HUMAN EEG POTENTIALS BEFORE EXPRESS SACCADDES

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Abstract

Using EEG backward averaging method there were fast negative and positive potentials found before regular short latency saccades and express-saccades. These potentials can reflect different stages of presaccadic preparation which include processes of saccadic system release of central fixation, attention disengagement from the central stimulus, decision making and activation of premotor cortical and subcortical structures. There were two schemes of visual stimulus presentation used - "step" and with a 200-ms "gap". Analysis of parameters and spatiotemporal dynamics of potentials allowed us to assume that express-saccades appear in conditions when the previously selected motor program and prediction of the target location coincides with the real coordinates of the target. At that optimum preparation of neuronal structure and a high level of readiness and attention are necessary. Decreasing an express-saccade latency can be the result of participation of main oculomotor areas of motor and saccadic planning in express-saccades initiation, particularly by direct signal transferring from the cortex to the saccadic brainstem generator, by-passing superior colliculus. Moreover, to successfully start initiation process and generate express-saccades, release from central fixation and attention disengagement has to begin in advance.

Key words: EEG potentials, saccades, attention disengagement

INTRODUCTION

To study the attention disengagement process in saccade programming in 1967 Saslow et al. developed an experimental paradigm with a delay of peripheral trigger stimulus presentation after the central fixation stimulus offset (Saslow, 1967). It is assumed that saccade preprogramming begins without information on peripheral stimulus, in which case latency period decreases by 30-80 ms (the "gap-effect") and express-saccades with a latency period from 80 up to 134 ms appear (Boch & Fischer, 1986; Fischer et al., 1987; Fischer & Rampsberger, 1986; Gomez et al., 2002).

Fischer and his colleagues made a major contribution to the investigation of express-saccade phenomenon. They combined the processes of attention disengagement and decision making into the decision making stage. They assumed that appearance of express-saccades resulted from attention disengagement when the central stimulus disappeared and from making decision on saccade

initiation, excited by the state of free attention. Herewith it was assumed that the decision making stage ends earlier than the target appears. The position of this target must be known to calculate the motor command. According to B. Fischer et al. attention disengagement takes about 70 ms, decision making - 20-60 ms and calculation of saccade parameters - 90-130 ms which corresponds to express-saccade latency period. By the authors' assumption express-saccade generation is connected with the shortest way of visual information transferring from retina via visual cortex and superior colliculus to brainstem saccadic generator (Fischer & Rampsberger, 1986; Goldberg, 2002; Neggers et al., 2005; Schiller and Tehovnik, 2005). Some authors suppose that in the normal state frontal oculomotor fields together with superior colliculus, using the time in interstimulus interval, are responsible for express-saccade generation (Dias & Bruce, 1993; Rivaud et al., 1994). There are also studies showing the important role of posterior parietal

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cortex (analogue of the lateral intraparietal area in monkey) in this process (Andersen et al., 1990, Pierrot-Deseilligny et al., 1991, Ben Hamed & Duhamel, 2002). There are other points of view on the nature of the “gap-effect”. Ross S. and Ross L. (Ross and Ross, 1981) made an assumption that fixation stimulus offset is the signal that provides the information on the time of saccadic target presentation. A similar to this hypothesis was expressed by G. Reulen (Reulen, 1984), according to which disappearance of the fixation point initiates off-signal appearance on retina. This signal can intensify or accelerate the processes of stimulus specific sensor processing, decision making and motor command. Such point of view on the nature of “gap-effect” is still popular and called “fixation offset-effect” (Dick et al., 2005). Neurophysiological studies of primates showed a reciprocal interaction of fixation and motor neurons in many oculomotor structures (Bon & Lucchetti, 1992; Munoz & Wurtz, 1993). In this connection there was a hypothesis expressed that fixation point offset in the “gap”-scheme leads to oculomotor system release from fixation and activation of specific processes in it which are connected with saccade preparation, initiation and execution (Rohrer & Sparks, 1993; Abrams & Dobkin, 1994; Tam & Ono, 1994; Pratt, 1998). It was shown that some subjects (“express-makers”) are able to execute a great number of express-saccades (up to 90% of the total amount) not only in “gap”, but even in “overlap” conditions, which is explained by suppression of their fixation mechanisms (Biscaldi et al. 1996).

So there are two major hypotheses on the “gap-effect” nature - “cognitive” which explains the “gap-effect” by attention and decision making processes that take place at the early stage of visual processing, and “motor” - by later processes of premotor preparation in the oculomotor system (Saslow, 1967; Boch & Fischer, 1986; Goldberg et al., 2002; Gomez et al., 2002). The study of premotor EEG-potentials before express-saccades is an adequate method of studying the cortical nature of these processes. The aim of the research was the analysis of spatiotemporal characteristics of human brain presaccadic potentials during fixation and target stimulus presentation with a “delay” at monocular stimulation of the right and the left eye.

METHODS

Subjects

8 healthy volunteers aged between 20 - 25 years (4 men and 4 women) participated in the experiments. 7 subjects had a right asymmetry profile (dominant right hand and eye), one was an ambidexter (by hand and eye). To

determine an asymmetry profile some standard tests were used: M. Annett questionnaire (Annett, 1972), Rosenbach’s test, hole-in-the-card test, etc. (Chapman and Chapman, 1987).

Stimuli and apparatus

Subjects were sitting in an armchair in a dark chamber equipped for the purpose of the experiment. EEG was registered monopolarly at 11 areas of a cortex - F3, F4, Fz, P3, P4, Pz, T3, T4, Cz, O1, O2 et 3 subjects and at 8 areas of a cortex - F3, F4, Fz, P3, P4, Pz, O1, O2 et 5 subjects under the scheme 10-20 by using the electroencephalograph EEG 16S “Medicor” (Hungary); (a time constant was 1; the frequency filter top level was at 70 Hz). Horizontal eye movements were registered by using the electrooculogram (EOG) bipolarly (a time constant was of 0.3). C-shaped electrodes were attached at the external edges of eyes.

To carry out the experiment, to make the analysis and for the data storage we used PC-compatible computer and integrated system CONAN-m (Russia). Signals were digitalised for each 5 ms.

A red light emitting diode (10 deg. min. dia) which was used as a fixation point was placed on a horizontal axis of the hemisphere at the distance of 60 cm directly in front of the subject’s eyes. Other two diodes were placed at visual angles of 10° to the left and right of the central one. They also served as peripheral visual targets for saccadic movements. We used monocular stimulation of the right and the left eye.

Task

Duration of the central fixation stimulus varied from 700 up to 1000 ms (a step equaled 100 ms), and peripheral - from 1000 up to 1300 ms (a step - 100 ms). Duration of diode brightness decreasing equaled 600 ms. Two experimental paradigms of visual stimuli performance were used: I) Step (control scheme) - the consecutive switching on of the peripheral targeted visual stimulus followed the switching off of the central fixation one; II) Gap - switching on of the peripheral targeted visual stimulus followed the central fixation visual one with interstimuli interval of 200ms.

Procedure

We used self-initiation method: each stimulus realization was initiated by the subject with button pressing, simultaneously central fixation stimulus was switched on. The subject was instructed to fix a gaze on the central fixation stimulus and as soon as peripheral stimuli was switched on to move eyes to them. While brightness of

peripheral stimuli was decreasing, the subject had to release the pressed button as fast as possible, and then transfer his gaze to the central stimulus.

Both of the above described paradigms of visual stimulation were applied randomly in the same experiment. Each of the two peripheral visual stimuli was switched on at random order. Visual stimuli were presented with blocks of 36 realizations. There were presented 288-432 stimuli during two-tree experiments to each subject.

Data analysis

For each subject there were carried out two kinds of selected average EEG before regular short latency saccades with "medium" latency (mode 20 ms) and before express-saccades with latency period from 90 to 120 ms. The first kind was backward average: the beginning of saccade served as the trigger of them, it was registered at EOG and coincided with the spike potential peak at EEG. Another kind was direct average: the moment of switching on of peripheral target stimuli served as the trigger of them. The interval of averaging made 1000 - 800 ms up to the trigger and 300 ms afterwards. Correction of zero level was carried out at a segment of averaging from 500 ms prior to the beginning of eyes movement to 100 ms after saccade beginning. 30-60 stimulus realizations served for the average data. Besides, there was carried out grand averaging of EEG at the group of subjects.

The amplitude and spike latency of the allocated potentials were measured at each subject. The maximal amplitude of fast positive or negative potentials was measured from the peak of the previous negative or positive fluctuation.

The average values, standard deviations etc. have been calculated and cover the data of all examined subjects. For a more detailed study of spatiotemporal dynamics of average potentials amplitude, there was used a method of computer graphics like an "EEG-mapping" with step of 10 ms. The number of potential focuses in each zone have been consequentially mapped with the step of 10 ms and individually calculated for each examined subject. Resulting individual data have been used for calculation of group averages and for statistical testing.

Statistical analyses were performed using statistical package SPSS 10.1. and spreadsheet processor EXCEL. Wilcoxon nonparametric test was used for comparison of reaction time average values distribution and EEG-potentials parameters. Method of autocorrelation proved that all observations (saccadic latencies and averaged EEG-potentials) were independent of each other.

RESULTS

Saccadic latency (reaction time)

Analysis of saccade latency period durations showed that "interstimulus interval" introduction during stimulus presentation led to saccade latency period shortening by 23-70 ms ("gap-effect", $p < 0.05$, tab.1). At that in six of the eight subjects many (21-30%) express-saccades appeared with a latency period of 90 to 120 ms. In four of these subjects express-saccades also appeared during consecutive stimulus presentation. In 77% cases there were more express-saccades of the direction contralateral to the stimulated eye than of the ipsilateral - to the left during stimulation of the right eye and to the right during stimulation of the left eye ($p < 0.05$, tab.2).

EEG-potentials

Analysis of averaged EEG potentials, obtained by backward averaging from saccade beginning, showed that each subject had a complex of fast potentials different polarity: spike potential, N -1 ("minus one") and -1 potentials in the saccade latency period, N -2, -2, N -3 and -3 potentials in the interstimulus interval (fig.1). Potential amplitude ranged from 0.5 to 9.4 V.

Negative presaccadic potentials

N-1 wave

N-1 potential was registered before the beginning of saccade (fig. 1-4). Average latency of its peak was 52 ± 19 ms before regular short latency saccades and 37 ± 12 ms before express-saccades. N-1 potential amplitude before express-saccades was much bigger than before regular short latency saccades: 2.66 ± 1 V and 2.04 ± 1.5 V respectively ($p < 0.05$, fig.5a). Herewith stimulating the left eye before express-saccades, the peak latency of N-1 potential before the express-saccades to the left was higher than before the saccades to the right ($p < 0.05$, pic.5b).

There are differences shown in the spatiotemporal dynamics of N-1 potential before express-saccades and before regular short latency saccades. Before regular short latency saccades N-1 potential focus in 69% cases was localized in the hemisphere contralateral to the movement, more often in the parietal areas ($p < 0.05$, fig.2). There was no contralaterality in the position of N-1 potential focus before express-saccades. Presenting stimulus to the right eye on the right in 50% cases the maximum N-1 potential amplitude was registered in the right frontal area, and in 43% cases - in the frontal-sagittal area. Presenting stimulus to the left eye on the left N-1 potential focuses in 85% cases dominated in both hemispheres with equal probability. Herewith there was a

Table 1. Stimuli and stimulation for both eyes.

subjects	Stimuli, stimulation of the right eye					
	10° to the left			10° to the right		
	Step N/M $\pm\sigma$	GAP N/M $\pm\sigma$	Δ	Step N/M $\pm\sigma$	GAP N/M $\pm\sigma$	Δ
IH	46 / 174 $\pm$ 40*	28 / 125 $\pm$ 38*	49	27 / 178 $\pm$ 40*	42 / 113 $\pm$ 40*	65
MB	49 / 185 $\pm$ 40*	47 / 129 $\pm$ 26*	56	43 / 169 $\pm$ 48*	46 / 132 $\pm$ 39	37
HF	50 / 203 $\pm$ 24*	64 / 177 $\pm$ 28*	26	39 / 195 $\pm$ 38*	38 / 163 $\pm$ 29*	32
KJ	42 / 225 $\pm$ 40*	41 / 161 $\pm$ 30*	64	43 / 237 $\pm$ 20*	47 / 168 $\pm$ 26*	70
ДН	42 / 246 $\pm$ 34*	40 / 170 $\pm$ 38*	66	45 / 208 $\pm$ 35*	26 / 157 $\pm$ 20*	52
AH	40 / 152 $\pm$ 20*	40 / 118 $\pm$ 20 *	34	36 / 151 $\pm$ 20*	30 / 119 $\pm$ 30 *	32
TE	47 / 214 $\pm$ 40*	35 / 158 $\pm$ 40*	56	44 / 250 $\pm$ 70	18 / 221 $\pm$ 70	29
CE	50 / 180 $\pm$ 40*	37 / 138 $\pm$ 40*	42	50 / 220 $\pm$ 70*	47 / 175 $\pm$ 50*	45
subjects	Stimuli, stimulation of the left eye					
IH	44 / 200 $\pm$ 40*	42 / 162 $\pm$ 70*	38	41 / 178 $\pm$ 38*	50 / 138 $\pm$ 60*	40
MB	50 / 170 $\pm$ 37*	48 / 140 $\pm$ 46*	30	40 / 150 $\pm$ 28*	49 / 127 $\pm$ 28*	23
HF	50 / 207 $\pm$ 30*	66 / 154 $\pm$ 35*	38	50 / 202 $\pm$ 30*	60 / 138 $\pm$ 30*	64
KJ	50 / 232 $\pm$ 30*	40 / 165 $\pm$ 38*	67	40 / 219 $\pm$ 30*	34 / 165 $\pm$ 50*	54
ДН	48 / 245 $\pm$ 46*	44 / 187 $\pm$ 40*	58	34 / 215 $\pm$ 40*	27 / 164 $\pm$ 30*	51
AH	50 / 162 $\pm$ 30*	51 / 130 $\pm$ 40 *	32	43 / 160 $\pm$ 30*	42 / 123 $\pm$ 40 *	37
TE	45 / 209 $\pm$ 40*	28 / 164 $\pm$ 50*	45	40 / 221 $\pm$ 50	35 / 202 $\pm$ 50	19
CE	50 / 200 $\pm$ 40*	42 / 132 $\pm$ 40*	68	48 / 182 $\pm$ 30*	34 / 134 $\pm$ 30*	48

transition of the focuses from the left hemisphere to the right one (fig.3). In 66% cases the maximum amplitude was registered in the central or parietal-sagittal areas ($p < 0.05$). During contralateral stimulation of the right eye on the left or of the left eye on the right N-1 potential focuses before express-saccades in 42% cases dominated in temporal and occipital areas of the right hemisphere (fig.4), in 31% cases in frontal and occipital areas of the left hemisphere and in the parietal-sagittal area.

N-2 wave

N-2 potential was observed at the end of the interstimulus interval before peripheral stimulus onset (fig.1-4). Average peak latencies were 175 ± 22 ms before

regular short latency saccades and 142 ± 19 ms before express-saccades ($p < 0.05$), amplitudes: 1.65 ± 1.1 V and 2.83 ± 1.2 V respectively ($p > 0.05$). Before regular short latency saccades N-2 potential in 75% cases dominated in different areas of the right hemisphere during stimulation of the right eye and during contralateral stimulation of the left eye on the right ($p < 0.05$, fig. 2). In the left hemisphere N -2 potential focuses were usually observed only during ipsilateral stimulus presentation to the left eye on the left.

Before express-saccades localization of N-2 wave focuses depended on the saccade direction. In 80% cases there was domination of N -2 focuses in the hemisphere contralateral to the saccade direction, which N-1 potential

Table 2. Step and GAP during stimulation

subjects	Stimulation of the left eye				Stimulation of the right eye			
	10° to the left		10° to the right		10° to the left		10° to the right	
	Step	GAP	Step	GAP	Step	GAP	Step	GAP
IH	0	19	7.3	28	2.2	39	7.4	36
MB	4	25	20	53	2	47	21	40
HF	0	24	0	40	0	22	0	29
KJ	0	7.5	0	15	0	7.3	0	2.4
DH	0	0	0	0	0	0	0	0
AH	2	25	7	38	7.5	50	3	33
TE	0	25	0	14	0	28	0	11
CE	2	50	7	35	3.9	49	0	17

lacked ($p < 0.05$). Herewith in 50% cases there were simultaneous focuses in the sagittal and in one of the lateral areas (fig.3). Irrespectively of the stimulated eye, during presentation of the stimulus on the left N -2 potential focuses most often dominated in the right parietal area (fig. 3, 4).

N-3 wave

N-3 potential was observed at the beginning of interstimulus interval (fig. 1-4). Average peak latencies were 249 ± 36 ms before regular short latency saccades and 231 ± 32 ms before express-saccades ($p < 0.05$), amplitudes: 1.89 ± 1.1 V and 2.69 ± 1.6 V respectively ($p > 0.05$). Before express-saccades during stimulation of the left eye N-3 potential peak latency before saccades to the left was bigger than before the saccades to the right, the same as in N-1 potential ($p < 0.05$, fig. 5b). Before regular short latency saccades there was no simple dependence on the stimulated eye and saccade direction found in localization of N-3 potential focuses. All in all there was a tendency observed that during contralateral presentation of stimulus to the stimulated eye N-3 potential focuses were more often localized in parietal-occipital areas of the left hemisphere, and during ipsilateral presentation - in one of the sagittal areas or in the right frontal area.

Spatiotemporal dynamics of N-3 potential was substantially different before express-saccades: 1) before express-saccades N-3 potential focuses had a similar

Figure 1. Presaccadic potentials (mkV = microvolts).

localization in all subjects; 2) in 65% cases they dominated in frontal- or parietal-sagittal areas of the brain ($p < 0.05$, fig. 3, 4). Presenting stimuli to the right eye and to the left eye on the left N-3 wave focuses were localized in sequence during 20-30 milliseconds in one of the sagittal areas, then in one of the lateral areas or vice versa (in the lateral and then in the sagittal area) ($p < 0.05$; fig.4). Stimulating the left eye on the right in most cases (60%) N-3 potential was observed in the frontal sagittal area, and

presenting stimulus on the left - in the parietal-sagittal area (fig.3).

Figure 2. N-2 potential in 75% cases dominated in different areas of the right hemisphere.

Positive presaccadic potentials

P-1 wave

P-1 potential was observed at the very beginning of saccade latency period right after peripheral stimulus onset (fig.1-4). Before express-saccades are often followed by spike potential. Most often (in 80% cases) this phenomenon was observed during contralateral stimulus presentation to the left eye on the right. Average peak latencies were 106 ± 30 ms before regular short latency saccades and 83 ± 15 ms before express-saccades ($p < 0.05$). P-1 potential amplitude before express-saccades, the same as in N-1 potential amplitude, was much bigger than before regular short latency saccades 3.06 ± 2 V and 1.73 ± 0.8 V respectively ($p < 0.01$).

Localization of P-1 positive potential focuses did not depend on to which eye visual stimulus was presented. Before regular short latency saccades in 85 % cases during contralateral stimulation and in 50 % cases before ipsilateral stimulation P-1 potential focuses prevailed in the hemisphere ipsilateral to the stimulated eye ($p < 0.05$) (fig.2). Before express-saccades P-1 potential in 60 % cases was observed in the right hemisphere and in 13 % cases in the left one. Before express-saccades of the direction contralateral to the stimulated eye, in all the right-handed subjects in 80 % cases P-1 positive potential focuses appeared in one of the sagittal areas (most often in the frontal area), then they transferred to the right hemisphere, most often to the parietal area (fig. 4). Before express-saccades of the direction ipsilateral to the stimulated eye there was an intersubject variability in

distribution of -1 potential focuses. The express-saccades could be localized either in the left or in the right hemisphere or in the frontal-sagittal area depending on the subject (fig.3).

P-2 wave

P-2 potential was observed in the interstimulus interval before peripheral stimulus onset (fig.1-4). Average peak latencies were 211 ± 28 ms before regular short latency saccades and 181 ± 31 ms before express-saccades ($p < 0.05$), amplitudes: 1.61 ± 1 and 2.5 ± 0.9 V respectively ($p > 0.05$).

Irrespective of the latency period duration spatiotemporal dynamics of P-2 potential depended more on saccade direction, than on the stimulated eye. Before regular short latency saccades P-2 potential had a clear localization only during contralateral stimulus presentation. Herewith stimulating the right eye in 57 % cases P-2 potential focuses were observed in frontal- and central-sagittal area, stimulating the left eye in 80 % cases the potential had two and more sequential peaks in one of the areas of the left hemisphere and in sagittal areas, mostly in the frontal- and central-sagittal area. Before express-saccades irrespective of the stimulated eye during stimulus presentation on the right P-2 potential in 55 % cases dominated in the right hemisphere, at that in the occipital areas half as much again than in the frontal and the parietal ones.

Figure 3. The express-saccades could be localized either in the left or in the right hemisphere or in the frontal-sagittal area depending on the subject.

Presenting stimuli from the left P-2 potential (in 46 % cases) dominated in the frontal- and parietal-sagittal areas, less often in the left hemisphere (fig.3-4). Before express-saccades P-2 potential more often than before the regular

short latency saccades was observed in the right hemisphere, at that during stimulus presentation to the right eye on the right this domination was complete ($p < 0.05$).

Figure 4. Presenting stimuli from the left P-2 potential (in 46 % cases) dominated in the frontal- and parietal-sagittal areas, less often in the left hemisphere.

P-3 wave

P-3 potential in most cases was in the “gap” period at the moment or after central fixation stimulus offset (fig.1-4). Average peak latencies were 290 ± 32 ms before regular short latency saccades and 267 ± 26 ms before express-saccades ($p < 0.05$). P-3 potential amplitude before regular short latency saccades was 1.57 ± 0.4 V and 2.2 ± 1.1 V respectively ($p > 0.05$). Using direct averaging from the moment of peripheral stimulus offset there was P1 potential corresponding to P-3 potential found. It had an advance nature, and peak latency of this potential was -6.5 ± 31 ms before regular short latency saccades and -90.5 ± 31 ms before express-saccades ($p < 0.01$), and amplitude was 3.2 ± 2.1 V and 3.4 ± 2.1 V respectively ($p > 0.05$). 1 potential amplitude using direct averaging from the moment of peripheral stimulus onset was much bigger than the amplitude of the same P-3 potential, but using backward averaging from the beginning of saccade ($p < 0.05$).

Before regular short latency saccades during ipsilateral stimulation either of the right or of the left eye P-3 potential focuses most often (in 50 % cases) dominated in different areas of the right hemisphere prevailing in F4 and 2 areas. During contralateral stimulation of the right eye in 57 % cases P-3 potential focuses were localized in different areas of the left hemisphere, and during contralateral stimulation of the left eye they were localized

mostly (in 61 % cases) in one of the sagittal areas ($p < 0.05$).

Before express-saccades spatiotemporal dynamics of this potential depended more on the stimulated eye and rarely on the stimulus localization. Stimulating the right eye in 50 % cases P-3 potential dominated in the left frontal area contralateral to the direction of movement. Stimulating the left eye P-3 wave focuses dominated in the parietal, temporal and occipital areas of the contralateral right hemisphere, at that twice as often in the occipital area than in other areas (fig. 3). In which case using direct averaging from the moment of peripheral stimulus onset maximum amplitude values of the corresponding 1 potential before express-saccades in 71 % cases were registered in parietal-occipital areas ($p < 0.05$).

We should also mention that peak latency of all the potentials preceding express-saccades (irrespectively of their polarity) significantly much smaller than in the corresponding potentials preceding regular short latency saccades ($p < 0.05$). At the same time peak latency of the potentials N-1, N-3, P-1 and P-2 preceding left-directed short regular saccades and peak latency of the potentials N-1 preceding left-directed express-saccades during stimulation of the right eye were significantly smaller than in the corresponding cases during stimulation of the left eye ($p < 0.05$, fig.5c).

DISCUSSION

Introduction of the “gap” during presentation of visual information leads to decreasing of saccadic latency and appearance of short latency express-saccades (“gap”-effect). This phenomenon is explained by anticipatory release from fixation, attention disengagement and increase of oculomotor system readiness during the “gap” period (Saslow, 1967; Shulgovsky et al., 2006; Boch & Fischer, 1986; Fischer & Breitmeyer, 1987; Fisher & Weber, 1993; Gomez et al., 2002; Suzuki & Hirai, 2000). Self-initiation method also increases the total level of active attention and readiness of subjects for saccade realization, which can explain the appearance of express-saccades in some subjects even during consecutive stimulus presentation (Suzuki and Hirai, 2000).

There were no lateral differences in the quantity of express-saccades revealed before express-saccades to the left and to the right (Rivaud et al., 1994). In our study there were more express-saccades observed in the direction contralateral to the stimulated eye. It can be assumed that this fact is connected with peculiarities of visual information conduction during monocular stimulation. In these conditions visual stimuli are projected from

contralateral semifield of vision on the temporal part of retina from which the information is transferred to the hemisphere contralateral to the stimulated eye and to the saccade direction by more rapid retino-tecto-thalamo-cortical tract (Springer & Deutsch, 1981), which can be the reason of saccade latency period decreasing.

Express-saccade generation mechanism is not precisely clear yet. According to the hypothesis of B. Fischer and E. Rampsberger (Fischer & Rampsberger, 1986) this mechanism is connected with the shortest way of visual information transferring from retina through lateral geniculate body, striatal cortex and superior colliculus to the brainstem saccadic generator. Comparison of saccade latency with the clinic data led to the assumption that express-saccades are reflexive movements and can be generated at the level of superior colliculus (Fischer & Rampsberger, 1986; Fisher & Weber, 1993; Rivaud et al., 1994). At that the most wide-spread in psychophysiology "block" model of saccadic generation, which includes the processes taking place in saccade latency period: attention, decision making and computation of movement parameters, is abstracted from the processes taking place at the stage of stimulus expectation (Fischer and Breitmeyer, 1987; Fisher & Weber, 1993; Mayfrank et. al, 1986).

The results that we drew show that for express-saccade generation the processes that take place at fixation period are important. Peak latencies of all the potentials preceding express-saccades were much smaller than before regular short latency saccades, therefore preparation of express-saccades begins later and happens rapidly. In the earlier studies of our laboratory there was shown a stronger intensity of PMN1 slow negative wave (analogue to CNV wave) before express-saccades as compared to the long latency ones (Shulgovskiy et al., 1995). It seems therefore that higher level of activation, attention and anticipation creates prerequisites for successful preliminary preparation of express-saccades. It can be assumed that in the conditions of our experiment, during indefinite stimulus presentation in the left or the right visual hemyfield express-saccades appear in case of coincidence of preselected program of the future movement with real coordinates of saccadic target in the conditions of optimum preparation of neuronal structure of movement in the course of experiment.

Presaccadic potentials in saccade latency period

N-1 wave

We found differences in the parameters of presaccadic potentials before express-saccades as compared to regular short latency saccades. In this study, as well as in the previous ones, it is shown that N-1 is observed with high

probability before regular short latency saccades in the parietal area contralateral to saccade direction (Slavutskaiy et al., 1998; Moiseeva et al., 2004; Shulgovsky, 2006). Human lateral posterior parietal area is an analogue of monkey LIP zone. Neurons of parietal cortex are discharged in 50-70 milliseconds before the beginning of contralateral direction saccade and they encode its parameters into motor coordinates (Andersen and Gnadt, 1989; Shibasaki, 1980). That is why we made an assumption that N-1 potential reflects command processes, initiating a saccade, and corresponds to the N-10 potential of motor initiation before hand movements which was found earlier (Shibasaki, 1980; Deecke et al., 1984). Introduction of insterstimulus interval has an indubitable influence on motor processes of saccadic initiation. Significant amplitude increase of N-1 potential suggests increase of the signal to starting of express-saccade as compared to regular short latency saccades. Absence of contralaterality in location of N-1 potential focuses, their domination in lateral frontal, temporal and occipital areas, in the frontal- and parietal-sagittal area and maximum amplitude value in the central- and parietal-sagittal areas suggests special nature of this potential. It is known that main eye fields which are situated on medial surface of frontal lobes - supplementary eye field (SEF) and supplementary motor area (SMA), dorsomedial part of prefrontal cortex (DMPF), as well as anterior cingulate cortex (ACF) are projected in the frontal and central sagittal area (Pierrot-Deseilligny, 2002). These structures have the outputs to brain stem saccadic generator which are independent from the superior colliculus (Tehovnik et al., 2000). The obtained data allows assuming that there is a contribution of main eye fields of motor and saccadic planning to express-saccade initiation, particularly through direct transfer of the signal from cortex to saccadic generator, by-passing superior colliculus. This can initiate optimum motor program and shorten latency period. Medial part of parietal cortex, homologue of monkey 7a field which is directly relevant to spatial attention processes, is projected to the parietal sagittal zone (Andersen & Gnadt, 1989). It is possible that high-amplitude N-1 potential in this area before express-saccades reflects increased level of attention that is the result of insterstimulus interval introduction and has an influence on all stages of movement preparation, including initiation processes.

N-1 wave

N-1 potential was located in saccade latency period and its focuses were observed in frontal, parietal and temporal oculomotor fields of both hemispheres. In our previous

studies we proposed that N-1 potential corresponds to -50 potential of motor initiation found earlier before hand movements (Deecke et al., 1984; Shulgovsky et al., 1995; Slavutskaia et al., 1998; Moiseeva, 2004; Shulgovsky et al., 2006). Before regular short latency saccades irrespectively of the stimulated eye and direction the saccades of this potential prevailed in the hemisphere ipsilateral to the stimulated eye. It is possible that this potential reflects the processes of active inhibition of oculomotor structures of ipsilateral hemisphere that are a necessary element of saccade initiation command processes.

Before express-saccades N-1 potential amplitude was much higher than before regular short latency saccades, the same as N-1 potential amplitude. Moreover it merged with spike potential more often than before regular short latency saccades. The obtained data can tell about strengthening of saccadic initiation process during express-saccade generation. There was regular replacement of N-1 positive potential focuses found during saccade latency period both in frontal and parietal oculomotor areas, and in frontal-sagittal area. This reflects the activity of above mentioned main oculomotor eye fields. The obtained results allow us to assume that N-1 potential before express-saccades reflects the processes of saccadic programming which includes both the stages of decision making and of saccade initiation. The proof of this hypothesis is the data on the absence of dependence of N-1 potential parameters on saccade direction. Similar data was obtained earlier in our laboratory (Shulgovsky et al., 2006).

Presaccadic potentials in interstimulus interval

According to present conceptions, during the interstimulus pause there happen processes of saccadic system release from central fixation, attention disengagement from the central stimulus and preparation processes, which include preliminary activation of premotor cortical and subcortical structures according to the program previously selected from memory (Fischer, Ramsperger, 1986; Becker, Rohrler, Sparks, 1993; Abrams, Dobkin, 1994; Gomez et al., 1995; Tam, Ono, 1994; Pratt, 1998; Tanaka, Shmojo, 2001). It can be assumed that the potentials found in this interval in our study reflect these processes to some extent.

N-2 wave

N-2 potential before express-saccades was observed at the end of interstimulus interval in the hemisphere contralateral to the movement direction. At that when

stimuli were presented on the left its focuses were most often registered in the right parietal area. This fact gives a ground to suppose that before express-saccades N-2 potential reflects final stages of saccade anticipation as a preliminary activation of initiating structures. Localization of N-2 potential in parietal cortex of the right hemisphere at the end of interstimulus interval can also be connected with attention processes. Right hemisphere domination in the processes of spatial attention and visual perception are well known (Mayfrank et al., 1986; Naatanen, 1992; Moiseeva et al., 2004). According to the studies of neuronal activity of monkeys, lateral intraparietal area is considered to be the "neuronal substrate of attention" (Ben Hamed & Duhamel, 2002; Goldberg et al., 2002, p. 205). Simultaneous localization of N-2 potential focuses in sagittal areas also confirms its connection with spatial attention processes (Andersen & Gnadt, 1989).

Before regular short latency saccades N-2 potential was localized not only at the end of interstimulus pause, but also at the beginning of latency period. As a rule it prevailed in the right hemisphere with peak values in parietal and temporal areas (Moiseeva et al., 2004), which also allows us to assume that there are processes of sensor perception and attention reflected in N-2 potential.

P-2 wave

In the second half of interstimulus interval before express-saccades there was found P-2 positive potential. Its parameters were significantly different from those of P-1 potential. The same as for N-2 potential, its amplitude was higher using direct averaging method from the moment of peripheral target onset than using the averaging backward from eye movement. Before regular short-latency saccades P-2 potential focuses prevailed in the left hemisphere, as well as in the frontal- and central-sagittal areas. We have already mentioned above that main oculomotor areas of motor and saccadic planning are projected into these areas. The important role of the left hemisphere in human anticipation activity is well-known (Milner, 1971). Due to this fact we suppose that P-2 potential has a complicated nature which reflects both the processes of sensor processing and movement preparation. It was found that before express-saccades spatiotemporal dynamics of P-2 potential depended on the direction of saccade. This gives us ground to assume that this potential reflects movement preparing processes that have anticipation nature. Domination of positivity focuses before saccades in the frontal- and parietal-sagittal areas, as well as in the left hemisphere can confirm our assumption, because main cortical structures of saccadic planning (FEF, SEF, SMA, DMPF, ACF) are projected

into these areas of cortex. It is possible that one of the conditions of express-saccade appearance is correspondence of spatial location of target stimulus to the selected program. P-2 potential focuses before express-saccades to the right dominated in the right hemisphere, which never occurred before regular short latency saccades. As we mentioned before, the right hemisphere dominates in the processes of spatial attention (Mayfrank et al., 1986; McIntosh et al., 1994). It is possible that P-2 potential before express-saccades reflects inclusion of the attention processes into motor preparation. Confirmation of this fact can be P-2 potential appearance in the parietal-sagittal area where dorsomedial parts of the field, homologous to 7a field of monkeys, are projected. These area is leading in the processes of sensor processing and selective attention and one of their functions is integration of eye position and retinotopic visual information, necessary for spatial analysis (Bremmer et al., 1997; Andersen & Gnadt, 1989).

N-3 wave

Spatiotemporal dynamics of N-3 potential development was significantly different before express-saccades and before regular short latency saccades. Before regular short latency saccades localization of this potential had great individual differences, and before express-saccades it dominated in most cases in the frontal- or parietal-sagittal areas. Negativity localization in the frontal-sagittal area gives us a ground to assume the connection of N-3 potential with the processes of movement program formation and probabilistic prediction, and in the parietal-sagittal area with the processes of selective sensor attention (Pierrot-Deseilligny, 2002). Negativity in the central parietal area can also reflect the influence of non-specific thalamo-parietal system, taking part in formation and offset of attention focus (Naatanen, 1992). Peak latency of N-3 potential enables us also to connect the nature of this potential with fixation release and attention disengagement. Release from fixation on the central point is an active process which is connected with the process of attention disengagement and its shift to the assumed place of target appearance, and it happens earlier than before regular short latency saccades (Suzuki and Hirai, 2000).

P-3 wave

At the very beginning of interstimulus interval there was P-3 potential observed. Spatiotemporal dynamics of this potential was different during stimulation of the right and the left eye, and its focuses often dominated in parietal-occipital or occipital areas. At that the maximum amplitude values of P-1 potential, which using direct

averaging method corresponds to P-3 potential, were registered in parietal-occipital areas. Basing on these facts we assume that P-3 potential reflects the processes of sensor processing of fixation stimulus (off-signal) offset (Reulen, 1984). Switching on frontal and sagittal areas during development of P-3 and N-3 early potentials in the interstimulus pause and dependence of their topography on the saccade direction can also point at the reflection in these potentials of motor attention processes, which include anticipation processes of movement preparation. Therefore spatiotemporal dynamics of both positive and negative components of averaged EEG-potential in the interstimulus interval before express-saccades enables us to assume that there is a compatibility of either "motor" or "cognitive" theory of Gap-effect. It can be that during the interstimulus pause there take place both the processes of sensor processing and attention disengagement, and the processes of motor preparation.

CONCLUSION

The study of presaccadic potentials showed a complex nature of express-saccades. Latency period shortening and the process of its generation are connected with modulation of cortical neuronal chains that are involved in sensor, motor and cognitive functions at all the stages of presaccadic preparation. Latency period duration in psychophysiological studies indicates the level of attention and activation. The data that we obtained allow us to assume that express-saccades appear in the conditions of increased level of activation and attention in combination with successful processes of motor anticipation. Significant amplitude increase of N-1 and P-1 potentials and their domination in the frontal-, central- and parietal-sagittal areas reflect increase of command signal for the beginning of an express-saccade. Express-saccade latency period shortening can also be explained by inclusion of efferent way from the main oculomotor areas of saccadic planning directly to the saccadic generator, by-passing superior colliculus. Spatiotemporal dynamics of N -2, -2, N-3 and -3 potentials in the interstimulus interval gives evidence to the fact that at this stage there happen such processes as sensor processing of fixation stimulus offset, motor program formation and prognostic movement prediction, sensor and spatial attention, release from fixation, attention disengagement and its offset, as well as preliminary activation of oculomotor neurons of the lateral intraparietal area.

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