<.0005	0.39
		Right Occipital	6.59	0.003	0.20
	Probe	Midline Central	8.94	<.0005	0.25
		Left Temporoparietal	6.38	0.003	0.19
		Right Temporoparietal	8.19	0.001	0.23

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