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The Strength of Alpha and Gamma Oscillations Predicts Behavioral Switch Costs

Amy L. Proskovec^{a,b,c}, Alex I. Wiesman^{b,c}, and Tony W. Wilson^{a,b,c}

^aDepartment of Psychology, University of Nebraska - Omaha, NE, U.S.A.

^bCenter for Magnetoencephalography, University of Nebraska Medical Center (UNMC), Omaha, NE, U.S.A.

^cDepartment of Neurological Sciences, UNMC, Omaha, NE, U.S.A.

Abstract

Cognitive flexibility is often examined using task-switch paradigms, whereby individuals either switch between tasks or repeat the same task on successive trials. The behavioral costs of switching in terms of accuracy and reaction time are well-known, but the oscillatory dynamics underlying such costs are poorly understood. Herein, we examined 25 healthy adults who performed a task-switching paradigm during magnetoencephalography (MEG). All MEG data were transformed into the time-frequency domain and significant oscillatory responses were imaged separately per condition (i.e., switch, repeat) using a beamformer. To determine the impact of task switching on the neural dynamics, the resulting images were examined using paired-samples *t*-tests. Whole-brain correlations were also computed using the switch-related difference images (switch – repeat) and the switch-related behavioral data (i.e., switch costs). Our key results indicated stronger decreases in alpha and beta activity, and greater increases in gamma activity in nodes of the cingulo-opercular and fronto-parietal networks during switch relative to repeat trials. In addition, behavioral switch costs were positively correlated with switch-related differences in right frontal and inferior parietal alpha activity, and negatively correlated with switch effects in anterior cingulate and right temporoparietal gamma activity. In other words, participants who had a greater decrease in alpha or increase in gamma in these respective regions had smaller behavioral switch costs, which suggests that these oscillations are critical to supporting cognitive flexibility. In sum, we provide novel data linking switch effects and gamma oscillations, and employed a whole-brain approach to directly link switch-related oscillatory differences with switch-related performance differences.

Corresponding Author: Tony W. Wilson, Ph.D., Center for Magnetoencephalography, University of Nebraska Medical Center, 988422 Nebraska Medical Center, Omaha, NE 68198, Phone: (402) 552-6431, Fax: (402) 559-5747, twwilson@unmc.edu.

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Keywords

cingulo-opercular network; fronto-parietal network; magnetoencephalography (MEG); oscillatory activity; task switching

1. Introduction

Cognitive control refers to the ability to flexibly adjust thoughts and behavior to enact current goals,¹ and one constituent of cognitive control is the ability to shift between various tasks to meet changing environmental demands.² One method for assessing such cognitive flexibility is via a task-switch paradigm, in which an individual either switches between tasks or repeats the same task on successive trials. Decreased performance (e.g., slower reaction times) is often observed in switch relative to repeat trials, and these so-called switch costs are often used as a measure of cognitive control.³ That is, smaller switch costs are indicative of greater cognitive control, and vice versa. Importantly, it is widely believed that a myriad of sub-processes underlie switch costs, including interference from the previous task-set, recall and application of the current task rules, and updating of stimulus-response mappings.^{2,4}

Not surprisingly, a network of neural regions has been implicated in task-switching. Specifically, when using a mixed block/event-related design, previous functional magnetic resonance imaging (fMRI) studies have demonstrated the sustained involvement of a cingulo-opercular network throughout the performance of task blocks relative to control blocks.⁵⁻⁸ This network includes anterior prefrontal, anterior cingulate, and anterior insula/frontal opercular regions. Additionally, the more transient trial-by-trial recruitment of a fronto-parietal network has also been observed during task-switch performance when employing an event-related analytical approach. This network spans the dorsolateral and ventrolateral prefrontal cortices, premotor cortices, supplementary motor area, inferior and superior parietal lobules, and intraparietal sulci.⁵⁻⁸ Generally, nodes within these networks are activated more strongly when switching tasks.^{5,9-15} Additionally, the differential recruitment of prefrontal and posterior parietal regions during task-switch performance has been shown to covary with the behavioral costs associated with task-switching.^{5,14,16}

Beyond the fMRI literature, neurophysiological studies, primarily employing electroencephalography (EEG), have investigated the oscillatory dynamics underlying task-switch performance. These studies have shown that alpha oscillations are consistently implicated in task switching, with stronger decreases often observed during switch relative to repeat trials both preceding target onset (i.e., preparatory period),¹⁷⁻²² but see²³, and following target onset (i.e., reactive period)^{18,20,24,25} in cued task-switch paradigms. Some studies have also demonstrated that better task-switching performance is associated with decreased alpha activity in frontal and parieto-occipital electrodes.^{19,22,26} Beyond alpha activity, greater increases in theta activity,^{17,27,28} and stronger decreases in beta activity^{17,29}, have also been observed when a task switch is imminent. Finally, one recent study linked increased theta activity in frontal midline and right centroparietal electrodes to

reduced behavioral variability (i.e., increased efficiency of cognitive control) during task-switch performance.²⁸

While the aforementioned EEG studies have provided invaluable insight on the oscillatory activity underlying task-switch performance, they have been limited in anatomical specificity, as source localization of the observed effects was not performed. Additionally, none of these studies identified switch effects on gamma-band (i.e., >30 Hz) oscillations, perhaps due to the difficulty of detecting and isolating higher-frequency brain oscillations with EEG. Interestingly, a previous magnetoencephalography (MEG) study did localize switch effects during task-switch performance, and found that theta activity in left inferior frontal and bilateral superior frontal areas, alpha activity in the right inferior parietal and left superior frontal regions, and beta activity in the right frontal and inferior parietal cortices was modulated by extradimensional task switching (i.e., switching between two sets of rules).³⁰ Unfortunately, the nature of the switch-related differences were not detailed (e.g., stronger decrease in oscillatory activity in one condition relative to the other, etc.), which limited functional interpretation of the results.

The goal of the present study was to utilize a whole-brain MEG approach to investigate the oscillatory dynamics underlying task-switching, and to identify the relationship between switch-related differences in oscillatory activity and behavioral switch costs. To this end, healthy adults performed a task-switching experiment while undergoing MEG, and the resulting data was transformed into the time-frequency domain and imaged using a beamformer. We hypothesized stronger decreases in alpha and beta activity, along with greater increases in gamma activity during switch relative to repeat trials within nodes of the cingulo-opercular and fronto-parietal networks, which have been widely linked to task-switching in the fMRI-based literature. Additionally, we predicted that participants would perform worse on switch trials (i.e., longer reaction times), but that those who exhibited greater decreases in alpha or beta activity and/or increases in gamma activity in prefrontal and posterior parietal regions during switch trials would perform better (i.e., demonstrate less of a switch cost) than individuals who exhibited less of an oscillatory difference between switch and repeat (i.e., no-switch) trials.

2. Methods and Materials

2.1 Subject Selection

We studied 25 healthy adults (13 females; *Age*: 27.28, *SD*: 4.25, range: 20-35) who were recruited from the local community. Exclusion criteria included any medical illness affecting central nervous system function, neurological or psychiatric disorder, history of head trauma, current substance abuse, and ferromagnetic implants. After providing a complete description of the study, written informed consent was obtained from participants following the guidelines of the University of Nebraska Medical Center's Institutional Review Board, which approved the study protocol.

2.2 Experimental Paradigm

During MEG recording, participants sat in a nonmagnetic chair within a magnetically-shielded room and performed a task-switching experiment (Figure 1). Target stimuli were digits ranging from 1-9, except the number 5 which was excluded from the set of possible targets. Each trial began with the presentation of a centrally-presented crosshair for 2700 $\pm$ 100 ms. Then, a single digit was centrally presented within a square or a diamond of equal dimensions for 2500 ms. If surrounded by a square, the participant was instructed to respond via button-pad as to whether the digit was less than or greater than 5. If surrounded by a diamond, the participant responded as to whether the digit was odd or even. Participants used their right index and middle fingers to make responses. The digit was surrounded by a square on 50% of the trials, and trial order was pseudo-randomized such that 50% of trials were a repeat of the previous rule and 50% were a switch away from the previous rule. Thus, participants could not anticipate when a switch in task would occur. Each trial lasted 5200 $\pm$ 100 ms, and there were 100 trials per condition, resulting in a total run-time of ~17.5 minutes.

2.3 MEG data acquisition

Recordings occurred in a one-layer magnetically-shielded room with active shielding engaged, and neuromagnetic responses were sampled continuously at 1 kHz using an acquisition bandwidth of 0.1–330 Hz and a 306-sensor Elekta system (Elekta, Helsinki, Finland). MEG data from each participant were individually corrected for head motion and noise reduced using the signal space separation method with a temporal extension.^{31,32}

2.4 MEG Coregistration & Structural MRI Acquisition and Processing

Preceding MEG measurement, four coils were attached to the participant's head and localized, together with the three fiducial points and scalp surface, with a 3-D digitizer (Fastrak 3SF0002, Polhemus Navigator Sciences, Colchester, VT, USA). During MEG recording, an electric current with a unique frequency label (e.g., 322 Hz) was fed to each coil, inducing a measurable magnetic field which allowed each coil to be localized in reference to the sensors throughout the recording session. Since coil locations were also known in head coordinates, all MEG measurements could be transformed into a common coordinate system. With this coordinate system, each participant's MEG data were coregistered with structural T1-weighted neuroanatomical data before source space analyses using BESA MRI (Version 2.0; BESA GmbH, Grafelfing, Germany). These data were acquired with a Philips Achieva 3T X-series scanner using an eight-channel head coil (TR: 8.09 ms; TE: 3.7 ms; field of view: 240 mm; slice thickness: 1 mm; no gap; in-plane resolution: 1.0 $\times$ 1.0 mm). Structural MRI data were aligned parallel to the anterior and posterior commissures and transformed into Talairach space, along with the functional images, after beamforming (see section 2.6).

2.5 MEG Time-Frequency Transformation and Statistics

A high-pass filter of 0.5 Hz, low-pass filter of 200 Hz, and notch filter of 60 Hz (width: 2 Hz) were applied to the MEG time series data. Cardiac and eye blink artifacts were then removed using signal-space projection (SSP), which was accounted for during source

reconstruction.³³ The continuous magnetic time series was divided into epochs of 5000 ms duration, from -2500 to 2500 ms, with the onset of the target stimulus being defined as 0 ms, and the baseline being defined as the 600 ms before target presentation (i.e., -600 to 0 ms). Epochs contaminated with artifacts were rejected based on a fixed threshold method, supplemented with visual inspection. Briefly, for each individual, the distribution of amplitude and gradient values across all trials was determined, and those trials containing the highest amplitude and/or gradient values relative to the full distribution were rejected based on amplitude and gradient thresholds. Importantly, these thresholds were determined individually for each participant, as inter-individual differences in head size, proximity to the sensors, and related variables strongly affect the amplitude of MEG signals, since magnetic field strengths decrease exponentially as the distance between the electric current (brain) and the detector (MEG) increases. Additionally, in some participants, non-artifactual trials were also randomly excluded so that the total number of accepted trials used in the final analyses did not differ between conditions. All trials where the participant responded incorrectly were also excluded from analysis, and two participants were excluded entirely due to poor performance (e.g., very delayed responses, difficulty staying awake, etc.). This reduced the final sample size to 23 participants. On average, 78.04 and 78.17 accepted trials per participant were used from the repeat and switch conditions, respectively, and this was not significantly different between conditions $t(22) = -0.35$, $p = .727$.

The artifact-free epochs were transformed into the time-frequency domain using complex demodulation, and the resulting spectral power estimations were averaged across all trials to generate time-frequency plots of mean spectral density. These sensor-level data were normalized per time-frequency bin using the baseline power per frequency bin (i.e., mean power during the -600 to 0 ms time period).

The time-frequency windows used for imaging were determined by statistical analysis of the sensor-level spectrograms across all trials (repeat + switch) and all gradiometers during the target period. Each data point in the spectrogram was first evaluated using a mass univariate approach based on the general linear model (GLM). To reduce the risk of false positive results while maintaining reasonable sensitivity, a two-stage procedure was adopted. In the first stage, one-sample t -tests were conducted on each data point and the output spectrogram of t -values was thresholded at $p < .05$ to identify time-frequency bins containing potentially significant oscillatory activity across all participants and both conditions. In stage two, the time-frequency bins that survived this threshold were clustered with temporally and/or spectrally neighboring bins that were also significant. A cluster value was then computed by summing the t -values of all data points in the cluster. Nonparametric permutation testing was then used to derive a distribution of cluster-values and the significance level of the observed clusters (from stage one) were tested directly using this distribution.^{34,35} For each comparison, at least 10,000 permutations were computed. Based on these analyses, only the time-frequency windows that contained significant oscillatory events across all participants and both conditions were subjected to the beamforming (i.e., imaging) analysis. Thus, a data-driven approach was utilized for determining the time-frequency windows that were entered into the source reconstruction.

2.6 MEG Source Imaging & Statistics

Neural oscillatory activity was imaged for each condition independently through an extension of the linearly constrained minimum variance vector beamformer,³⁶⁻³⁸ which calculates source power for the entire brain volume by employing spatial filters in the time-frequency domain. The single images were derived from the cross spectral densities of all combinations of MEG gradiometers averaged over the time-frequency range of interest,³⁶ and the solution of the forward problem for each location on a grid specified by input voxel space. Following convention, the source power in these images was normalized per participant using a separately averaged pre-stimulus noise period (i.e., baseline) of equal duration and bandwidth.³⁷ Thus, the normalized source power was computed for the statistically-determined time-frequency bands over the entire brain volume per participant at $4.0 \times 4.0 \times 4.0$ mm resolution. Each participant's functional images were then transformed into standardized space (Talairach) using the transform that was previously applied to the structural images and spatially resampled to 1 mm isotropic voxels (see section 2.4). MEG pre-processing and imaging used the Brain Electrical Source Analysis (version 6.1) software.

To determine the effects of task-switching, the resulting 3D maps of brain activity were statistically evaluated using a random effects, mass univariate approach based on the GLM. Essentially, two-tailed paired-samples *t*-tests per time-frequency bin were conducted to identify the effect of task-switching (i.e., switch vs. repeat). All output statistical maps were displayed as a function of alpha level, thresholded at $p < .005$, and adjusted for multiple comparisons using a spatial extent threshold (i.e., cluster restriction; $k = 200$ contiguous voxels) based on the theory of Gaussian random fields.³⁹⁻⁴¹ Of note, we also conducted nonparametric permutation testing using a cluster-based method similar to that performed on the sensor-level spectrograms (see section 2.5), to control for Type 1 error, and our results were virtually identical between the two methods.

2.7 Whole-brain Neurobehavioral Correlation Maps

To identify brain regions in which switch-related oscillatory differences were directly related to behavioral switch costs, we first computed difference maps (switch – repeat) per participant for each time-frequency bin containing significant switch-related effects identified in the previous analysis. We then performed whole-brain Pearson correlations using each participant's difference map and their respective reaction time (RT) difference (switch - repeat) on the task. These whole-brain correlation maps were displayed as a function of alpha level, and adjusted for multiple comparisons using a cluster restriction ($k = 200$ contiguous voxels). Note that we did not center the switch-repeat RT difference before computing the neurobehavioral correlation (i.e., simple regression) maps, because this would only have changed the value of the intercept in the model, while leaving the relationship between the predictor and dependent variable unchanged.

3. Results

3.1 Behavioral Analysis

As expected, task performance differed between conditions, such that participants were significantly more accurate when performing repeat ($M = 97.08\%$, $SD = 2.84\%$) relative to switch trials ($M = 95.82\%$, $SD = 3.37\%$; $t(22) = 2.71$, $p = .013$; Figure 1). Participants also responded significantly faster during repeat ($M = 1149.47$ ms, $SD = 208.86$ ms) relative to switch trials ($M = 1204.07$ ms, $SD = 216.75$ ms; $t(22) = -4.49$, $p < .001$). Thus, the average switch cost was 54.59 ms ($SD = 12.16$ ms).

3.2 Sensor-Level Analysis

Statistical analyses of the time-frequency spectrograms revealed a significant cluster of decreased alpha (8-12 Hz) oscillatory activity following target presentation from 350 to 1550 ms ($p < .001$, corrected; Figure 2). Additionally, a significant cluster of decreased beta (16-20 Hz) activity was observed from 300 to 1000 ms ($p < .001$, corrected). Finally, a significant cluster of increased gamma (68-76 Hz) activity was detected from 125 to 825 ms ($p < .001$, corrected). These three oscillatory responses were observed in many posterior gradiometers, near the bilateral parietal and occipital cortices, across all participants and conditions, and Figure 2 depicts the two sensors among this larger set of gradiometers that showed the peak responses for alpha/beta and gamma. As the aforementioned responses were relatively sustained, we split each into two non-overlapping time bins of equal duration, and source reconstructed the resulting time-frequency windows for each condition independently. Additionally, as the focus of the present study was on the oscillatory dynamics serving task-switching, we restricted our source-space analyses to the time period in which these effects would be maximal, and other brain responses (e.g., motor) minimal. Thus, we applied a beamformer to the following windows: 8 to 12 Hz from 350 to 750 ms and 750 to 1150 ms, 16 to 20 Hz from 300 to 650 ms and 650 to 1000 ms, and 68 to 76 Hz from 125 to 475 ms and 475 to 825 ms.

3.3 Beamformer Analysis

To investigate the oscillatory dynamics associated with task-switching, paired-samples t -tests were computed between the repeat and switch whole-brain maps, and a cluster-correction was applied to each resulting statistical parametric map (SPM). Our results indicated significant switch-related effects on alpha (8-12 Hz) activity in the right inferior frontal gyrus, insula, and lateral occipital cortex from 350 to 750 ms, as well as in the left intraparietal sulcus and superior parietal lobule from 350 to 1150 ms (Figure 3; all p 's $< .005$, corrected). Significant switch-related alpha differences were also detected in the right middle temporal gyrus and postcentral gyrus from 350 to 750 ms, and bilateral cuneus from 750 to 1150 ms (all p 's $< .005$, corrected). Additionally, significant switch-related effects on beta (16-20 Hz) activity were observed in the left premotor cortex from 300 to 650 ms (Figure 3; $p < .005$, corrected). These effects dissipated in the later time window (650-1000 ms) and there were no significant beta differences between conditions from 650 to 1000 ms. Across all regions, the aforementioned differences reflected stronger decreases in alpha or beta activity during switch relative to repeat trials.

Gamma activity (68-76 Hz) in the left superior occipital gyrus, right cerebellum, anterior cingulate, and left anterior prefrontal cortex was significantly modulated from 125 to 475 ms by task-switching, such that stronger increases in gamma activity were detected during switch relative to repeat trials (Figure 4; all p 's < .005, corrected). Additionally, switch-related effects on gamma activity in the left inferior parietal were found from 475 to 825 ms, with increases in gamma activity observed during switch trials, while during repeat trials activity within these regions remained near baseline levels (Figure 4; all p 's < .005, corrected).

3.4 Neurobehavioral Correlation Analysis

To identify links between switch-related oscillatory differences and behavioral switch costs, whole-brain correlation maps were computed separately using the alpha, beta, and gamma difference images (switch – repeat) and RT differences between conditions (switch – repeat). The alpha neurobehavioral correlation results were strikingly similar across the 350 to 750 ms and 750 to 1150 ms time bins, and thus the reported results are collapsed across the entire 350 to 1150 ms window. Specifically, for each participant we averaged the 350 to 750 ms map and 750 to 1150 ms map together for each condition independently. We then computed difference maps by subtracting the time-averaged repeat image from the time-averaged switch image for each participant, and these maps were entered into the neurobehavioral correlation analysis pipeline. This revealed that switch-related alpha differences in the right inferior and superior frontal gyri and inferior parietal were positively correlated with switch-related RT differences (Figure 5; all p 's < .005, corrected). In other words, across these three regions, the greater the decrease in alpha activity during switch relative to repeat trials, the smaller the behavioral switch cost. Additionally, a significant negative relationship was observed in the left cerebellum between switch-related alpha differences and switch costs (Figure 5; p < .005, corrected), such that the greater the decrease in alpha activity during switch relative to repeat trials, the larger the switch cost tended to be. There were no significant neurobehavioral correlations involving beta activity. Finally, switch-related differences in gamma activity in the dorsal anterior cingulate cortex and right temporoparietal junction from 475 to 825 ms were negatively correlated with switch-related differences in RT (Figure 6; all p 's < .005, corrected). That is, the stronger the increase in gamma activity within these regions during switch relative to repeat trials, the smaller the behavioral switch cost tended to be. Of note, inspection of the gamma neurobehavioral scatterplots suggested a potential bimodal distribution with regards to the right temporoparietal junction. To further probe this, we conducted Shapiro-Wilk tests of normality on switch-related differences in RT and differences in right temporoparietal junction gamma activity. The results indicated that switch-related differences in RT were normally distributed, while differences in right temporoparietal gamma were marginally not normal. As such, we computed a Spearman's rho correlation between switch-related differences in RT and the data from the right temporoparietal junction peak voxel. In agreement with the findings using Pearson correlations, a significant negative correlation between switch-related differences in RT and switch-related differences in right temporoparietal gamma activity was observed. Thus, similar results were obtained regardless of whether a Pearson's or Spearman's correlation was utilized.

4. Discussion

In this study, we characterized the spatiotemporal oscillatory dynamics underlying task-switching, and examined whether switch-related differences in oscillatory activity were related to behavioral switch costs. Our results indicated stronger decreases in alpha and beta activity, and greater increases in gamma activity, within nodes of the cingulo-opercular and fronto-parietal networks when a switch in task was performed. Additionally, the stronger the decrease in alpha activity within right prefrontal and inferior parietal cortices, and the stronger the increase in gamma activity within anterior cingulate and right temporoparietal regions during switch relative to repeat trials, the smaller the behavioral decrement when switching tasks. These findings are discussed in further detail below.

To our knowledge, this is the first study to directly tie gamma oscillations to task switching. While novel, these effects were anticipated, as a growing number of neurophysiological studies have shown that increased gamma activity is central to many cognitive processes, including attention, working memory, and long-term memory, while also serving a role in feature binding.^{42,43} Additionally, increases in frontal gamma have been observed in other tasks which probed cognitive control.^{44,45} Not surprisingly, multimodal EEG-fMRI experiments have demonstrated a positive relationship between the fMRI blood-oxygen-level dependent (BOLD) signal and gamma oscillations during cognitive processing.⁴⁶⁻⁴⁹ That is, increased gamma oscillations are commonly observed in the same regions as fMRI activations, and given our task and the regions involved the same would likely hold here. With regards to alpha and beta activity, a negative relationship with the BOLD signal is often observed during task performance, such that decreased alpha and/or beta oscillations are associated with fMRI activations within similar regions.^{46-48,50,51} Such decreases in alpha or beta activity are commonly believed to reflect the active engagement of a neural region,⁵²⁻⁵⁵ and in congruence with the EEG-based literature,^{18,20,24,25} stronger decreases in alpha and beta activity were observed when a switch in task-set was necessary.

Taken together, the direction (increases vs. decreases) and anatomical location of these switch-related effects largely complement the fMRI-based literature demonstrating stronger recruitment of both cingulo-opercular and fronto-parietal networks during task-switching.^{5,9-15} Specifically, evidence suggests that the cingulo-opercular network is involved in the domain-independent and stable maintenance of task-set information, with the dorsal anterior cingulate tied to interference and feedback monitoring processes, the anterior insula linked to rule implementation, and the anterior prefrontal cortex implicated in more specific and higher-order representations (e.g., plans, strategies, subgoals).^{7,56,57} Additionally, the anterior insula and dorsal anterior cingulate are believed to function together in a saliency network, to select the most relevant external stimuli and internal goals for further processing.⁵⁸ Our data extend upon this work by implicating alpha and gamma oscillations within this cingulo-opercular network in task-switch performance, and stress the flexibility of gamma oscillations within the dorsal anterior cingulate for effective cognitive control.

The fronto-parietal network is believed to complement the cingulo-opercular network and have greater involvement in the transient and rapid adjustment of top-down cognitive control.⁷ In particular, the intraparietal and superior parietal regions of the dorsal attention

network (DAN) are closely associated with the top-down allocation of attention to goal-relevant information,⁵⁹ and within a similar vein, decreased alpha oscillations within posterior parietal regions have been tied to attentional processes.^{60,61} Thus, the sustained and stronger alpha decreases we observed within these regions during task-switching were not surprising. Also implicated in attention are the right temporoparietal and inferior frontal regions of the ventral attention network (VAN), which have been linked to the detection of behaviorally relevant stimuli,⁶² and our data suggests that the flexible recruitment of these attention-related regions facilitates cognitive control processes. Additionally, these results align with previous fMRI- and EEG-based studies that reported switch-related effects in right prefrontal regions,^{9,22,25,63} including one study that found the same neurobehavioral correlation between switch-related difference in right frontal alpha activity and switch-related difference in task performance.²² Beyond involvement in the VAN, the right inferior frontal cortex is also intimately tied to the inhibition of response tendencies,⁶⁴ which may be particularly relevant for task-set inertia accounts of switch cost effects. That is, switch costs may in part reflect interference from the previous task and the perseverance of the no longer relevant prior stimulus-response mapping, which would need to be inhibited.⁶⁵ On the flip side of this, processes which select and enact the relevant stimulus-response mappings would also need to be in place, and the posterior superior frontal gyrus has been linked to the implementation of learned arbitrary stimulus-response associations.⁵⁶ Thus, our results further bolster the importance of these areas in task-switching by directly linking oscillations within these regions to switch cost effects.

Finally, alpha oscillations within the right inferior parietal and left cerebellum were also related to performance. Previous research suggests that the right inferior parietal is particularly important for the processing of symbolic numbers and the performance of mental arithmetic,^{66,67} and as our task involved numeric stimuli and numerical decisions, it is perhaps not surprising that the stronger recruitment of this region was linked to better task performance in this specific experiment. In contrast, the stronger recruitment of the cerebellum during switch trials was associated with larger switch costs. The cerebellum is believed to generate error codes that are fed forward to regions in the fronto-parietal network, which in turn rapidly adjust behavior accordingly.⁷ Potentially, the switch trials which propagated the strongest error signals were those which also required more extensive and time-consuming top-down control mechanisms, which behaviorally manifested as longer reaction times. Future studies will need to further probe these possibilities.

Per the results as a whole, it is interesting to note that the regions demonstrating a relationship with behavior were quite distinct from the regions in which significant differences between the switch and repeat conditions were found. One potential explanation for this is that the regions related to behavior (i.e., neurobehavioral correlations) were less involved in the actual task switching component and more involved in the actual computations needed for task performance. Thus, these regions did not show up in the switch versus repeat comparisons, but were significant in the neurobehavioral correlations because they were actively performing the necessary processing (i.e., odd/even determination and greater than/less than 5) and consequently more active in the processing-intensive trials where reaction times were slower. Conversely, the same logic would apply to why the regions that were significantly different in the conditional comparisons (i.e., switch

vs repeat) were not significantly correlated with behavior. Of course, this interpretation is largely speculative and future studies are needed to further sort this out.

While the present study offers novel insight into the spatiotemporal oscillatory dynamics underlying task-switch performance, it was not without limitations. For example, by design, our task targeted reactive cognitive control processes; however, as eluded to in the introduction, neural oscillations have also been observed during preparatory cognitive control processes.¹⁷⁻²² As such, future investigations could utilize a cued task-switch paradigm and similar whole-brain approach as that applied here to characterize the spatiotemporal oscillatory correlates of anticipatory cognitive control. Additionally, our study focused on younger adults, but healthy aging has been linked to declines in executive control processes including task-switching, and age-related differences in the neural activity underlying task-switch performance have been observed.⁶³ Thus, future studies should characterize the effects of aging on the oscillatory dynamics serving task-switching. Investigating sex differences in this context should also be a goal of future studies. Finally, we did not investigate switch-related differences in functional connectivity between the areas identified in our analyses, and previous EEG-based studies have demonstrated task-switching effects on oscillatory functional connectivity between electrodes.^{23,24} Thus, examining functional connectivity in future MEG work would also likely be a fruitful approach.

5. Conclusions

This study utilized MEG and a task-switch paradigm to characterize the oscillatory activity underlying cognitive flexibility, and was the first to directly link switch-related effects on neural oscillations to behavioral switch costs via a whole-brain multispectral approach. Our results suggest that the flexible recruitment of cingulate, frontal, and parietal resources is integral to successfully meeting the increased cognitive control demands imposed by a switch in task, and highlight the importance of alpha, beta, and gamma oscillations within the cingulo-opercular and fronto-parietal networks in task-switching.

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Highlights

- Task-switching costs are well known, but their oscillatory signature is unclear
- Adults performed a task-switching paradigm during magnetoencephalography (MEG)
- MEG data were subjected to a beamformer and advanced oscillatory analysis methods
- Task-switching distinctly modulated behavior, alpha, beta, and gamma oscillations
- Switch effects on alpha and gamma oscillations were tied to behavioral switch costs

Figure 1.

Top: Task-switch paradigm. A trial began with the presentation of a fixation cross for 2700 +/- 100 ms, followed by a digit surrounded by a square (50% of trials) or a diamond for 2500 ms. Digits ranged between 1-9, with the number 5 excluded. Participants responded via button pad whether the digit was less than or greater than 5 for squares, and odd or even for diamonds. Half of the trials were a switch away from the previous rule, while the remaining repeated the previous rule. Bottom: Behavioral results with accuracy (% correct) depicted in the left panel, and reaction time (ms) in the right panel. Performance differed between switch and repeat trials, such that participants were less accurate and took longer to respond during the switch (blue) relative to the repeat (red) condition ($p < .05$).

Oscillations in the Parieto-occipital Cortices

Figure 2.

Time-frequency spectrograms with time (ms) shown on the x-axis and frequency (Hz) denoted on the y-axis. Percent power change was computed for each time-frequency bin relative to the respective bin's baseline power (−600 to 0 ms). The color legends are displayed to the right. Data represent two peak sensors, collapsed across conditions and averaged across all participants, located near the parieto-occipital cortex. The same sensors were used in all participants. A strong increase in gamma activity occurred following target onset, while strong decreases in alpha and beta activity began slightly later. All three responses were relatively sustained.

Figure 3.

Significant switch effects ($p < .005$, corrected) on alpha (8-12 Hz) and beta (16-20 Hz) oscillatory activity following target presentation are displayed. Top: Alpha activity in the right inferior frontal cortex, right anterior insula, right lateral occipital cortex, left intraparietal sulcus, and left superior parietal lobule was modulated by task-switching from 350-750 ms. Switch-related alpha differences in the left intraparietal sulcus and superior parietal lobule were also sustained from 750-1150 ms (not shown). Bottom: Beta activity in the left premotor cortex was modulated by task-switching from 300-650 ms. All effects reflect stronger decreases in alpha or beta activity during switch relative to repeat trials.

Figure 4.

Significant switch effects ($p < .005$, corrected) on gamma (68-76 Hz) oscillatory activity following target presentation are displayed. Gamma activity in the anterior cingulate, left anterior prefrontal cortex, superior occipital cortex, and right cerebellum from 125-475 ms (top section), and in the left inferior parietal from 475-825 ms (bottom section) was modulated by task-switching. All effects reflect stronger increases in gamma activity during switch relative to repeat trials.

Figure 5.

Switch-related differences (switch – repeat) in alpha (8-12 Hz) activity in the right inferior frontal gyrus, inferior parietal, and superior frontal gyrus from 350-1150 ms following target onset were positively correlated with switch-related differences in reaction time (switch costs), while switch effects on left cerebellar alpha activity were negatively correlated with switch costs. Images have been thresholded at ($p < 0.005$, corrected). Scatterplots representing these relationships are shown to the right utilizing data from the peak voxels of the whole-brain correlation maps.

Figure 6.

Switch-related differences (switch – repeat) in gamma (68-76 Hz) activity in the dorsal anterior cingulate and right temporoparietal junction from 475-825 ms following target onset were negatively correlated with switch-related differences in reaction time (switch costs). Scatterplots representing these relationships are presented to the right utilizing the data from the peak voxels of the whole-brain correlation maps. All maps are shown at a threshold of $p < .005$, corrected.