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## **Brain oscillatory activity associated with switch and mixing costs during reactive control**

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## Abstract

Task-switching paradigms, which involve task repetitions and between-task switches, have long been used as a benchmark of cognitive control processes. When mixed and single-task blocks are presented, two types of costs usually occur: the *switch cost*, measured by contrasting performance on switch and repeat trials during the mixed-task blocks, and the *mixing cost*, calculated as the performance difference between the *all-repeat* trials from the single-task blocks and the repeat trials from the mixed-task blocks. Both costs can be mitigated by informational cues that signal the upcoming task switch beforehand. Recent electroencephalographic (EEG) studies have started unveiling the brain oscillatory activity underlying the switch cost during the preparatory cue-target interval, thus targeting proactive control processes. Less attention has instead been paid to the mixing cost and, importantly, to the oscillatory dynamics involved in switch and mixing costs during reactive control. To fill this gap, here we analyzed the time-frequency data obtained during a task-switching paradigm wherein the simultaneous presentation of task cues and targets increased the need for reactive control. Results showed that while alpha and beta bands were modulated by switch and mixing costs in a similar gradual fashion, with greater suppression going from switch to repeat and *all-repeat* trials, theta power was sensitive to the switch cost with increased power for switch than repeat trials. Together, our findings join previous studies underlining the importance of theta, alpha and beta oscillations in task-switching and extend them by depicting the oscillations involved in switch and mixing costs during reactive control processes.

## 1. Introduction

*“Repetita iuvant”*

While this ancient Latin quote was not coined with reference to task-switching, a common finding in the cognitive control literature is that switching from one task to another incurs a significant “switch cost” as compared to repeating the same task. Yet, there is also a “mixing cost” when contrasting performance on the *all-repeat* trials from the single-task blocks and the repeat trials from the mixed blocks (Monsell, 2003; Rubin & Meiran, 2005). The switch cost is generally taken as an index of a phasic task-set reconfiguration process, which operates on a trial-by-trial basis to flexibly switch between different tasks and which itself includes multiple sub-processes such as retrieval of current rules and appropriate stimulus-response mappings from memory, resolution of carryover interference from the previous trial, suppression of the no longer relevant task-set and activation of the new relevant one (Monsell, 2003). Conversely, the mixing cost is thought to reflect higher memory demands and sustained cognitive control processes to maintain multiple task-sets active during the mixed block (e.g., Braver, Reynolds, & Donaldson, 2003; Rubin & Meiran, 2005).

Support for the dissociation between the processes underlying switch and mixing costs comes from different lines of evidence. For example, from a normal aging perspective, older adults usually show larger mixing costs but similar switch costs with respect to their younger counterparts (e.g., Kray & Lindenberger, 2000; Mayr, 2001; Moretti, Semenza, & Vallesi, 2018). At the neural level, functional magnetic resonance imaging (fMRI; Braver et al., 2003) and resting-state electroencephalographic (EEG) studies (Ambrosini & Vallesi, 2016) link switch and mixing costs to the activity of left-lateralized and right-lateralized prefrontal areas, respectively. As concerns event-related potential (ERP) studies, the picture is instead much less clear-cut as both common and unique ERPs have been reported for the two

types of costs (e.g., Goffaux, Phillips, Sinai, & Pushkar, 2006; Tarantino, Mazzone, & Vallesi, 2016; Wylie, Murray, Javitt, & Foxe, 2009; see Karayanidis & Jamadar, 2014, for a review).

In addition to ERP studies, in the last decade there has been a steep increase in research into the oscillatory activity involved in switching or repeating a task. In contrast to the switch cost, the oscillatory dynamics underlying the mixing cost have received much less attention. Moreover, the majority of EEG time-frequency task-switching studies focused on proactive control processes, namely, those processes that develop during the cue-target interval allowing preparation for a task switch or a task repetition (e.g., Cooper, Wong, McKewen, Michie, & Karayanidis, 2017; Cunillera et al., 2012; López, Pusil, Pereda, Maestú, & Barceló, 2019). However, many real-life situations do not afford anticipatory preparation. For instance, while driving, we can either encounter a warning signal that lets us know in advance that a road change is coming up on our drive, or it may also happen that an unexpected falling rock prompts us to suddenly change direction. How does the brain behave in the latter situation? In order to address this question, here we investigated the oscillatory neural activity associated with switch and mixing costs during a task-switching paradigm stressing reactive control processes. To begin with, the following paragraph provides an overview of the brain oscillations observed in previous task-switching studies. Regarding the switch cost, a general finding is that switch trials are related to greater power increases in fronto-parietal theta oscillations as compared to repeat trials. This has led to the hypothesis that theta band could represent a possible frequency signature of the goal-directed and updating processes required to switch task, in line with mounting evidence linking increased theta to the “need for cognitive control” (Cavanagh & Frank, 2014). In support of this claim, theta power over fronto-parietal electrodes was shown to increase when participants were proactively cued to shift categorization rule during a cued-Wisconsin card sorting task (Cunillera et al., 2012). In another cued task-switching study, Cooper and colleagues (2017) also found greater theta power over fronto-parietal electrodes along with enhanced phase coherence across trials in response to switch cues (see also López et al., 2019, for

further evidence of greater fronto-parietal theta and fronto-temporal delta phase connectivity for switch cues). Taken together, these studies suggest a role for theta oscillations in switch-related proactive cognitive control. In addition, there is also evidence for the involvement of theta oscillations after target onset. For example, the use of a single-trial regression approach in a recent study showed that switch trials with increased mid-frontal theta power during both preparatory and post-target intervals were associated with smaller switch costs (Cooper et al., 2019).

In contrast to enhanced theta activity, a different pattern has usually been found for alpha oscillations with lower power for switch versus repeat trials both during the preparatory cue-target interval (e.g., Cunillera et al., 2012; Foxe, Murphy, & De Sanctis, 2014; Murphy, Foxe, & Molholm, 2016; but see Cooper et al., 2019; Mansfield, Karayanidis, & Cohen, 2012) and after target onset (e.g., Rapela, Gramann, Westerfield, Townsend, & Makeig, 2012; Sauseng et al., 2006). In the majority of these studies, alpha suppression had a parieto-occipital scalp distribution but, in some work, it was also observed over central (Cunillera et al., 2012) and frontal electrodes (Foxe et al., 2014) or in frontal magnetoencephalography (MEG) reconstructed regions (Proskovec, Wiesman, & Wilson, 2019). A plausible explanation for the decrease of alpha activity during switch trials is that alpha oscillations would reflect the involvement of a suppressive top-down mechanism, in charge of diverting attention away from competing, distracting task-sets (Foxe et al., 2014). Another, not mutually exclusive, explanation is that a decrease in alpha activity during switch trials could index an increase in the retrieval of relevant information from memory (Sauseng et al., 2006).

Lastly, there is also evidence for the sensitivity of beta oscillations to task-switching contexts (e.g., Cooper et al., 2017; 2019; Gladwin, Lindsen, & de Jong, 2006). As an example, Cunillera and colleagues (2012) observed that relative to repeat cues, switch cues during the cue-target interval were linked to decreased beta power across the scalp, though being more pronounced over posterior-occipital regions. In addition, a recent MEG work with a similar reactive paradigm as the one used here also reported

switch-related beta decrease in the left premotor cortex (Proskovec et al., 2019). A motor interpretation of beta has often been embraced to explain the finding of decreased beta oscillations during switch trials.

Concerning the mixing cost, we are aware of only two previous studies<sup>1</sup> examining brain oscillations associated with *all-repeat* trials and repeat trials from the mixed blocks. Both studies, however, had aims different from ours. The first study (Enriquez-Geppert & Barceló, 2018) investigated age-related changes in theta and beta oscillations by specifically considering the functional networks underlying the target-P300 potential. The second study (Cooper et al., 2017) focused primarily on the role of fronto-parietal theta oscillations during proactive control processes and, hence, time-frequency analysis was restricted to cue-locked activity. The findings by Cooper and colleagues (2017) showed that fronto-parietal theta was sensitive to both switch and mixing costs as it increased significantly from *all-repeat* trials to repeat trials, and from repeat trials to switch trials.

Summarizing the aforementioned EEG studies, it becomes clear that specific brain frequencies are differentially modulated by the requirement to switch or repeat a task. However, since switch and mixing costs have been rarely compared and, when done, the focus was mainly on proactive control, it is still unsettled whether switch and mixing costs in reactive control tasks are tied to similar or distinct frequency bands as those found for proactive control. To improve our understanding of switch and mixing costs during reactive control, we conducted time-frequency analysis of a previous EEG dataset

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<sup>1</sup> During the revision process, we found out another very recent time-frequency study comparing switch and mixing costs (McKewen et al., 2020). We report it here for the reader's benefit. Of note, however, this study too tackled a different research question than the present work, as it investigated whether phase-locked and nonphase-locked power in the time-frequency EEG signal were differentially modulated by switch and mixing costs. Moreover, the specific focus of the study was on time-frequency effects usually observed at frontal and parietal sites, such that all the analyses were performed on two a-priori selected electrodes (FCz and Pz).

from our laboratory (Capizzi, Ambrosini, Arbula, Mazzonetto, & Vallesi, 2016). The key design feature of that study was the simultaneous cue-target presentation. Accordingly, there was no opportunity for anticipatory preparation as the target color was the only cue that indicated the specific task to be implemented on any given trial. Therefore, in this task-switching scenario a successful switch operation depended exclusively on the involvement of strong stimulus-driven control mechanisms, which in turn allowed us to compare switch and mixing costs during reactive control.

## **2. Method**

### **2.1 Participants**

Fifty-four university students<sup>2</sup> (mean age: 22.8 years, age range: 21–29 years, 14 men, all right-handed) voluntarily took part in the experiment and received cash reimbursement for their time. All participants were native Italian speakers, with normal or corrected-to-normal visual acuity and normal color vision. They gave informed consent prior to their inclusion in the study, which was approved by the Bioethical Committee of the Azienda Ospedaliera di Padova in compliance with the Declaration of Helsinki. All participants reported no history of neurological or psychiatric disorders.

### **2.2 Procedure and Task**

The general procedure and task are described in detail in Capizzi et al. (2016).

In brief, as depicted in Figure 1, stimulus material consisted of visually presented three-dimensional words that could be categorized according to either verbal or spatial sorting rules. The verbal rules

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<sup>2</sup> Participants were the same as in Capizzi et al. (2016). However, unlike our previous study where data from 6 participants were discarded, here we used all the participants' data according to the different analysis pipeline followed in the present study (see the Data Analysis section for further details).

required participants to classify the words according to two grammatical dimensions: *gender* (female/male) and *name* (proper/common), whereas the spatial rules regarded the *roll* (clockwise/counterclockwise) and *pitch* (upward/downward) rotations. In total, there were 18 proper names, divided into 9 proper female names and 9 proper male names, and 18 common names, divided into 9 common female names and 9 common male names.

Verbal and spatial tasks were presented separately, with half of the participants starting with the verbal tasks and the other half with the spatial ones. Each word could be written in one of four colors: red, blue, green or brown. In the task-switching condition, the blue and red colors signaled the specific task to be performed on any given trial (see Figure 1 for further details). In the single-task condition, the colors also changed randomly between brown and green in order to match all the stimuli along the perceptual dimension, but participants were instructed not to pay attention to the color of the words. For both verbal and spatial tasks, there were two single-task blocks (one for each categorization rule, e.g., gender and name) and four task-switching blocks each comprising 32 trials. Repeat and switch trials were presented in a pseudo-random order to guarantee roughly the same number of trials per condition. The experimental blocks were preceded by a short practice session that allowed participants to familiarize themselves with the specific task rules.

Both behavioral and EEG data were collapsed across spatial and verbal tasks after having confirmed comparable behavioral and EEG effects ( $p > .05$ ) as in our previous study (see Capizzi et al., 2016).

--- Figure 1 about here---

### **2.3 EEG recording**

EEG was recorded using BrainAmp amplifiers (BrainProducts, Munich, Germany) from 64 Ag/AgCl electrodes that were mounted on an elastic cap (EASYCAP GmbH, Germany) according to the extended 10–20 system. Electrooculography (EOG) activity was measured through an electrode placed under the



left eye and also monitored through the scalp electrodes placed in the proximity of both eyes. Impedances for each channel were measured and adjusted until they were kept below 10 k $\Omega$  before testing. An electrode positioned at FCz and another placed at AFz served as the online reference and ground electrodes, respectively. Raw data were digitized at a sampling rate of 500 Hz and bandpass filtered between .1 and 100 Hz.

### **3. Data analysis**

#### **3.1 Behavioral Data Analysis**

Data were analyzed in terms of both accuracy and response times (RTs). To improve normality, raw RT data and accuracy scores were, respectively, log- and arcsine-transformed before statistical analyses. For the RT analysis, the first trial of each task-switching block (2.08% of all the trials), anticipations (RT < 150 ms; 3 trials) and errors (6.02% of the remaining trials) were discarded. Additionally, for each participant trials with an RT above or below 2 *SDs* from their individual task mean condition were treated as outliers and rejected (4.02% of the remaining trials). For the accuracy analysis, the first trial of each task-switching block was removed.

For both correct RTs and accuracy scores, switch and mixing costs were computed by calculating, respectively, the difference between switch and repeat trials and between repeat and *all*-repeat trials. We then assessed the statistical significance of switch and mixing costs by means of two-sample *t* tests against zero. The Cohen's *d* was used as a measure of the effect size (Cohen, 1977).

#### **3.2 Electrophysiological Data Analysis**

Signal preprocessing was performed using BrainVision Analyzer 2.0 (Brain Products GmbH), custom Matlab (Mathworks, Natick, MA) scripts and functions from the EEGLAB environment (version 13.4.4b; Delorme & Makeig, 2004). The continuous EEG was filtered offline using a .5 Hz highpass filter (Butterworth zero-phase, 48 dB/oct) and subjected to an ocular correction algorithm based on independent component analysis (ICA) as implemented in BrainVision. After correcting for eye movements and blink activity, data were exported to EEGLAB and lowpass filtered at 45 Hz (cutoff) using a zero-phase Kaiser-windowed sinc FIR filter (beta = 6.317, transition bandwidth = 10 Hz; see Widmann, Schröger, & Maess, 2015). Channel rejection was then performed by means of the “*clean\_rawdata*” EEGLAB plugin using an autocorrelation parameter of 0.7071 (Mullen et al., 2013). The resulting noisy channels (1 channel in 11 datasets, 5 channels in 1 dataset) were interpolated using spherical splines (Perrin, Pernier, Bertrand, & Echallier, 1989). After interpolation, EEG data were re-referenced to the average of all of the electrodes and segmented into epochs of 3500 ms (1500 ms prestimulus and 2000 ms corresponding to the time interval during which the word was presented; see Figure 1). This wide range avoided edge artifacts resulting from time-frequency decomposition. The first trial of each task-switching block and trials associated with incorrect behavioral responses were excluded from the segmentation. Epochs were corrected in the time domain using a prestimulus interval of [-200 0] ms and screened for artifacts and/or outliers with four different methods (see Delorme, Sejnowski, & Makeig, 2007). The following criteria were applied according to a preliminary examination of our sample aimed at optimizing artifact rejection: 1)  $\pm 100 \mu\text{V}$  for the standard extreme values thresholding; 2) current drifts larger than  $\pm 50 \mu\text{V}/\text{epoch}$  and  $R^2 > .3$  for the linear trend test; 3)  $SD > 7$  (for each channel) and  $SD > 3$  (for all channels) for the improbability test; and 4)  $SD > 7$  (for each channel) and  $SD > 3$  (for all channels) for the kurtosis test. Epochs containing data points exceeding any of these criteria were excluded from further analyses. As a result, a mean of 9.13% of the epochs were rejected. The minimum number of retained epochs in each experimental condition was 50.

Time-frequency decomposition was performed on clean epochs via complex Morlet wavelet convolution. We extracted Event-Related Spectral Perturbation (ERSP) in the frequency range between 4 and 45 Hz (resolution: 1 Hz) using a number of cycles that varied from 4 cycles at the lowest frequency (4 Hz) up to 22.5 at the highest frequency (45 Hz) in linearly increasing steps, with a temporal resolution of approximately 20 ms. ERSPs were expressed in decibel relative to the mean power in the baseline interval (-1000 -500 ms prestimulus).

Statistics were performed via a Threshold Free Cluster Enhancement (TFCE) method, which avoids a-priori assumptions about data while enabling correction for multiple comparisons (Smith & Nichols, 2009). Specifically, TFCE has been shown to be more sensitive than traditional cluster-mass methods given that threshold, rather than cluster, of each data point is computed. The TFCE analyses included all the 64 channels, the entire epoch length (2000 ms), and all the frequencies range from 4 to 45 Hz (20000 permutations;  $p < .05$ ). Please note that oscillations in the gamma band ( $> 30$  Hz) were not considered here due to the possible influence of artefactual muscular activity. Three separate TFCE analyses were performed. The first two TFCE assessed the statistical significance of the ERSP switch and mixing effects by contrasting, respectively, ERSPs in switch vs. repeat trials and those in repeat vs. *all*-repeat trials. A third TFCE tested for the interaction between ERSP switch and mixing effects by contrasting them.

### **3.3 Time-frequency – Behavior Correlation Analysis**

Pearson's correlation was used to test for relationship between behavioral switch and mixing costs and time-frequency measures. Specifically, we computed the correlations between the participants' switch and mixing RT costs and the ERSP switch and mixing effects. As for the time-frequency analysis detailed above, we considered all the frequencies, time points, and channels, and assessed the statistical significance of the time-frequency – behavior correlation results using the TFCE method. This allowed

avoiding the circularity problem (Kriegeskorte, Lindquist, Nichols, Poldrack, & Vul, 2010). In order to control for possible biases due to a negative correlation between switch and mixing effects, we report only significant spatio-temporo-spectral data points for which the correlation between switch and mixing ERSP effects was not significant.

## **4. Results**

### **4.1 Behavioral results**

Descriptive statistics are reported in Table 1. As expected from a task-switching paradigm, RT analysis showed reliable switch and mixing costs ( $M = .102$ ,  $SD = .034$ ,  $t_{(53)} = 21.73$ ,  $p < .001$ ,  $d = 2.96$ , and  $M = .121$ ,  $SD = .047$ ,  $t_{(53)} = 18.79$ ,  $p < .001$ ,  $d = 2.56$ , respectively) (Figure 2A). Analysis on the accuracy scores paralleled the RT findings with significant switch and mixing costs also for accuracy ( $M = .10$ ,  $SD = .07$ ,  $t_{(53)} = 10.85$ ,  $p < .001$ ,  $d = 1.48$ , and  $M = .06$ ,  $SD = .11$ ,  $t_{(53)} = 3.82$ ,  $p < .001$ ,  $d = .52$ , respectively) (Figure 2B).

--- Table 1 and Figure 2 about here---

### **4.2 Time-frequency results**

The TFCE analysis performed with a standard threshold value ( $p = .05$ ) showed significant clusters of relatively sustained and broadly distributed oscillatory activity involving theta, alpha and beta frequencies. In order to refine the results and evaluate their robustness, a further TFCE analysis was thus performed using a more conservative threshold ( $p = .00001$  instead of  $.05$ ). The use of a more stringent threshold also allowed improving the scalp-based localization of the observed brain oscillations by revealing clusters that were more spatially distinct. The results of both analyses are reported here for

completeness but, of note, only the results from the conservative one are graphically represented, as they better depict the scalp-based localization of brain oscillations. The reader is referred to the Supplementary material for visualization of the TFCE results obtained with the conventional alpha value. Figure 3 shows the time-frequency plots for the three trial types (switch, repeat, *all-repeat*) over nine representative frontal (F3, Fz, F4), central (C3, Cz, C4) and parietal (P3, Pz, P4) electrodes. Overall, the ERSP results clearly involved an event-related increase in power for frequencies in the theta range (4-7 Hz), as well as a sustained event-related decrease in power for frequencies mainly comprised in the alpha range (8-15 Hz), accompanied by a less sustained event-related decrease in power for frequencies in the beta range (16-30 Hz). These ERSP modulations were generally more pronounced for switch as compared to repeat trials and, even more, for repeat as compared to *all-repeat* trials.

--- Figure 3 about here---

#### **4.2.1 ERSP switch effect**

The TFCE on the ERSP switch effect showed a significant cluster of oscillatory activity in the theta range (4-7 Hz), which was due to a stronger event-related increase in power for switch compared to repeat trials. Such theta cluster was present from 900 to 1800 ms over fronto-central and right fronto-temporal electrodes (Supplementary Figure A, bottom). The control TFCE analysis confirmed this result by showing a significant theta effect (across 1000-1600 ms) over fronto-central electrodes (Figure 4A, B). A significant cluster with a stronger decrease of power for frequencies mainly included in the alpha range (8-15 Hz) for switch relative to repeat trials was also observed in a time window spanning from 700 ms to the end of the epoch. This alpha effect was widely distributed across the scalp but strongest over anterior mid-frontal and bilateral centro-parietal electrodes (Supplementary Figure A, middle). The control analysis confirmed this result (across 1000-1600 ms) by revealing a frontal and left-lateralized posterior scalp distribution (Figure 4C, D).

Additionally, from 700 to 1800 ms there was a significant cluster with a stronger decrease in beta activity (16-30 Hz) for switch compared to repeat trials, which was broadly distributed over left fronto-central and right centro-parietal electrodes (Supplementary Figure A, top). This result was confirmed in the control analysis (across 900-1600 ms), which showed a central scalp distribution more lateralized to left electrodes (Figure 4E, F).

--- Figure 4 about here---

#### 4.2.2 ERSP mixing effect

The TFCE contrasting repeat and *all*-repeat trials showed significant ERSP mixing effects in theta, alpha and beta frequencies. Specifically, two clusters<sup>3</sup> of theta activity were detected. A first significant cluster with a greater increase in theta activity for *all*-repeat trials as compared to repeat trials was observed from 200 to 400 ms over left fronto-central and bilateral occipito-temporal electrodes. A second significant cluster with greater increase in theta power for *all*-repeat relative to repeat trials was found from 900 to 1200 ms over posterior electrodes (Supplementary Figure B, bottom). None of these results, however, survived the conservative threshold in the control TFCE analysis.

Regarding the alpha band, a significant sustained cluster with a stronger decrease in alpha activity for repeat compared to *all*-repeat trials was found from 200 ms to end of the epoch across all the scalp and noticeable especially over bilateral fronto-parietal electrodes (Supplementary Figure B, middle). During the same time window (200 ms–end of the epoch), there was also a significant cluster with a stronger

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<sup>3</sup> A third significant cluster with greater theta suppression for repeat relative to *all*-repeat trials was also observed from 1300 ms to the end of the epoch over right fronto-temporal and left centro-temporal-parietal electrodes. Since participants' RTs were shorter than 1300 ms ( $M = 945$  ms in the repeat condition), this theta cluster was no longer considered here as it probably captured a post response process.

decrease in beta power for repeat than *all*-repeat trials involving mainly right central and bilateral parietal electrodes (Supplementary Figure B, top). Both results were confirmed in the control analysis (8-15 Hz: 400 ms-end of the epoch; 16-30 Hz: 400-1600 ms), which clarified the frontal and most pronounced right central and bilateral parietal scalp distribution for alpha band (Figure 5A, B), and the more posterior distribution for beta band (Figure 5C, D).

--- Figure 5 about here---

#### **4.2.3 ERSP switch by mixing effect interaction**

The TFCE testing for the interaction between switch and mixing effects revealed significant differences in theta, alpha and beta frequencies. As concerns theta band, switch and mixing effects significantly differed during two time windows: an earlier one, from 100 to 400 ms, and a later one, from 1100 to 1800 ms. During the first time bin, theta ERSP switch and mixing effects had opposite sign over central and bilateral occipito-temporal electrodes. During the later time bin, a significant cluster was observed over fronto-central electrodes, with a stronger theta ERSP switch effect as compared to the mixing one (Supplementary Figure C, bottom). None of these theta results, however, survived the control analysis. As regards alpha activity, the ERSP mixing effect was stronger than the switch one from 200 ms to the end of the epoch over bilateral anterior and posterior electrodes (Supplementary Figure C, middle). Likewise, during a similar sustained time bin (200 ms-end of the epoch), there was a greater beta ERSP mixing effect relative to the switch effect, which involved right fronto-central and bilateral parieto-occipital electrodes (Supplementary Figure C, top). Both results were replicated in the control analysis in the 600-1100 ms time window. As concerns their scalp-based localization, the control analysis showed a significant effect for frequencies mainly included in the alpha range (8-15 Hz) over right frontal and

bilateral occipital electrodes (Figure 6A, B), as well as a significant beta effect (16-30 Hz) distributed across three separate electrode sites: fronto-central, left parietal and right occipital (Figure 6C, D).

--- Figure 6 about here---

#### **4.3 Time-frequency – Behavior Correlation Results**

Regarding the switch cost, two clusters showed significant time-frequency – behavior correlations. A first cluster involved high theta and low alpha frequencies (7-10 Hz) over parieto-occipital electrodes in a time window ranging approximately from 1000 to 1400 ms (Figure 7, top topoplot). This positive correlation indicates that participants who had a more negative ERSP switch effect (i.e., greater decrease in alpha power for the switch as compared to the repeat condition) exhibited a smaller behavioral switch cost (Figure 7, top scatterplot). A second significant cluster concerning high alpha-low beta frequencies (11-20 Hz) was observed during 600-1200 ms over mid-frontal and bilateral occipito-temporal electrodes (Figure 7, bottom topoplot). As for the first cluster, there was a positive correlation between the behavioral switch cost and the ERSP switch effect such that a greater decrease in high alpha/low beta power in the switch condition was associated with a smaller switch cost (Figure 7, middle and bottom scatterplots). Of note, these results were confirmed in a similar analysis performed using Spearman's correlations, which are less sensitive to both deviations from the normal distribution and outlier observations. The only difference between the two correlation approaches regarded the second cluster, which in the Spearman's correlation analysis included frequencies in the range from 11 to 15 Hz. No significant correlations emerged between behavioral and oscillatory activity for the mixing cost.



--- Figure 7 about here---

## 5. Discussion

In the present study, we investigated the brain oscillatory dynamics involved in switch and mixing costs during a task-switching paradigm emphasizing reactive cognitive control processes. As will be detailed below, our results complement previous findings on the switch cost and add to current knowledge on the mixing cost and the difference between switch and mixing costs when advance preparation is not afforded. Behaviorally, strong switch and mixing costs were observed as expected in this kind of paradigm. At the electrophysiological level, the mass univariate approach applied to time-frequency data showed the involvement of theta, alpha and beta oscillations in both switch and mixing costs, albeit with some significant differences mainly concerning their spatio-temporal dynamics. We discuss these time-frequency results in what follows starting with alpha and beta frequencies, as they were modulated by switch and mixing costs in a similar manner, and concluding with theta band, which behaved differently for switch and mixing costs.

With regard to frequencies comprised between 8 and 15 Hz, collectively labeled here as alpha band to differentiate them from a clear beta cluster spanning from 16 to 30 Hz (see Figure 3), a marked decrease was observed during switch relative to repeat trials (the ERSP switch effect), as well as during repeat compared to *all*-repeat trials (the ERSP mixing effect). A further analysis on the interaction between switch and mixing effects also showed a greater alpha ERSP mixing effect compared to the ERSP switch effect. The robustness of these alpha results is supported by the finding that they were replicated using a very conservative  $p$  value threshold ( $p = .00001$ ). The use of a more stringent threshold also improved the separation between spatially-distinct clusters associated with switch and mixing effects, thus enabling a better scalp-based localization of such effects. In particular, the control analysis helped clarify that, although frontal and posterior alpha frequencies were both involved in switch and mixing effects,

the alpha ERSP switch effect was stronger over left-lateralized posterior electrode sites. By contrast, the ERSP mixing effect had a more widespread distribution with marked frontal, right central and bilateral scalp localization. These differences were then reflected in the switch by mixing interaction analysis, which showed a greater alpha ERSP mixing effect over right frontal and bilateral occipital electrodes. The presence of alpha activity over frontal and posterior electrodes is in line with previous time-frequency task-switching studies (Foxye et al., 2014; Proskovec et al., 2019). What is interesting to note, however, is the fact that while the switch effect appeared to be more related to left-lateralized alpha activity, the mixing effect was linked to more bilateral and slightly more right-lateralized activity. With the proper caution, as necessary when speculating about scalp-based effects, these findings fit with the idea that switch and mixing costs could be mediated by more left-lateralized and right-lateralized brain activity, which in the literature has been linked to the operation of transient and more sustained aspects of cognitive control, respectively (e.g., Ambrosini & Vallesi, 2016; Braver, Reynolds, & Donaldson, 2003). Supporting this argument, the difference between repeat and *all*-repeat trials occurred earlier and was more sustained in time than that concerning switch and repeat trials. A final difference concerning alpha oscillations was that high theta/low alpha frequencies (7-10 Hz) over parieto-occipital electrodes were positively correlated to the RT switch cost but not the mixing cost.

In general, the switch-related alpha suppression observed here converges with previous work reporting: 1) stronger decreases in alpha activity for switch trials (Cunillera et al., 2012; Foxye et al., 2014; Sauseng et al., 2006), and 2) positive relationships between suppressed alpha activity and behavioral switch costs (Proskovec et al., 2019; Verstraeten & Cluydts, 2002). Interestingly, of the aforementioned studies both Proskovec et al. (2019) and Sauseng et al. (2006) employed a task-switching paradigm similar to the one used here as cue and target coincided in time, thus specifically stressing reactive control processes. Corroborating such previous reports, our findings support the conclusion that switch-related processes in reactive control tasks are partly reflected by greater alpha suppression, in contrast to other studies

that employing a cue-target interval have found increased, rather than decreased, alpha power for switch cues (Cooper et al., 2019; Mansfield et al., 2012). Future studies manipulating the opportunity for advance preparation (i.e., presence or absence of a preparatory interval) in the same design will help clarify the opposite pattern of alpha increase/decrease associated with switch trials in the context of proactive and reactive tasks, respectively. Importantly, extending the work by Proskovec et al. (2019) and Sauseng et al. (2006), both of which lacked a single-task condition, we added that alpha activity was also sensitive to the mixing cost, being more suppressed during repeat relative to *all*-repeat trials. As regards the functional meaning of alpha band in task-switching, it is generally thought it could index the recruitment of a suppressive top-down mechanism, which would divert attention away from the task-sets competing with the one to be correctly applied in the task at hand (Cunillera et al., 2012; Foxe et al., 2014). Using an overlapping cue-target paradigm as here, Sauseng and colleagues (2006) furthered the idea that a greater alpha suppression during switch trials could also reflect an increase in the retrieval of relevant information from memory. Both explanations hold for our results, in that they showed a gradual modulation of alpha activity from the most demanding switch trials, requiring stronger memory and attentional suppression of the previous task-set, to repeat trials, which also required the maintenance of two task-sets, to the least difficult *all*-repeat trials. Of note, the difference in alpha suppression between switch and repeat trials was not as great as that between repeat and *all*-repeat trials. This result aligns with previous studies showing that, when switch and repeat trials have the same probability to be presented within a block, some reconfiguration sub-processes could also take place on repeat trials, albeit to a lesser degree than what required on switch trials (e.g., Brass & von Cramon, 2004; Capizzi, Fehér, Penolazzi, & Vallesi, 2015; Nicholson, Karayanidis, Poboka, Heathcote, & Michie, 2005). In our specific case, the lack of a preparatory interval and the used trial sequence with equal probability for switch and repeat trials might have partly encouraged the recruitment of similar

attentional suppression and memory processes also during repeat trials to maintain the two very demanding task-sets active throughout the mixed block.

Echoing the alpha results, the same pattern of marked power decrease for switch relative to repeat trials and for repeat relative to *all*-repeat trials was reported in the beta frequency range (16-30 Hz).

Beta differences as a function of the mixing effect emerged early after stimulus onset ( $\approx 200$  ms, 400 ms in the control analysis), whereas for the switch effect beta modulations occurred later in time, at approximately 700 ms (1000 ms in the control analysis). Again, as for the alpha band, the ERSP mixing effect observed in the beta frequency range was greater than the ERSP switch effect and beta power decreases were related to the behavioral switch cost only. Finally, all the beta results survived a very conservative statistical threshold.

Unlike theta and alpha, beta oscillations in task-switching have been usually neglected or just reported but not thoroughly addressed, perhaps because the functional role of the beta band in cognitive processes is the least understood of all the frequency bands (e.g., Engel & Fries, 2010). Moreover, beta oscillations during task-switching have been primarily related to sensorimotor functions (movement execution and/or preparation; e.g., Cooper et al., 2019). With regard to the beta effects observed here, our data speak against a strict motor-related interpretation of beta activity. A first argument is that, as generally illustrated in Figure 3, the scalp distribution of beta oscillations was not confined to sensorimotor scalp regions. Beta activity was also localized to scalp regions not compatible with underlying motor areas (e.g., parietal and occipital, besides from frontal) and this is particularly evident for the ERSP mixing effect (see Figure 5D). Second, participants with greater high-alpha/low-beta (11-20 Hz) suppression around the time of response selection/execution ( $\approx 600$ -1200 ms) had smaller switch costs, whereas there was no relationship between beta modulations and the behavioral mixing cost. It is, thereby, difficult to reconcile this pattern with the idea of beta as a mere correlate of motor functions, as responses were given in the same manner in all trial types. In light of these lines of

evidence, it is more plausible to conclude that in our task beta oscillations reflected the involvement of non-motor processes. This assertion finds support in recent studies showing that beta oscillations across non-motor areas are associated with a number of cognitive processes such as working memory, long-term memory and decision making (see Spitzer & Haegens, 2017, for a review). More germane to the current work, our findings of similar alpha and beta modulations by switch costs (i.e., greater suppression for switch compared to repeat trials) confirm the results by Proskovec and colleagues (2019), who also found greater beta decreases for switch relative to repeat trials during an overlapping cue-target task-switching task. Extending this work with the comparison of repeat and *all*-repeat trials, a plausible explanation for the finding of a gradual beta suppression from switch to repeat, and from repeat to *all*-repeat trials, is that beta suppression in demanding reactive control tasks could be linked to interference control processes, as found in other cognitive control tasks, such as the Stroop task, where a stronger beta suppression has been reported for incongruent trials as compared to congruent ones (Tafuro, Ambrosini, Puccioni, & Vallesi, 2019).

A final key result of this study concerned oscillatory activity in the theta frequency band. Unlike alpha and beta oscillations, which were modulated by switch and mixing costs in a quite similar gradual fashion, a more puzzling picture arose for the theta band. As concerns the switch cost, we found that a significant difference in mid fronto-central and right fronto-temporal theta started to emerge in a late time window (900-1800 ms), with increased theta power for switch relative to repeat trials. The topographical distribution of this theta effect was basically the same after the stringent control analysis applied to our data, which confirmed its fronto-central scalp distribution (see Figure 4B).

Significant theta effects were also found in the mixing cost analysis, which revealed two clusters of theta modulation (see Supplementary Figure B). A first significant cluster, characterized by increased theta power over left fronto-central and bilateral occipito-temporal electrodes for *all*-repeat trials as compared to repeat trials, was observed during an early time window (200-400 ms). This early cluster

was followed by a later one (900-1200 ms), which showed increased theta for *all-repeat* relative to repeat trials over posterior electrodes. The interaction analysis further clarified this pattern of data by showing that, while during the early time window, theta increased for switch relative to repeat trials and, conversely, for *all-repeat* compared to repeat trials, in the late time window theta activity was greater for the switch effect as compared to the mixing effect. However, the involvement of theta activity in the mixing cost and the interaction between switch and mixing costs did not survive a more conservative control analysis threshold. Therefore, these findings will not be discussed further, as they probably represent some spurious or at least less robust results, which call for cautiousness with respect to a possible role of theta in the mixing cost.

In contrast to the mixing cost, the increase in theta power during switch trials was a robust finding that strongly supports the importance of this frequency band in task-switching abilities. On a general level, our theta findings fit well with the recognized role of theta as the frequency band reflecting the “need for cognitive control” (Cavanagh & Frank, 2014). In support of this, increased theta power is usually observed in those conditions requiring greater cognitive control engagement such as the incongruent trials in the Stroop or the Flanker task (e.g., Ergen et al., 2014; Hanslmayr et al., 2008; Nigbur, Ivanova, & Stürmer, 2011). Our results bolster this view of theta, since the higher cognitive control required on switch trials was reflected in an increase of theta oscillations. On a more specific level, as briefly mentioned in the Introduction, mid-frontal oscillations in the theta frequency band have been proposed as a crucial neural signature of specific switch-related processes. In particular, it is assumed that theta oscillations would index the involvement of goal-directed and updating task-set reconfiguration processes. Of importance, a relationship between increased fronto-parietal theta (measured as phase connectivity across the scalp) and switch trials has been also established after target onset when task-set reconfiguration could not be completed beforehand during the preparatory period (Cooper et al., 2015). In this condition, task-set reconfiguration is thought to be postponed until

the presentation of the target, whose attributes and corresponding response mappings cannot be predicted in advance (e.g., Karayanidis et al., 2009). Joining this prior work, the enhancement of theta oscillations found in our study likely reflects the recruitment of poststimulus task-set reconfiguration processes, related to the implementation of reactive control in the most demanding switch trials. To conclude, taking all the above-mentioned results into account, the present study significantly extends previous research by depicting the brain oscillations involved in switch and mixing costs during reactive control processes. While alpha and beta frequencies are involved in switch and mixing costs, theta oscillations instead seems to play a major role in task-switching abilities.

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## Figure legends

### Figure 1. Trial structure. Schematic representation of events and responses in the task-switching

**blocks.** “Sara” is the Italian version of the name “Sarah”, “mago” is the Italian word for “wizard”, and “luca” is the Italian version of the name “Luke”. Fix stands for fixed, ITI for inter-stimulus interval, Stim for stimulus. All the words, including the proper names (i.e., “sara” and “luca” in the figure), were presented in lowercase letters. When the task was spatial and the color of the word was written in red, participants had to classify the word (e.g., “sara”) according to roll rotation (counterclockwise in the figure) by pressing a specific left-sided (or right-sided) response key (counterbalanced across participants). When the color of the word changed from red to blue, participants had to switch to pitch rotation (e.g., upward for “mago” and downward for “luca” in the figure). On verbal blocks, participants had to decide whether words like “sara” were a female or a male name. For words written in blue, they instead had to decide whether words like “mago” and “luca” referred to either common or proper names.

### Figure 2. Behavioral results.

The boxplots show the distributions of the participants’ log-transformed RTs (A) and arcsine-transformed accuracy (B) for the three trial types. The central line of the box represents the median, the edges of the box are the first and third quartiles, the whiskers represent 1.5 times the interquartile difference, and the red crosses represent outlier data points.

### Figure 3. ERSP results.

The figure shows the ERSP data for the three trial types (switch, repeat, *all*-repeat, from top to bottom) over nine representative frontal (F3, Fz, F4), central (C3, Cz, C4) and parietal (P3, Pz, P4) electrodes. ERSPs are reported in the frequency range between 4 and 45 Hz with a 1-Hz resolution (y axis) during a time window ranging from -960 to 2960 ms, where 0 marks stimulus onset, and with a temporal resolution of approximately 20 ms. ERSPs are expressed in decibel relative to the mean power in the baseline interval (-1000 -500 ms prestimulus) and are depicted using a color map where hot and cold colors represent, respectively, event-related increase and decrease in power (range: from -5 to 5 dB).

**Figure 4. ERSP switch effect.**

The figure shows the results of the TFCE analysis for the clusters associated with significant switch effects for the frequencies in the theta (4-7 Hz, A-B), alpha (8-15 Hz, C-D), and beta (16-30 Hz, E-F) ranges. The plots in panels A, C, and E represent the time courses of the ERSPs in the three trial types (*all-repeat*, in green; *repeat*, in orange; *switch*, in red) for the frequencies composing each significant cluster (4-7 Hz, 8-15 Hz, and 16-30 Hz, respectively), averaged across the electrodes showing the largest switch effect, as indicated by the black circles in the topoplots on the right. The topoplots in panels B, D, and F represent the scalp distribution of the *T* values averaged across both the same frequencies indicated above and the time points within the time windows of statistical significance, which are indicated by the horizontal black lines drawn above the x axes in the corresponding plots on the left.

**Figure 5. ERSP mixing effect.**

The figure shows the results of the TFCE analysis for the clusters associated with significant mixing effects for the frequencies in the alpha (8-15 Hz, A-B), and beta (16-30 Hz, C-D) ranges. Conventions are as in Figure 4.

**Figure 6. ERSP switch by mixing effect interaction.**

The figure shows the results of the TFCE analysis for the clusters associated with significant interactions between switch and mixing effects for the frequencies in the alpha (8-15 Hz, A-B), and beta (16-30 Hz, C-D) ranges.

Conventions are as in Figure 4.

**Figure 7. Brain-behavior correlation results.**

The figure shows the topoplots for the clusters associated with significant time-frequency – behavior (i.e., high theta-low alpha frequencies, 7-10 Hz, and high alpha-low beta frequencies, 11-20 Hz – RT switch cost) correlation effects in the TFCE analysis.



**Table 1. Descriptive statistics for behavioral results.**

	<i>All-repeat</i>		Repeat		Switch	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Reaction Times (ms)	715	97	945	131	1180	151
Reaction Times (log)	2.84	0.06	2.96	0.06	3.07	0.06
Accuracy (%)	95	4.8	93	3.7	87	6.8
Accuracy (arcsine)	1.38	0.11	1.32	0.09	1.22	0.10

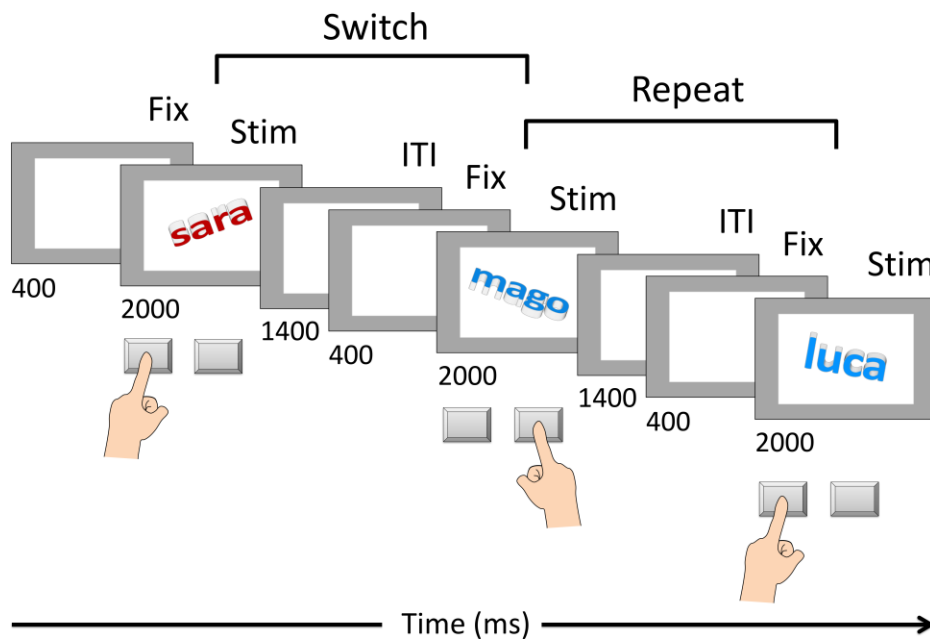


Figure 1.

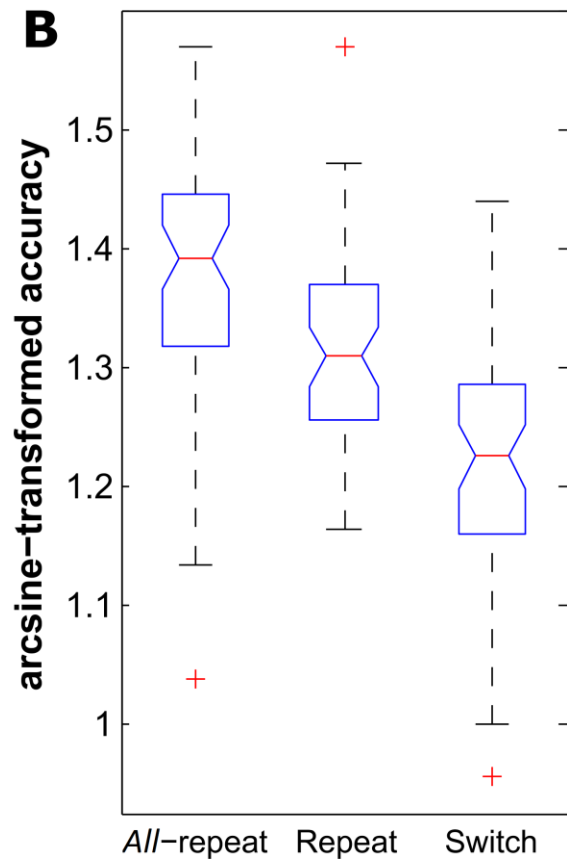
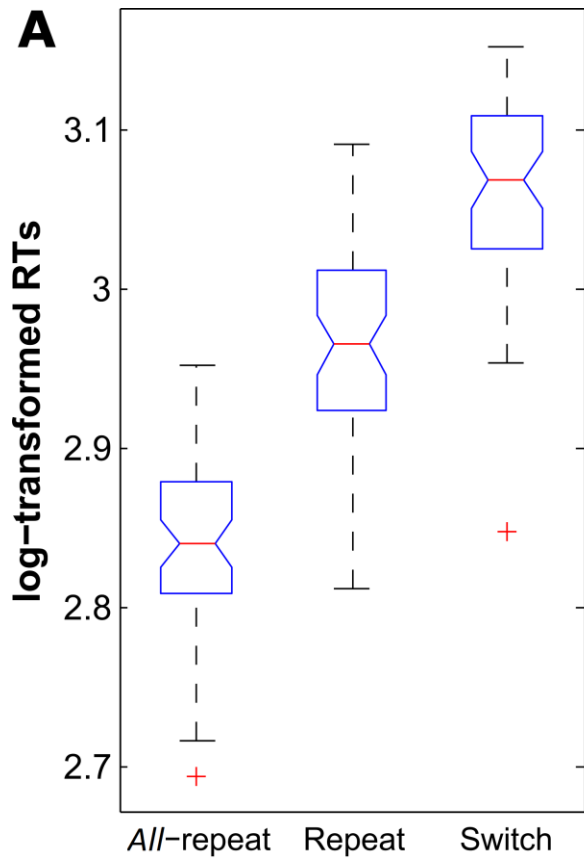


Figure 2

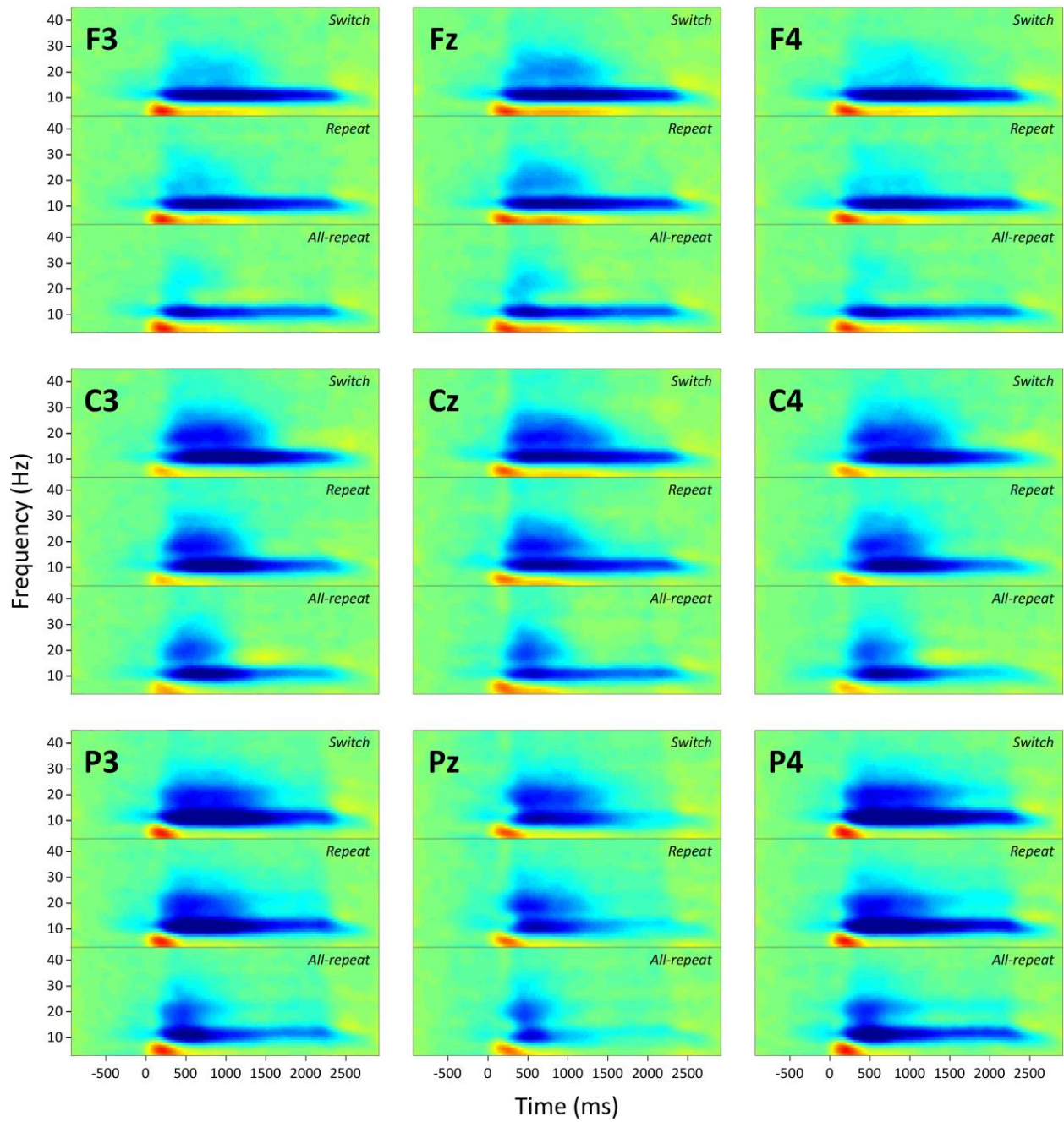


Figure 3

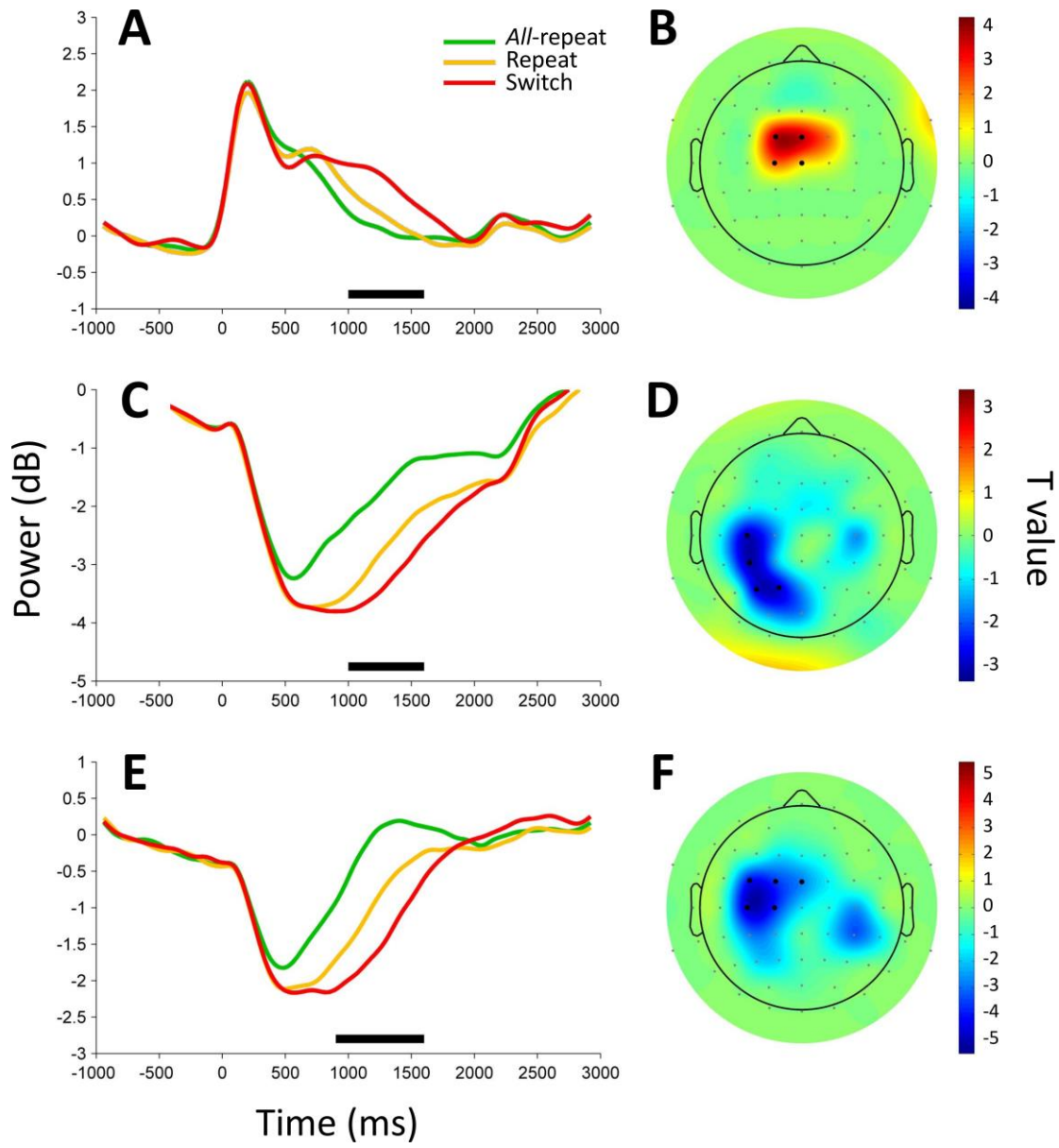


Figure 4

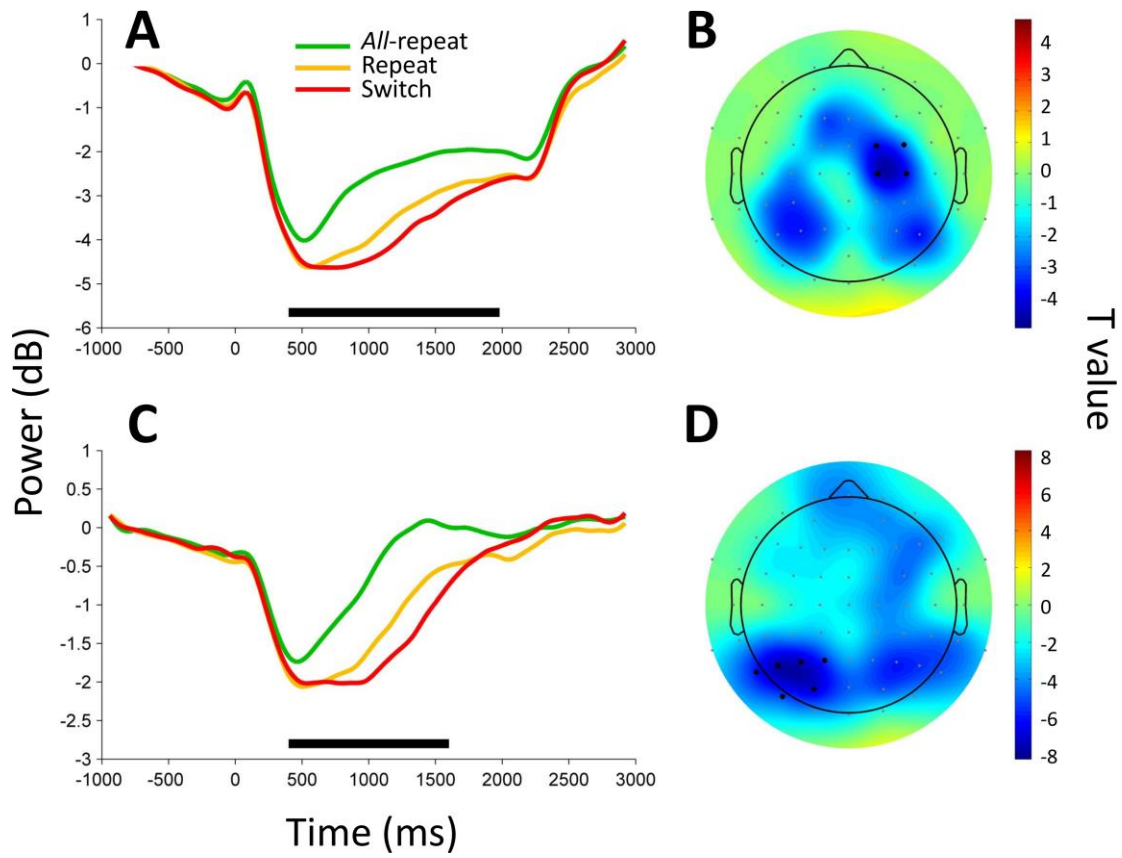


Figure 5

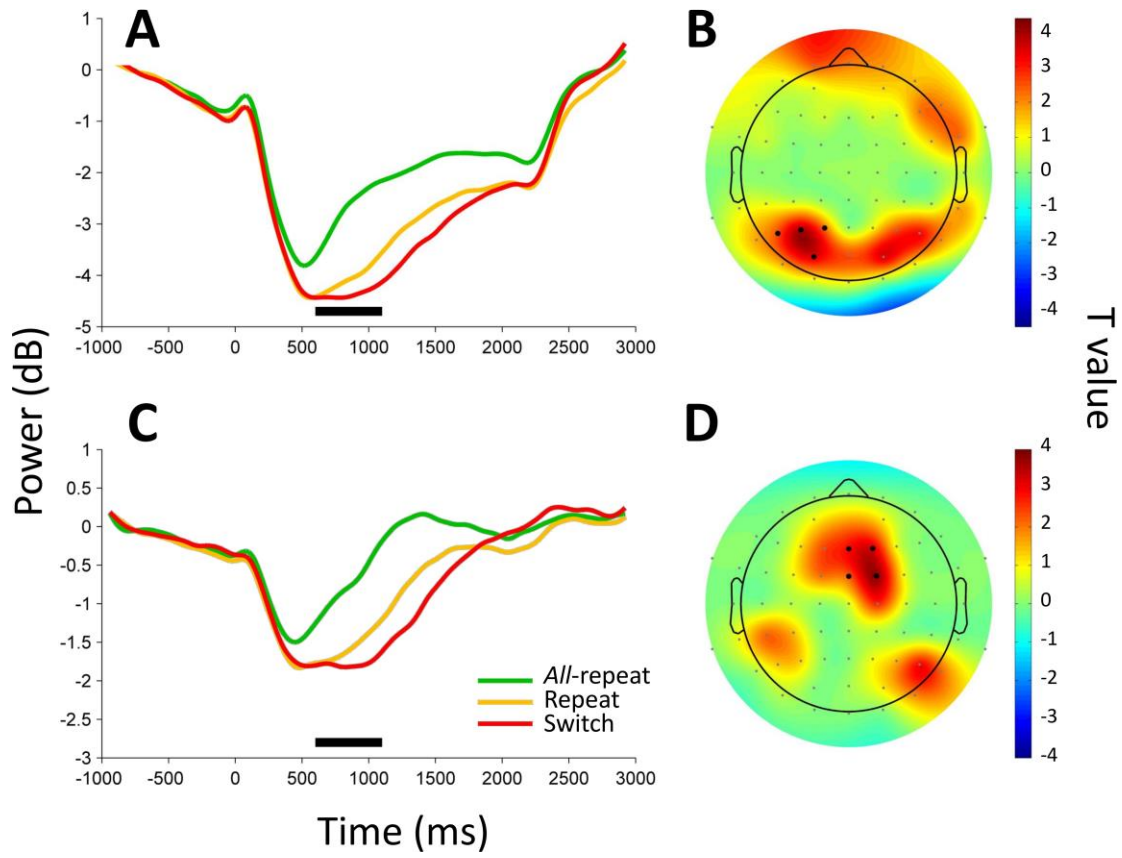


Figure 6

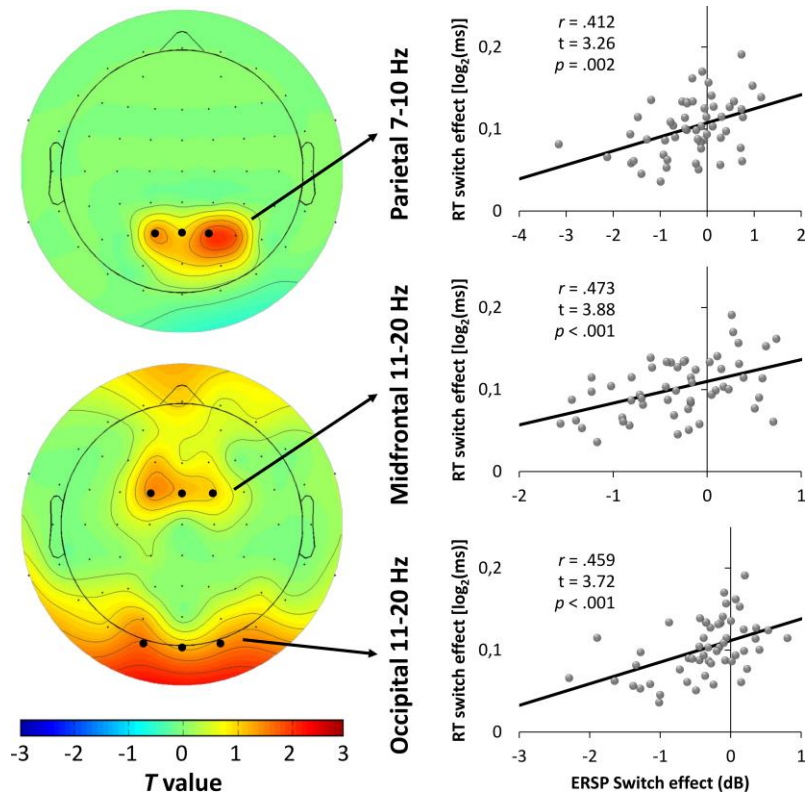


Figure 7.