ERRATA

Erratum: Functional Brain Organization of Global and Local Visual Perception: An Event-Related Potentials Study [*Human Physiology*, vol. 36, no. 5, pp. 518–534]¹

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Abstract—Adult subjects were asked to recognize a hierarchical visual stimulus (a letter) while their attention was drawn to either the global or local level of the stimulus. Event-related potentials (ERP) and behavioral indices (reaction time and percentage of correct responses) were measured. An analysis of behavioral indices showed the global level precedence effect, i.e. the increase in a small letter recognition time when this letter is a part of incongruent stimulus. An analysis of ERP components showed level-related (global vs. local) differences in the timing and topography of the brain organization of perceptual processing and regulatory mechanisms of attention. Visual recognition at the local level was accompanied by (1) stronger activation of the visual associative areas (P_z and T_6) at the stage of sensory features analysis (P1 ERP component), (2) involvement mainly of inferior temporal cortices of the right hemisphere (T_6) at the stage of sensory categorization (P2 ERP component), and (3) involvement of prefrontal cortex of the right hemisphere at the stage of selection of the relevant features of the target (N2 ERP component). Visual recognition at the global level was accompanied by (1) pronounced involvement of mechanisms of early sensory selection (N1 ERP component), (2) prevailing activation of parietal cortex of the right hemisphere (P_4) at the stage of sensory categorization (P2 ERP component) as well as at the stage of the target stimulus identification (P3 ERP component). We suggested that perception of the hierarchical stimulus at the global level is related primarily to the analysis of its spatial features in the dorsal visual system whereas the perception at the local level primarily involves an analysis of the object-related features in the ventral visual system.

Keywords: visual perception, global/local recognition, dorsal and ventral visual systems, ERP.

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INTRODUCTION

How do people perceive complex visual objects: from the whole to details or from details to the whole? This is a key issue in studying the mechanisms of processing visual information. Behavioral studies that exploited hierarchically arranged visual stimuli proposed by Navon [1–3], which are large objects (letters or figures) composed of similar small objects, showed the global level advantage, i.e. more rapid and accurate recognition of the object as a whole. When the local and global levels are represented by different elements, the subject's attention is drawn primarily to the large object because of the precedence effect of the global level thus causing the increase in the recognition time of the small object. This impact of the global features precedence onto recognition of a small object is referred to as the global interference effect. In Navon's opinion [2], per-

ceiving a complex object as a whole is based on the ability of the visual system to extract the spatial structure or spatial arrangement that unite small details into a whole and treat it as a separate object feature. According to the concept of Navon, this property of the perception does not imply any preliminary analysis of details. Navon [2] pointed out that the effect of global precedence is not an absolute rule, and how it manifest itself depends on the numerous sensory and cognitive factors. Nonetheless, a common tendency to holistic perception is one of the most important features of the objective perception of the world.

Although perception of hierarchical stimuli has been extensively studied, it still remains an open question at what stage of the visual information processing the advantage of the global level does appear, and, even broader, what the specific brain mechanisms are that underlie the perception of the whole and details. One of the most common views relates the specifics of global vs. local recognition to the brain mechanisms of low- vs.

¹ In the original article, there were many translation error. Here the article is reproduced in full with corrections.

high-frequency spatial filtering of the visual signals at the early stages of analysis [4–7]. The effect of the global level precedence is assumed to be a result of more rapid processing of the low frequencies of a visual stimulus, information about which is delivered to the associative cortical areas through the magnocellular visual pathways [7]. A rapid processing of visual signals is favorable for the perception of the global shape [2]. A reduced sensitivity of the visual system to signals with low spatial frequency or a removal of the low frequency components out of the signal affects the perception of the global stimulus features and leads to a reduction or disappearance of the global interference effect [4, 5]. A removal of the high frequency component of a visual signal reduces the probability of recognizing the target stimulus at the local level [6]. Some neuroimaging studies [8, 9] demonstrate a predominant activation of the medial part of the occipital cortex (the projection of parvocellular visual pathway) during recognition of the hierarchical stimuli at the local level, whereas the lateral part of this area (the projection of the magnocellular visual pathway) is activated during recognition at the global level. At the same time, it has been reported [10] that, during random alternation of the recognition levels of a hierarchical letter, the filtering of spatial frequency has no any specific influence on the parameters of the target signal recognition at the global or local level. Besides, the analysis of the event related brain potentials (ERP) did not show any direct link between local/global perception and the early sensory processing of the spatial frequency of visual signal. According to [6], the ERP dependence on the spatial frequency of the hierarchical figures did not appear earlier than 200 ms post-stimulus. As reported in [11], the global- vs. local-specific ERP features appeared in the inferior temporal areas only for the N250 component and only in the distributed attention condition when a subject had to recognize a target stimulus at either the global or local level. In the selective attention condition, there were no differences in ERP between the global and local recognition: in both cases, early P1 positivity in the extrastriate cortex was higher than in the free observation condition. The authors of [11] explain the differences in the recognition of visual objects at the global and local levels by an involvement of different mechanisms of attention which, in turn, may vary depending on the cognitive task at hand. It was shown in the ERP study of patients with damaged frontoparietal brain regions [12] that perceptual grouping during recognition of the hierarchical stimuli at the global level is controlled by the modulatory influence of the fronto-parietal attention network. As reported in [8], the perception of a target stimulus at the local level was accompanied by an increased local blood flow in the inferior temporal cortical areas activity of which is related to selective analysis of the categorical features of an object [13]. In similar experimental condition, an increase in N2 component was observed by Han et al. [14] in the frontal cortex and ventral visual associative

areas. The data mentioned above suggest that the system of spatial attention is involved primarily in recognizing the global aspect of complex stimuli whereas attention to the categorical features is involved into recognizing the local aspect. The specifics of perception of the whole and details can depend on an interaction between the bottom-up processes and various top-down mechanisms that modulate the processing of visual information.

In the present study, we tried to reveal the brain organization of the sensory-specific and regulatory components of the global and local recognition under the condition of directed attention. To that end, we analyzed different components of ERP confined to various sensory and associative cortices.

METHODS

Twelve healthy adult subjects (eight men and four women) participated in the study. They were right-handed (according to self-reports) and had normal or corrected to normal vision. All subjects gave their informed consent to participate in this study. After the preliminary EEG analysis, the data of only ten subjects aged from 20 to 36 (seven men and three women) were subjected to further analyses.

The experiment was designed and conducted using the EEGExProc software (written by S.D. Dyachenko). The EEG was recorded with Neurotravel 24 D COM computer electroencephalograph (ATES MEDICA, Russia). The stimuli were presented with 15-inch CRT display with 75 Hz frame rate (Samatron 55E). The subject responses were recorded using the joystick buttons (Genius, Usb-07).

The test stimuli shown on the screen were the hierarchically organized large capital letters H, E, and O each consisting of small capital letters arranged in a 5×5 matrix [15] (Fig. 1). The size of a large letter (the global aspect of the stimulus) was 2.5×3.5 angular degrees horizontally and vertically, respectively. The size of a small letter (the local aspect of the stimulus) was 0.35×0.5 angular degrees. According to the published data, these sizes were optimal for the precedence of the global level [3]. The H and E letters were target stimuli: the subjects were asked to determine which of these two letters appeared on the global or local level. In the course of the experiment, three types of hierarchical stimuli were presented in the central visual field: incongruent (Fig. 1, 1), congruent (Fig. 1, 2), and neutral, the latter containing O element on either level (Fig. 1, 3). In order to fixate the subjects' gaze, a small cross of 0.35×0.5 angular degrees was shown at the center of the screen over entire experiment. The cross disappeared whenever a relevant stimulus appeared. Although, according to Navon's original experimental design, the hierarchical stimuli were shown in different quadrants of the screen, we used a central presentation with a fixation cross instead. This was done in order to reduce the eye movement-related artifacts in EEG recordings. The

effect of global precedence is preserved under these experimental conditions as was shown by our previous behavioral study [16] and the results of other authors [11, 15].

The arrows of 1.3×1.7 angular degrees served as warning stimuli (Figs. 1, 4 and 5) [15]. The direction of the arrow indicated at which level (global or local) the test stimulus should be recognized. The half of the subjects pressed one of the two response buttons with their right index finger when recognized target letter "H" and the other response button with right middle finger when recognized target letter "E". The other half of the subjects used the inverse mapping between the fingers and target letters.

The subjects performed the task while sitting in a comfortable chair (with viewing distance of 1 m) in a dark shielded chamber. The experimental session consisted of a series of 120 trials. The hierarchical stimuli of each type (incongruent, congruent, and neutral) were presented 40 times (20 trials for each global and local level). The type of the test stimulus and the required level of recognition alternated in a pseudorandom order. At the beginning of each trial, the fixation cross was shown in the central visual field for a time varying from 750 to 1250 ms. It was replaced by a warning stimulus exposed for 120 ms. Then, the fixation cross reappeared on the screen and remained there for 3000 to 3500 ms following by a test stimulus with 80 ms exposure time. According to the given instruction, a subject had to decide which of the two letters, H or E, were shown on the level indicated by a warning signal (global or local) and then press the appropriate response button. The subjects were asked to perform this task as quickly as possible without errors.

The EEG was recorded continuously during each trial at a sampling rate of 250 Hz within a frequency range of 0.1–70 Hz. EEG was recorded from the following leads: frontal ($F: F_3, F_4, F_z$), frontal inferior ($Fi: F_7, F_8$), temporal anterior ($Ta: T_3, T_4$), temporal posterior ($Tp: T_5, T_6$), central ($C: C_3, C_4, C_z$), parietal ($P: P_3, P_4, P_z$), and occipital ($O: O_1, O_2$) using a digitally linked mastoids as a reference. Electrode placement corresponded to the international 10–20 system. The eye movement artifacts were monitored by recording the electrical activity from two frontal pole electrodes (Fp_1, Fp_2). Artifact-free EEG segments that included 300 ms prestimulus and 1000 ms poststimulus periods were averaged individually for each subject, each EEG channel, and each of 6 experimental conditions: (local, global) $\times$ (congruent, incongruent, and neutral). The amplitudes of successive positive and negative target-related ERP components were analyzed. In order to find out the time boundaries of the ERP components we used a superposition of subjects' individual ERP curves. Since the component boundaries are location-specific, the curves were superimposed separately for each lead. The ERP components were enumerated according the order of their appearance which is one of the standard methods [17]. The time boundaries of ana-

Fig. 1. Different types of hierarchical visual stimuli. Test stimuli: 1, incongruent; 2, congruent; 3, neutral. Warning stimuli: 4, attention is drawn to the global aspect of the hierarchical letter; 5, attention is drawn to the local aspect of the hierarchical letter.

lyzed components were as follows (in ms): P1, 60–110; N1, 100–180; P2, 180–270; N2, 240–320; P3, 320–450 in the occipital and temporal posterior leads; P1, 50–90; N1, 80–130; P2, 120–250; N2, 185–270; P3, 270–380 in the frontal, central, temporal, and parietal leads. An amplitude of each component (positive or negative) was measured as a local ERP waveform extremum (maximum or minimum) within the component-specific boundaries. The mean over the prestimulus period voltage level served as a reference. The impact of experimental conditions onto the amplitudes of ERP components was studied with RM ANOVA (Greenhouse–Geisser corrected). In pairwise comparisons, the Bonferroni correction was used. The statistical relationships between ERP and behavioral parameters were estimated with Pearson's correlation coefficient.

RESULTS

Behavioral Study

In order to assess the effect of the experimental conditions on the accuracy (percentage of correct responses) and the recognition speed (the inverse of reaction time, RT) of a hierarchical stimulus, we used a multivariate analysis of variance (MANOVA) where CONDITION (global, local) and STIMULUS (congruent, incongruent, or neutral) were the within-subject factors. Table 1 shows the mean values of the behavioral parameters and their standard deviations.

The MANOVA showed that the time of correct recognitions of a hierarchical letter (RT) depended on CONDITION ($F(1, 9) = 8.755, p = 0.016$) and STIMULUS ($F(2, 8) = 8.608, p = 0.010$). The interaction of these factors ($F(2, 8) = 5.290, p = 0.034$) was also significant. The mean RT was significantly higher during recognition of a small letter as compared to a large letter. As

Table 1. Mean values and standard deviations of behavioral indices for a hierarchical letter recognition

Condition	Stimulus	RT, ms		Accuracy, %		N
		Mean	SD	Mean	SD	
Global level recognition	congruent	943.86	149.62	97	3.49	10
	incongruent	1011.06	159.62	94	6.15	10
	neutral	957.06	233.82	96	3.94	10
Local level recognition	congruent	1037.20	227.41	95	7.24	10
	incongruent	1160.20	210.15	89	7.37	10
	neutral	979.51	230.93	98	3.49	10

compared to congruent stimuli, the incongruent stimuli were recognized longer at both global and local levels. Pairwise comparison showed that the STIMULUS-related differences in RT were significant for the small letter recognition only: the recognition time for incongruent stimulus was longer than for both congruent ($p = 0.013$) and neutral ($p = 0.005$) stimuli. The accuracy of recognition of the target stimulus was affected significantly only by STIMULUS ($F(2, 8) = 8.751, p = 0.01$): the incongruent stimuli were recognized less accurately than the congruent or neutral stimuli ($p = 0.01$ and $p = 0.01$, respectively).

Since the data reported above showed the presence of the global level interference effect in our subjects, we considered the whole group as a representative sample for further studying the specifics of brain organization of global and local perception.

ERP Analysis

As a first step, the RM ANOVA of the ERP amplitude was performed with the following within-subject factors: ERP COMPONENT (P1, N1, P2, N2, P3); CONDITION (global, local), STIMULUS (congruent, incongruent, and neutral), and LOCATION (17 levels according to the number of EEG channels).

Testing for the within-subject effects that involve ERP COMPONENT (Table 2) revealed different reactivity of ERP components to a change in the level of hierarchical letter recognition and showed a regional specificity in changes of various ERP components depending on the recognition level and stimulus type. These results allowed us for applying RM ANOVA analyses separately for each ERP component.

Each of the ERP components was subjected to ANOVA with CONDITIONS, STIMULUS, and LOCATION (O, P, C, F, Fi, Ta , and Tp) as within-sub-

ject factors. The HEMISPHERE (left, right) factor was also included into RM ANOVA in order to test for the potential interhemispheric differences. The within-subject effects for all analyzed ERP components are shown in Table 3.

Analysis of the amplitude of early positive *component P1* pointed to its regional specificity (LOCATION factor): P1 component was most pronounced in the caudal regions of both hemispheres under various experimental conditions (Fig. 2). In all the studied experimental conditions, the P1 amplitude was higher in the right hemisphere than in the left one (HEMISPHERE factor). No other significant main effects concerning the P1 amplitude were found. Although CONDITION and STIMULUS factors did interact, the pairwise comparisons revealed no significant differences.

P1 component showed different reactivity to a change in CONDITION and STIMULUS depending on the cortical location and hemisphere (Fig. 2).

An analysis of STIMULUS $\times$ LOCATION interaction showed a pronounced regional specificity of the early ERP positive component during recognition of an incongruent stimulus ($F(1.9, 17.2) = 10.707, p = 0.001$) with most of the activation found over occipital and inferior temporal cortices. It was found that P1 amplitude was higher in the occipital areas than in the frontal inferior areas ($O > Fi: p = 0.050$). Also, P1 amplitude in inferior temporal cortices was higher than in the frontal ($Tp > F: p = 0.043$) and temporal anterior regions ($Tp > Ta: p = 0.008$).

An analysis of CONDITIONS $\times$ STIMULUS $\times$ LOCATION interaction revealed that, during recognition of the stimulus global aspect, statistically significant regional differences in the P1 amplitude were only observed in the case of the neutral stimulus ($F(1.8, 15.9) = 10.551, p = 0.002$). In the latter experimental situation, the maximum P1 amplitude was

Fig. 2. At the top of the figure shown is the mean amplitude of P1 ERP component (in μV) during recognition of the global (I, III) and local (II, IV) aspects of the hierarchical stimulus in the left (I, II) and right (III, IV) hemisphere regions for congruent (1), incongruent (2), and neutral (3) stimuli. The vertical lines above each column correspond to the standard error of the mean (SEM). At the bottom of the figure: shown is the average ERP in the temporal posterior lead of the left (T_5) and right (T_6) hemispheres during recognition of the global (V) and local (VI) aspects of the hierarchical stimulus. The dotted, solid, and dashed lines correspond to congruent, incongruent, and neutral stimulus respectively.

Table 2. RM ANOVA results: tests of within-subjects effects that involve ERP COMPONENT factor (Greenhouse–Geisser corrected)

Within-subject factors	<i>df</i> 1	<i>df</i> 2	<i>F</i>	<i>Sig.</i>
CONDITION × ERP COMPONENT	2.735	24.614	3.667	0.029
STIMULUS × ERP COMPONENT	3.898	35.082	1.491	0.227
LOCATION × ERP COMPONENT	3.382	30.439	7.734	0.000
CONDITION × STIMULUS × ERP COMPONENT	3.489	31.401	2.091	0.113
CONDITION × LOCATION × ERP COMPONENT	6.444	57.996	1.559	0.171
STIMULUS × LOCATION × ERP COMPONENT	7.709	69.384	1.962	0.067
CONDITION × STIMULUS × LOCATION × ERP COMPONENT	7.547	67.926	2.284	0.034

observed in the occipital leads (*O*). In case of recognition of the local aspect of a stimulus, the regional differences in P1 amplitude were found for the incongruent ($F(2.4, 21.3) = 10.474, p < .001$) and neutral ($F(2.7, 24.3) = 6.967, p = 0.02$) stimuli. The maximum of P1 amplitude was observed in the occipital leads (*O*) when the neutral stimulus was presented. When the incongruent stimulus was shown, P1 amplitude reached its maximal value in the temporal posterior leads (*TP*). During recognition of the local aspect, the P1 amplitude in the temporal posterior leads depended significantly on the stimulus type ($F(1.6, 14.5) = 4.393, p = 0.039$) and reached its maximum for the incongruent stimulus ($p = 0.010$) when compared to the neutral stimulus. In the very same leads, the P1 amplitude tended to be higher ($F(1, 9) = 3.242, p = 0.065$) during recognition of the local aspect of incongruent stimulus than during recognition of the global aspect.

The interhemispheric asymmetry in P1 amplitude (higher values were observed in the right hemisphere) was most pronounced during recognition of a small letter belonging to an incongruent stimulus ($F(1, 9) = 19.451, p = 0.002$), which was reflected in a significant CONDITION × STIMULUS × HEMISPHERE interaction. A significant right-hemispheric asymmetry was found in the temporal posterior leads ($T_6 > T_5; p = 0.038$). In addition, the P1 amplitude in the right inferior temporal area was significantly higher during recognition of the local aspect of an incongruent stimulus than during recognition of the global aspect ($p = 0.029$). The changes in the early positive ERP component in the T_6 lead caused by experimental condition variations are shown in Fig. 2 (V, VI).

Testing for the within-subject effect with the CONDITIONS × STIMULUS × LOCATION (P_z, C_z, F_z) factorial design limited to the sagittal leads only showed a significant 3-way interaction ($F(2.9, 26.5) = 4.391, p = 0.013$). Analysis of this interaction demonstrated a significant influence of the factor STIMULUS on the P1 amplitude in the sagittal parietal area during recognition of the local aspect of a stimulus ($P_z: F(1.5, 13.2) = 5.996, p = 0.020$). In the local condition, the P1 amplitude was higher for incongruent than for neutral stimuli ($p = 0.01$). As in the inferior temporal area of the right

hemisphere (T_6), the P1 amplitude was higher for local than for global recognition ($p = 0.029$) in P_z lead.

Thus, the most pronounced amplitude differences in the early positive ERP component, which were related to the level of the recognition of a hierarchical stimulus, were found for incongruent stimulus in the sagittal parietal (P_z) and temporal posterior (TP) leads: in P_z and T_6 , the P1 amplitude for incongruent stimuli was higher when the target signal was shown at the local level; in addition, the amplitude was higher in the right than in the left inferior temporal area.

In order to clarify a functional role of neurophysiological mechanisms underlying P1 component generation it is worth to make a comparison between P1 amplitude and behavioral indices of the task performance efficiency. To that end, we computed correlation coefficients between the RT and response accuracy on the one hand and P1 amplitude on the other. The correlation pattern was analyzed separately for each EEG channel and each experimental condition. A significant positive correlation between P1 amplitude and the accuracy was found in the parietal sagittal lead ($P_z: r = 0.745; p = 0.021$) for recognition of the global aspect of a neutral stimulus, in the left occipital lead ($O_1: r = 0.729; p = 0.025$) for recognition of the local aspect of a neutral stimulus, and in the left frontal inferior ($F_7: R = 0.773; p = 0.014$) as well as the right temporal posterior ($T_6: r = 0.720; p = 0.028$) leads for recognition of the local aspect of an incongruent stimulus. The latter finding confirms the functional significance of P1 changes in the T_6 revealed by the ANOVA. No significant negative correlations were found between the accuracy and the P1 amplitude.

The correlation pattern for RT vs. P1 amplitude turned out to be less clear: the correlation sign varied with the lead location. In the caudal regions, mostly negative correlations (the higher the P1 amplitude, the lower the RT) were observed. Significant correlations were detected in the left occipital lead ($O_1: r = -0.782; p = 0.012$) during recognition of the local aspect of a neutral stimulus. The similar correlation was found in the parietal sagittal lead ($P_z: r = -0.687; p = 0.053$) during recognition of the local aspect but this time of an incongruent stimulus. As we already mentioned above,

ERP components

Within-subjects factors	P1				N1				P2				N2				P3			
	<i>df</i> 1	<i>df</i> 2	<i>F</i>	<i>p</i>	<i>df</i> 1	<i>df</i> 2	<i>F</i>	<i>p</i>	<i>df</i> 1	<i>df</i> 2	<i>F</i>	<i>p</i>	<i>df</i> 1	<i>df</i> 2	<i>F</i>	<i>p</i>	<i>df</i> 1	<i>df</i> 2	<i>F</i>	<i>p</i>
CONDITION					1	9	2.921	0.91									1	9	6.884	0.028
STIMULUS																				
HEMISPHERE	1	9	4.476	0.063													1	9	6.537	0.031
LOCATION	1.62	14.58	10.905	0.000					2.2	20.2	11.940	0.000	2.54	22.9	8.694	0.001	1.7	15.8	11.934	0.001
CONDITION × STIMULUS	1.71	15.37	5.233	0.022	1.9	17.8	3.579	0.049					1.78	16.1	13.693	0.000				
CONDITION × HEMISPHERE																				
CONDITION × LOCATION									3.2	28.7	7.852	0.000	2.87	25.82	2.926	0.054				
STIMULUS × HEMISPHERE																				
STIMULUS × LOCATION	3.77	33.89	3.465	0.019					4.3	38.6	5.020	0.000	4.64	41.81	5.890	0.000				
HEMISPHERE × LOCATION									1.8	16.0	2.759	0.098								
CONDITION × STIMULUS × HEMISPHERE	1.84	16.59	3.782	0.047					1.5	13.5	3.074	0.090	1.42	12.81	4.660	0.040				
CONDITION × STIMULUS × LOCATION	2.52	22.67	2.598	0.086					4.5	36.5	2.202	0.087								
CONDITION × HEMISPHERE × LOCATION									4.1	36.9	3.082	0.027	3.44	30.98	4.903	0.005	3.40	30.59	3.778	0.017
STIMULUS × HEMISPHERE × LOCATION									4.6	41.2	2.594	0.044								
CONDITION × STIMULUS × HEMISPHERE × LOCATION									4.3	38.9	4.274	0.005								

for P_z , the maximum of P1 amplitude was attained for the local aspect of incongruent stimulus. In contrast, positive correlations (the RT increased with increasing P1 amplitude) predominated over the frontal regions: significant positive correlations were found for frontal ERPs and corresponding RTs when a small letter belonging to a congruent stimulus had to be recognized (F_z : $r = 0.686$; $p = 0.041$ and F_4 : $r = 0.682$; $p = 0.042$).

Thus, the above correlation analysis suggests the existence of a link between the amplitude of P1 component in the visual cortex, on the one hand, and the effectiveness of the recognition of a hierarchical stimulus, on the other. In general, when compared to all the other experimental cross-conditions, the early stage of the incongruent stimulus recognition at the local level is characterized by more pronounced activation of the parietal sagittal and inferior temporal regions of the right hemisphere.

The results of the RM ANOVA for *N1 negativity* (Table 3) showed a significant effect of CONDITION factor—N1 component was more pronounced during recognition of a target stimulus at the global ($-2.8 \pm 0.17 \mu V$) than local level ($-2.1 \pm 0.4 \mu V$)—and a significant CONDITION $\times$ STIMULUS interaction. Analysis of this interaction showed that, for a neutral stimulus, the N1 amplitude was significantly higher ($F(1, 9) = 8.066$, $p = 0.019$) when the target stimulus was at the global than local level (-2.9 ± 0.34 and -1.5 ± 0.52 , respectively). There were no significant condition-related differences for other stimulus types.

The N1 amplitude in sagittal leads (P_z , C_z , and F_z) did not depend significantly on any experimental factor. Since LOCATION factor did not exert any influence on the N1 amplitude, we did not analyze the regional specifics of the reactivity of this component.

In the caudal cortical regions, the N1 amplitude correlated positively with RT. When the global aspect of a hierarchical letter was recognized during presentation of a congruent stimulus, a significant correlation was found for the right temporal posterior lead (T_6 : $r = 0.662$, $p = 0.037$) while during presentation of an incongruent stimulus, a significant correlation was found in the left temporal posterior lead (T_5 : $r = 0.639$, $p = 0.047$). During recognition of the local aspect of the congruent stimulus, a positive correlation was found in the right occipital lead (O_2 : $r = 0.677$, $p = 0.031$).

The N1 amplitude in the frontal cortical regions correlated negatively with RT. Significant negative correlations were found in the left frontal (F_3 : $r = -0.638$, $p = 0.048$) and sagittal frontal (F_z : $r = -0.639$, $p = 0.048$) leads when incongruent stimulus was shown and the target aspect was global. No significant correlations between N1 amplitude and accuracy were found.

Thus, the above analysis of N1 reactivity showed that this component was most pronounced during recognition of the global aspect of a hierarchical letter, especially in case of the neutral stimulus. We did not find a uniformly signed correlations between N1 amplitude

and RT across different cortical areas. An involvement of the frontal regions at this stage of information processing resulted in the performance improvement especially during the recognition of the incongruent stimulus at the global level, while ERP negatation in the caudal regions resulted in RT increase.

The results of RM ANOVA for *P2 component* are shown in Table 3. Figure 3 demonstrates how P2 amplitude varies under different experimental conditions in various cortical areas. Pronounced regional differences in this component were observed in all experimental conditions (LOCATION) with the maximum of P2 amplitude attained in the frontal areas. In all experimental conditions, there was also a significant right-hemispheric asymmetry of the P2 amplitude (higher values in the right hemisphere) in the parietal area ($P_4 > P_3$; $F(1, 9) = 7.173$, $p = 0.025$). The observed asymmetry reflects itself in a significant HEMISPHERE $\times$ LOCATION interaction.

In the central and frontal areas, the P2 amplitude was higher during stimulus recognition at the global than local level (CONDITION $\times$ LOCATION interaction, C : $F(1, 9) = 9.704$, $p = 0.012$; F : $F(1, 9) = 9.774$, $p = 0.012$). Significant differences between the global and local recognition were found in the central and frontal leads of the right hemisphere only (CONDITION $\times$ HEMISPHERE $\times$ LOCATION interaction, C_4 : $F(1, 9) = 22.934$, $p = 0.001$; F_4 : $F(1, 9) = 11.885$, $p = 0.007$). Figure 3 (V and VI) demonstrates different reactivity of this ERP component in the frontal regions during recognition of the global and local aspects of a stimulus.

The recognition of a local vs. global aspect of a hierarchical letter resulted in the different P2 reactivity in the right and left hemispheres, and this difference, in turn, depended on the stimulus type (CONDITION $\times$ STIMULUS $\times$ HEMISPHERE interaction). The inter-hemispheric asymmetry, i.e. the higher amplitude in the right hemisphere, was observed during recognition of the local aspect of an incongruent stimulus ($F(1, 9) = 5.417$, $p = 0.045$).

Analysis of CONDITION $\times$ STIMULUS $\times$ LOCATION and CONDITION $\times$ STIMULUS $\times$ LOCATION $\times$ HEMISPHERE interactions showed that, when a hierarchical stimulus was recognized at the global level, the significant stimulus-related differences in the P2 amplitude were found in the parietal regions (P : $F(1.5, 13.7) = 4.789$, $p = 0.034$): the maximal amplitude of this component was observed for the incongruent stimulus while the minimal amplitude corresponded to the neutral stimuli ($p = 0.006$). The right hemispheric asymmetry of the P2 amplitude was observed in the parietal regions during recognition of the global aspect of both the incongruent and congruent stimuli: ($P_4 > P_3$: $F(1, 9) = 13.086$, $p = 0.006$ and $P_4 > P_3$: $F(1, 9) = 14.731$, $p = 0.002$, respectively). In addition, in the parietal and inferior temporal areas of the right hemisphere, the opposite changes in the P2 amplitude were found for the two levels of recognition of incongruent stimulus: during recognition of the global level, the amplitude

Fig. 3. At the top of the figure shown is the mean amplitude of P2 ERP component (in μV) during recognition of the global (I, II) and local (III, IV) aspects of the hierarchical stimulus in the left (I, II) and right (III, IV) hemisphere regions for congruent (1), incongruent (2), and neutral (3) stimuli. The vertical lines above each column correspond to the standard error of the mean (SEM). At the bottom of the figure shown is the average ERP in the frontal lead of the left (F_3) and right (F_4) hemispheres during recognition of the global (V) and local (VI) aspects of the hierarchical stimulus. Notations are as in Fig. 2.

of this component was higher in the parietal lead (P_4 : $p = 0.003$) whereas during recognition of the local level, the same parameter was higher in the temporal posterior lead (T_6 : $p = 0.029$). During local recognition, the P2 amplitude tended to be higher in the temporal posterior lead of the right hemisphere than in the symmetrical lead of the left hemisphere ($T_6 > T_5$: $F(1, 9) = 4.526$, $p = 0.062$).

The results of RM ANOVA for the sagittal leads (P_z , C_z , F_z) indicate that the P2 amplitude was higher during the recognition of letters at the global than local level. However, the only significant pairwise differences were found for the frontal cortex (F_z : $F(1, 9) = 6.674$, $p = 0.03$). Therefore, the influence of CONDITION factor varies depending on the ERP scalp location leading to the significant CONDITION $\times$ LOCATION interaction ($F(1.4, 12.9) = 4.769$, $p = 0.038$).

Thus, in general, the amplitude of the P2 component reached its maximum over the anterior associative regions. In the very same cortical areas, the P2 amplitude was higher during recognition of the global than local aspect of a stimulus, this effect being stronger in the right hemisphere. It is worth mentioning the specifics of involvement of the right visual associative cortices into the processing the incongruent stimulus at the global vs. local level: the parietal area (P_4) showed greater activation during the recognition of the global aspect, whereas the inferior temporal area (T_6) was stronger activated during the recognition of the stimulus local aspect. Similar condition-related difference was observed in the right inferior temporal area for P1 positivity.

Linear correlation analysis revealed significant positive correlations between P2 amplitude in the frontal regions of the right hemisphere and the recognition accuracy of the global aspect of the congruent stimulus (C_4 : $r = 0.670$, $p = 0.048$; F_4 : $r = 0.682$, $p = 0.043$; F_8 : $r = 0.691$, $p = 0.048$). Note that, it is those regions where the P2 reactivity was more pronounced during recognition of the global aspect of the congruent stimulus than in the other cortical areas (Fig. 3 (V)). During recognition of the global aspect of incongruent stimuli, the P2 amplitude negatively correlated with the accuracy. Significant negative correlations were found in the central and frontal cortical regions (C_4 : $r = -0.759$, $p = 0.018$; C_z : $r = -0.676$, $p = 0.046$; F_3 : $r = -0.679$, $p = 0.040$; F_4 : $r = -0.849$, $p = 0.004$; F_z : $r = -0.767$, $p = 0.016$; F_7 : $r = -0.690$, $p = 0.040$; F_8 : $r = -0.886$, $p = 0.001$). Similar negative correlations were also found between the P2 amplitude and the accuracy of the recognition of the global aspect of the neutral stimuli (C_3 : $r = -0.774$, $p = 0.014$; F_3 : $r = -0.801$, $p = 0.009$; F_4 : $r = -0.816$, $p = 0.007$; F_z : $r = -0.738$, $p = 0.023$; F_7 : $r = -0.762$, $p = 0.017$; F_8 : $r = -0.708$, $p = 0.033$; T_4 : $r = -0.678$, $p = 0.045$).

The accuracy of the recognition of the local aspect of a congruent stimulus correlated positively with P2 amplitude in the right caudal regions (O_5 : $r = 0.764$, $p = 0.017$; T_6 : $r = 0.632$, $p = 0.068$). No significant correla-

tion was found between the P2 amplitude and the accuracy of the recognition of the local aspect of incongruent and neutral stimuli.

The P2 amplitude in the right parietal area correlated negatively with the RT during recognition of the global aspect of a congruent stimulus (P_4 : $r = -0.684$, $p = 0.047$). Note that, in this cortical region, the stimulus-related P2 reactivity was most pronounced with maximal P2 amplitude during recognition of the global aspect of the congruent stimulus. A negative correlation was also found between P2 amplitude and RT during recognition of the local aspect of the congruent stimulus: significant correlations were found for the occipital and temporal anterior leads in the right hemisphere (O_2 : $r = -0.652$, $p = 0.047$; T_4 : $r = -0.689$, $p = 0.040$) as well as for the parietal sagittal area (P_z : $r = -0.684$, $p = 0.042$). Significant negative correlations were also found between P2 amplitude and RT for incongruent stimuli: in the occipital areas of both hemispheres and the left temporal posterior area during global recognition (O_1 : $r = -0.699$, $p = 0.036$; O_2 : $r = -0.691$, $p = 0.044$; T_5 : $r = -0.655$, $p = 0.046$), in the occipital regions of both hemispheres during local recognition (O_1 : $r = -0.701$, $p = 0.035$; O_2 : $r = -0.779$, $p = 0.023$).

Under all experimental conditions N2 component usually resided on top of a large positivity and did not leave the "positive zone" when measured against the reference computed over the prestimulus period. Because of that, in order to assess the impact of experimental conditions onto N2 component, we measured the relative amplitude. The latter was computed as the difference between the maximal and minimal ERP values found within the time boundaries of N2 component (see Method).

Table 3 shows the results of the statistical analysis of the N2 relative amplitude and Fig. 4 shows its mean value for different EEG leads and various experimental conditions. The dependence of the N2 relative amplitude on the cortical location (LOCATION factor) was observed under all experimental conditions: it was most pronounced in the frontal and central regions and less pronounced in the temporal regions. At the same time, the N2 amplitude depended not only on the location but also on the level of recognition of a hierarchical stimulus (CONDITION $\times$ LOCATION interaction). During recognition of the large letter, N2 amplitude was maximal in the central cortical regions while during recognition of the small letter the N2 amplitude reached its maximum in the frontal regions. Besides, during global recognition N2 amplitude attained maximal value in the central area of the left hemisphere only, whereas during local recognition a relative peak in N2 amplitude was observed in the frontal region of the right hemisphere (CONDITION $\times$ HEMISPHERE $\times$ LOCATION interaction). In the right frontal region, the N2 amplitude tended to be higher during recognition of the local than global aspect of the stimulus (F_4 : $F(1, 9) = 3.192$, $p = 0.063$). Figure 4 (V, VI) illustrates the frontal N2 reactivity during global and local recog-

Fig. 4. Mean value of relative amplitude of the N2 ERP component (in μV) during recognition of the global (I, II) and local (III, IV) aspects of the hierarchical stimulus in the left (I, II) and right (III, IV) hemisphere regions for congruent (1), incongruent (2), and neutral (3) stimuli. The vertical lines above each column correspond to the standard error of the mean (SEM). Notations are as in Fig. 2.

dition. The amplitude of N2 component in different cortical areas depended differently on the stimulus type (STIMULUS $\times$ LOCATION interaction). In the parietal areas, the maximum of N2 amplitude was found for the congruent stimuli; this value was significantly higher than N2 amplitudes for either the incongruent ($p = 0.014$) or the neutral stimuli ($p = 0.044$). In the frontal regions, no significant stimulus-related differences in N2 amplitude were found. In the central regions, the N2 component was significantly higher for the neutral stimulus as compared to the congruent or incongruent stimuli ($p = 0.03$ and $p = 0.032$, respectively).

Thus, the analysis of regional reactivity of N2 showed the predominant involvement of the right frontal cortex when hierarchical stimuli were recognized at the local level. The amplitude of N2 in the central cortical regions took the highest value for the neutral stimulus for both global and local levels of recognition with higher N2 amplitude during global recognition. The latter effect was most pronounced in the left hemisphere. The maximal involvement of parietal areas was observed for congruent stimuli irrespective of the level of recognition.

The analysis of CONDITION $\times$ STIMULUS interaction showed that the N2 amplitude reached its maximum during the recognition of the global level of the neutral stimulus with N2 amplitude being significantly higher for neutral stimuli than congruent or incongruent stimuli ($p = 0.002$, $p = 0.024$, respectively). During recognition of a small letter, the stimulus-related differences in N2 amplitude were found for the right hemisphere only. In the right hemisphere, the maximum of N2 amplitude was found for congruent stimuli: this value was significantly higher for the congruent than the neutral stimuli ($p = 0.020$), and it tended to be higher for the congruent than for incongruent stimuli ($p = 0.069$). The hemispheric specificity in N2 reactivity to experimental condition and stimulus type reflected in a significant CONDITION $\times$ STIMULUS $\times$ HEMISPHERE interaction.

The analysis of N2 reactivity in the sagittal leads revealed no significant differences.

The negative correlations between the N2 amplitude and the recognition time for a large letter were found for the centro-parietal regions of the left hemisphere and sagittal areas: in P_3 ($r = -0.800$, $p = 0.01$), P_z ($r = -0.771$, $p = 0.015$) and C_3 ($r = -0.757$, $p = 0.018$) dur-

ing recognition of the global aspect of the congruent stimulus; in P_3 ($r = -0.667$, $p = 0.050$), P_z ($r = -0.787$, $p = 0.012$), and C_3 ($r = -0.702$, $p = 0.035$) during recognition of the global aspect of incongruent stimulus; in P_3 ($r = -0.792$, $p = 0.011$), C_3 ($r = -0.644$, $p = 0.061$), and in T_3 ($r = -0.702$, $p = 0.035$) during recognition of the global aspect of neutral stimulus. When a small letter was recognized, similar negative correlations between N2 and RT were found for the congruent stimulus in the central area of the left hemisphere (C_3 : $r = -0.691$, $p = 0.039$).

The functional link between N2 component and performance effectiveness resulted in positive correlation between N2 amplitude and the accuracy with the statistically significant correlations found in two cases: first, for the left central lead during recognition of a large letter within the incongruent stimulus (C_3 : $r = 0.698$, $p = 0.049$) and, second, for the right temporal posterior lead during recognition of a small letter within the incongruent stimulus (T_6 : $r = 0.865$, $p = 0.003$).

It is worth of notice that positive correlations between N2 amplitude and recognition accuracy were observed for centro-parietal areas of the left hemisphere under almost all experimental conditions whereas the same N2 vs. accuracy correlation for the right temporal posterior lead (T_6) was found only during recognition of the local aspect of an incongruent stimulus. Note that, in the inferior temporal area of the right hemisphere, the other ERP components (P1, P2) also correlated in a specific way with the recognition of local aspect of the incongruent stimulus.

Thus, although the N2 amplitude followed a similar topographical pattern across all experimental conditions being most pronounced over central and frontal cortices, still it was characterized by some region-related specifics in its reaction to experimental cross-conditions. It is noteworthy that the relatively high N2 amplitude is reached in the central area of the left hemisphere and that the N2 amplitude in this area correlated positively with the motor response speed under all experimental conditions.

The results of ANOVA for the *P3 component* are shown in Table 3. The amplitude of this ERP component was characterized by pronounced regional differences similar across all experimental conditions (the main effect of LOCATION factor). The maximum of P3 amplitude was reached in the parietal leads (P : 13.683 ± 1.052 μ V) where it was significantly higher than in the occipital (O : 7.712 ± 1.014 μ V; $P > O$, $p = 0.002$), temporal anterior (Ta : 8.262 ± 0.486 μ V, $P > Ta$, $p = 0.005$), and temporal posterior (Tp : 4.860 ± 0.675 μ V, $P > Tp$, $p < 0.001$) leads. The asymmetry of this ERP component was observed for all cortical areas (the main effect of HEMISPHERE factor): P3 amplitude was higher in the right (9.737 ± 0.364 μ V) than left (9.013 ± 0.252 μ V) hemisphere. Generally, the P3 amplitude was higher during recognition of a large (9.843 ± 0.341 μ V) than small (9.149 ± 0.661 μ V) letter (the main effect of CONDITION factor). Most pronounced CONDI-

TION-related differences in P3 amplitude were observed in the right parietal region (P_4 : $F(1, 9) = 5.488$, $p = 0.043$), which was reflected in a significant CONDITION $\times$ HEMISPHERE $\times$ LOCATION interaction. The stimulus type did not have any impact onto P3 amplitude: neither main effect of the factor nor its interactions with any other factors were found.

Some significant statistical relationships between P3 amplitude and the recognition accuracy were found only for global recognition. We found significant positive P3 amplitude vs. accuracy correlations in the central and frontal cortical areas during recognition of the global aspect of a congruent stimulus (C_4 : $r = 0.762$, $p = 0.017$; C_z : $r = 0.890$, $p = 0.001$; F_3 : $r = 0.869$, $p = 0.003$; F_4 : $r = 0.820$, $p = 0.007$; F_z : $r = 0.766$, $p = 0.016$; F_7 : $r = 0.726$, $p = 0.027$; F_8 : $r = 0.857$, $p = 0.003$). Significant negative correlations were found in the same brain regions during recognition of the global aspect of an incongruent stimulus (F_3 : $r = -0.678$, $p = 0.045$; F_z : $r = -0.761$, $p = 0.017$; F_8 : $r = -0.743$, $p = 0.002$). We did not find any other significant correlations between the P3 amplitude and the behavioral indices.

DISCUSSION

The results of the present work show that, during recognition of the hierarchical visual stimuli at the global and local levels, the evoked brain electrical activity (EA) is characterized by a certain temporal and topographical specificity.

Condition-related alterations of ERP could be detected at relatively early stages of information processing. We found more pronounced reactivity of the P1 component in visual associative areas during recognition of a hierarchical stimulus at the local vs. global level, it was especially salient for the incongruent stimuli. An increase in P1 amplitude, when attention is drawn to the local level of the hierarchical stimulus, was also reported by other researchers [6, 14, 18]. However, some studies show either an opposite effect of the recognizing level onto P1 amplitude, i.e. a higher amplitude during stimulus recognition at the global than local level [19], or a lack of any impact of the level of recognition on the P1 amplitude [11, 20]. The differences in the P1 amplitude that we found, i.e., the higher amplitudes during recognition of incongruent stimuli at the local level, were significant in P_z and T_6 leads located over the dorsal parietal (Brodmann's areas 7) and the inferior temporal (Brodmann's areas 37) cortices, respectively [21]. The functional significance of such ERP differences is confirmed by the fact that, for the local aspect of an incongruent stimulus, the P1 amplitude positively correlated with the recognition speed for P_z and recognition accuracy for T_6 . It is shown that P1 positivity reflects a selective attention-related increase in the neuronal activity in the sensory-specific visual areas [22]. The P1 positivity is thought to be generated by the sources located in the dorsal parietal and/or inferior temporal cortices [23]. The dorsal pari-

etal cortex is primarily involved in the processing of the spatial features of the external signals and is a part of the visual-spatial attention system [24–27], whereas the inferior temporal cortex, being a part of the ventral visual system, participates mainly in object perception [13, 27]. Our results suggest a stronger involvement of inferior temporal cortex in the recognition of the hierarchical incongruent stimuli at the local level. That allows for the two important conclusions to be drawn about the brain organization of the local level recognition. First, the recognition of details requires more intensive information processing at the initial stage of sensory analysis than does the identification of the stimulus as a whole. Second, at this stage of analysis, the recognition of details is based on the extraction of spatial (dorsal visual systems) along with object (ventral visual systems) features of a stimulus. The increase in the amplitude of the P1 component in the associative visual areas may reflect the participation of the recurrent neuronal circuits in the early sensory-specific analysis of stimuli at the local level. According to the Reverse Hierarchy Theory of visual perception [28], the associative cortex exerts top-down influence onto the activity of sensory-specific projection areas to ensure a more precise selection and processing of relevant features. It has been shown [28, 29] that backward visual masking reduces the efficiency of the recognition of a hierarchical stimulus at the local but not the global level. The authors of [28, 29] attributed this effect to the involvement of the feedforward hierarchy in the case of the global features processing and of the feedback (or reverse) hierarchy in the case of the processing of the local features.

The N1 ERP component reflects the processes of visual sensory discrimination [21, 23, 30, 31]. According to the results of the present work, the N1 negativity, unlike the P1 component, had higher amplitude during recognition of a large than small letter, especially for neutral stimuli. This indicates a stronger involvement of sensory selection mechanism into perception of the hierarchical stimulus at the global level. The N1 amplitude in the frontal region positively correlated with the recognition speed of a large letter. A higher N1 amplitude during recognition of the global aspect of the hierarchical letter was also reported in [20, 32]. These results, along with those for P1 component, suggest that early stages of sensory processing may be of less importance for discriminating the stimulus features on the global than local level. However, there seems to be no reason to consider the global recognition as a process of lesser complexity as compared to the process of local recognition. This point is supported by the results of analysis of the ERP components with longer latencies.

According to [19], P2 positivity which reflects the activation of visual associative cortical areas during analysis of the discriminative features of the target stimulus [27], was even higher in the global than in local perception. Our data do not show any general difference in P2 amplitude in the global vs. local perception. How-

ever we found some topographically specific condition-related differences in the reactivity of P2 component. In the P_4 lead located above the parietal cortex of the right hemisphere the P2 amplitude was higher during global than local recognition whereas in the T_6 lead located above the inferior temporal cortex of the same hemisphere, the inverse relationships were observed, i.e. the P2 amplitude was higher during local than global recognition. This observation is consistent with the results of the fMRI study of the brain activation during compound shape recognition in adults [33]. This study showed that the parietal areas were activated during presentation of the target stimuli at the global level, whereas the inferior temporal areas were activated in response to the target stimuli presented at the local level. An activation of the visual ventral regions in macaque monkeys was reported during recognition of the hierarchical letter at the local level [34]. The functional significance of interregional differences in P2 amplitude during global vs. local perception is supported, first, by the presence of the positive statistical correlation between the amplitude of this component in the right parietal area (P_4) and the speed of recognition of a large letter and, second, by the presence of the positive correlation between the amplitude of this component in the right inferior temporal area (T_6) and the accuracy of the recognition of a small letter. Taking into account the discussed above specifics in information processing in the dorsal and ventral visual systems one can suggest that, when attention is drawn to the global level of a hierarchical stimulus, the process of categorizing of a target signal is based primarily on the analysis of the stimulus spatial properties; in contrast, when attention is drawn to the local level, the object features used as the main source of information for categorization.

We found that the P2 amplitude depended on the level of recognition of a hierarchical letter not only in the caudal visual areas but also in the anterior associative areas, the ERP component being higher in the right central and frontal leads during global recognition. In addition, the P2 amplitude positively correlated with the accuracy of the recognition of a large letter. In the literature, there is evidence that the P2 component over the anterior cortex has a different origin from that over the caudal cortex regions. If, as it was mentioned above, the caudal P2 is associated with the processing of the categorical features of a target visual stimulus [27], the frontal P2 is associated with the activating influence of the DA reward system onto the anterior associative cortex [35]. Based on the ERP comparison between experimental conditions differing in reward expectation, Potts et al. [35] suggested that P2 might reflect the activity of the motivation modulating system which signals whether the analyzed object features correspond to the target stimulus parameters thus preparing the mechanism of top-down selective attention for the further processing of the stimulus. As reported in [36], where ERP were studied in oddball task, the P2 component was detected over the fronto-central cortices if and only

if the target stimuli were shown. This finding is in favor of the idea that the frontal P2 might be related to the mechanism of the stimulus relevance estimation. Our data suggest that such processes of “positive reinforcement” are likely to be more intensive during the global rather than local perception.

Analysis of N2 negativity indicates that the amplitude of this component in the right frontal lead (F_4) was higher during recognition of the local rather than global aspect of the stimulus. The literature data on N2 reactivity during perception of hierarchical visual stimuli are controversial. For example, a higher amplitude of this component during recognition of the local features were reported in [14], while an opposite effect, i.e. a higher N2 amplitude during recognition of the global features, was found in [6, 19, 20, 37]. This controversy may be related not only to the diversity of experimental conditions but also to the existence of functionally and topographically different ERP negative components sharing the same time interval spanned from 200 to 300 ms. According to the data reviewed in [38], the N2 negativity in the anterior associative cortex reflects the involvement of cognitive control processes which include conflict monitoring, inhibition of inadequate reactions, and choice making. An increase in N2 amplitude in various prefrontal areas is accompanied by the activation of metabolism in the anterior cingulate gyrus [39, 40]. That finding confirms a close relationship between this ERP component and cognitive control. The relatively higher N2 amplitude in the frontal lead of the right hemisphere during local recognition may reflect a relatively higher demand to the cognitive control when a small letter is recognized as part of the hierarchical stimulus. The N2 negativity over the caudal cortical regions differs from the frontal N2 with respect to both the localization of its cortical source and its functional meaning. In the visual associative areas, the N2 amplitude grows along with the visual attention load [38, 41] and the source of this component may be localized in the parietal or inferior temporal cortex [41]. Although we did not see any significant level-related (global vs. local) changes in caudal N2 component, still, in temporal posterior lead (T_6), the N2 amplitude positively correlated with the accuracy of small letter recognition. The latter finding may provide some additional support for the participation of the ventral visual system in the recognition of local elements of hierarchical stimuli, and we may assume the involvement of mechanism of categorical features selection.

The results of the present study show that the P3 amplitude was the highest in parietal leads in all experimental conditions. That allows us to consider this component as a “classic” P3 (P3b) which is different from the fronto-central P3 (P3a) caused by a novel stimulus presentation [42, 43]. The classic P3 is observed under different experimental conditions, when a subject reacts to already known target stimulus or performs mental operations on it. These operations include comparing of the incoming information with the internal model of

a target stimulus following by a decision if the two match [43]. According to the data reviewed in [42, 43], P3 positivity is generated by the large-scale neuronal network linking the parietal, temporal, frontal cortices, and limbic structures including the cingulate cortex. The amplitude of this component depends not only on the similarity between the perceived stimulus features and those stored in the internal model of the target but also on whether attention is focused on the target. Indeed, the P3 amplitude increases when a subject focuses attention on the stimulus but decreases with the diversion of attention or when task complexity is growing [44]. In the present study, the amplitude of P3 positivity was found to be generally higher during recognition of the target signal at the global than local level, and the global vs. local difference reached its maximum in the right parietal region. Similar data on the different P3 amplitude during global vs. local perception was reported in [20]. The higher P3 reactivity during recognition of a large letter indicates that more intensive processing may be needed for the identification of the target signal and more attention resource is allocated when recognizing the global aspect of the stimulus.

Special consideration deserves the issue of hemispheric specialization in the processing of the whole vs. details of a visual compound stimulus. In our study, no one-to-one relationship was found between the level of stimulus recognition, on the one hand, and the predominant involvement of a particular hemisphere into the visual information processing, on the other. In most cases, the ERP amplitude turned out to be higher in the right hemisphere. According to our results, at the early stage of analysis (P1 component) as well as at the final stage of identification of a visual object (P3 component), the right hemisphere structures were involved to a greater extent irrespective of the recognition level or the stimulus type. At the same time, our data showed that, in some cortical regions, the degree of the right hemispheric asymmetry of ERP components depended on a combination of the experimental factors. Indeed, during global recognition, P2 component associated with the categorical features processing demonstrated the right hemispheric asymmetry in the anterior associative cortex whereas P3 component usually associated with stimuli classification was characterized by the right hemispheric asymmetry in parietal regions. During local recognition, the right hemispheric asymmetry of positive ERP components (P1, P2) was found in the inferior temporal areas. The predominant involvement of the right but not the left inferior temporal area into the recognition of the local aspect of a hierarchical stimulus seems to be related to the way the visual information is processed in the ventral visual pathway: the higher activation of the right inferior temporal cortical region during object features recognition [45, 46].

The opposite interhemispheric asymmetry was observed in the central regions, where the amplitude of the N2 was higher in the left hemisphere, and interhemispheric differences reached statistical significance

during recognition of the global aspect of stimuli. The fact that N2 amplitude in the left central area positively correlates with the speed of subject response in all the experimental conditions suggests that the left hemispheric asymmetry may be related to the superposition of two negativities: the negative ERP deviation within the time interval of 180–300 ms and the readiness potential in the left motor cortex reflecting preparation for the right hand motor response. It is known that when the experimental paradigm does not require a delayed response, the maximum of the readiness potential attained within the time interval from 150 to 300 ms after the appearance of the target signal [47].

Our results are not consistent with the common view on the specific role of the right vs. left hemisphere in the perception of the global vs. local aspects of a compound visual stimulus. The evidence on the possible functional specialization of hemispheres in processing the whole and details first came from neuropsychological studies in patients with local lesions to temporoparietal brain regions [48] and later was supported by neuroimaging studies [8, 33, 49]. However, in healthy subjects, several studies [6, 9, 50] failed to find either the predominant involvement of the right hemisphere into the global recognition or the left hemisphere predominant involvement into the local recognition. Moreover, an inverse asymmetry pattern was found in [51], i.e. a more pronounced activation of the right occipital area during local recognition and the left occipital area during global recognition.

It is possible that the absence of any specific involvement of the left hemisphere into the local aspect processing may be related to the specifics of the experimental procedure. First, stimuli were shown under the condition of the directed but not distributed attention; second, a large letter consisted of a small number of elements (5×5 matrix) thus reducing a perceptual salience of the large letter, and finally, subjects were asked to make two-choice responses. According to [52], all these conditions reduce the probability of observing the interhemispheric asymmetry during recognition of the global and local aspects of a hierarchical letter.

CONCLUSIONS

In general, the results of this study suggest that the advantage of the global level is not a result exclusively of specific sensory analysis or exclusively of attention mechanisms because of the difference in the brain organization of both the sensory and attention functional components during hierarchical letter recognition. The early stage of sensory processing of a visual pattern reflected in the ERP P1 amplitude; this processing is more intensive during recognition of details than of the whole and it involves both dorsal and ventral structures of the visual systems. During an analysis of discriminative features of an object (sensory categorization), intensity of which is reflected in P2 amplitude, there observed the specific involvement of the right parietal

cortex during global recognition vs. the right inferior temporal cortex during the local recognition. This finding may be in favor of the view that perception of the global aspect of visual hierarchical objects is based mainly on the analysis of their spatial properties whereas perception of the details is based on the analysis of object-related features. The analysis of P3 reactivity indicates that the late stage of sensory-specific processing (i.e. identification of the target stimulus) is more intensive during recognition of the global level and it is accompanied by the activation of the dorsal visual associative areas of predominantly the right hemisphere.

Also, the level-dependent differences in functioning of brain regulatory systems during global and local perception were observed as early as at the early stages of information processing. The process of the early sensory recognition, which is related to the activation of the exogenous visual attention and reflected in N1 amplitude, is more intensive during global than local perception. The results of the analyses of the anterior P2 and N2 components reported in this paper along with the literature data allow us to suggest that the reward modulatory system is more involved during global recognition whereas the cognitive control is of relatively more importance during recognition of the local elements.

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