

NATIONAL RESEARCH UNIVERSITY HIGHER SCHOOL OF ECONOMICS

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BASIC RESEARCH PROGRAM

WORKING PAPERS

SERIES: PSYCHOLOGY WP BRP 28/PSY/2014

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Attentional lapses are usually viewed as a result of deterioration in cognitive control. Current theories suggest that deterioration in the cognitive control may be related to an increase in alpha rhythm power, although it is not clear whether this notion can be generalized outside of the visual task modality. In the current study power of prestimulus alpha-band oscillations was analyzed during performance of the modified auditory condensation task, which creates high attentional load. Prestimulus lower alpha-band power was found to decrease before erroneous responses, which can be viewed as attentional lapses related to decreased cognitive control, compared with correct responses. Prestimulus lower alpha-band power also gradually increased within continuous sequences of distractor stimuli separating adjacent target stimuli, thus reflecting gradual increase in the level of cognitive control mirroring increasing expectancy of the target stimuli. These findings demonstrate that the relation of alpha power to cognitive control level critically depends on the experimental task modality, and under conditions of the auditory attentional task higher alpha power may be an index of increased rather than decreased level of cognitive control.

JEL Classification: Z

Keywords: alpha oscillations, attention, electroencephalogram, prestimulus, cognitive control.

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⁸ The study was implemented in the framework of the Basic Research Program at the National Research University Higher School of Economics (HSE) in 2014.

Introduction

Attention lapses (or, in broader sense, cognitive control failures) have been extensively studied in psychophysiology during the last decade. In one of the pioneering studies by Weissman et al. [2006] it was shown by means of fMRI that lapses in attention were preceded by reduced activity in the frontal cortex, reduced task-related deactivation of the default-mode network, and reduced activity in the occipital cortex (importantly, the task used was visual); on the contrary, increased activation of the frontal cortex after the lapse supposedly reflected the compensatory mechanism, leading to improved performance. Thus the pattern found points to several potential causes of attentional lapses. Deactivation of the frontal cortex may reflect a decrease in the level of cognitive control, while the default-mode network activation is likely to be related to the state of mind-wandering, which may be viewed as a concurring task competing for cognitive resources and thus compromising the performance quality. Both these two causes may lead to disrupted processing of perceptual information - as indexed by reduced activation in sensory areas. Later research generally confirmed these notions. In particular, it was shown that errors are accompanied by decreased amplitudes of the contingent negative variation and P300 component [O'Connell et al., 2009], as well as reduced theta power [Cavanagh et al., 2009] – all of them being indexes of attention/cognitive control in general. A positive shift of responserelated ERPs before error commissions is also in line with the notion of the reduced cognitive control leading to errors [Ridderinkhof et al., 2003; Allain et al., 2004; Hajcak et al., 2005].

In early EEG studies it was also demonstrated that alpha rhythm decreases when a person is involved in intense mental activity [Martinson, 1939]; thus for a long time it was believed that alpha rhythm is the rhythm of inactivity, as it is usually depressed during activation of sensory systems.

In 1960 Lindsley suggested that there is a relationship between the functional state shift, the dynamics of EEG and attention [Lindsley, 1960]. A voluntary activity involving attention is accompanied by a certain EEG amplitude reduction in the alpha range [Shaw, 2003]. Lal and Bekiaris demonstrated that a situation requiring prolonged elevated level of attention is accompanied by increased power of theta oscillations and reduced alpha rhythm [Lal et al., 2007]. Many researchers noted that the dynamics of the EEG contributes to mental processes such as initiation and suppression of motor responses, decision-making, pattern recognition, decision under mnemonic tasks – that is, the processes that are associated with the involvement of attention [Klimesch et al., 2007; Pfürtscheller, Lopes da Silva, 1999].

At the moment there is a large and rapidly growing body of evidence demonstrating that changes in prestimulus occipital-parietal alpha power modulates attentive perception of visual stimuli. Most of that evidence stays in accord with the notion that increased alpha can be a correlate of cortical deactivation [Pfurtscheller et al., 1996] or of an active process of cortical inhibition [Klimesch et al., 2007]. In a pioneering study by Ergenoglu et al. [2004] it was found that lower values of alpha power preceded successful detection of near-threshold visual stimuli, while failures in detection were preceded by relatively higher values of alpha power.

Similar results were obtained in later experiments: it had been established, that a group of subjects, who successfully perceived briefly presented visual stimuli, demonstrated lower alpha power during prestimulus intervals [Hanslmayr et al., 2007]; moreover, participants discriminated near-threshold differences in visual stimuli better when alpha power was lower during the prestimulus interval [Dijk et al., 2008]. Experiments involving direct manipulations of brain activity demonstrated that transcranial magnetic stimulation (TMS) applied to parietal sites led to phosphene perception if the stimulation was preceded by low alpha rhythm power, conversely, no phosphenes were perceived if alpha power was high [Romei et al., 2008]. TMS rhythmically applied in the alpha range (10 Hz) led to better perception of visual stimuli (compared with TMS at 5 or 20 Hz), the fact that led to the conclusion that alpha oscillations are actively involved in perception and attention.

Repetitive inhibitory TMS applied to the intraparietal sulcus or to the frontal eye field, in turn, both impairs identification of visual objects and abolishes anticipatory alpha desynchronization. This observation supported the view that the visual cortex is under the control of the frontoparietal attentional network [Capotosto et al., 2009]. Thus a general understanding of the parietal alpha may be that it reflects top-down preparation for an ongoing task. Interestingly, besides objective performance measures, subjective attentional state ratings also negatively correlate with prestimulus alpha power [Macdonald et al., 2011].

The pattern obtained for visual tasks is not limited to the parietal or occipital alpha: both occipital and sensorimotor (mu rhythm) alpha were elevated before error commission [Mazaheri et al., 2009] in the Go/noGo task. Later still, comparison of the psychophysical data to changes in spontaneous prestimulus alpha revealed that pronounced occipital alpha is more strongly related to performance deterioration (compared to sensorimotor mu rhythm) [Chaumon and Busch, 2014].

Similar results were obtained in experiments using somatosensory stimulation in which

mu rhythm (recorded at central electrodes) was measured. Lower mu power was accompanied by better detection rate in a tactile task [Jones et al., 2010]. Direction of spatial attention to a particular body part (left or right) during a somatosensory task led to mu rhythm reduction at corresponding brain areas [Anderson and Ding, 2011; Ede et al., 2011]; interestingly this was also accompanied by greater occipitoparietal alpha power [Anderson and Ding, 2011]. Inversely, in a somatosensory working memory task, mu rhythm became greater over task-irrelevant brain regions [Haegens et al., 2010].

Analogous studies in the auditory modality are much less numerous, and they rather concentrate on sophisticated relations of prestimulus EEG to stimulus-locked ERPs [for example, see Barry et al., 2014, 2000]. This seems surprising, since one of the first studies investigating relations of EEG to perception and performance used auditory stimulation [Makeig and Jung, 1996].

Several studies directly measured relation between attentional lapses and changes in stimulus-locked alpha power on a longer timescale. In the study by Compton et al. [2009; 2011], alpha power was found to decrease in the intertrial intervals after the erroneous trials (compared with the correct ones), which may be interpreted as a compensatory activation of the cognitive control mechanism. In studies investigating changes in alpha power preceding erroneous responses, it was found that alpha gradually increases before error commission, and the effect can be detected up to 20 seconds preceding errors [O'Connell et al., 2009]. This fact can again be interpreted in terms of changes in top-down cognitive control level – specifically in terms of its gradual decline during a repetitive task performance.

It is worth noting that in the studies of Compton et al. [2009, 2011] and O'Connel [2009] attentional tasks in visual modality were used, and the experimental effect was most pronounced at parietal and occipital sites. Thus, considering the known relation between the posterior alpha rhythm and visual cortex activation, the evidence on the relation between alpha power and cognitive control can be reevaluated in the following way: increased cognitive control focused on visual processing may lead to activation of visual sensory areas, leading to alpha power suppression. On the contrary, decreased cognitive control would lead to deactivation of visual areas accompanied by an increase in alpha power.

Moreover, as shown by Mo et al. [2013], higher visual alpha power values were accompanied by higher activity of the default-mode network; this finding also casts doubt on the possibility to use alpha-power changes as a direct indicator of cognitive control level.

Thus, a non-visual attentional task may be needed to study the role of alpha oscillations in cognitive control mechanism in separation from the alpha activity related to the visual scene analysis or the default-mode network activation. Data obtained from experiments involving somatosensory stimulation [Anderson and Ding, 2011; Ede et al., 2011] allow assuming that the analysis of alpha oscillations used as a cognitive control level indicator should not be restricted to the occipitoparietal regions. Still, to the best of our knowledge, there were no studies measuring prestimulus alpha power dynamics relative to the cognitive control on a longer time-scale - beyond studies in visual modality mentioned above.

According Klimesch [Klimesch, 1997; Klimesch, 1999], the alpha range is not functionally uniform and can be divided into distinct sub-ranges. Attention and procedural memory correspond to changes in the lower alpha sub-range, while semantic memory is related to changes in the higher alpha band. Consequently, it seems useful to analyze alpha-range separately within these sub-ranges to better identify its specific changes in relation to cognitive control/attention.

Most studies dedicated to understanding the mechanism of attentional failures use various kinds of continuous performance tasks. In this study we used the condensation task, which presumably is more demanding in terms of cognitive resources than most other tasks since it requires more cognitive operations to be performed. According to the classical form of the condensation task [Posner, 1964; Gottwald, Garner, 1975] participants are required to pay attention to two stimulus features simultaneously, and to make a decision based on feature combination (i.e. conjunction). During such tasks participants commit a significant number of erroneous responses related to attentional failures. In the present study, the condensation task was modified and frequent distractors were additionally interposed in the way similar to the oddball task [Sutton et al., 1965]; frequent distractors allow studying the dynamics of brain activity during the intervals between the target stimuli, while they create stronger attentional emphasis on the target stimuli. The prestimulus alpha rhythm preceding distractors is of interest because if it reflects the current level of cognitive control and is common for auditory and visual modalities; one may expect that it will gradually decrease from the first distractor to the last one in the row. This hypothesis is based on the idea that immediately after presentation of a target stimulus, another target is the least expected, while expectation of the target probability gradually increases along the sequence of distractors, with a corresponding gradual increase in cognitive control level.

The aim of this study was to investigate the role of alpha band oscillations as a potential mechanism of distribution of attention during the auditory condensation task and, and in a broader view, in regulation of cognitive control within the auditory modality.

Methods

Participants

The study was conducted on 44 university students 18-22 years of age (mean age 19 years). All participants had normal hearing, normal or corrected to normal vision and reported no auditory, neurological or mental illness or previous instances thereof. Participants were asked to refrain from consuming psychotropic drugs, alcohol, tea and coffee, as well as to have enough sleep on the day before the experiment. An informed consent was obtained and signed by the participants before the experiment, and they were also asked to fill a short questionnaire concerning their current physical and mental state.

Materials

Experimental settings. The experiment was performed in a sound-attenuated chamber with standard ceiling lighting. Participants were comfortably seated onto encephalographic chair with adjustable headrest and armrests. A 19" LCD monitor was in front of them at their chest level.

Electrophysiological recording. Electroencephalogram (EEG) was recorded with NVX-52 system (Medical Computer Systems, Russia) with Neocortex Pro software (Neurobotics, Russia) from 32 EEG electrodes in accordance with the international 10-10% system and one electrooculographic electrode, referred to linked earlobes, with a forehead grounding electrode. Impedance was kept lower then $10 \text{ k}\Omega$ in all channels. The filter bandpass was 0.5–200 Hz.

Auditory stimulation and experimental procedure. Auditory stimuli were presented to the participants by means of E-Prime software (Psychology Software Tools, Inc., U.S.A.) through a high-quality stereo headset with in-ear design, which additionally reduces ambient noises. Five pre-recorded auditory tones were presented. Four of them ("targets") were sinusoidal signals of either 500 Hz ("low") or 2000 Hz ("high") – either a pure tone ("pure") or the same tone with broadband noise admixed to the signal ("noised"). Thus the 4 stimuli were named in

the instruction presented to the participants as (1) "low pure", (2) "low noised", (3) "high pure", and (4) "high noised". The distractor was a pure 400 Hz tone. The duration of all stimuli was 40 ms, with rise and fall time 10 ms each, and approximately 85 dB loud.

Behavioral responses were obtained from the participants with the help of a handheld gamepad. Participants were instructed to hold the miniature gamepad in their dominant hand, and press one of the two buttons with the thumb in response to target stimuli, trying to avoid moving their hand and arm.

The table below specifies the conjunction contingencies between the two stimulus features ("high/low" and "pure/noised") comprising the set of the 4 target stimuli, and the response required for the left and right buttons of the gamepad. In response to pure high and to low noised sounds participants were asked to press the left button; in response to low pure and high noised sounds participants were asked to press the right button. Although the rule is simple, the task cannot be solved at above chance level by relying on any single feature but it rather requires mental conjunction of the two features.

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

	High	Low
Pure	Left button	Right button
Noised	Right button	Left button

Participants were also informed that after each response they would receive the feedback signal: if they pressed the correct button, a "thumbs up" schematic sign would be briefly presented on a LCD screen in front of them, and in the event of incorrect response a "thumbs down" sign would be presented.

Before the main part of the experiment participants were made familiar with the stimuli: while the printed table was in front of the subject, all four stimuli were manually played to

him/her twice, each one loudly named by the experimenter ("low pure", "low noised" etc.). Then the stimuli were manually repeated without annotations as many times as needed until the participants would confirm that they could easily identify each of them if prompted to. To ensure that errors made in experiment are related to the binding process, two control behavioral series were performed. These series involved discrimination of the same stimuli by a single feature (pith or noisiness separately) rather than by the combination of features: these control series produced error rate below 1%.

The experiment was comprised of 6 experimental sessions. Each session consisted of 200 stimuli of 5 types (see above) intermixed in a random order. The four targets were presented with equal probability ratio (1:1:1:1); the ratio of targets to distractors was 1:4 (fig. 1). The stimuli were presented with random SOA of 2500 ± 500 ms (flat distribution). The time between a response and the next stimulus was kept to not less than 500 ms by prolonging SOA if needed. Feedback signal appeared 500 ms after the responses and was presented for 500 ms.

Participants were asked to press one button at time, but the instruction did not stress the necessity of speeded responses or the necessity of response even in case when the decision was not made (i.e. participants were implicitly allowed to omit responses).



Fig. 1. Example of stimulus sequences and responses required during the experiment: different target stimuli (color notes) of different pitch and with or without admixed noise (notes with stars and rounded notes correspondingly), requiring left (L) or right (R) button presses, are randomly presented interspersed between distractors (black notes).

Data extraction and analysis

Behaviour. Behavioral outcome of each trial could be one of the following: correct response (pressing the correct button), error (pressing the wrong button), response omissions (failure to press any button). In the event of multiple key pressings only the first response was taken into analysis. Omissions were not analyzed because only 7 of the 44 participants made more than 10 omissions during the experiment.

EEG. For the purpose of EEG analysis, all sessions except the first one (which was a training one) performed by a participant were taken into account (i.e. 5 sessions). EEG was analyzed within the EEGLAB [Delorme, Makeig, 2004] toolbox for MATLAB (Mathworks, USA). EEG artifacts were manually rejected, and electrooculographic artifacts were corrected based on conventional recursive least squares regression [Gómez-Herrero et al., 2006].

EEG was analyzed at the four central electrodes (Fz, Cz, Pz, Oz) during the one-second period preceding the stimulus onset (-1000 - 0 ms). Alpha EEG power values were calculated using Fourier transformation with Hanning window superimposed. EEG power values were calculated in the total alpha range (8-12 Hz) and in two sub-ranges: the Higher alpha (10-12 Hz) and Lower alpha (8-10 Hz). EEG power values were calculated and averaged out within each participant, separately for each type of stimuli (target and distractors), for different positions of distractors (fig. 1), and for different outcomes (correct or erroneous response after target stimulus presentation) – for targets only. Only the data from the participants with more than 60 correct artifact-free trials were taken into analysis. Data from participants, who made less than 10 errors, were excluded from the analysis. Due to these restrictions statistical analysis was performed on a subgroup of 37 participants.

Statistical analysis

Prestimulus alpha power values preceding correct responses and errors, and prestimulus alpha power values for different distractor positions were analyzed separately by means of repeated measures variance analysis (ANOVA).

The following factors were used: RESPONSE (2 levels for correct response and errors), ELECTRODE (4 levels) and DISTRACTOR POSITION (4 levels). Greenhouse-Geisser correction was applied if needed. Data are presented as Mean ± Standard Error of Mean (M±SEM) unless otherwise specified.

Results

Behavior

While performing the modified condensation task, participants made errors in 19.6 ± 1.9 % of trials, omissions in 3.4 ± 0.7 % of all trials (N=44). For the subgroup of participants included into the EEG analysis these values were 19.2 ± 1.8 % and 2.7 ± 0.4 % for errors and omission accordingly (N=37).

Lower alpha (8-10 Hz)

Analysis of the behavioral outcomes produced two main results: alpha power was higher at parietal sites (F(3,108) = 8.55, p < .001, fig. 2A), and alpha power was decreased preceding erroneous responses compared to correct responses (F(1,36) = 7.57, p = .009, fig. 2B). Interaction of RESPONSE and ELECTRODE factors was not significant (F(3, 108) = .34, ns).

Comparison of the EEG power during prestimulus epochs for different distractor positions revealed alpha to increase from the first distractor to the fourth (F(3,108) = 3.65, p = .01, fig. 2C). Alpha power for distractor stimuli was also always higher at parietal sites (F(3, 108) = 8.55, p < .001). There was also a significant interaction between factors ELECTRODE and DISTRACTOR POSITION (F(9, 324) = 2.67, p = .005, fig. 2C), reflecting more dynamic changes at posterior (occipital and parietal) sites.

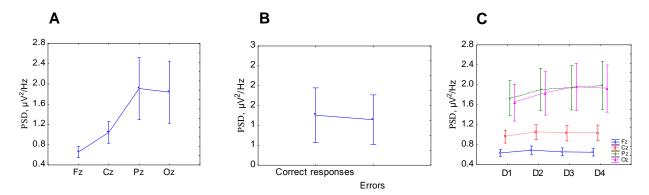


Fig. 2. Prestimulus lower alpha power. (A) Dependence of lower alpha power upon electrode. (B) Lower alpha power before correct response and errors. (C) Lower alpha power in dependence upon distractor position.

Higher alpha (10-12Hz)

Analysis of higher alpha power values for different behavioral outcomes revealed only a significant influence of electrode location (F(3, 108) = 9.0, p < .001): higher values were predictably obtained in the parietal and occipital sites (see fig. 3A). Response accuracy did not affect the higher alpha power (F(1, 36) < 0.01, ns) and interaction between factors ELECTRODE and RESPONSE was also non-significant (F(3, 108) = 0.6, ns).

Similar results were obtained when analyzing the role of distractor position. Only ELECTRODE factor was significant (again, with alpha more pronounced in parietal and occipital sites F(3, 108) = 10.2, p < .001). Impact of the DISTRACTOR POSITION factor was non-significant (F(3, 108) = 1.8, ns), as well as the interaction between DISTRACTOR POSITION and ELECTRODE factors (F(9, 324) = 1.5, ns).

Overall alpha (8-12 Hz)

The results obtained for the whole alpha range were similar to the ones obtained for the higher alpha rhythm frequencies (10-12 Hz). Comparison of higher alpha power values for different behavioral outcomes revealed only the significant influence of electrode location ((F(3, 108) = 10.32, p < .001), with higher values obtained in the parietal and occipital sites (see fig. 4A). Accuracy of the responses did not affect the higher alpha power (F(1, 36) = 0.4, ns), and interaction between factors ELECTRODE and RESPONSE was also non-significant (F(3, 108) = 0.8, ns).

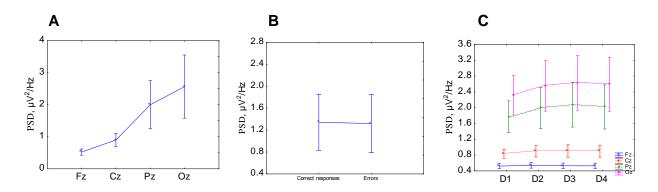


Fig. 3. Prestimulus higher alpha power. (A) Dependence of higher alpha power upon electrode; (B) Higher alpha power before correct response and errors. (C) Higher alpha power in dependence upon distractor position.

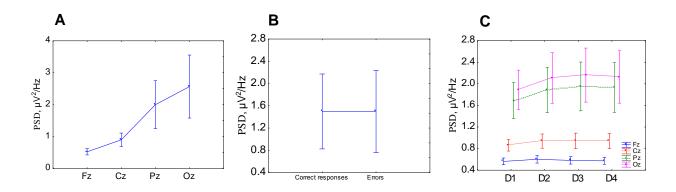


Fig. 4. Prestimulus overall alpha power. (A) Dependence of overall alpha power upon electrode. (B) Overall alpha power before correct response and errors. (C) Overall alpha power in dependence upon distractor position.

Analysis of the role of distractor position showed that only ELECTRODE factor was significant (with alpha more pronounced at parietal and occipital sites F(3, 108) = 11.27, p < .001). Impact of DISTRACTOR POSITION factor was pronounced at tendency level (F(3, 108) = 2.15, p = .09), as well as interaction between factors DISTRACTOR POSITION and ELECTRODE (F(9, 324) = 1.86, p = .06, fig. 4C).

Discussion

All participants confirmed that they clearly understood the instruction and that they were able to discern the stimuli well, and still they made errors during about 20% of trials. Control behavioral series involving discrimination of the same stimuli by a single feature (either pith, or noisiness separately) produced error rate below 1%. That suggests the nature of the performance failures was not related to any difficulties in sensory-related processing per se.

The percentage of errors in the current experiment was higher than in the experiments of Dyson and Quinlan [2003], or in [Chernyshev et al., 2014] who used a similar condensation task, although in a more common form without distractors. Thus introduction of distractors into the condensation makes the task more difficult for the participants. Another distinctive feature of the participants' behaviour during the modified condensation task used in the current study was the virtual absence of response omissions - compared to the traditional condensation task without

distractors [cf. Chernyshev et al., 2014]. Probably, introduction of distractors, leading to the increase in the time between targets presentation, allowed better mobilization or preparation to respond (see also a discussion on alpha power preceding distractors below), which in turn led to lowered amount of response omissions, but did not improve the overall performance. This does not contradict the understanding that feature binding in auditory modality may be automatic, accomplished within the relatively early time window after the stimulus onset and does not rely on late processes [Gomes et al., 1997]; thus increased target-to-target time affects the specific response property (such as its commission within a limited time window), but does not affect the success rate in general task performance.

The main electrophysiological finding of this study was that prestimulus EEG power in the alpha range was lowered before erroneous responses compared to correct responses. This result is partially consistent with our previous findings concerning the alpha-band reduction during a condensation task without distractors [Chernyshev et al., 2014]. Still there are some differences: first, the effects mentioned above were found in the full range of the alpha rhythm (8-13) Hz, while in the current study reduction in alpha power was expressed predominantly in the lower range of this band (8-10 Hz). Second, in the current study the effect was found preceding erroneous button presses, while in our previous study [Chernyshev et al., 2014] reduction in alpha power was found preceding response omissions.

Alpha depression is usually associated with general activation of the central nervous system and increased level of wakefulness [Tkachenko et al., 2013; Barry et al., 2004]; thus, suppression of alpha oscillations can be attributed to cortical activation [Pfurtscheller et al., 1996]. Increased alpha can also be a correlate of active process of cortical inhibition [Klimesch et al., 2007].

Seemingly, our findings are in contradiction with the data obtained by O'Connell et al. [2009], and do not support the presence of common mechanisms of cognitive control related changes in alpha power for visual and auditory modalities. Rather, since the current task was auditory, the decrease in alpha range power (especially pronounced at parietal and occipital sites) could signify a disinhibition of visual processing, meaning that attention was probably diverted from the relevant auditory modality to some other activity. It is likely that at the moments preceding errors the participants were involved in some sensory or mental activity, with their focus of attention diverted away from the auditory task. Thus the notion that occipital-parietal alpha reduction is directly related to changes in cognitive control is not supported by current results. Our data also do not contradict the findings of Weissman et al. [2006], who

pointed out that attentional lapses may be accompanied by increased analysis of some irrelevant stimuli with greater activation of corresponding cortical areas.

Another important electrophysiological finding of the current study is that alpha power gradually increased in a row of distractor – i.e. through a period of waiting for the next target stimulus. Apparently, immediately after presentation of a target stimulus another target is the least expected, while expectation of the target gradually increases along the sequence of distractors. Increased apprehension of the growing target probability should entail the increase in the level of cognitive control.

The character of alpha power change observed across distractors presentation also does not support the view of occipital-parietal alpha depression being a general index of increased cognitive control. Since, according to Klimesch [Klimesch et al., 2007], the intensity of alpha oscillations is an expression of specific inhibition, we can conclude that within the row of distractors an inhibition of the visual cortex develops. This inhibition may be an indirect index of preparation for the perception and analysis of the next target in auditory modality. In a way this picture is similar to the results of Haegens et al. [2010], who found greater mu rhythm over task-irrelevant regions while performing somatosensory working memory task.

Our data also contradict the inferences in Compton's study [2009]. Compton and colleagues used visual Stroop color identification task and analyzed alpha depression after errors as an index of cognitive control. But again, in our view, in Compton et al. study, more prominent decrease of alpha power was related not only to the enhanced cognitive control per se but to the enhanced processing of relevant visual information. This is also plausible, because in Carp and Compton [2009] maximal alpha suppression was seen in parietal areas.

Taken together, current study and the other studies, performed in the visual modality, point out that alpha oscillations (especially, parietal alpha) reflect modality specific processing changes in relevant cortical areas, rather than they can be used as a direct measure of cognitive control.

One of the complimentary explanations of the decreased alpha oscillations preceding errors is the mental state of mind-wandering, which is known to entail deterioration in attentional concentration on the overt ongoing task [Smallwood et al., 2003; Smallwood and Schooler, 2006]. During the post-experimental interview most of the subjects indicated that they indeed were occasionally involved in task-unrelated thoughts throughout the experiment. They usually

defined it as randomly distracting thoughts having no relation to the experimental conditions.

Mind wandering was shown to be characterized by decreased occipital alpha power (9-11 Hz) compared to task-related activity [Braboszcz and Delorme, 2011] – the finding compatible with the results obtained in the current study (considering both the sign of the change in alpha power and the frequency sub-range). It is worth to be noted still, that Braboszcz and Delorme used rather specific primary task to compete with the state of mind wandering – namely breathe counting, not very common in the field of mind wandering research.

On the other hand, the mind wandering explanation of decreased alpha is in contradiction with the study directly measuring alpha activity and activity of the default mode network (DMN), in which higher visual alpha was accompanied by higher activity of DMN [Mo et al., 2013]. Since mind wandering (task-unrelated and stimulus-independent experience) is associated with higher activity of DMN [Stawarczyk et al., 2011], decreased alpha preceding errors is likely to be related to other mental process(es).

It should be noted that decreased alpha power in relation to mind wandering was observed in explicitly non-visual conditions – in dark room that prevented any visual processing [Braboszcz and Delorme, 2011], while in the study of Mo et al. [2013] the increase in alpha power was found only during eyes-open condition, and no such effect was present in eyes-closed condition. Thus the findings of Braboszcz and Delorme [2011] seem to be more relevant for the interpretation of our data obtained during a non-visual task, and the mind wandering explanation is a valid alternative explanation.

Interestingly, the results obtained in the current study were only significant in the lower alpha sub-range, which, according to Klimesch, reflects attentional information processing [Klimesch, 1997; Klimesch, 1999]. Therefore, again, it is likely that in our experiment, the alpha power decrease preceding errors and alpha power increase in expectation of a target may be explained by alternating allocation of attention between the relevant auditory task and some irrelevant activity. The latter could be either visual processing of objects located within the participants' field of vision, or mind-wandering, or both. Most likely both of the irrelevant activities contributed to the effects observed during periods of decreased cognitive control level; future experiments may be needed to distinguish the relative role of the two processes.

To conclude, the findings of the current study demonstrate that alpha band power should not be viewed as a simple and direct index of cognitive control in attention-dependent tasks, and the sign of the effect depends on the experimental task modality. Specifically, under the auditory attentional task higher level of cognitive control may be related to an increase rather than decrease in alpha band power.

References

Allain, S., Carbonnell, L., Falkenstein, M., Burle, B., Vidal, F., 2004. The modulation of the Ne-like wave on correct responses foreshadows errors. Neurosci. Lett. 372, 161–166. doi:10.1016/j.neulet.2004.09.036

Anderson, K.L., Ding, M., 2011. Attentional modulation of the somatosensory murhythm. Neuroscience 180, 165–180. doi:10.1016/j.neuroscience.2011.02.004

Barry R.J., Clarke A.R., McCarthy R., Selikowitz M., Rushby J.A., Ploskova E. EEG differences in children as a function of resting-state arousal level. Clin. Neurophysiol. 2004. V. 115(2). P. 402-408.

Barry, R.J., De Blasio, F.M., De Pascalis, V., Karamacoska, D., 2014. Preferred EEG brain states at stimulus onset in a fixed interstimulus interval equiprobable auditory Go/NoGo task: a definitive study. Int. J. Psychophysiol. Off. J. Int. Organ. Psychophysiol. 94, 42–58. doi:10.1016/j.ijpsycho.2014.07.005

Barry, R.J., Kirkaikul, S., Hodder, D., 2000. EEG alpha activity and the ERP to target stimuli in an auditory oddball paradigm. Int. J. Psychophysiol. 39, 39–50. doi:10.1016/S0167-8760(00)00114-8

Braboszcz, C., Delorme, A., 2011. Lost in thoughts: neural markers of low alertness during mind wandering. Neuroimage 54, 3040–3047. doi:10.1016/j.neuroimage.2010.10.008

Capotosto, P., Babiloni, C., Romani, G.L., Corbetta, M., 2009. Frontoparietal Cortex Controls Spatial Attention through Modulation of Anticipatory Alpha Rhythms. J. Neurosci. 29, 5863–5872. doi:10.1523/JNEUROSCI.0539-09.2009

Cavanagh, J.F., Cohen, M.X., Allen, J.J.B., 2009. Prelude to and Resolution of an Error: EEG Phase Synchrony Reveals Cognitive Control Dynamics during Action Monitoring. J. Neurosci. 29, 98–105. doi:10.1523/JNEUROSCI.4137-08.2009

Carp, J., Compton, R.J., 2009. Alpha power is influenced by performance errors. Psychophysiology 46, 336–343. doi:10.1111/j.1469-8986.2008.00773.x

Chaumon, M., Busch, N.A., 2014. Prestimulus neural oscillations inhibit visual perception via modulation of response gain. J Cogn Neurosci 26, 2514–2529. doi:10.1162/jocn_a_00653

Dijk, H. van, Schoffelen, J.-M., Oostenveld, R., Jensen, O., 2008. Prestimulus Oscillatory

Activity in the Alpha Band Predicts Visual Discrimination Ability. J. Neurosci. 28, 1816–1823. doi:10.1523/JNEUROSCI.1853-07.2008

Dyson, B.J., Quinlan, P.T., 2003. Feature and conjunction processing in the auditory modality. Perception and Psychophysics 65, 254–272.

Ede, F. van, Lange, F. de, Jensen, O., Maris, E., 2011. Orienting Attention to an Upcoming Tactile Event Involves a Spatially and Temporally Specific modulation of Sensorimotor Alpha- and Beta-Band Oscillations. J. Neurosci. 31, 2016–2024. doi:10.1523/JNEUROSCI.5630-10.2011

Eichele, T., Debener, S., Calhoun, V.D., Specht, K., Engel, A.K., Hugdahl, K., Cramon, D.Y. von, Ullsperger, M., 2008. Prediction of human errors by maladaptive changes in event-related brain networks. Proc. Natl. Acad. Sci. 105, 6173–6178. doi:10.1073/pnas.0708965105

Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., Uresin, Y., 2004. Alpha rhythm of the EEG modulates visual detection performance in humans. Brain Res. Cogn. Brain Res. 20, 376–383. doi:10.1016/j.cogbrainres.2004.03.009

Gottwald R.L., Garner W.R. Filtering and condensation tasks with integral and separable dimensions. Perception & Psychophysics. 1975. V. 18. P. 26-28.

Haegens, S., Osipova, D., Oostenveld, R., Jensen, O., 2010. Somatosensory working memory performance in humans depends on both engagement and disengagement of regions in a distributed network. Hum. Brain Mapp. 31, 26–35. doi:10.1002/hbm.20842

Hajcak, G., Nieuwenhuis, S., Ridderinkhof, K.R., Simons, R.F., 2005. Error-preceding brain activity: Robustness, temporal dynamics, and boundary conditions. Biological Psychology 70, 67–78. doi:10.1016/j.biopsycho.2004.12.001

Hanslmayr, S., Aslan, A., Staudigl, T., Klimesch, W., Herrmann, C.S., Bäuml, K.-H., 2007. Prestimulus oscillations predict visual perception performance between and within subjects. NeuroImage 37, 1465–1473. doi:10.1016/j.neuroimage.2007.07.011

Jones, S.R., Kerr, C.E., Wan, Q., Pritchett, D.L., Hämäläinen, M., Moore, C.I., 2010. Cued Spatial Attention Drives Functionally-Relevant Modulation of The Mu Rhythm in Primary Somatosensory Cortex. J. Neurosci. Off. J. Soc. Neurosci. 30, 13760–13765. doi:10.1523/JNEUROSCI.2969-10.2010

Klimesch W. EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. Brain Research Reviews. 1999. V. 29. P. 169-195

Klimesch W., Sauseng P., Hanslmayr S. EEG alpha oscillations: the inhibition-timing hypothesis. Brain Res. Rev. 2007. V. 53. P. 63-88.

Lal S., Bekiaris E. The reliability of sensing fatigue from neurophysiology. Auswireless

Conference, University of Technology, Sydney, 2007.

Lindsley D. B. Attention, consciousness, sleep & wakefulness. Handbook of Physiology / Eds. Field J., Magoun H.W., Hall V.E. Washington, DC: American Physiological Society. 1960. V. 3. P. 1553-1593.

Luria A. R. The working brain: An introduction to neuropsychology. – Basic Books, 1976. (in Russian)

Macdonald, J.S.P., Mathan, S., Yeung, N., 2011. Trial-by-Trial Variations in Subjective Attentional State are Reflected in Ongoing Prestimulus EEG Alpha Oscillations. Front. Psychol. 2. doi:10.3389/fpsyg.2011.00082

Makeig, S., Jung, T.P., 1996. Tonic, phasic, and transient EEG correlates of auditory awareness in drowsiness. Brain Res. Cogn. Brain Res. 4, 15–25.

Martinson D.M. A study of brain potentials during mental blocking. J. of Experimental Psychol. 1939. V. 24. P. 143-156.

Mazaheri, A., Nieuwenhuis, I.L.C., van Dijk, H., Jensen, O., 2009. Prestimulus alpha and mu activity predicts failure to inhibit motor responses. Hum. Brain Mapp. 30, 1791–1800. doi:10.1002/hbm.20763

Mo, J., Liu, Y., Huang, H., Ding, M., 2013. Coupling between visual alpha oscillations and default mode activity. NeuroImage 68, 112–118. doi:10.1016/j.neuroimage.2012.11.058

O'Connell, R.G., Dockree, P.M., Robertson, I.H., Bellgrove, M.A., Foxe, J.J., Kelly, S.P., 2009. Uncovering the Neural Signature of Lapsing Attention: Electrophysiological Signals Predict Errors up to 20 s before They Occur. J. Neurosci. 29, 8604–8611. doi:10.1523/JNEUROSCI.5967-08.2009

Romei, V., Brodbeck, V., Michel, C., Amedi, A., Pascual-Leone, A., Thut, G., 2008. Spontaneous Fluctuations in Posterior α-Band EEG Activity Reflect Variability in Excitability of Human Visual Areas. Cereb. Cortex 18, 2010–2018. doi:10.1093/cercor/bhm229

Pfurtscheller, G., Stancák Jr., A., Neuper, C., 1996. Event-related synchronization (ERS) in the alpha band - An electrophysiological correlate of cortical idling: A review. International Journal of Psychophysiology 24, 39–46. doi:10.1016/S0167-8760(96)00066-9

Pfurtscheller G., Lopes da Silva F.H. Event-related EEG/MEG synchronization and desynchronization: basic principles. Clin. Neurophysiol. 1999. V. 110. P. 1842-1857.

Posner M.I. Information reduction in the analysis of sequential tasks // Psychological Review. 1964. V. 71. P. 491.

Ridderinkhof, K.R., Nieuwenhuis, S., Bashore, T.R., 2003. Errors are foreshadowed in brain potentials associated with action monitoring in cingulate cortex in humans. Neuroscience

Letters 348, 1–4. doi:10.1016/S0304-3940(03)00566-4

Shaw J.C. The brain's alpha rhythms and the mind. A review of classical and modern studies of the alpha rhythm component of the electroencephalogram with commentaries on associated neuroscience and neuropsychology Elsevier. 2003. 360 p.

Smallwood J., Obonsawin M., Heim D. Task unrelated thought: the role of distributed processing. Conscious Cogn. 2003. V 12. P. 169-189.

Smallwood J., Schooler J.W. The restless mind. Psychol. Bull. 2006. V. 132. P. 946-958

Stawarczyk, D., Majerus, S., Maquet, P., D'Argembeau, A., 2011. Neural Correlates of Ongoing Conscious Experience: Both Task-Unrelatedness and Stimulus-Independence Are Related to Default Network Activity. PLoS One 6. doi:10.1371/journal.pone.0016997

Sutton S., Braren M., Zubin J. Evoked-potential correlates of stimulus uncertainty. Science. 1965. V. 150. P. 1187-1188

Takegata, R., Brattico, E., Tervaniemi, M., Varyagina, O., Näätänen, R., Winkler, I., 2005. Preattentive representation of feature conjunctions for concurrent spatially distributed auditory objects. Cognitive Brain Research 25, 169–179. doi:10.1016/j.cogbrainres.2005.05.006

Tkachenko, O. N., Lavrova, T. P., Dorokhov, V. B., Dementienko, V. V., & Sil'kis, I. G. (2013). Investigation of features of EEG changes at psychomotor disturbanses associated with microsleep. Zhurnal vyssheĭ nervnoĭ deiatelnosti imeni IP Pavlova, *63*(1), 141.

Weissman D.H., Roberts K.C., Visscher K.M., Woldorff M.G., 2006. The neural bases of momentary lapses in attention. Nat. Neurosci. 9 (7), 971–978.

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21