

Article

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## Influence of «sensory prehistory» on the ambiguous stimuli processing in the human brain

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**Abstract.** *Purpose* of this work is to study the effect of previous sensory information on the brain's processing of current visual stimuli. Bistable images (Necker cubes) with a high degree of ambiguity (HA) and a low degree of ambiguity (LA) were used as visual stimuli. *Methods.* In this paper, we used wavelets to identify features of the brain activity signals. A multivariate analysis of variance was used to compare behavioral characteristics. Spectral power and event-related spectral perturbations were compared via a cluster-based permutation test using the FieldTrip package for Matlab. *Results.* We found that when the HA stimuli followed the LA stimuli, the activity of neurons in the sensory areas decreased in the early processing stage but increased in the later stages. This result confirmed the hierarchical organization of processing, where the low levels processed the details of the stimulus, and the high levels represented its interpretation. We supposed that processing of HA and LA stimuli was similar at low levels due to their similar morphology. Therefore, the brain might use the LA stimulus template at low levels to reduce the demands when processing the details of the HA stimulus. When the LA stimulus followed the HA stimulus, a weakened response in the sensory regions accompanied a high response in the frontal cortex. It reflected activation of the top-down cognitive functions, detecting a mismatch between the LA stimulus and the HA stimulus template. *Conclusion.* These results expanded the existing knowledge about the sensory processing mechanisms.

**Keywords:** ambiguous stimuli, stimulus template, processing hierarchy, EEG, predictive coding theory.

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## Introduction

The brain uses sensory information to create an idea of the external environment. The published results indicate that the brain's processing of sensory information is organized hierarchically: at low levels, individual details are processed, while high levels interpret the information received as a whole. There is an opinion that the brain uses a priori knowledge (predictions) along with

sensory data to create an accurate representation of the external environment [1, 2].

There is a widespread tendency to view forecasts as high-level processes acting from top to bottom on mechanisms at a lower level of the hierarchy. For example, most of the literature suggests that forecasts lead to the formation of incentive patterns [3–5]. The brain correlates these patterns with external sensory information [6]: patterns are transmitted from high levels to low levels, while signals going in the opposite direction — from low to high levels of the hierarchy encode errors of such a mapping [7]. Thus, predictive signaling reflects downstream processes, and predictive error signaling represents upstream processing. These processes are interdependent and always interact with each other [1]. Thus, to date, there is sufficient evidence that forecasts are formed at different levels of processing and interact with each other through descending and ascending flows of information in the brain. [2, 8]. At the same time, the question of the exact mechanism underlying the comparison of forecasts and sensory data remains open.

In this paper, we consider the processing of repeatedly presented ambiguous visual stimuli (Necker cubes) with a low degree of ambiguity (low ambiguity, LA) and a high degree of ambiguity (high ambiguity, HA). During the receipt of messages from the subject about the interpretation of each visual stimulus, the following were recorded EEG signals and cube interpretation times (reaction time, RT). It is known from the literature that repeated exposure to an identical or similar sensory stimulus causes adaptation of the neural ensemble. This effect implies a decrease in neural response to repetitive stimuli [9] and applies to both low-level [10, 11] and high-level [12, 13] processes.

According to our previous works [14–16], the interpretation of stimuli with a high degree of ambiguity takes longer than the interpretation of stimuli with a low degree of ambiguity. The cubes LA and HA have almost the same morphology, so it can be assumed that they have a similar processing process at low levels. We also assume that the interpretation of the HA stimulus involves processes at higher levels; consequently, at these levels, its processing involves a large neural population, increasing the total processing time. Finally, we assume that the HA stimulus pattern appears at hierarchically higher processing levels than the LA pattern. As a result, the HA and LA patterns may have different effects on the processing of current stimuli.

## 1. Methods

**1.1. Subjects.** Twenty healthy subjects (16 men and 4 women) aged 20 to 36 years with normal or normalized visual acuity took part in the experiments. All of them gave written informed consent in advance to participate in the experiment. All participants were familiar with the experimental task and had not participated in such experiments in the last 6 months. Experimental studies were conducted in accordance with the Helsinki Declaration and approved by the Research Ethics Committee.

**1.2. Experimental procedure.** The Necker cube [17, 18] was used as an ambiguous visual stimulus. The subject, without any visual disturbances, interprets the 2D image of the Necker cube as a 3D object due to the specific position of the edges of the cube. Depending on the contrast of the inner edges, the Necker cube can be oriented either to the left or to the right (fig. 1, *a*). The contrast of the three middle lines centered in the left corner was used as a control parameter  $a \in [0, 1]$  ( $a$  — ambiguity level). The values  $a = 1$  and  $a = 0$  correspond to 0 (black) and 255 (white) pixels of the brightness of the inner lines using an 8-bit gray scale palette. Therefore, the control parameter can be defined as  $a = g/255$ , where  $g$  is the brightness of the inner lines. In our experiment, we use images of a Necker cube with 8 different levels of ambiguity (fig. 1, *a*). Half of them ( $a \in \{0.15, 0.25, 0.4, 0.45\}$ ) are considered left-oriented, the other half

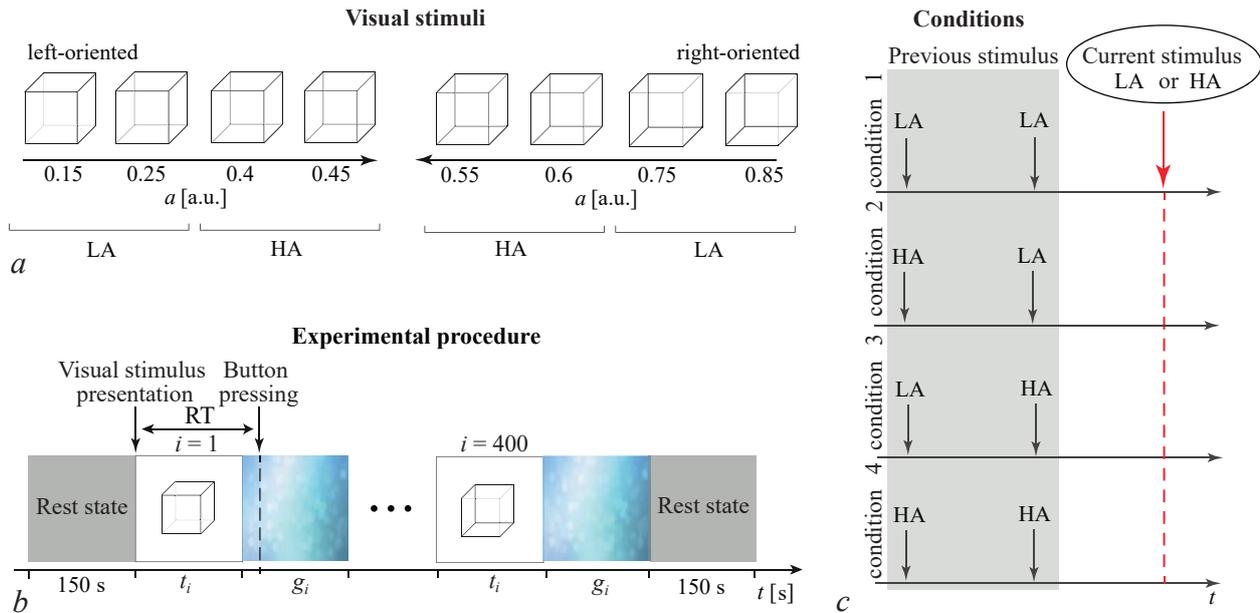


Fig. 1. *a* — Набор визуальных стимулов (кубов Неккера с различной степенью неоднозначности); *b* — схематическая иллюстрация экспериментальной процедуры, отражающая демонстрацию 400 кубов Неккера, чередующихся с демонстрацией абстрактных изображений. RT — время реакции испытуемого; *c* — экспериментальные условия

Fig. 1. *a* — Set of visual stimuli (Necker cubes with varying degrees of ambiguity); *b* — schematic illustration of an experimental procedure that reflects a demonstration of 400 Necker cubes alternating with a demonstration of abstract images. RT — subject's reaction time; *c* — experimental conditions

( $a \in \{0.55, 0.6, 0.75, 0.85\}$ ) right-oriented. For  $a \approx 0$  and  $a \approx 1$  (low-ambiguity (LA) images), cubes are easily interpreted as oriented left and right. For  $a \approx 0.5$ , identifying the orientation of the cube is a more difficult task, since we are dealing with images with a high level of ambiguity (HA).

Each image of the Necker cube was displayed in the center of the computer screen using black and gray lines on a white background. Images of Necker cubes (142 mm) were shown on a 24-inch BenQ LCD monitor with a spatial resolution of  $1920 \times 1080$  pixels and a refresh rate of 60 Hz. The subjects were located at a distance of 70...80 cm from the monitor with a viewing angle of about 0.25 rad.

The whole experiment lasted about 40 minutes for each participant, including short EEG recordings at rest (about 150 s) before and after the main part of the experiment. During the experimental sessions, cubes with predefined values of  $a$  (selected from the set in Fig. 1, *a*) were randomly demonstrated 400 times, each cube with a certain ambiguity was presented about 50 times. The scheme of the experimental session is shown in Fig. 1, *b*. Each  $i$ -th stimulus was presented during the time interval  $\tau_i$ , and the next ( $i+1$ ). The  $i$ -th stimulus was demonstrated after the time interval  $\gamma_i$ . The duration of the stimulus demonstration varied in the range of  $\tau \in [1, 1, 5]$  s.

For each stimulus, we evaluated the behavioral response by measuring the RT time, which corresponded to the time elapsed from the presentation of the stimulus to the pressing of the button (fig. 1, *b*).

**1.3. Recording and processing of EEG signals.** EEG signals were recorded using the monopolar registration method and the classical extended electrode placement scheme 10–10. We recorded 31 signals with two referents, A1 and A2, located on the earlobes, and a grounding electrode N located just above the forehead. The signals were obtained using Ag/AgCl cup

adhesive electrodes placed on the paste «Tien-20» (Weaver and Company, Colorado, USA). Immediately before the start of the experiments, we carried out all the necessary procedures to increase the conductivity of the skin and reduce its resistance with the help of an abrasive gel «NuPrep» (Weaver and Company, Colorado, USA). After the electrodes were installed, the resistance was monitored throughout the experiment. Usually the resistance values changed in the range of 2...5 com. An electroencephalograph was used to amplify and analog-to-digital conversion of EEG signals «Encephalan-EEGR-19/26» (company «Medikom MTD», Taganrog, Russian Federation) with multiple EEG channels and a two-button input device (keyboard). The raw EEG signals were filtered by a bandpass filter with a finite pulse characteristic with cut-off points of 1 Hz and 100 Hz and a 50 Hz notch filter using an integrated hardware and software package. The removal of eye blinking and heartbeat artifacts was carried out by the method of independent component analysis (ICA) using the software EEGLAB [19]. After the EEG preprocessing procedure, we excluded some tests due to high-amplitude artifacts and reviewed 320 of tests from the initial 400.

The recorded EEG signals were segmented into 4-second recordings, where each recording was associated with one demonstration of the Necker cube, including a 2-second interval before and a 2-second interval after the demonstration of the Necker cube. We calculated the spectral power for each test in the frequency range of 4...40 Hz using a wavelet transform with a Morlet wavelet [20]. The number of cycles ( $n$ ) was defined as  $n = f$ , where  $f$  is the frequency of the signal [21]. The wavelet analysis was performed in Matlab using Fieldtrip instrumentation. The intervals of 0.5 s on each side of the recording were reserved for calculating the power of the wavelet. As a result, we considered the power of the wavelet in the interval of 3 s, including the pre-stimulus state (from  $-1.5$  s to 0) and the activity associated with the stimulus (from 0 to 1.5 s). For the received wavelet power, we considered the spectral disturbances ERSP (Event-Related Spectral Power) associated with the event (presentation of a visual stimulus) using the normalization [activity associated with the stimulus — prestimulus state]/prestimulus state.

**1.4. Experimental conditions.** Two types of stimuli LA and HA were grouped and separated by conditions according to the ambiguity of the previous stimulus. Not only the ambiguity of the previous stimulus (the first previous one) was introduced into consideration, but also the ambiguity of the stimulus presented two cubes earlier (the second previous one). As a result, we considered four conditions for cubes LA and HA (fig. 1, c):

- condition 1 — both previous cubes have a low level of ambiguity (LA–LA);
- condition 2 — the first previous cube has a low level of ambiguity, and the second previous cube has a high level of ambiguity (HA–LA);
- condition 3 — the first previous cube has a high level of ambiguity, and the second previous cube has a low level of ambiguity (LA–HA);
- condition 4 — both previous cubes have a high level of ambiguity (HA–HA).

To keep the number of EEG recordings constant depending on the conditions and the subjects, we selected 16 events for each condition.

**1.5. Statistical analysis.** Statistical analysis at the group level was carried out for the values of the median reaction time, the median time of presentation of the visual stimulus and the ratio between left-sided and right-sided stimuli, as well as the ratio between the stimuli LA and HA. The main effects were evaluated using multivariate analysis of variance with the correction of Greenhouse-Gamer. We performed post hoc analysis using the Student's t-test for dependent samples and using the Wilcoxon test, depending on the normality of the samples. Normality was

tested using the Shapiro-Wilk test. We conducted a statistical analysis using the SPSS software. The tests used and their parameters are specified in the section «Results».

Spectral power and spectral disturbances were compared for different experimental conditions in the time, spatial and frequency domains using a t-test for dependent samples. Correction of multiple comparisons was based on the cluster permutation test and the Monte Carlo randomization method. The critical  $\alpha$ -level for the paired comparison was set to 0.05. The critical  $\alpha$ -level for the cluster test was set to 0.025. The minimum number of elements in the cluster was set to 2, and the number of permutations was 2000. The analysis was carried out using the Fieldtrip package for Matlab.

## 2. Results

**2.1. Reaction time.** We analyzed the effect of ambiguity of the previous stimulus separately for the current stimuli LA and HA. We compared RT subjects in four conditions (Methods and Fig. 1, c). Figure 2 demonstrates how RT differs under these conditions for the stimuli HA and LA. Multivariate analysis of variance revealed a significant effect of the experimental condition for both stimuli. For HA:  $F(3.57) = 10.787$ ,  $p < 0.001$ ; for LA:  $F(3.57) = 6.067$ ,  $p = 0.001$ .

For HA stimuli, we observed a minimum reaction time in condition 4, where the two previous stimuli also had a high level of ambiguity. On the contrary, the subjects demonstrated the maximum reaction time in the condition 1, where the two previous cubes had a low level of ambiguity. Post hoc analysis using the Wilcoxon criterion showed that the reaction time in

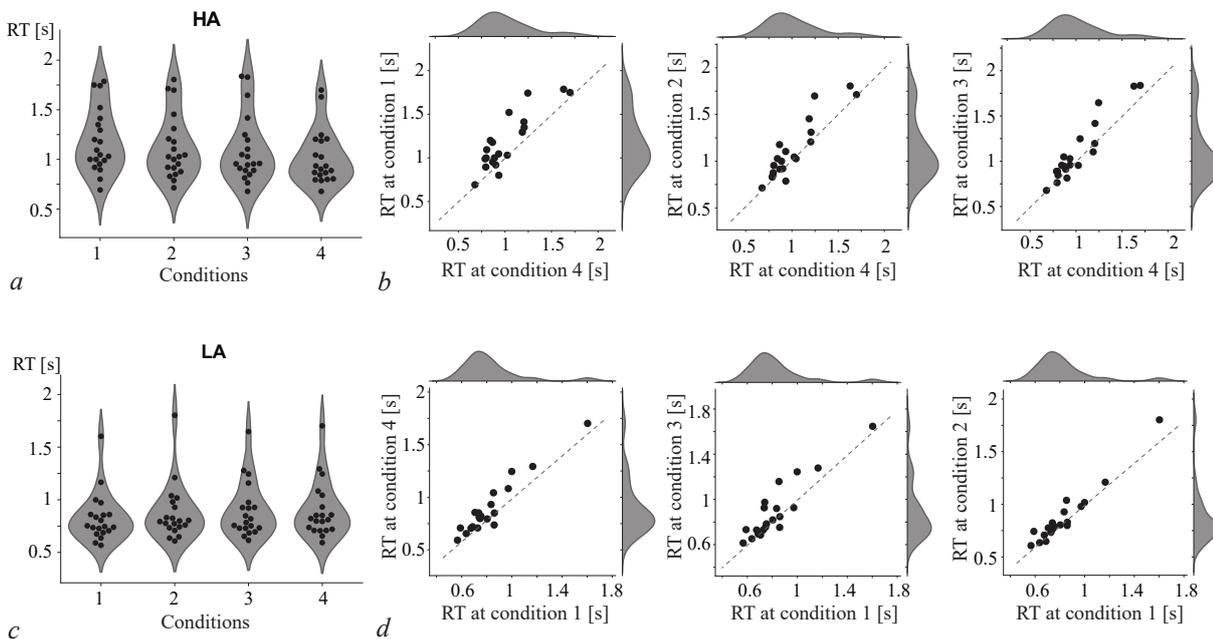


Fig. 2. *a* — Время реакции RT в четырех условиях для текущего стимула HA; *b* — парные различия между RT в различных условиях для текущего стимула HA; *c* — время реакции (RT) в четырех условиях для текущего стимула LA; *d* — парные различия между RT в различных условиях для текущего стимула LA

Fig. 2. *a* — Response time (RT) under four conditions for the current stimulus HA; *b* — paired differences between RT under different conditions for the current stimulus HA; *c* — response time (RT) under four conditions for the current stimulus LA; *d* — paired differences between RT under different conditions for the current stimulus LA

condition 4 ( $M = 1.01$  c,  $SD = 0.27$  c) was significantly lower compared to condition 1 ( $M = 1.18$  c,  $SD = 0.32$  c):  $Z = 3.547$ ,  $p < 0.001$ . The analysis of paired differences (Fig. 2, b) showed that 19/20 of the subjects showed an effect in the same direction as the group, and only one subject had an effect in the opposite direction. The reaction time in condition 4 was also lower than in condition 2 ( $M = 1.12$  s,  $SD = 0.32$  s):  $Z = 3.323$ ,  $p = 0.001$ . In this case, 2/20 subjects demonstrated an effect in the opposite direction, and one subject showed no effect. Finally, the reaction time in condition 4 was lower than in condition 3 ( $M = 1.09$  s,  $SD = 0.33$  s):  $Z = 2.696$ ,  $p = 0.007$ . The analysis of paired differences showed that 15/20 of the subjects showed an effect in the same direction as the group, 4/20 of the subjects showed an effect in the opposite direction, and one subject showed no effect. For the LA stimuli, we observed the minimum reaction time in condition 1, where the two previous stimuli also had a low level of ambiguity, and the maximum reaction time — in condition 4, where the two previous stimuli had a high level of ambiguity. The Wilcoxon test showed that the reaction time in condition 1 ( $M = 0.82$  s,  $SD = 0.23$  s) was significantly lower compared to condition 4 ( $M = 0.89$  s,  $SD = 0.26$  c):  $Z = 3.061$ ,  $p = 0.002$ . The analysis of paired differences showed that 18/20 of the subjects showed an effect in the same direction as the group. One subject demonstrated an effect in the opposite direction, and the other — none. The reaction time in condition 1 was also lower than the reaction time in condition 3 ( $M = 0.89$  s,  $SD = 0.25$  s):  $Z = 2.13$ ,  $p = 0.009$ . In this case, 4/20 of the subjects showed an effect in the opposite direction. Finally, the reaction time in condition 1 was lower than the reaction time in condition 2 ( $M = 0.87$  s,  $SD = 0.26$  s):  $Z = 2.67$ ,  $p = 0.008$ . The analysis of paired differences showed that 4/20 of the subjects had an effect in the opposite direction.

Finally, multivariate analysis of variance with the Greenhaus-Geisser correction showed that the median presentation time of the Necker cube did not change significantly depending on the conditions for both stimuli LA:  $F(1.3, 24.9) = 2.883$ ,  $p = 0.093$ , and for incentives HA:  $F(1.38, 26.3) = 1.646$ ,  $p = 0.214$ . The ratio between the number of left- and right-oriented current stimuli also did not change in the conditions for both LA stimuli:  $F(1.26, 29) = 3.604$ ,  $p = 0.059$ , and for incentives HA:  $F(1.9, 45.5) = 1.159$ ,  $p = 0.323$ . These results indicate that neither the time points at which the subjects were shown visual stimuli nor the orientation of the cube affect the reaction time in the conditions under consideration 1-4. This parameter is affected only by the ambiguity of previous visual stimuli.

To analyze how the previous orientation of the stimulus affected the reaction time, we introduced the coefficient  $\Theta$ , which characterizes the correspondence between the orientation of the current and previous stimuli. For each test  $\Theta = 1$  indicated that the current stimulus has the same orientation as the previous stimulus,  $\Theta = 2$  reflected the correspondence between the orientation of the current stimulus and the two previous stimuli. In contrast,  $\Theta = 0$  means that the current orientation of the stimulus is different from the previous orientation of the stimulus. The values of  $\Theta$  were averaged across all trials and compared between four conditions. The analysis of variance revealed the main factors for both HA stimuli:  $F(3.57) = 11.702$ ,  $p < 0.001$ , and for LA stimuli:  $F(3.57) = 2.913$ ,  $p = 0.042$ . Then we used multivariate correlation analysis to check whether  $\Theta$  correlates under these conditions with the reaction time of [22]. As a result, a weak correlation was observed for both stimuli HA:  $r(59) = 0.29$ , 95% CI [0.042 0.51],  $p = 0.02$ , and for LA incentives:  $r(59) = -0.25$ , 95% CI [-0.48 - 0.0004],  $p = 0.045$ . Finally, we found that the error rate does not change depending on the conditions for both the stimuli HA ( $M = 9.2\%$ ,  $SD = 10.4\%$ ):  $F(3.57) = 0.288$ ,  $p = 0.844$ , and for the stimuli LA ( $M = 1.7\%$ ,  $SD = 3.5\%$ ):  $F(3.57) = 0.497$ ,  $p = 0.686$ .

**2.2. Neural activity during the prestimul state.** According to the results described above, the ambiguity of the previous stimulus affected the time the subject spent identifying the current stimuli. RT was lower if the ambiguity level of the previous visual stimulus coincided with the ambiguity level of the current stimulus. This effect was stronger if two previously presented

stimuli had the same level of ambiguity (both LA or both HA). We assumed that the brain's processing of previous stimuli affects the prestimulus state of the current stimulus. So, after processing the LA stimuli (condition 1), it was more favorable for processing the current LA stimulus. In contrast, the prestimulus state after processing the HA stimuli was more favorable for processing the current HA stimulus. Accordingly, we compared the spectral power of the prestimulus state between condition 1 and condition 4 (fig. 3, *a*).

Comparing the prestimulus states formed after processing HA and LA stimuli, we found a significant negative cluster ( $p = 0.0475$ ) in the frequency range of 16...18.75 Hz, localized in the occipital (Oz) and parietal (Pz and CPz) regions of the brain (Fig. 3, *b*). The spectral power of this cluster in condition 4 ( $M = 1.7 \times 10^4$ ,  $SD = 7.2 \times 10^4$ ) was higher than in condition 1 ( $M = 1.5 \times 10^4$ ,  $SD = 6.2 \times 10^4$ ). The analysis of paired differences showed that 17/20 of the subjects showed an effect in the same direction as the group (fig. 3, *c*).

Note that the median time of presentation of the current stimulus had no significant differences for these conditions ( $Z = 1.307$ ,  $p = 0.191$ , Wilcoxon test). Also, no significant differences were observed for the ratio between the left and right orientations of the current stimulus ( $Z = 0.105$ ,  $p = 0.917$ , Wilcoxon test). Thus, we conclude that the observed change in spectral power was caused only by the ambiguity of the previous stimulus, but not by the duration of the experiment or the current orientation of the stimulus.

**2.3. Neural activity during brain processing of HA stimuli.** As described above, after processing two consecutive HA stimuli, cortical activity showed increased power of the  $\beta$  range in the occipital-parietal region of the brain. In this case, the brain processing of the current HA stimulus took less time (lower RT value) (fig. 2, *a*). In order to analyze the cortical activity underlying the decrease in reaction time in this state, we compared the spectral disturbances caused by visual stimulus processing between condition 1 and condition 4 within 0.35 s after the start of stimulus presentation. As a result, a significant positive cluster with  $p = 0.045$  was found. This cluster is located in the time range from 0.15 to 0.162 s after the start of the stimulus in

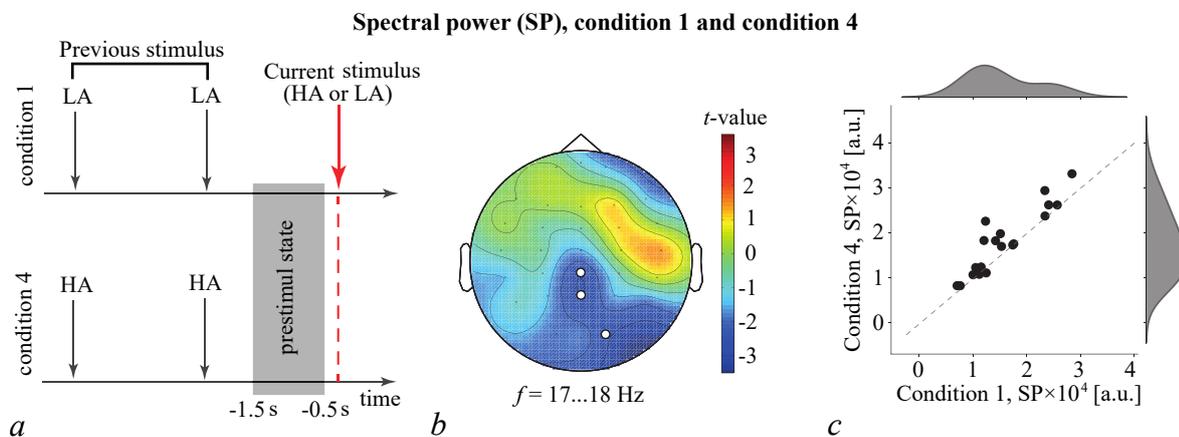


Fig. 3. Сопоставление престаимпульной спектральной мощности (SP) в условии 1 и условии 4: *a* — схематическое представление условий эксперимента; *b* — значение  $t$  отражает результат сравнения SP между условием 1 и условием 4 с использованием  $t$ -критерия. Кружочки показывают значимый кластер ( $p < 0.05$  с помощью  $t$ -критерия для парных выборок с кластерной поправкой для множественных сравнений); *c* — распределение парных различий отражает изменение SP между условием 1 и условием 4 у всех участников (цвет online)

Fig. 3. Comparison of the prestimulus spectral power (SP) in *condition 1* and *condition 4*: *a* — schematic representation of the experimental conditions; *b* — the value of  $t$  reflects the result of the comparison between SP in *condition 1* and *condition 4*. The circles show a significant cluster ( $p < 0.05$  using the  $t$ -test for paired samples with cluster correction for multiple comparisons); *c* — the distribution of pairwise differences reflects the change in SP between *condition 1* and *condition 4* for all participants (color online)

the frequency range 17.5...17.75 Hz and localized in the right occipital (O2), parietal (P4, P8) and temporal (Tp8) regions of the brain (Fig. 4, *a*). The ERSP in this cluster in condition 1 ( $M = 0.17$ ,  $SD = 0.45$ ) was higher than in condition 4 ( $M = -0.09$ ,  $SD = 0.31$ ). The analysis of paired differences showed that 15/20 of the subjects showed an effect in the same direction as the group (fig. 4, *b*).

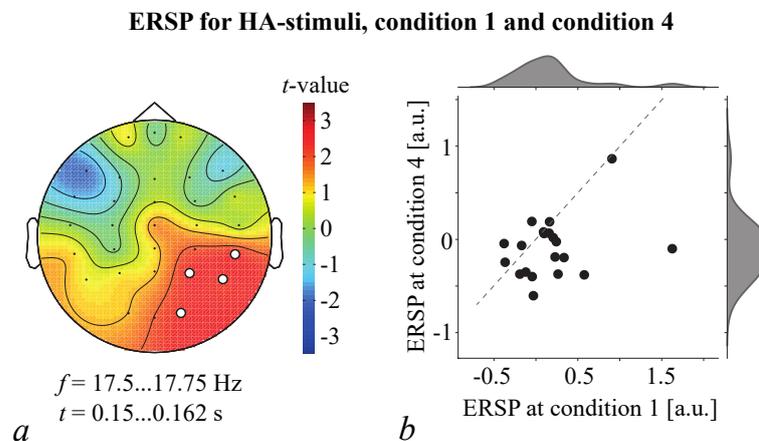


Fig. 4. Сопоставление спектральных возмущений, вызванных стимулом (ERSP), во время обработки HA стимула в условии 1 и условии 4: *a* — значение  $t$  отражает результат сравнения ERSP между условием 1 и условием 4. Кружочки показывают значимый кластер ( $p < 0.05$  с помощью  $t$ -критерия парных выборок с кластерной поправкой для множественных сравнений); *b* — распределение парных различий показывает изменение ERSP между условием 1 и условием 4 в группе участников (цвет online)

Fig. 4. Comparison of spectral perturbations caused by the stimulus (ERSP) during the processing of the HA stimulus in *condition 1* and *condition 4*: *a* —  $t$ -value reflects the result of the comparison between the ERSP in *condition 1* and *condition 4*. The circles show a significant cluster ( $p < 0.05$  using the  $t$ -test of paired samples with cluster correction for multiple comparisons); *b* — the distribution of paired differences shows the change in ERSP between *condition 1* and *condition 4* in the group of participants (color online)

**2.4. Neural activity during brain processing of LA stimuli.** Comparing the spectral disturbances caused by the brain processing of the LA stimulus between condition 1 and condition 4, we found four negative and two positive clusters. The first positive cluster with  $p = 0.0105$  is located in the time range 0.26...0.35 s after the start of the stimulus in the frequency range 19...23.75 Hz and localized in the right occipital (Oz, O2), parietal (P4, P8) and temporal (TP8) regions of the brain (Fig. 5, *a*). The ERSP in this cluster in condition 1 ( $M = 0.18$ ,  $SD = 0.44$ ) was higher than in condition 4. ( $M = -0.12$ ,  $SD = 0.25$ ). The analysis of paired differences showed that 17/20 of the subjects showed an effect in the same direction as the group. The second positive cluster with  $p = 0.0105$  is located in the time range 0.3...0.35 s in the frequency range 25.75...28 Hz and localized in the right occipital (O2) and parietal (P4 and P8) regions of the brain (Fig. 5, *b*). The ERSP in this cluster in condition 1 ( $M = 0.18$ ,  $SD = 0.45$ ) was higher than in condition 4 ( $M = -0.09$ ,  $SD = 0.21$ ). The analysis of paired differences showed that 18/20 of the subjects showed an effect in the same direction as the group.

Negative clusters were observed within 0.15 s after the start of the stimulus in the  $\beta$ - and  $\theta$ -range frequency zones (fig. 6). The first cluster with  $p = 0.031$  manifested from the beginning of the stimulus to 0.098 s in the frequency range of 17.25...19 Hz and included EEG sensors in the right frontal (F4, F8), frontocentral (FC4) and right temporal (T4) regions of the brain (fig. 6, *a*). Event-Related Spectral Power in this cluster in condition 1 ( $= -0.11$ ,  $SD = 0.25$ ) was lower than in condition 4 ( $= 0.17$ ,  $SD = 0.28$ ). The analysis of paired differences showed that 16/20 of the

## ERSP for LA-stimuli, condition 1 and condition 4

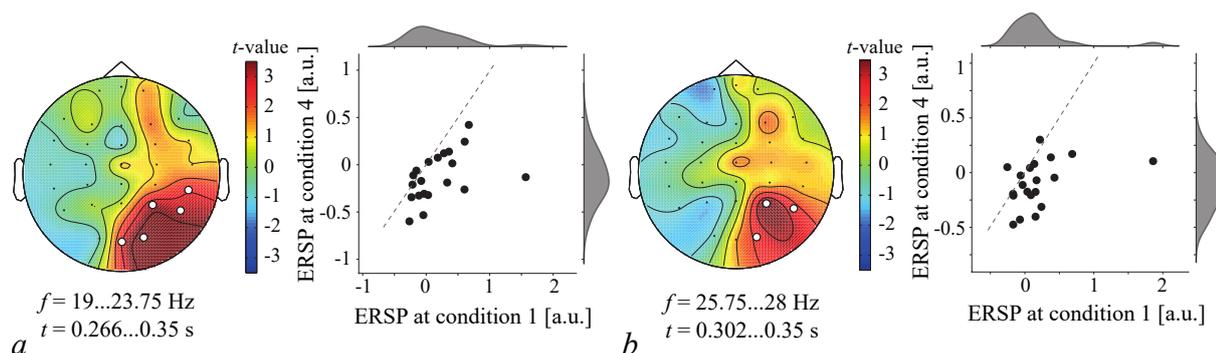


Fig. 5. Два положительных кластера (*a*, *b*) отражают результат сопоставления ERSP во время обработки LA стимула в условии 1 и условии 4: *a* — значение *t* отражает результат сравнения ERSP между условием 1 и условием 4. Кружочки показывают значимый кластер ( $p < 0.05$  с помощью *t*-критерия для парных выборок с кластерной поправкой для множественных сравнений); *b* — распределение парных различий показывает изменение ERSP между условием 1 и условием 4 в группе участников (цвет online)

Fig. 5. Two positive clusters (*a*, *b*) reflect the result of ERSP matching during LA stimulus processing in *condition 1* and *condition 4*: *a* — *t*-value reflects the result of the comparison between the ERSP in *condition 1* and *condition 4*. The circles show a significant cluster ( $p < 0.05$  using the *t*-test of paired samples with cluster correction for multiple comparisons); *b* — the distribution of paired differences shows the change in ERSP between *condition 1* and *condition 4* in the group of participants (color online)

subjects showed an effect in the same direction as the group.

The second cluster with  $p = 0.036$  is located from the beginning of the stimulus to 0.018 s in the frequency range of 5.25...5.75 Hz and included left-sided parietal (P3), central-parietal (CPz, CP3), left-sided temporal (T3) and left-sided frontal (F3) EEG sensors (Fig. 6, *b*). The ERSP in this cluster in condition 1 ( $M = -0.12$ ,  $SD = 0.17$ ) was lower than in condition 4 ( $M = 0.14$ ,  $SD = 0.44$ ). The analysis of paired differences showed that 16/20 of the subjects showed an effect in the same direction as the group. The third cluster with  $p = 0.045$  was located in the time range from 0.094 s to 0.142 s after the start of the stimulus at a frequency of 6.25 Hz and was localized in the middle frontal (Fz) and front-central (FCz), as well as in the left temporal (T3) and front-temporal (FT7) regions the brain (fig. 6, *c*). Event-Related Spectral Power in this cluster in condition 1 ( $= -0.11$ ,  $SD = 0.15$ ) was lower than in condition 4 ( $= 0.13$ ,  $SD = 0.36$ ). The analysis of paired differences showed that 17/20 of the subjects showed an effect in the same direction as the group.

The fourth cluster with  $p = 0.046$  is located in the time range 0.066...0.074 s after the start of the stimulus at a frequency of 5.25 Hz and included middle frontal (Fz) and front-central (FCz) sensors, as well as left temporal (T3) and central parietal (CPz) sensors (fig. 6, *d*). Event-Related Spectral Power in this cluster in condition 1 ( $= -0.09$ ,  $SD = 0.14$ ) was lower than in condition 4 ( $= 0.14$ ,  $SD = 0.36$ ). The analysis of paired differences showed that 16/20 of the subjects showed the same effect as the group.

## Discussion of the results

When perceiving sequentially presented ambiguous stimuli — Necker cubes — the ambiguity of the previous stimulus affects the processing of the current visual stimulus by the brain. It was shown that the subject processes the stimulus faster if its ambiguity coincides with the ambiguity of the previously presented stimuli. It can be assumed that the populations of neurons involved

ERSP for LA-stimuli, condition 1 and condition 4

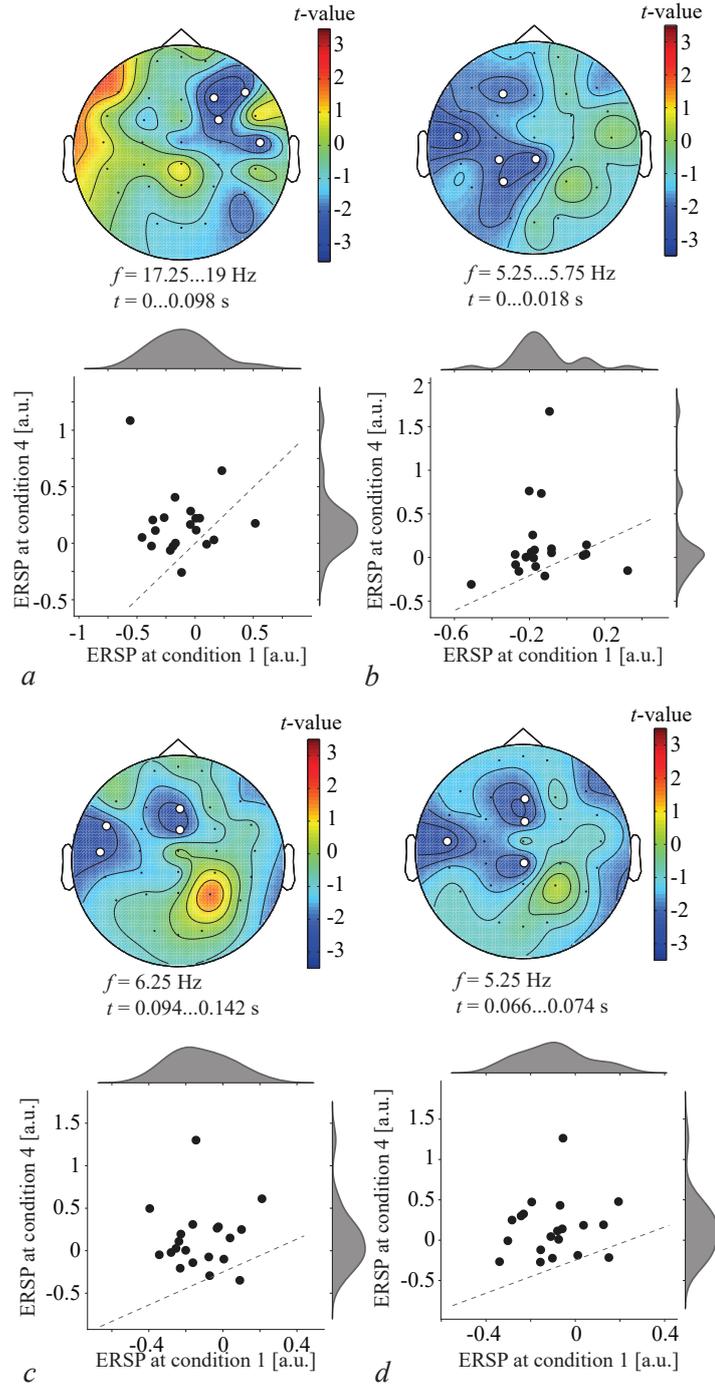


Fig. 6. Отрицательные кластеры (*a-d*), отражающие результат сопоставления ERSP во время обработки стимула LA между условием 1 и условием 4. Значение  $t$  отражает результат сравнения ERSP между условием 1 и условием 4 для всех датчиков ЭЭГ. Кружочки показывают значимый кластер ( $p < 0.05$  с помощью  $t$ -критерия для парных выборок с кластерной коррекцией для множественных сравнений). Распределение парных различий показывает изменение ERSP между условием 1 и условием 4 у всех участников (цвет online)

Fig. 6. Negative clusters (*a-d*) reflecting the result of ERSP comparison during LA stimulus processing between *condition 1* and *condition 4*. The value of  $t$  reflects the result of comparing the ERSP between *condition 1* and *condition 4* for all EEG sensors. The circles show a significant cluster ( $p < 0.05$  using the  $t$ -criterion for paired samples with cluster correction for multiple comparisons). The distribution of paired differences shows the change in ERSP between *condition 1* and *condition 4* for all participants (color online)

in the processing of previous stimuli remain active during the subsequent prestimulus period. To confirm this, we compared the pre-stimulus period after processing the stimuli HA and LA and found an increase in the power of the  $\beta$  range in the occipitoparietal region of the cerebral cortex in the first case. Activation of populations of neurons before processing a stimulus may be associated with the emergence of a prestimular pattern [3, 4].

According to [23], the stimulus pattern appears as a result of expectations. If this is the case, then for a faster response, the subjects expect a stimulus with a high level of ambiguity (HA) after two HA stimuli. However, we present stimuli randomly, and the probability of seeing a stimulus HA after two cubes of HA is small. Subjects are more likely to expect an LA stimulus after two HA. Finally, the subjects should determine the orientation of the Necker cube (i.e. left/right orientation), but not the level of its ambiguity (i.e. LA or HA). Therefore, the expectation and the resulting pattern should include the orientation of the stimulus. Given the above, the subjects should react faster to the stimulus with the same orientation as the previous one. However, our results show that the similar orientation of the current and previous visual stimulus does not cause a faster response.

According to the review [1], stimulus patterns appear at different levels of the sensory processing hierarchy. We assume that the orientation of the stimulus characterizes a high-level pattern, whereas the pattern at lower levels reflects the morphology of the stimulus. The neural response during HA stimulus processing increases for two possible reasons. Firstly, the HA stimulus has an indeterminate orientation, so to determine it, it is necessary to involve larger populations of neurons at high levels of the processing hierarchy. Secondly, the morphology of HA stimuli is more complex. Along with similar characteristics (the outer faces of the cube), the Necker cube with a high level of ambiguity has a higher contrast of the inner faces. Thus, in order to process the HA stimulus, it is necessary to obtain more sensory data, which leads to higher activation of neurons at low levels of the sensory processing hierarchy. Since the orientation of the previous stimulus does not affect the brain's processing of the current visual stimulus, we do not consider a high-level pattern. On the contrary, we focus on low-level templates.

We conducted a comparative analysis of brain activity associated with processing a visual stimulus with a high level of ambiguity in two cases: the previous stimulus was a stimulus with a low level of ambiguity (LA) and the previous stimulus was a stimulus with a high level of ambiguity (HA). We observed higher power in the  $\beta$ - and  $\theta$ -ranges in the occipital and parietal regions of the brain in the first case for  $t < 0.15$  s. The increased power of the  $\theta$  band in the parietal region indicates increased requirements for information processing, leading to the attraction of additional cognitive resources [24, 25]. The high power of the  $\beta$  range in the occipital and parietal regions characterizes the tasks associated with endogenous descending processes, including the processing of ambiguous visual stimuli [26]. In [27], bistable visual stimuli (face — saxophone) were presented to the subjects after images that were clear representations of the face or saxophone. Similarly to our results, an increase in power in the  $\beta$  range was observed in the occipital and parietal regions when processing an ambiguous stimulus after an unambiguous one. The authors reported that the subjects mostly interpreted the ambiguous picture as a face. The power of the  $\beta$  range was higher if the ambiguous figure followed the saxophone, and not the image of the face. Since the unambiguous stimulus was part of the ambiguous one, it was assumed that their morphology was similar. Thus, the authors suggested that the enhanced neural response was associated with high-level processes related to the interpretation of the stimulus as a whole, and not with low-level processing of individual signs of the stimulus. We do not consider the influence of orientation of visual stimuli. Therefore, higher processing stages responsible for the interpretation of the stimulus as a whole were excluded from the analysis. We came to the conclusion that the higher power of the  $\theta$ - and  $\beta$ -ranges may be related to the processing of features of HA stimuli that are

not similar to LA stimuli (for example, internal faces). We observe a higher reaction for  $t > 0.15$  s after the stimulus is presented, which confirms this assumption.  $t < 0.15$  c can be associated with the low levels at which the outer contours of the Necker cube are processed. These stimulus features are similar for cubes with low and high levels of ambiguity. Therefore, we assume similar activity of neurons at these processing levels for the stimulus LA and HA.

A comparative analysis of brain activity was carried out, which is associated with the processing of a visual stimulus with a low level of ambiguity in two cases. The previous stimulus was a stimulus with a low level of ambiguity (LA) and the previous stimulus was a stimulus with a high level of ambiguity (HA). Similarly, the neural response in the occipital and parietal regions of the brain remains unchanged for  $t < 0.15$  s. For  $t > 0.15$  c, we observe an increase in the power of the  $\beta$ -range in the parietal region for the previous stimulus LA. This confirms our assumption that stimuli LA and HA similarly at earlier stages, and higher stages of processing stimuli HA require additional resources. An unexpected effect is the higher power of the  $\beta$ - and  $\theta$ -range observed for  $t < 0.15$  s for the previous HA stimulus. The power of the  $\theta$  band in the medial frontal region increases when the LA stimulus follows the HA stimulus. The frontal-medial amplitude of ERP (Event-Related Potential) increases in situations that require a lot of cognitive control. A recent review by [28] links the frontal-medial amplitude of ERP with two components of cognitive control — detection of inconsistency with the perceptual pattern and reaction slowdown. Finally, in the review [29] it is shown that  $\theta$ -power in the frontal-medial region increases when performing tasks within the framework of classical interference paradigms. The power of the  $\beta$  range in the right frontal cortex is usually associated with the downward control of the reaction [30]. This cognitive function is activated in tasks requiring rapid termination.

The absence of differences in the occipital and parietal cortex at earlier stages ( $t < 0.15$  s) may indicate that the brain formed the corresponding patterns at low processing levels regardless of the ambiguity of the previous stimulus. This may be the result of a similar morphology of the outer faces of the cubes HA and LA. At the same time, the activation of cognitive control may reflect a significant initial discrepancy between the cube template ON and the sensory data obtained at earlier stages of processing. The HA stimulus is processed at higher levels compared to the LA stimulus. Thus, the HA pattern appears at higher levels than the LA pattern. The brain matches incoming sensory information with a template of high-level stimuli to minimize processing costs. Sensory data at low levels is insufficient to match this pattern. The brain tries to build low-level patterns from high-level patterns. This mechanism goes through the interaction between the downstream processes associated with the adaptation of the template and the upstream processes associated with the detection of matching errors. Thus, when the LA stimulus follows the HA-stimulus, top-down control is required to translate the template from high-level to low-level processing. This hypothesis coincides with the point of view proposed in the review [1]. The authors suggested that higher levels of the processing hierarchy extract features of high-order stimuli and use them to create a set of predictions that can be quickly adapted. They also assume that these predictions are transmitted to low levels of processing via direct links. The authors associate these direct connections with downstream processes, which allows information to be transferred between high and low levels and skip intermediate levels. Our results show that these descending processes include conflict control and reaction control, which are localized through neural activity in the frontal-medial cortex, anterior cingulate cortex and right inferior frontal cortex.

## Conclusion

In this paper, the influence of the ambiguity of the previous stimulus on the processing of the current one was analyzed. At the behavioral level, it was found that subjects respond more quickly to HA stimuli following HA stimuli. At the same time, a faster response to LA stimuli follows LA stimuli. EEG analysis shows that when the HA stimulus follows the LA stimulus, neural activity in the sensory (occipital-parietal) areas weakens at the early stage of processing, but increases at the last stages. This indicates a hierarchical organization of processing, where low levels process the details of the stimulus, and high levels represent its interpretation. This also confirms the fact that at low levels, the processing of HA and LA stimuli is similar due to similar morphology. Therefore, the brain uses the LA stimulus pattern at low levels to reduce the cost of processing the details of the HA stimulus. When the LA stimulus follows the HA stimulus, a weakened neural response in sensory areas accompanies a high response in the frontal cortex. Namely, we observe a high power of the  $\theta$  range in the medial frontal cortex and a high power of the  $\beta$  range in the right frontal cortex. We believe that these are electroencephalographic markers of descending processes associated with the detection of a mismatch between the LA stimulus and the HA stimulus pattern. The detected markers can be further used to create brain-computer interfaces for attention analysis and error control of the operator performing routine operations related to visual information processing [31–34].

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