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# **THETA, ALPHA AND BETA BAND MODULATIONS DURING AUDITORY CONDENSATION TASK PERFORMANCE**

**BASIC RESEARCH PROGRAM**

**WORKING PAPERS**

**SERIES: PSYCHOLOGY  
WP BRP 81/PSY/2017**

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## ***SERIES: PSYCHOLOGY***

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# **THETA, ALPHA AND BETA BAND MODULATIONS DURING AUDITORY CONDENSATION TASK PERFORMANCE<sup>8</sup>**

Outcome of a behavioral response can be detected either internally at the time of the response commission, or externally through a feedback signal. In both cases, a number of brain networks that subserve cognitive control are recruited, all networks having certain distinctive signatures in electroencephalographic oscillations. Yet most studies in the field have several limitations. First, typical behavioral tasks depend heavily upon inhibition of prepotent responses – thus they mostly exploit control of the motor threshold rather than the full range of processes related to cognitive control. Second, these studies were conducted in the visual modality, leaving it unclear whether the oscillatory phenomena found in these studies truly relate to cognitive control or they reflect effects specific to the tasks used. Here, we studied outcome-related adjustments by analyzing response-related and feedback-related modulations of theta, alpha, and beta band activity in the auditory version of the condensation task, which bears no inherent dependence upon inhibition of prepotent responses and which is administered in the auditory modality. Frontal midline theta (FMT) activity was enhanced after errors compared with correct trials, and after negative feedback compared with positive feedback. Alpha band suppression in the parieto-occipital region was enhanced in the late post-error interval. Frontal beta oscillatory activity was increased on correct trials during positive feedback onset. These findings indicate that several separate neuronal networks are involved in post-error and post-feedback adjustments: the midfrontal performance monitoring network, the parietal attentional network, and the frontal reward-processing network. Our findings extend the current knowledge concerning the functional role of theta, alpha, and beta band oscillations in cognitive control beyond a limited range of tasks and beyond the visual modality.

JEL Classification: Z

Keywords: cognitive control, attention, error detection, theta oscillations, alpha oscillations, beta oscillations

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<sup>8</sup> The study was implemented in the framework of the Basic Research Program at the National Research University Higher School of Economics (HSE) in 2017.

## Introduction

The set of neurocognitive processes responsible for flexible and adaptive goal-directed behavior are usually described collectively as “cognitive control” [Yeung, 2014]. The systems involved in cognitive control support such functions as sustained attention, which promotes proper allocation of brain resources, retention and activation of task rules (stimulus-response mappings), and inhibition of irrelevant motor responses. Improper functioning of any of these systems predisposes to performance errors [van Driel et al., 2012; Navarro-Cebrian et al., 2013]. A success or failure of a behavioral action invokes an array of neurocognitive processes that are attempting to develop relevant adaptations in brain functioning and promote optimized performance. Importantly, evaluation of trial outcomes may be either internal (driven by endogenous processes) or external (driven by a feedback stimulus) [Holroyd et al., 2004]. Such phenomena can be studied in the behavioral domain and by using various psychophysiological methods.

Using the time-frequency analysis of the electroencephalogram (EEG) provides helpful insights into the mechanisms of cognitive control and the ensuing behavioral flexibility. A number of important phenomena were found by studying theta, alpha, and beta oscillations. A negative trial outcome (including both internal error and negative feedback detection) evokes a profound increase in the power of frontal midline theta (FMT) oscillations [Yeung et al., 2004; Cohen et al., 2007; Cavanagh et al., 2009; Christie and Tata, 2009; Cohen et al., 2009; van de Vijver et al., 2011; Cavanagh and Frank, 2014; Novikov et al., 2015]. Suppression of the power of alpha oscillations over the parietal and occipital cortical areas is believed to reflect adjustments of attention; this effect can be observed mostly in tasks that require sustained attention [Carp and Compton, 2009; Mazaheri et al., 2009; van Driel et al., 2012]. Prefrontal beta oscillations tend to increase in response to positive feedback; this phenomenon is believed to be an electrophysiological signature of the process that signals maintaining current task rules [van de Vijver et al., 2011].

Most studies of cognitive control – including those mentioned above – use behavioral tasks that require inhibition of irrelevant prepotent responses (such as the Simon task, the flanker task and the Stroop task); thus, they inherently involve asymmetrical stimulus-to-response mapping and they essentially exploit just one specific aspect of cognitive control – namely motor inhibition. Other mechanisms involved in cognitive control remain out of focus in most studies in the field.

Further, the tasks used in these studies typically involve visual stimuli, leaving unsettled the question of whether the effects reported are hallmarks of visual processing or whether they reflect the true mechanisms of cognitive control.

In the current study, we used an auditory condensation task, which is a modification of the generic condensation task [Garner, 1974; Gottwald, Garner, 1975; Posner, 1964]. This task is a valid experimental tool for studying cognitive control by means of electrophysiological measures such as event-related potentials and EEG oscillations [Novikov et al., 2015; Novikov et al., 2017; Chernyshev et al., 2015].

The condensation task produces a high cognitive load, and it requires a high level of sustained attention [Chernyshev et al., 2015]. Importantly, this task has symmetrical stimulus-to-response mapping, thus it does not have a strong dependence on inhibition of prepotent responses. All stimuli presented in this task are target stimuli, and thus they produce no congruency or oddball effects. In addition, it is based on auditory stimuli, allowing an investigation in a non-visual domain. These considerations mean that an auditory condensation task is promising because it allows a comparison of correct and erroneous trials and it is free of many of the confounding factors inherent in many other behavioral tasks used within the area of research.

In a recent study, which used the auditory condensation task [Novikov et al., 2015], a feedback signal was given immediately after the behavioral response not allowing dissociating response-related and feedback-related phenomena. Moreover, only positive feedback was administered in that task, and this unsymmetrical feedback procedure for correct and erroneous trials limited the potential for the direct evaluation of time-frequency effects under the condensation task against the body of the literature. Additionally, that study did not attempt to probe oscillatory effects in the beta band.

In the current study, feedback was given with a sufficient delay after response commission, allowing the measurement of both error-related and feedback-related brain events separately within each trial. We focused on the distinction between correct and erroneous behavioral responses, and we analyzed theta, alpha, and beta oscillations.

The present study aimed to find:

(1) whether specific modulations of theta, alpha, and beta oscillations can be observed in a task that involves no inhibition of prepotent responses;

(2) whether these effects, which have been extensively studied in the visual modality, can be detected in a task that is based on non-visual stimulation.

## **Materials and methods**

### **Participants and experimental conditions**

Twenty-six volunteers participated in the study (mean age  $23.0 \pm 0.9$  years). All volunteers had normal or corrected-to-normal vision and normal hearing; they reported no auditory, neurological, or mental disorders. The experiments were carried out in accordance with the Declaration of Helsinki and its amendments and were approved by the ethics committee of the National Research University Higher School of Economics. Informed consent was signed by participants before the experiment. Experiments were conducted in a sound-attenuated chamber.

### **Stimuli**

Auditory stimuli were presented using E-Prime software (Psychology Software Tools, Inc., USA) through a stereo headset with in-ear design at a sound pressure level of 90 dB. We used four auditory stimuli that varied in timber ('violin' or 'calliope') and pitch ('low' 440 Hz, A4, or 'high' 523.25 Hz, C5). The four stimuli were named in the instruction presented to the participants as 'violin low', 'calliope low', 'violin high', and 'calliope high'.

The tones were synthesized using Microsoft GS Wavetable SW Synth integrated into Microsoft DirectX (Microsoft Corporation, Redmond, WA, USA). For each tone, only the stationary plateau part was taken from original digital recordings of sufficient length. The resulting duration of all auditory stimuli was 100 ms. Artificial rise and fall periods (each 10 ms in duration) were created by linearly decreasing amplitude represented in the dB scale. Mean square amplitudes of all auditory stimuli recordings were digitally equalized. Digital sound editing was done using Anvil Studio (Willow Software, Lake Forest Park, WA, USA), Audacity (Free Software Foundation, Boston, MA, USA), and MATLAB (MathWorks Inc., Natick, MA, USA).

Visual feedback stimuli were used: a positive visual feedback was a large black contour thumbs-up sign on a gray background, and a negative visual feedback was a thumbs-down sign, which was produced by rotating the thumbs-up sign by  $180^\circ$  (see Figure 1).

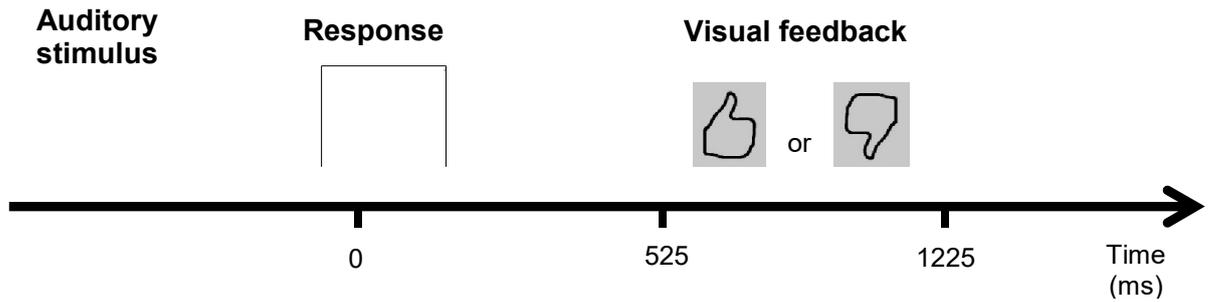


Figure 1. A schematic illustration of the experimental behavioral task. See text for details.

## Design and procedure

An auditory two-choice version of the condensation task was used [Chernyshev et al., 2015; Novikov et al., 2015]. A schematic layout of the experiment is depicted in Figure 1, and stimulus-to-response contingencies are given in Table 1.

The experiment was split into six identical blocks; after each block, participants had an opportunity to have a short rest. During each block, 100 auditory stimuli were presented; the four stimuli were presented with equal probabilities (25:25:25:25) interleaved in a quasi-random order, with random stimulus onset asynchrony (SOA) of  $4000 \pm 500$  ms (uniform distribution).

**TABLE 1. Response contingencies in the experimental task: this table was read as well as handed in printed form to the participants before the experiment**

Sound pitch	Sound timbre	
	Violin	Calliope
High	Left button	Right button
Low	Right button	Left button

Participants were instructed to hold the gamepad in their right hand and to press one or the other of the two specified buttons with their thumb in response to the stimuli. The stimulus-to-response mapping used in the current version of the condensation task is represented in Table 1. The table specifies the conjunction contingencies between the two stimulus features ('violin'/'calliope' and 'high'/'low') comprising the set of the four stimuli, and the response required to the left and right buttons of the gamepad. Though the task rules were simple, the task could not be solved at above chance level via processing any single feature but instead it required a mental conjunction of both features. For familiarization, the participants were offered a table (the same as Table 1), which was given to them printed in a large font on a sheet of paper for free viewing and then removed before the start of EEG recording.

Visual feedback was presented in all six experimental blocks, 525 ms after participants' responses; the duration of the feedback stimulus was 700 ms. Depending on the correctness of the response, participants were presented with positive or negative visual feedback. The meaning of the feedback stimuli was explained in the instruction read to the participants before the start of the experiment. Feedback was presented only if response time was greater than 300 ms. If response time exceeded 1700 ms, feedback stimuli were supplemented with a word 'Faster' on the monitor; such 'urged' trials were later excluded from the EEG analysis.

Before the start of the experimental blocks, the participants were familiarized with the auditory stimuli: the experimenter manually played them to the participants and named them orally, and then the participants were blind-tested with the stimuli. During this test, all of the participants easily named all of the stimuli correctly, and all of them stated confidently that they could clearly hear the difference between all of the stimuli and knew which button corresponded to each stimulus.

The instruction given to the participants informed them that they were to press one of the two buttons as specified in the table, but it did not tell them to respond as fast as possible, nor did it force them to make random choices if they were not sure which response was correct.

## **Electrophysiological recording and EEG preprocessing**

The EEG was recorded using an NVX-52 system (Medical Computer Systems, Moscow, Russia) with Neocortex Pro software (Neurobotics, Moscow, Russia) from 27 electrodes in accordance with the modified international 10-10% system and 1 electrooculogram electrode, with a linked earlobe reference. The band-pass filter was 0.1–200 Hz, and sampling rate was 1000 Hz. Electrode-to-skin impedance was kept below 10 k $\Omega$  for all channels.

EEG analysis was performed within MATLAB (MathWorks Inc., Natick, MA, USA) using custom-written scripts and built-in functions of EEGLAB toolbox [Delorme and Makeig, 2004]. High-amplitude artifacts exceeding 300  $\mu\text{V}$  were rejected from the data. Signals in bad channels were replaced by spherical interpolations over the neighborhood electrodes. Independent component analysis (ICA) was performed, and components related to eye movements were manually selected and rejected from the data. Finally, we substituted signals in channels contaminated with electromyographic activity by spherical interpolation over the neighborhood electrodes; we selected for this procedure those channels in which the spectral power in 25-45 Hz range exceeded 1.5 standard deviations above the mean value taken over the total number of channels $\times$ blocks $\times$ subjects in the experimental sample (approximately 2% of channels $\times$ blocks $\times$ subjects).

In order to reduce volume conduction effects, current source density (CSD) transformation was applied to EEG data using an open-source CSD toolbox [Kayser and Tenke, 2006a]. CSD transformation can be applied to low-resolution EEG [Kayser and Tenke, 2006b].

Response-locked epochs for each condition were extracted from the data. Epochs were included in the EEG analysis only if they met the following conditions:

(1) the response time was within 300-1700 ms range. Thus, 'urged' responses and trials with abnormal RTs were excluded from the analysis;

(2) we excluded trials with multiple responses that were occasionally performed by some participants and which could contaminate post-response EEG data;

(3) only correct trials committed within sequences of correct trials and only single errors committed between correct trials were included in the analysis. This was done in order to exclude post-error and pre-error effects influencing the trials that immediately follow or immediately precede erroneous responses.

The CSD signal in each channel was translated into the time-frequency domain using wavelet transformation within sliding time windows at 20 ms steps. Morlet wavelets with frequencies ranging from 2 to 40 Hz in steps of 1 Hz were used; the number of cycles was linearly increased from 2 (on the lowest frequency) to 37.5 (on the highest frequency), providing an equal tradeoff between time and frequency resolutions over the whole frequency range.

For each time-frequency bin and each electrode, we calculated non-phase-locked spectral power averaged over the subsets of trials used for the analysis. First, we calculated the mean

total power by averaging the squared norms of the complex amplitudes over the trials. Next, we calculated phase-locked power by averaging the complex amplitudes over the trials, and then taking squared norm of this average. Non-phase-locked power was calculated as the difference between the total power and the phase-locked power. Spectral power values were converted to logarithmic units (decibels). We averaged data within each of five consecutive time points using a rectangular time window, thus increasing the step of spectral data representation from 20 to 100 ms; this was done in order to improve the signal to noise ratio.

Since all participants committed less erroneous trials than correct trials, we did a trial number matching procedure, which equalized the number of trials across conditions. This was needed to equalize the variance of the mean non-phase-locked power estimate, avoiding a bias in the estimation of the mean difference in the non-phase-locked power between conditions.

To contrast correct and erroneous responses (which were the focus of the analyses reported here), the trial matching procedure involved a response time matching procedure as follows. We used all trials from a condition that was less frequent throughout the experiment, and for each of these trials we selected a matching trial from the other condition with the closest response time (each trial could be taken only once). This procedure equalized mean RTs within each pair under comparison, allowing us to compare correct trials with erroneous trials on compatible timelines.

### **General strategy of statistical EEG data analysis**

Within all the permutation statistical analyzes described below, we used two types of paired statistical comparisons. First, for each condition, spectral power values were compared with the respective baseline prestimulus values (within-condition analysis). Next, spectral power values were compared between correct trials and erroneous trials (cross-condition analysis). We applied this statistical approach to compare correct trials with erroneous trials.

For such analyses, values of non-phase-locked power for each subject and each condition were organized into 4D matrices with the following dimensions: rostrality (7 levels: from frontal to occipital electrodes), laterality (5 levels: from left to right), oscillation frequency (29 levels: 2 to 30 Hz) and time (20 levels: -500 to 1400 ms). Such 4D matrices were used for ROI-free analyses.

T-statistics was applied independently to each data point. Then, for all such comparisons, we applied TFCE-based permutational statistical testing as described below.

## ROI-free EEG data analysis

In order to describe the general picture of brain oscillations under the behavioral procedure used, we did a whole-data permutational analysis free of any assumptions concerning electrode locations, oscillation frequency, and time. We used the whole range of valid RTs specified above.

For this analysis, we did a response time matching procedure within each participant's data: we used all trials from a condition that was less frequent throughout the experiment (erroneous trials), and for each of these trials we selected a matching trial from the other condition (correct trials) with the closest response time (each trial could be taken only once).

The baseline was calculated by averaging the spectral power over the -500-0 ms pre-stimulus time window (independently for each electrode and each frequency). We used a common baseline for the two conditions under comparison because we focused on post-stimulus effects and aimed to get rid of possible pre-stimulus variation effects.

In the within-condition analysis, we calculated the difference between the spectral power value in each data bin of the 4D matrix and the corresponding baseline power values, thus obtaining event-related spectral perturbations (ERSP). In the cross-condition comparisons, we performed a bin-by-bin subtraction of the power values contained in the 4D matrices of the conditions being compared. Both the within-condition and cross-condition matrices calculated for each subject were subjected to the same group-level statistical procedures as follows. For each spatial-time-frequency data bin, we compared its vector mean value against zero. For the within-condition analysis, this is equivalent to comparing the bin with the baseline; for the cross-condition analysis, this is equivalent to comparing the corresponding bins between two conditions.

In order to deal with the multiple comparison problem, we performed the following statistical procedure. First, we calculated paired t-statistics for each data bin independently, producing a matrix of t-scores, and then we applied the threshold-free cluster enhancement (TFCE) algorithm [Smith and Nichols, 2009] to this matrix, which resulted in a new matrix of TFCE-scores of the same dimensionality and size. Positive and negative t-scores were transformed to TFCE scores using two independent runs of the algorithm. After that, we shuffled the initial data by flipping the sign of all the bins in the matrix for randomly selected subsets of subjects, and repeated the calculation of TFCE matrix on this shuffled data; this permutational procedure was repeated 1000 times. At each permutation step, we obtained the maximal

(positive) and the minimal (negative) TFCE-score over the entire matrix, and then we constructed two distributions: one for the maximal and the other for the minimal values. Finally, for each bin of the non-shuffled TFCE matrix (independently), we calculated the quantiles of “minimal” and “maximal” distributions the value in this bin falls into, thus obtaining permutation-based p-value for this bin.

The results reported here were considered significant at  $p < 0.05$ . It is important to note that the permutation procedure described above provides correction for multiple comparisons in spatial- and time-frequency domains. For illustrative purposes, we plotted projections of the 4D data space onto 2D scalps using averaging within theta, alpha, and beta bands (4-7, 8-13, 15-25 Hz respectively) as well as within consecutive time windows.

### **ROI definition**

The current study primarily aimed at testing error-related and feedback-related events. Thus, we defined the following *a priori* ROIs based on previous research.

ROI 1 – error-related and feedback-related FMT oscillations: 4-7 Hz, frontal midline electrodes Fz, Fcz, Cz [Yeung et al., 2004; Cohen et al., 2007; Cavanagh et al., 2009; Christie and Tata, 2009; Cohen et al., 2009; van de Vijver et al., 2011; Cavanagh and Frank, 2014; Novikov et al., 2015].

ROI 2 – attention-related posterior alpha oscillations: 8-13 Hz, parieto-occipital electrodes Pz, O1, Oz, O2 [Klimesch, 1999; Carp and Compton, 2009; Mazaheri et al., 2009; van Driel et al., 2012; Novikov et al., 2015].

ROI 3 – feedback-related frontal beta oscillations: 15-25 Hz, electrodes overlaying prefrontal areas F3, Fz, F4 [Cohen et al., 2007; Marco-Pallares et al., 2008; van de Vijver et al., 2011; Cunillera et al., 2012].

### **ROI-based EEG data analysis using the whole range of RTs**

In order to give a more focused description of the time-frequency dynamics, we averaged data across electrodes within each of the ROIs. Again, we did both within-condition and cross-condition comparisons. Averaging across electrodes within ROIs produced 2D matrices that were subjected to the TFCE and permutation statistical testing in a way similar to the procedure described above. Results were represented as time-frequency ERSP plots.

# Results

## ROI-free EEG data analysis

First, we performed a whole-data analysis of non-phase-locked oscillations, unrestricted by any *a priori* assumptions concerning spatial electrode locations, frequency bands or time windows, using a 4D TFCE-based permutational statistics as described in Methods. Figure 2 provides illustrations of these results as projections of the 4D data space onto a sequence of 2D scalp maps collapsed within EEG frequency bands and representative time windows.

Within the theta range (Figure 2, top panels), significant activations at the frontal midline regions were evident in the pre-response, post-response and feedback time windows. During the pre-response time, FMT was equally strong on correct and erroneous trials. This involved midline electrodes Fz, Fcz, and their nearest neighbors over the left hemisphere. Post-response FMT revealed error-related activity, with a strong maximum at Fcz. Feedback activity was very strong and significant, involving three frontal midline electrodes (Fz, Fcz, and Cz), and extending to the nearest lateral electrodes (with significant differential effects found on the left side of the scalp only).

Alpha oscillations (Figure 2, middle panels) were significantly suppressed over the whole scalp through the whole trial duration. During the pre-response and post-response time, the greatest suppression was at lateral central electrodes, with a local minimum on the left side (C3 and Cp3), and with an additional weaker symmetrically located local minimum on the right side. The effect did not differ significantly between correct and erroneous trials. During the feedback presentation, the topography of the alpha suppression was different, with the strongest effect at the parieto-occipital region. It was stronger on erroneous trials, leading to a significant difference between errors and correct trials at the parieto-occipital region, with some predominance on the left side.

Beta oscillations (Figure 2, bottom panels) were significantly suppressed through the pre-response and post-response periods. This suppression largely disappeared during most of the feedback period – with the exception of the posterior sites, where suppression continued throughout most of the trial. The frontal feedback-related increase in the power of beta oscillations became evident around the feedback onset and lasted throughout the feedback. On correct trials, it was significant on frontal electrodes such as Fz and its neighbors on the left side. On erroneous trials, such feedback-related activity was weaker and statistically insignificant.

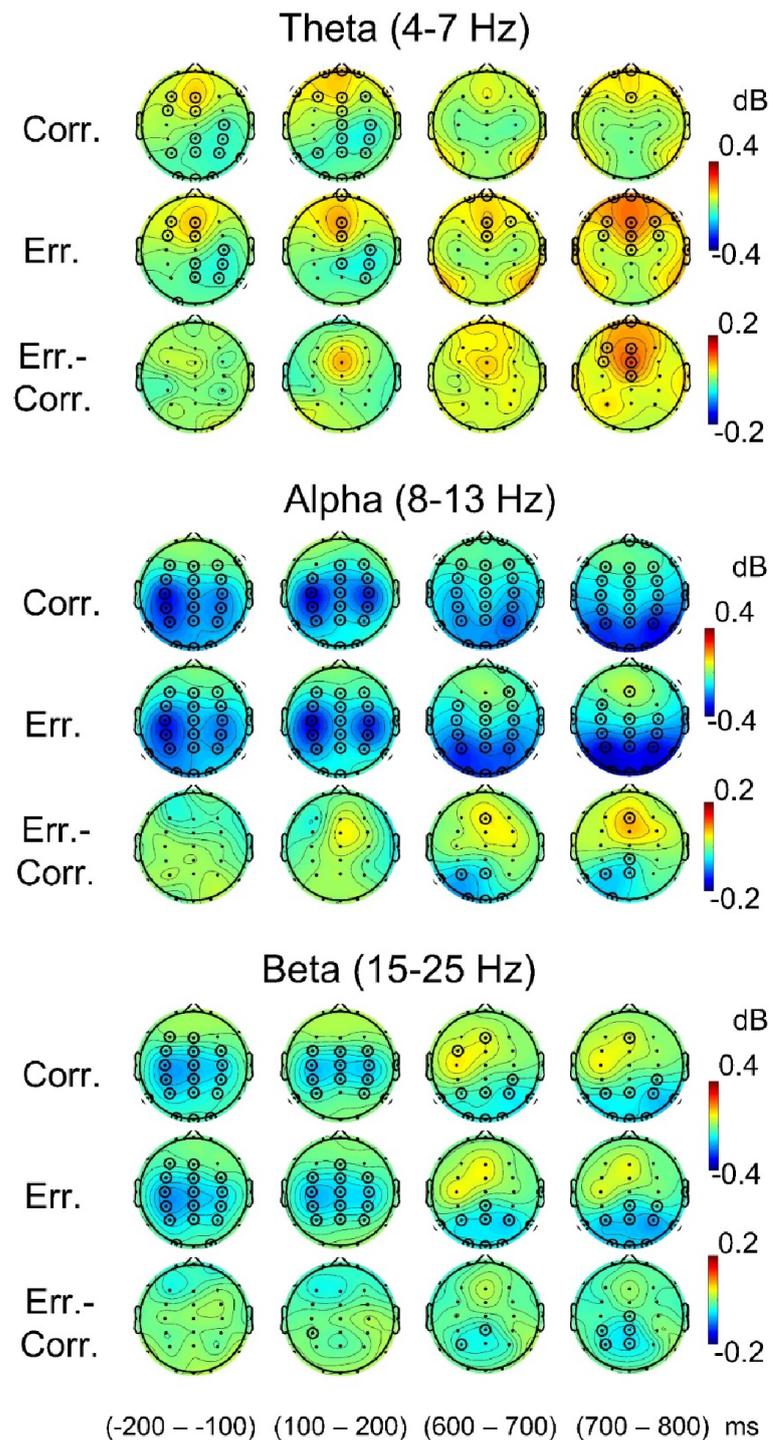


Figure 2. Topographical maps of non-phase-locked theta, alpha, and beta band activity.

Within each panel for theta, alpha, and beta bands:

*top*: spatial distribution of event-related spectral perturbations (ERSP) on correct trials;

*middle*: spatial distribution of ERSP on erroneous trials; *bottom*: spatial distribution of ERSP

difference between erroneous and correct trials.

Time intervals relative to the behavioral response are indicated at the bottom and represent ‘pre-response-’, ‘post-response-’, ‘early feedback-’ and ‘late feedback-related’ time windows correspondingly. Significant electrodes ( $p < 0.05$ , 4-D TFCE permutation statistics) are highlighted by black circles. Abbreviations: “Corr.” – trials with correct responses, “Err.” – trials with erroneous responses, “Err. - Corr.” – difference between erroneous and correct responses.

## ROI-based EEG data analysis using the whole range of RTs

Next, we did a more focused time-frequency analysis of non-phase-locked oscillatory activity within ROI locations using 2D TFCE-based permutational statistics as described in Methods. Figure 3 provides illustrations of these results as time-frequency ERSP plots.

At frontal midline ROI 1 centered on Fcz (Figure 3, left panel), non-phase-locked theta activity was clearly visible. In the pre-response interval, theta activity was significant on both correct and erroneous trials. On correct trials, theta activity ceased at the time of the behavioral response commission, while on erroneous trials it continued well through the post-response period up to approximately 400 ms. The difference was significant within the 100-400 ms interval, thus evidencing the presence of the error-related FMT effect. During feedback, there was a strong increase in theta, which commenced approximately 150-200 ms after the feedback onset and lasted throughout the whole feedback duration. No evidence of such an increase of theta activity was present on correct trials. The difference between erroneous and correct trials was also significant starting from approximately 150-200 ms after the feedback onset and lasting throughout the whole feedback, thus evidencing presence of the feedback-related FMT effect.

Within the parieto-occipital ROI 2 (Figure 3, middle panel), suppression of non-phase-locked alpha oscillations was significant throughout the entire period of analysis, with the strongest suppression during the pre-response period and during the feedback. Pre-response alpha suppression was equally strong on correct and erroneous trials. Feedback-related activity apparently had an earlier onset on erroneous trials compared with correct trials. A comparison of erroneous and correct trials revealed that alpha suppression was indeed stronger on erroneous trials. Significant difference started around 350-400 ms after the response, i.e. before the feedback onset, and the differential effect continued throughout the whole feedback time period, with the strongest initial part of the differential effect from approximately 400 to 700-800 ms after the behavioral response.

At the prefrontal ROI 3 (Figure 3, right panel), on correct trials there was a significant increase in the non-phase-locked low beta range within the pre-response period, while there was no such increase on erroneous trials. On correct trials, there was a strong increase of non-phase-locked oscillations in the frequency range from 14-15 to 25-27 Hz starting before the feedback onset and lasting throughout the whole feedback and further beyond the feedback period.

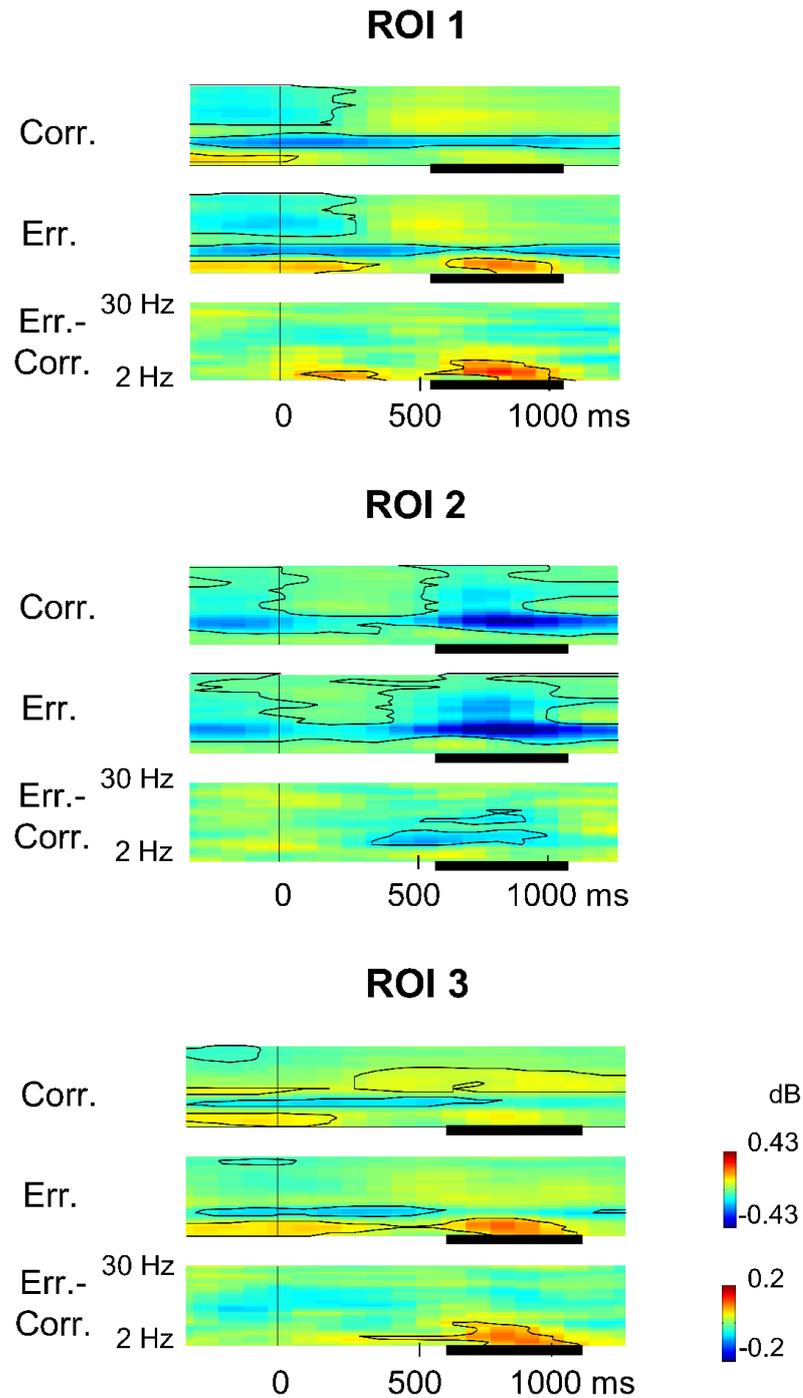


Figure 3. Time-frequency plots of non-phase-locked activity within ROIs. *top*: ERSP averaged across ROI 1 (Fz, Fcz, Cz) illustrating FMT oscillations; *middle*: ERSP averaged across ROI 2 (Pz, O1, Oz, O2) illustrating posterior alpha oscillations; *bottom*: ERSP distribution averaged across ROI 3 (F3, Fz and F4) illustrating prefrontal beta oscillations. Within each panel from top to bottom: dynamics of ERSP on correct trials, dynamics of ERSP on erroneous trials, dynamics of ERSP difference between erroneous and correct trials. Black contours show significant time-frequency areas ( $p < 0.05$ , 2-D TFCE permutation statistics). Time is shown relative to the behavioral response. Horizontal black rectangle on the time axis indicates feedback presentation.

# **Discussion**

## **Summary of results**

We observed clear evidence of both error-related and negative feedback-related FMT oscillations. Alpha oscillations were significantly suppressed over almost all electrodes throughout the whole trial, with greater suppression at lateral electrode locations over sensory-motor regions around the response time, and greater suppression at parieto-occipital areas around the time of the feedback presentation. The latter was stronger on erroneous trials compared with correct trials. Sensorimotor beta oscillations were significantly suppressed around the response time. At the time of the feedback presentation, prefrontal beta oscillations were significantly increased only on correct trials.

## **FMT oscillations**

Before the response, FMT power was significantly increased compared with the baseline level on both correct and erroneous trial types. The most prominent power of theta-band oscillations appeared at the mid-frontal electrodes with a maximum at Fz and Fcz electrode sites. We can interpret this phenomenon as an index of the processes that reflect stimulus processing, activation of task rules, initiation of motor programs, etc. Supposedly, this process is related to conflict processing resulting from the necessity to commit a choice between the two alternative behavioral responses; the major sources of FMT are known to be located in the medial prefrontal cortex [Womelsdorf et al., 2010; Cavanagh and Frank, 2014]. This pre-response theta activation did not differ between erroneous and correct trials, thus our data do not provide evidence of a relation between pre-response theta activation and task performance accuracy.

Soon after the behavioral response, theta FMT was significantly increased after erroneous responses, while there was no evidence of such an increase after correct responses. The difference between correct and erroneous responses was significant within the midline frontal ROI 1. This post-error FMT burst is believed to reflect error detection [Luu and Tucker, 2001; van Driel et al., 2012; Navarro-Cebrian et al., 2013; Novikov et al., 2015].

Error-related EEG activity in the low-frequency range is believed to be associated with error detection at the level of movement monitoring: this phenomenon was observed mostly for the total theta oscillations rather than for phase-locked theta oscillations, evidencing that this effect can be explained by an increase in theta power rather than by an increase in theta

synchronization (phase-locking) [Yordanova et al., 2004; Kolev et al., 2009]. The increased theta power after incorrect responses has its sources in the medial prefrontal cortex; currently there is a general agreement that it represents the need for increased cognitive control [Ridderinkhof et al., 2004; Debener et al., 2005; Cohen et al., 2008; Doñamayor et al., 2012]. The error-related FMT activity may be viewed as an index of the internal error detection [Holroyd et al., 2004].

After feedback onset, FMT power was significantly elevated on erroneous trials compared with correct trials. This effect is believed to reflect detection of a mismatch between expected and actual outcomes [Cohen et al., 2007, 2009; Cavanagh et al., 2010; van de Vijver et al., 2011]. The feedback-related FMT activity may be viewed as an index of the external error detection [Holroyd et al., 2004].

Our findings evidence that under conditions of the auditory condensation task typical FMT effects may be observed, similar in frequency, timing and topography to those reported using a substantially different class of behavioral tasks based on suppression of prepotent responses [Ridderinkhof, 2002; Ridderinkhof et al., 2004; Dudschig and Jentsch, 2009; van Driel et al., 2012]. Our findings also agree with an earlier demonstration of an error-related FMT effect in a substantially different version of the condensation task [Novikov et al., 2015].

## **Posterior alpha oscillations**

The power of alpha oscillations was significantly suppressed over most of the scalp on all trial types. Alpha suppression is believed to be a sign of cortical disinhibition: such disinhibition serves to recruit a variety of neurocognitive processes when demand in top-down control arises [Klimesch et al., 2007]. Alpha suppression is supposedly related to an adaptive increase in the level of attention required for effective performance in a behavioral task [Carp and Compton, 2009; Compton et al., 2011; Cohen and Ridderinkhof, 2013].

For a prolonged time around the behavioral response, the effect was most strongly pronounced at left lateral electrodes. All participants in the current study used their right dominant hands to commit responses during the experiment, thus this observation agrees with reports describing mu-rhythm desynchronization in the hemisphere contralateral to the hand being used [Szurhaj et al., 2001]. This effect can be explained as action preparation or processes related to decision making, such as evidence integration [Pineda, 2005; Tosoni et al., 2014].

Within the later post-response time interval (continuing beyond the feedback onset), we found that the depression of posterior alpha power was significantly stronger on erroneous trials

than on correct trials. Similar effects were reported in the literature, and they were regarded as evidence of an adaptive increase in sustained attention following error detection [Carp and Compton, 2009; Mazaheri et al., 2009; Novikov et al., 2015].

In line with a recent report using a different version of the condensation task [Novikov et al., 2015], our results agree with the literature. Alpha-band modulations observed in the current study can be interpreted in terms of cognitive control and attentional adjustments.

### **Frontal beta oscillations**

We observed strong modulations of beta power over the prefrontal cortex. The behavioral task used in the current experiment was cognitively demanding [Chernyshev et al., 2015]; according to the literature, the modulation of beta-band activity in the prefrontal cortex was observed to accompany various intense cognitive processes such as action planning [Siegel et al., 2011], cognitive control [Zhang et al., 2015], working memory [Babiloni et al., 2004], etc.

Importantly, in our study, we detected a significant increase in beta power on correct trials during the positive feedback stimulus, while there was no evidence of such an effect on erroneous trials. Prominent increases in beta power following the positive feedback onset were observed in prefrontal electrode sites F3, Fz and F4, confirming the results reported by Cunillera et al. [2012]. Our findings agree with studies that found enhanced beta oscillations in the prefrontal cortex induced by positive feedback during reinforcement learning [Cohen et al., 2007; van de Vijver et al., 2011], as well as gambling tasks [Marco-Pallares et al., 2008]. Beta oscillations are believed to reflect the involvement of frontal, striatal, and hippocampal structures in relation to reward processing [Mas-Herrero et al., 2015].

### **Conclusions**

This study aimed at an in-depth probing of error-related and feedback-related modulations of the EEG oscillatory activity in theta, alpha, and beta bands during the performance of an auditory condensation task. Such activity has been investigated only in a very narrow class of behavioral tasks, all of which involved visual stimuli and asymmetrical stimulus-to-response mapping, while they were taxing motor inhibition needed to overcome prepotent responses rather than attention per se.

Our findings demonstrate that under a demanding attentional task, which had symmetrical stimulus-to-response mapping, a full range of error-related and feedback-related phenomena in the oscillatory domain can be observed. Our results extend the current knowledge concerning error- and feedback-related modulations of theta, alpha, and beta band activity to an attentional task that involves no inhibition of prepotent responses. Importantly, our findings extend this knowledge to the auditory modality. Thus, the auditory condensation task proves to be a promising and effective tool for investigating the nature of cognitive control and related phenomena.

Our findings confirm and extend the current knowledge concerning the functional role of theta, alpha, and beta band oscillations in cognitive control beyond a limited range of tasks and beyond the visual modality. Additionally, the current findings highlight the role of at least three brain networks involved in cognitive control: the medial prefrontal network (which is related to assessing the need for increased cognitive control), the parietal attentional network (which is related to sustained attention), and the frontal network (which is related to positive reward processing).

## **Acknowledgements**

The authors would like to acknowledge the invaluable contribution of Anna A. Lapina in conducting the experiments. The authors are very grateful to Evgenii E. Kalenkovich for designing important aspects of the framework used for the current data analysis.

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