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Title
Neuronal adaptation in the course of the prolonged task improves visual stimuli processing

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Abstract

Brain optimally utilizes resources to resist mental fatigue during the prolonged period of cognitive activity. Neural mechanisms underlying long-term cognitive performance remain unknown. We show that during 40-minutes visual stimuli classification task, subjects improve behavioral performance in terms of response time and correctness. We observe that the prestimulus θ and α power grows during the experiment manifesting the mental fatigue. The prestimulus β power, in its turn, increases locally in the region, engaged in the ongoing stimulus processing, that may reflect the neuronal adaptation. Our results evidence that the neuronal adaptation is enhanced in the course of the experiment reducing the cognitive demands required to activate the stimulus-related brain regions.

Introduction

Since the brain resource is limited, human exhibits mental fatigue during the prolonged periods of cognitive activity. The mental fatigue is negatively correlated with human attention and results in the decrease of the behavioral performance (Mizuno et al. (2011)). The bulk of literature describes the cortical activity underlying mental fatigue and attention. Thus, the mental fatigue is accompanied with the shift of EEG power toward the low-frequency bands, e.g. δ ($1-4$ Hz), θ ($4-8$ Hz), and α ($8-13$ Hz) (Phipps-Nelson et al. (2011); Wascher et al. (2014)), while high-frequency activity, e.g. β ($15-30$ Hz) and γ (>30 Hz) typically decreases in amplitude (Lal and Craig (2001)). Attention, in turn, is characterized by the low α- and high β-band spectral power. In particular, low α- and high β-band power during the prestimulus period reflects increased attention and predicts better performance in the ongoing task (Van Dijk et al. (2008); Gola et al. (2013)).

At the same time, cognitive performance is not necessary to decrease while accomplishing prolonged resource-demanding tasks. For instance, the increased reward makes the subject to improve behavioral performance even after the fatigue-induced session (Jimura et al. (2010); Krebs et al. (2010)). It evidences that the brain spends cognitive resources in the way to reserve it for future use (Christie and Schrater (2015)). The Ref. (Benoit et al. (2019)) relates the strategy the brain utilizes the cognitive resources with a fatigue-induced performance decrement, but not with the subjective fatigue. It manifests that the resource reallocation is controlled by the endogenous cognitive mechanisms regardless of the subjective feelings. According to the recent review (Shenhav et al. (2017)), the neural activity underlying the cognitive resource rearrangement and cognitive performance is yet to be determined.

In this work, we subject the group of volunteers to the prolonged (~ 40 min) task. The task requires the participants to quickly percept the successively presented bistable visual stimuli and report one of their possible interpretations right after presentation. On the behavioral level, subjects improve their performance in the course of the task: they reduce their response time along with the number of errors. We suppose that this observation can be referred to as the training effect and suggest that the within-experiment training is one of the possible mechanisms of the optimal cognitive resource utilization.

The previous works reported that the training in the particular task allowed the subjects to improve their behavioral performance. In the visual task, training improved the efficiency of high-level visual processing, which therefore provided less ambiguous sensory information to the decision-related brain networks (Yang et al. (2014)). While in Ref. (Yang et al. (2014)) the training period has lasted for three days, our results suggest that the training effect is notable even within a 40-min session.

The brain's ability to enhance its cognitive performance in the course of training was previously described by Tang and Posner (Tang and Posner (2009)). They distinguished two different types of training - network training and state training(Tang and Posner (2014)). The network training involves the practice of a specific task (e.g., attention, working memory) and thus exercises the specific task-related brain areas and networks (Petersen and Posner (2012)). The state training involves exercises, e.g., meditation that might alter the brain state in general (Tang et al. (2007)). The network training, in its turn, may use a fixed task difficulty where performance shows improvement over trials or the adaptive training in which task difficulty adjusts as learning occurs (Tang and Posner (2014)). Given above, we suppose that our current study deals with the brain network training performed in the fixed difficulty fashion.

According to (Tang and Posner (2014)), the neuronal mechanisms underlying the training effect remain poorly understood. Some studies report the increased activation of the task-related brain networks in the course of training. In contrast, others observe the decrease of the task-related activity of the corresponding brain structures (Buschkuehl et al. (2012)). It also appears that the direction of the effect depends heavily on the type of training. For instance, the increased task-related brain activity may reflect the need for increased effort to solve more complicated tasks during adaptive training (Jensen et al. (2012)). Thus, there is no complete understanding of how brain activity changes during the training.

To address this issue, we consider the cortical activity on the EEG sensor level in θ (4-8 Hz), α (8-12 Hz), and β (15-30 Hz) frequency bands in the course of the experiment. We observe that the training changes the brain activity not only during the stimulus processing stage but during the prestimulus period as well. The prestimulus θ and α-band power grow in the course of the experiment that indicates the mental fatigue caused by the increased time spent performing the task. The prestimulus β-band power increases in the right hemisphere that may reflect the activation of the attention network. Finally, we show that

the prestimulus β-band power increases locally in the region, engaged in the ongoing stimulus processing, that may reflect the neuronal adaptation (Henson and Rugg (2003)). We hypothesize that the neuronal adaptation is enhanced in the course of the experiment reducing the cognitive demands required to activate the stimulus-related brain regions.

Methods

Participants

Twenty healthy subjects (11 males and 9 females) aged from 26 to 35 with normal or corrected-to-normal visual acuity participated in the experiments. All of them provided written informed consent in advance. All participants were familiar with the experimental task and did not participate in similar experiments in the last six months. The experimental studies were performed under the Declaration of Helsinki and approved by the local Research Ethics Committee of the Innopolis University.

Visual stimuli

The ambiguous visual stimulus was the Necker cube. (Kornmeier et al. (2011); Hramov et al. (2017)). A subject without any perceptual abnormalities perceives the Necker cube as a 3D-object due to the specific position of the cube's edges. The Necker cube can be interpreted as left- or right-oriented depending on the contrast of the inner edges. The contrast of the three middle edges centered in the left middle corner was used as a control parameter $a \in [0,1]$. The values $a = 1$ and $a = 0$ correspond, respectively, to 0 (black) and 255 (white) pixels' luminance of the inner lines using the 8-bit gray-scale palette. Therefore, the control parameter was defined as $a = g/255$, where g is the brightness of the inner lines. In our experiment, we used the Necker cube images with 8 different ambiguity levels (see Fig. 1, a. Half of them ($a \in \{0.0, 0.15, 0.4, 0.45\}$) are considered as left-oriented (LO) and another half ($a \in \{0.55, 0.6, 0.85, 1\}$) as right-oriented (RO). While for $a \approx 0$ and $a \approx 1$ (low ambiguous (LA) images) the cubes can easily be interpreted as left- and right-oriented, for $a \approx 0.5$ the identification of the cube orientation is a more difficult task since we deal with highly ambiguous (HA) images (Hramov et al. (2018); Maksimenko et al. (2017)). The 14.2-cm Necker cubes were drawn by black and gray lines on a white background at the center of a 24" BenQ LCD monitor with a spatial resolution of 1920×1080 pixels and a 60-Hz refresh rate. The subjects located at a 70–80 cm distance from the monitor with a visual angle of approximately 0.25 rad.

Experimental protocol

The whole experiment lasted ≈ 40 min for each participant, including short recordings of the resting EEG state (≈ 150 s) before and after the main part of the experiment. During experimental sessions, the Necker cubes with predefined values of a (chosen from the set in Fig. 1, a) were randomly demonstrated 400 times, each cube with a particular ambiguity was presented about 50 times.

The scheme of the experimental session is shown in Fig. 1, b. Each i-th stimulus was presented for time interval τ_i, followed by the time interval γ_i of the abstract image presentation (see Fig. 1, c). The participants were instructed to press either left or right key with respectively left or right hand to report their interpretation of the orientation (left or right) of each cube. The consecutively presented images affect the perception of previously demonstrated cubes. For example, if the subject observed several left-oriented cubes in a row, then his/her perception was stabilized to the left-oriented cube, even if the next cube was right-oriented. Such phenomenon is referred to as a stabilization effect (Leopold et al. (2002)). To reduce this effect, the duration of the stimulus exhibition varied in the range of $\tau \in [1, 1.5]$ s. Moreover, a random variation of the control parameter a also prevented the perception stabilization. Lastly, to draw away the observer's attention and make the perception of the next Necker cube independent of the previous one, different abstract pictures were exhibited for about $\gamma \in [3, 5]$ s between subsequent demonstrations of the Necker cube images. For each cube, we estimated a behavioral response by measuring the response time (RT), which corresponded to the time passed from the stimulus presentation to the button pressing (Fig. 1, d) and the error (if the subject's interpretation differs from the actual cube orientation).

EEG acquisition and preprocessing

We recorded the EEG signals using the monopolar registration method (a 10–10 system proposed by the American Electroencephalographic Society Nuwer et al. (1998)). We recorded 31 signals with two reference electrodes A1 and A2 on the earlobes and a ground electrode N just above the forehead. We used the cup adhesive Ag/AgCl electrodes placed on the "Tien–20" paste (Weaver and Company, Colorado, USA). Immediately before the experiments started, we performed all necessary procedures to increase skin conductivity and reduce its resistance using the abrasive "NuPrep" gel (Weaver and Company, Colorado, USA). Usually, the impedance varied within a 2–5 kΩ interval during the experiment. The electroencephalograph "Encephalan-EEG-19/26" (Medicom MTD company, Taganrog, Russian Federation) with multiple EEG channels and a two-button input device (keypad) performed amplification and analog-to-digital conversion of the EEG signals. This device possessed the registration certificate of the Federal Service for Supervision in Health Care No. FCP 2007/00124 of 07.11.2014 and the European Certificate CE 538571 of the British Standards Institute (BSI). The raw EEG signals were sampled at 250 Hz,

filtered by a band-pass FIR filter with cut-off points at 1 Hz (HP) and 100 Hz (LP) and by a 50-Hz notch filter by embedded a hardware-software data acquisition complex. Eyes blinking and heartbeat artifact removal was performed by Independent Component Analysis (ICA) using EEGLAB software (Delorme and Makeig (2004)). The recorded EEG signals presented in proper physical units (millivolts) were segmented into two sets of 4-s trials, including 2-s pre-stimulus (baseline) activity and 2-s post-stimulus activity. Data were then inspected manually and corrected for remaining artifacts.

Trials selection and experimental conditions

After the EEG preprocessing procedure, we excluded some trials due to high-amplitude artifacts. To keep the number of EEG trials constant for each cube ambiguity, we considered 320 trials out of the initial 400, including 40 trials for each ambiguity. To define the experimental conditions, we divided the whole experimental session into six non-overlapping fragments (T_i) of the equal length (Fig. 2, a). For each fragment, we selected 40 trials with an equal proportion of RO and LO stimuli, as well as LA and HA stimuli. Such a selection of the trials enables neglecting the effects caused by the cube orientation and complexity. For each segment, we averaged RT across the 20 trials corresponding to LA and HA stimuli and compared the mean RT values across the conditions $T_1 \dots T_6$ in the group of subjects.

EEG time-frequency analysis

Time-frequency analysis of EEG trials was carried out using Morlet wavelet with the number of cycles for each frequency f as $f/2$. The wavelet power E was calculated in the $4-30$ Hz frequency band and averaged over the frequency bands of interest: θ ($4-8$ Hz), α ($8-12$ Hz) and β ($15-30$ Hz). The pre-stimulus oscillatory activity was averaged over the time interval from -0.5 s to 0 s. The post-stimulus oscillatory activity was contrasted by the activity in the pre-stimulus period subtracting the mean of baseline values followed by dividing by the mean of baseline values ('*percent*' mode) and considered in the time interval from 0 s to 0.5 s. The results of the time-frequency analysis were averaged over trials for each subject belonging to each fragment ($T_1 \dots T_6$).

Following (Maris and Oostenveld (2007)), a group-level spatio-temporal non-parametric cluster-based statistical test was used to address the statistical significance of the θ, α and β oscillatory activity changes in the pre-stimulus and post-stimulus states between the different conditions T_i. Here, a pairwise comparison of samples between the conditions was performed via paired sample t-test with a critical level of $p_{pairwise}$ set to 0.01. The critical level for non-parametric cluster-based statistical test $p_{cluster}$ was set to 0.05. The number of random permutations was 2000. The time-frequency analysis and non-parameteric cluster-based statistical tests were performed using MNE package for Python 3.7 (Gramfort et al. (2013)). To estimate the inter-hemispherical asymmetry of pre-stimulus oscillatory activity in the θ, α and β bands between the conditions T_i, the EEG spectral power of the corresponding frequency bands was averaged over the EEG sensors placed in the left hemisphere (LH) {O1, P3, T5, CP3, TP7, C3 T3, FC3 FT7, F3, F7, FP1} and the right hemisphere (RH) {O2, P4, T6, CP4, TP8, C4, T4, FC4, FT8, F4, F8, FP2}.

Results

Behavioral results First, we compared RT across the fragments T_i via a repeated-measures ANOVA with two factors: ambiguity (LA vs HA) and fragment ($T_1 \dots T_6$). As a result, ANOVA with the Greenhouse Geisser correction revealed the significant main effect for fragment ($F_{2.31,44.05} = 9.63, p < 0.001$) and ambiguity ($F_{1,19} = 59.66, p < 0.001$), whereas the interaction effect $fragment \times ambiguity$ was insignificant ($F_{2.47,46.93} = 1.06, p = 0.366$). We concluded that RT changed similarly between the fragments regardless of the stimulus ambiguity. Therefore, for further analysis, we combined LA and HA stimuli on each fragment.

The post-doc analysis via the Bonferroni-corrected paired-samples t-test revealed a monotonous decrease of RT across the fragments $T_1 \dots T_6$ with the maximal statistically significant difference achieved between the beginning (T_1) and the end (T_6) of the experiment (ΔRT=0.189$\pm$0.043SE, $df = 19$, $t = 4.318$, $p = 0.006$) (Fig. 2, a). A similar tendency was observed for the error rate (Fig. 2, b): an ANOVA with the Greenhouse Geisser correction revealed a significant effect for the fragment ($F_{2.75,52.38} = 3.386, p = 0.028$). The posthoc analysis with the paired samples t-test displayed the maximal statistically significant difference between T_1 and T_6 (Δ=1.74$\pm$0.64SE, $df = 19$, $t = 2.733$, $p = 0.013$). The Bonferroni-corrected p-value was 0.198. The obtained results demonstrated that both the RT and the error rate decreased in the course of the experiment. We supposed that the most significant difference in the neuronal activity should be observed between the fragments T_1 and T_6. For these conditions, we compared RT between the HA and LA cubes (Fig. 2, c). The repeated-measures ANOVA with the Greenhouse Geisser correction showed a significant decrease of RT between the conditions ($F_{1,19} = 18.64, p < 0.001$) and between the HA and LA cubes ($F_{1,19} = 50.48, p < 0.001$). The interaction effect was insignificant ($F_{1,19} = 1.08, p = 0.312$). For the LO and RO cubes (Fig. 2, d) the repeated measures ANOVA with the Greenhouse Geisser correction revealed a significant change in RT among different conditions ($F_{1,19} = 20.714, p < 0.001$). In contrast, RT changed insignificantly between LO and RO cubes ($F_{1,19} = 1.56, p = 0.227$). Finally, we found that the interaction effect was also insignificant

($F_{1,19} = 0.084, p < 0.775$). This analysis evidenced that a change in RT between the T_1 and T_6 conditions was independent of the cube ambiguity and orientation. Given above, cortical activity was compared between T_1 and T_6 conditions based on 40 trials per condition, including the equal proportion of the LA and HA stimuli as well as LO and RO stimuli.

Rest-state and prestimulus activity. At the first stage, we analyzed how the subject's condition changed in the course of the experiment. Since the human condition affects the brain activity regardless the presented stimuli or the task, we analyzed the EEG spectral power in the θ-, α- and β-frequency bands in three experimental conditions: the rest-state (the phase of the experiment before the first stimulus was presented), the prestimulus state at the beginning of the experiment (T_1) and the prestimulus state at the end of the experiment (T_6). For each experimental condition, the set of 40 EEG trials (0.5-s length) was considered.

Figures 3 (*a,c,e*) illustrate the way the EEG spectral powers in the θ, α and β bands change in the left (LH) and right hemispheres (RH). Figures 3 (*b,d,f*) show the topograms of t-values reflecting the power changes in these bands in the T_6 versus T_1 conditions.

In the θ-band (Fig. 3, *a*) the repeated measures ANOVA with the Greenhouse-Geisser correction revealed insignificant changes in the spectral power between the hemispheres ($F_{1.00,19.00} = 0.18, p = 0.676$) as well as between the experimental conditions ($F_{1.058,20.096} = 0.18, p = 0.124$). The interaction effect *hemisphere* $\times$ *condition* was also insignificant ($F_{1.067,20.268} = 0.823, p = 0.383$). At the same time, the cluster-based statistical analysis with permutations revealed that the prestimulus state at the end of the experiment is characterized by the increasing power over the particular EEG channels (Fig. 3, *b*).

In the α-band (Fig. 3, *c*), the repeated measures ANOVA with the Greenhouse-Geisser correction revealed a significant change of the power E_α between the experimental conditions ($F_{1.46,27.84} = 9.713, p = 0.002$) and between the hemispheres ($F_{1.00,19.00} = 4.944, p = 0.039$). The interaction effect *condition* $\times$ *hemisphere* was insignificant ($F_{1.27,24.146} = 1.378, p = 0.264$). The post-hoc analysis with Bonferroni-corrected paired samples t-test demonstrated that E_α(RH) exceeded E_α(LH) ($\Delta E_\alpha = 9.06 \times 10^3 \pm 4.07 \times 10^3 \mathrm{SE}, p = 0.039$). The value of E_α in the rest-state did not differ significantly from $E_\alpha(T_1)$ ($p = 1.0$), while $E_\alpha(T_6)$ significantly exceeded both $E_\alpha(T_1)$ ($\Delta E_\alpha = 15.9 \times 10^3 \pm 4.84 \times 10^3 \mathrm{SE}, p = 0.012$) and E_α during the rest-state ($\Delta E_\alpha = 12.8 \times 10^3 \pm 3.01 \times 10^3 \mathrm{SE}, p = 0.001$).

The obtained results demonstrated that the analyzed group of participants exhibited the right-lateralization of the α-band spectral power. The lateralization in the prestimulus state did not change in the course of the experiment. The averaged α-band spectral power in the prestimulus period at the beginning of the experiment did not differ from the rest-state. Finally, the averaged α-band spectral power in the prestimulus period increased in the course of the experiment. The cluster-based statistical analysis with permutations revealed that the prestimulus state at the end of the experiment was characterized by the overall increase in the α-band spectral power when compared to the beginning of the experiment (Fig. 3, *d*). A significant increase of α-band spectral power was observed for the channel clusters ($p < 0.01$) in the occipito-parietal area, frontal area, and temporal areas.

In the β-band (Fig. 3, *e*), the repeated measures ANOVA with the Greenhouse-Geisser correction revealed a significant change in the wavelet power E_β between the experimental conditions ($F_{1.531,29.094} = 4.654, p = 0.025$), while the changes in E_β between the hemispheres were insignificant ($F_{1.00,19.00} = 0.0, p = 0.988$). The repeated measures ANOVA revealed a significant interaction effect *condition* $\times$ *hemisphere* ($F_{2,38} = 7.619, p = 0.002$). The post-hoc analysis with the Bonferroni-corrected paired samples t-test demonstrated that E_β in the rest-state did not differ significantly from $E_\beta(T_1)$ ($p = 1.0$), and $E_\beta(T_6)$ did not significantly exceed both $E_\beta(T_1)$ ($p = 0.136$) and E_β during the rest-state ($p = 0.066$). Due to the significant interaction effect, the post-hoc analysis was performed via the pairwise comparison of E_β(LH, RH) in all experimental conditions as well as for E_β(LH) and E_β(RH) between different conditions. As a result, the paired samples t-test revealed that E_β(LH) and E_β(RH) differed neither for the rest-state ($df = 19, t = 0.423, p = 0.677$) nor for the prestimulus period at the beginning ($df = 19, t = 1.49, p = 0.151$) and at the end ($df = 19, t = -1.62, p = 0.121$) of the experiment. Having compared the T_1 condition with the rest-state, we found that neither E_β(LH) ($df = 19, t = -1.27, p = 0.218$), nor E_β(RH) ($df = 19, t = 0.562, p = 0.58$) differed significantly. Finally, having compared the T_6 and T_1 conditions, we observed a significant increase in E_β(RH) ($df = 19, t = 2.899, p = 0.009$) and an insignificant change in E_β(LH) ($df = 19, t = 0.565, p = 0.579$).

The obtained results demonstrated that the β-band power did not change at the beginning of the experiment when compared to the rest-state. In the course of the experiment, we observed an increase in the prestimulus β-band spectral power in the right hemisphere. The cluster-based statistical analysis with permutations revealed that the prestimulus state at the end of the experiment was characterized by a significant ($p < 0.01$) increase in the β-band spectral power for the channel cluster including channels F4, FC4, C4, CP4, Cz (Fig. 3, *f*).

Task-related activity. The task-related cortical activity on the EEG sensor level was analyzed by comparing the topograms of the θ-, α- and β-band spectral powers between the start (T_1) and the end (T_6) of the experiment. Figure 4 illustrates the channels clusters (circles) and the corresponding t-values (color scale) obtained during the 0.5-s interval following the presentation of the visual stimulus. Each topogram represented the spectral power averaged over a 0.1-s window mentioned in the legend under the topograms.

One could see that the clusters had different spatio-temporal properties in the different frequency bands. At the same time, no positive clusters appeared in these bands, indicating the overall increase of the task-related neuronal activation at the beginning of the experiment.

In the θ-band (Fig. 4, a), the earlier processing stage ($t < 0.1$ s) was characterized by the left-lateralized occipito-parietal cluster (O1 and P3 channels) and the mid-line centro-parietal cluster (CPz and Cz channels). For ($0.1 < t < 0.2$ s), the only left-lateralized occipito-parietal (O1 and P3) cluster was observed. The further processing ($t > 0.2$ s) was associated with the increased t-value over the parietal and temporal EEG sensors. For ($0.2 < t < 0.3$ s), there were two clusters (P3 and P8), while for ($0.3 < t < 0.4$ s), the only one cluster (P8) remained. Finally, for ($t > 0.4$ s), no clusters were found in the θ-frequency band.

The α-band power (Fig. 4, b) remained unchanged during the first 0.2 sec after the stimulus presentation. Then, for 0.2-0.3 s, we observed the bilateral negative cluster in the occipital area, including O1 and O2 EEG channels and the right-lateralized parieto-temporal cluster, including P4, P8, and TP8 EEG channels. For the 0.3-0.4 s, the size of the observed cluster decreased, and it became right-lateralized. Finally, the further increase of the processing time led to the cluster disappearance. The obtained results evidenced that at the end of the experiment, the task-related cortical activity was characterized by the increased α-band power in the occipital and right temporal areas during 0.2-0.3 s after the stimulus presentation.

In the β-frequency band (Fig. 4, c), the negative cluster was observed for the first 0.3 s after the visual stimulus presentation. At the earlier sensory processing stage ($t < 0.1$ s) it included the bilateral prefrontal cortical channels (Fp1, Fpz, Fp2), the right-lateralized frontoparietal area (Fz, F4, F8, FCz, FC4, Cz, C4, CPz, CP4, Pz) and the right temporal area (FT8, TP8). During the 0.1-0.2 s, the observed cluster was bilateral in the prefrontal cortex, but right-lateralized in the temporal region. For 0.2-0.3 s, the frontal cluster disappeared, and one could observe the remaining right-lateralized cluster in the occipital, parietal, and temporal cortex. Finally, no clusters were found for $t > 0.3s$ in the β-frequency band.

Discussion

Our results demonstrate that during a prolonged visual stimuli classification task, subjects enhance their performance in terms of the reduced reaction time and decision accuracy. This observation is not trivial since a prolonged cognitive activity may induce mental fatigue and, therefore, cognitive decline. Thus, we suppose that the brain implements a strategy for the optimal utilization of cognitive resources to resist mental fatigue and increase behavioral performance.

At the beginning of the experiment, we observe enhanced spectral power in the θ, α, and β frequency bands during the stimulus processing. The high β power has been observed in the right temporoparietal cortex and bilaterally in the prefrontal cortex, while high α and θ power – in the occipital and in both occipital and parietal areas, respectively.

The neuronal activity in the temporoparietal regions subserves the processing and storage of visuospatial information (Linden (2007); Rahm et al. (2014)). At the same time, the activation of the prefrontal cortex indicates that the task accomplishing requires additional cognitive resources. It is also confirmed by an increase of the task-related θ-band activity (Berger et al. (2019)). The task-related occipital α-power is associated with selective attention during stimulus processing. The low α-band power reflects the effective processing of attended stimuli (Zumer et al. (2014)). Having summarized, we suppose that at the beginning of the experiment, stimulus processing engages the resources of the frontoparietal cortical network. Moreover, the lower task-related α-band power in the occipital area at the end of the experiment is possible to reflect the enhanced brain ability to respond to the attended stimulus effectively.

The prestimulus activity in the θ, α, and β-bands changes in the course of the experiment. The prestimulus α-band power is higher in the right hemisphere during the rest-state and the prestimulus period. This lateralization doest not change in the course of the experiment. At the same time, α-band power grows during the experiment over the majority of the EEG sensors in both hemispheres. The θ- and β-band activity is bilateral in the rest-state and prestimulus period. However, at the end of the experiment, the β-band power increases in the right hemisphere, while the θ-band power grows bilaterally in the frontal-central, parietal, and temporal regions.

The prestimulus activity in the α and β bands is usually analyzed to characterize the subject's attention. A wide body of literature shows that α and β-band activities are relevant to attention in general and not restricted to the visual stimuli processing (Baumgarten et al. (2014); Anderson and Ding (2011); Bauer et al. (2012); Gola et al. (2013)). Attention modulates the prestimulus α- and β-band power (Baumgarten et al. (2014); Gola et al. (2013); Linkenkaer-Hansen et al. (2004)) and affects the stimulus processing accuracy. Thus, low α- and high β-band power during the prestimulus period is beneficial for sensory perception (Van Dijk et al. (2008); Gola et al. (2013)). The prestimulus θ- and α-band activities can serve as the markers of mental fatigue, i.e., the increased power in these bands reflects the subject's mental fatigue and causes the performance decrement (Wascher et al. (2014)). Taken together, the low prestimulus θ- and α-band power and the high β-power should predict the high performance and vice versa. On the contrary, we report that the high prestimulus spectral power in the θ-, α- and β- frequency bands accompany the performance increment.

According to (Boksem et al. (2012)), the lateralized α-band power reflects the attentional breadth during the stimulus processing. The attentional breadth characterizes the subject's ability to focus attention either on the global level (e.g., the forest) or local elements that make up the stimulus (e.g., the trees) Dale and Arnell (2013). Recent studies demonstrate that greater local attentional bias is observed after activating the left hemisphere, and a greater global bias is observed after activating the right hemisphere (Gable et al. (2013)). The α-band power over the right and left frontal-central sensors correlate with attentional breadth. The greater left frontal α power corresponds to faster responses to local targets and greater right frontal α power – to faster responses to global targets (Harmon-Jones and Gable (2009)). Previous findings suggest that prestimulus and rest-state α power lateralization (Pitchford and Arnell (2019b)) also predict the subject's performance in a global-local attention task (Boksem et al. (2012)).

We report the high α-band activity in the right hemisphere at rest as well as in the prestimulus state. Moreover, the lateralization does not change in the course of the experiment. Therefore, we can conclude that the subjects which initially have right-lateralized alpha-band power exhibit the global attentional bias and do not change it during the experiment. It coincides with the existing literature claiming that the attentional bias remains stable for at least ten days in multiple global/local tasks (Pitchford and Arnell (2019a)).

The increased prestimulus α power in the course of the experiment can be an electrophysiological indicator of mental fatigue (Boksem et al. (2005)). The prolonged task induces mental fatigue, increasing reaction times, misses, and false alarms. As discussed above, high α-band power predicts the low performance of the ongoing stimulus processing. Thus, it can be supposed, that increased α-band power at the end of the experiment is associated with mental fatigue, which should lead to the performance decline. The increased θ-band power, together with α-band power, can also manifest the mental fatigue. According to (Wascher et al. (2014)), the prestimulus θ-band power in the frontal area grows in the course of the experiment and negatively correlates with the behavioral performance. Another paper (Barwick et al. (2012)), relates mental fatigue with the increased θ-band power in the frontal-central and parietal regions.

High prestimulus β-band power in the right hemisphere can be related to the increasing human attention. There is a view that the human attentional brain network is overall lateralized to the right hemisphere (Vossel et al. (2014)). Some components of the attention (e.g., alerting and disengaging functions) are bilateral (Spagna et al. (2016)), while others (e.g., orienting and executive functions) are biased to the right hemisphere (Spagna et al. (2018)). According to (Spagna et al. (2015)), the executive functions subserve an interplay between alerting and orienting functions to maintain the state of readiness and focus attention towards the relevant features of a stimulus.

Taken together, the increased orienting and executive components of attention in the course of the experiment can be the possible reasons for the increase in behavioral performance. In this context, the performance can grow due to the enhanced effectiveness of the relevant stimulus features selection. At the same time, high prestimulus θ- and α- power contradict the definition of attentional state in general. Therefore, we cannot conclude unequivocally that the brain increases its attentional properties in the course of the experiment.

Finally, we introduce one more possible explanation for the increased performance in the course of the experiment. We observe that the prestimulus β-band power at the end of the experiment increases locally in the region, which is more engaged during the stimulus processing. Hence, we suppose that the preactivation of the stimulus-related cortical areas reduces the cognitive demands required for their activation during the stimulus processing (Myers et al. (2015)). The preactivation of the stimulus-related neuronal ensembles before the stimulus processing is also known as the neuronal adaptation (NA). The NA is considered as the evidence for the predictive coding theory (Rauss and Pourtois (2013)). NA is observed when the same visual stimulus is repeatedly presented with a brief interval and causes the reduced neural response to repeated compared with unrepeated stimuli Henson and Rugg (2003). The NA is supposed to arise from at least two types of neural activity. One explanation is that only the part of the neuronal ensemble is sensitive to stimulus recognition. Thus, the neurons that are not critical for recognizing the stimulus decrease their responses as the stimulus is repeatedly presented. In contrast, the neuronal populations carrying essential information continue to give a robust response. As a result, the mean firing rate becomes attenuated by stimulus repetition. This theory is supported by the first studies of unit cell recordings Wiggs and Martin (1998). The alternative explanation is the stimulus repetition reduces the response in the temporal domain Henson and Rugg (2003). In this theory, the neural processing network settles to a stable response more quickly in response to a repeated than novel stimulus, because the network connections involved in producing the response have been reinforced by a previous presentation of the same stimulus Henson et al. (2002). The NA affects the neuronal response in the occipital Kourtzi and Kanwisher (2000), parietal Naccache and Dehaene (2001), and frontal Wagner et al. (2000) cortical populations in the single-unit data as well as on the sensor level.

Taking together, we suppose that the training effect in the course of the experiment results in the preactivation of the stimulus-related regions in the β frequency band. The very recent work (Theves et al. (2020)) also relates the β-band spectral power to the training. The authors report on the enhanced β-band power over the central, temporal and the parietal sensors during an 80–400 ms window of the poststimulus onset (post- versus pre-training trials), while we observe that the β-band

spectral power decreases in the same areas during the same time window. At first glance, this issue can be addressed to different experimental paradigms. For example, (Theves et al. (2020)) compared two experiments carried out in different days, whereas in this work, we analyze a single experimental session performed in one day. It follows that the different mechanisms stay behind the training effect in these two paradigms. Besides, different stimuli are used, i.e., we consider visual stimuli only, while (Theves et al. (2020)) use visual stimuli together with auditory stimuli. Moreover, similar to our findings (Theves et al. (2020)) report on a significant decrease in the β-band power (post-training vs pre-training trials) at certain conditions. The authors relate this effect to the participant's perceptual template formation after the training and consider these results as the evidence for the predictive coding model. The predictive coding theory suggests that the brain creates sensory templates (Arnal and Giraud (2012)), which causes increasing β-band activity before the occurrence of an expected event that potentially reflects the mobilization of neuronal populations to encode the expected sensory inputs (Fujioka et al. (2012); Bernasconi et al. (2011)).

Additional information

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Competing interests

The authors declare that they have no competing interests.

Author contributions statement

AH, ML and VM designed and supervized the study, AK performed the experiments, AK analyzed behavioral data, NF analyzed EEG data, VM interpreted results, VM, AP, NF wrote the manuscript.

Data Accessibility

Data are available from the corresponding author (V.Maksimenko, maximenkovl@gmail.com) upon request.

Abbreviations

EEG – electroencephalography, HA – high ambiguity, LA – low ambiguity, LH – left hemisphere, NA – neuronal adaptation, LO – left orientation, RH – right hemisphere, RO – right orientation, RT – response time,

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Figure legends

Figure 1.

The set of visual stimuli (Necker cubes) with different degree of ambiguity a including (a) left-oriented (LO) and (b) right-oriented (RO) with high-ambiguity (HA) and low-ambiguity (LA). (c) Schematic illustration of experimental sessions. τ_i is the duration of the i-th cube presentation, γ_i is the interval between the i-th and $(i+1)$-th presentations. (d) Response time (RT) definition.

Figure 2.

The change in RT (a) and error rate (b) in the course of the experiment across the fragments $T_1 \dots T_6$. The difference in RT between HA and LA stimuli (c) and between LO and RO stimuli (d) at the beginning (T_1) and the end (T_6) of the experiment. Data are shown as group mean $\pm$ SE. $^*p < 0.05$ via repeated measures ANOVA.

Figure 3.

Upper row: EEG spectral powers in (a) θ-, (c) α- and (e) β-frequency bands in the left (LH) and right (RH) hemispheres during the rest-state and pre-stimulus period at the beginning (T_1) and at the end (T_6) of the experiment. Data are shown as group mean $\pm$ SE. $^*p < 0.05$ via a repeated measures ANOVA. Lower row: EEG channel clusters representing significant changes in (b) θ-, (d) α- and (f) β-frequency band spectral powers in T_6 versus T_1 conditions ($p_{pairwise} < 0.01$, $p_{cluster} < 0.05$).

Figure 4.

EEG channel clusters representing significant changes in the EEG spectral power in the θ-, α- and β-frequency bands at the end (T_6) versus the powers at the beginning (T_1) of the experiment ($p_{pairwise} < 0.01$, $p_{cluster} < 0.05$).

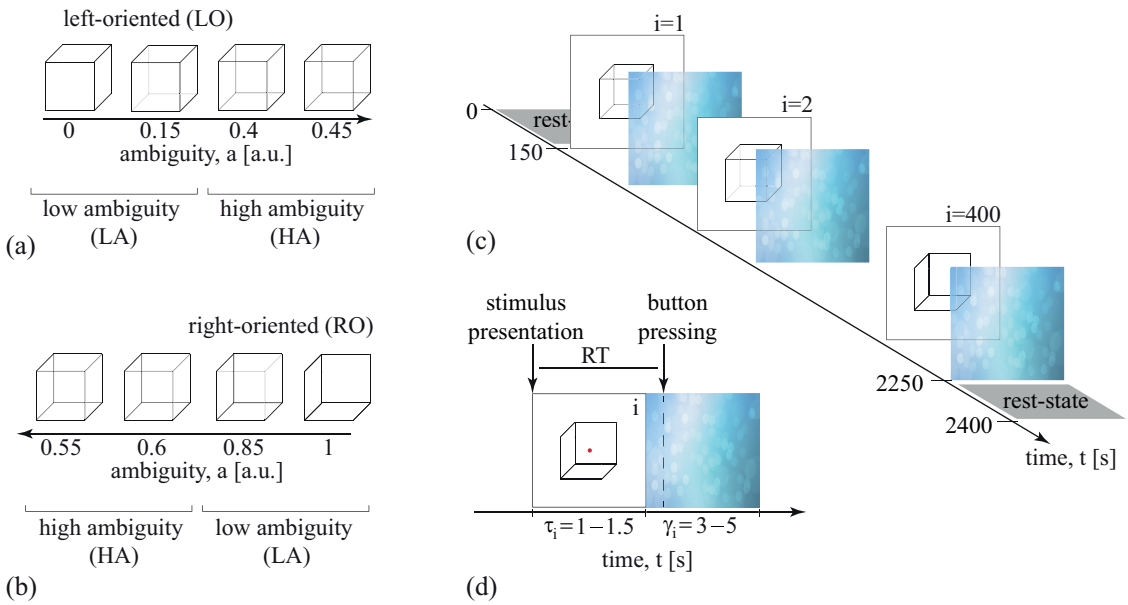

Figure 1

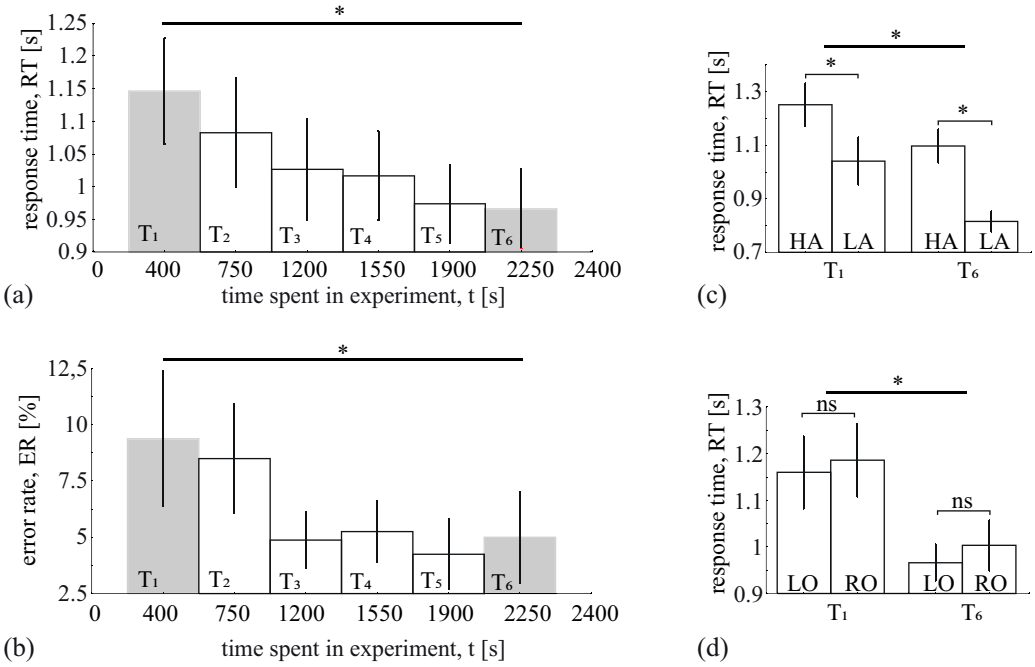

Figure 2

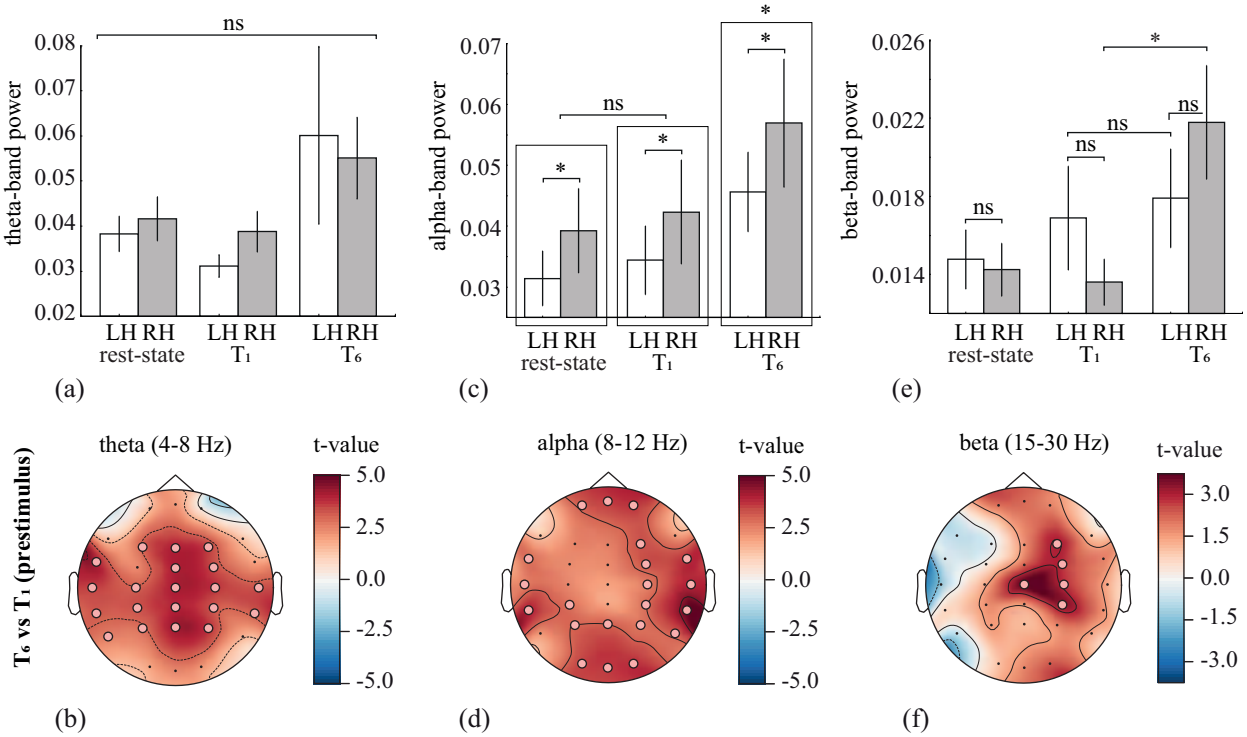
theta-band power
alpha-band power
beta-band power
ns
*
LH RH
rest-state
T1
T6
(a)
(c)
(e)
T6 vs T1 (prestimulus)
theta (4-8 Hz)
alpha (8-12 Hz)
beta (15-30 Hz)
t-value
(b)
(d)
(f)

Figure 3

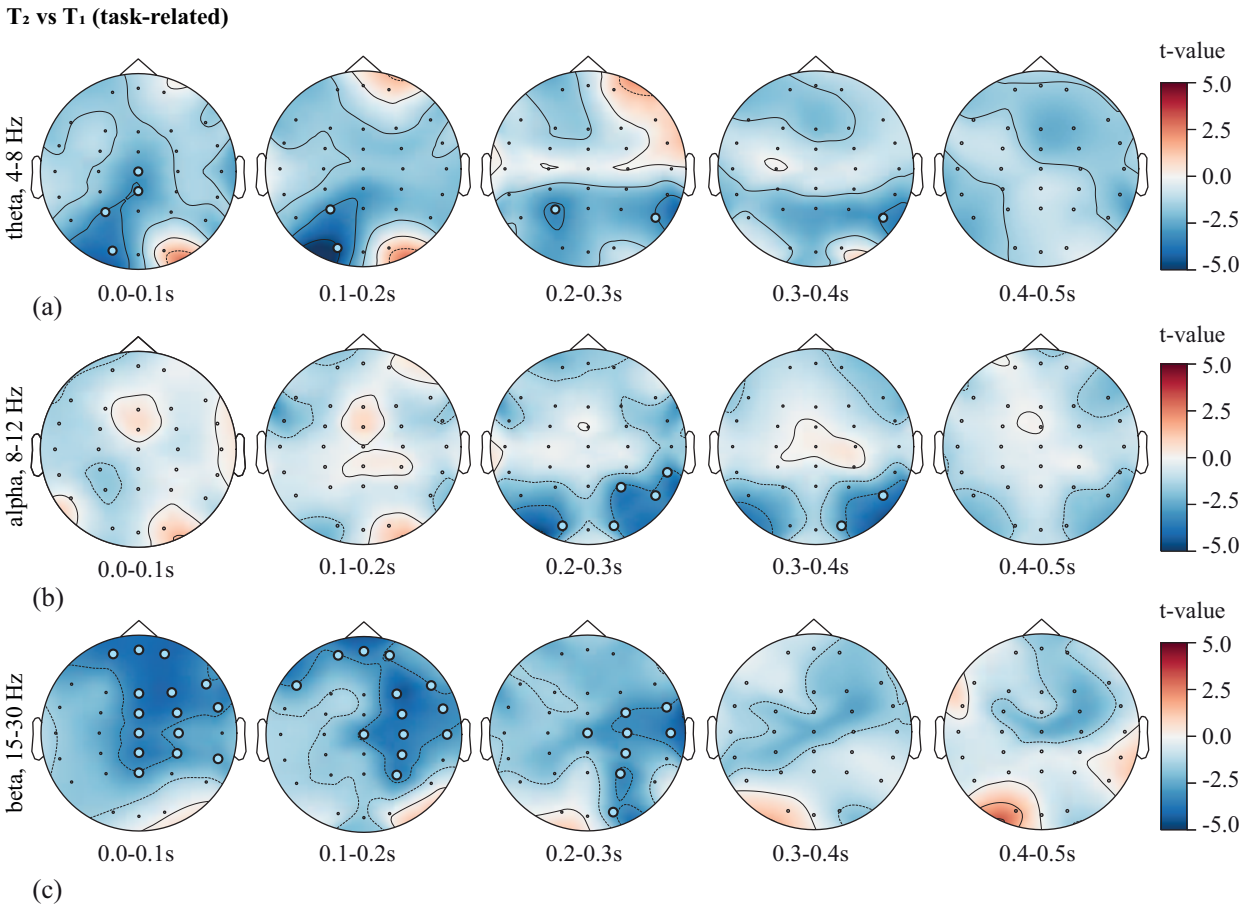
T₂ vs T₁ (task-related)
theta, 4-8 Hz
alpha, 8-12 Hz
beta, 15-30 Hz
0.0-0.1s
0.1-0.2s
0.2-0.3s
0.3-0.4s
0.4-0.5s
(a)
(b)
(c)
t-value
5.0
2.5
0.0
-2.5
-5.0

Figure 4