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Asymmetry between the upper and lower visual fields: An event-related potential study

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Abstract Using event-related potentials (ERPs), the present study examined the electrophysiological and attentional asymmetries between the upper visual field (UVF) and the lower visual field (LVF) while subjects were performing a target detecting task. The early ERP components showed a smaller P1 and a larger N1 in LVF than in UVF over the occipito-parietal areas, while the late components (N2 and P3) showed no difference between the two visual fields. In addition, the attention enhancement on the P1 component was greater in UVF than in LVF. These findings suggest that the function of the UVF and LVF differ in terms of both early visual information processing and attentional modulation.

Keywords: asymmetry, upper visual field, lower visual field, event-related potentials, attentional modulation.

Asymmetries of human visual information processing across visual fields have been an interesting issue in cognitive psychology and neuroscience. In addition to investigations of the asymmetries between the left and right visual fields that are believed to reflect the functional differences between the left and right hemispheres[1], a number of studies have proposed that visual processing also differs between the upper and lower visual fields[2,3]. Anatomically, in striate cortex of each hemisphere, the LVF is represented above the calcarine fissure, whereas the UVF is represented below the fissure. Accordingly, in extrastriate cortex, the LVF is represented dorsally and the UVF ventrally[4,5]. Behaviorally, LVF superiority has been found across a variety of tasks: simple reaction time[6], luminance threshold[7], temporal and spatial contrast sensitivities and visual acuity[3], perception of illusory contours[8], sensitivity to chromatic motion under isoluminant conditions[9], visually guided pointing[10] and spatial relocation memory task[11]. Moreover, some behavioral studies suggest that there might be attentional asymmetry between the upper and lower visual fields. For instance, He *et al.*[12] reported that attentional resolution was greater in the LVF than that in the UVF. Altpeter *et al.*[13] also found that patients with maculopathies sustained attention with the LVF better than with the UVF. Only a few studies found a UVF advantage, such as those using a lexical decision task[14] and in saccadic eye movement task[15]. It has been proposed by Previc[2] that there might be an ecological significance to the functional specialization of the UVF and LVF, which is in agreement with the functional segregation of the dorsal and ventral visual cortical pathways.

In contrast to the large numbers of behavioral studies, relatively few electrophysiological studies have examined asymmetries between the two vertical hemifields. One study using magnetoencephalograph (MEG) revealed stronger occipital activation in response to the LVF stimuli than to the UVF stimuli[16]; another MEG study reported direction-dependent apparent motion in UVF but not in LVF[17]. Several ERP studies consistently reported that the latencies of early components (P1 and N1) were shorter in LVF than in UVF[3,18]. However, the findings about the amplitude of ERPs varied across studies. The amplitude of early components (P1 and N1) between the UVF and LVF were similar in two studies[18,19], but different in another study[20]. Moreover, these studies did not report whether there was an asymmetry in the late ERP components (such as N2 and P3) between the UVF and LVF.

The findings reported for attention are equally confusing. Although the attentional modulation on early ERP components has been revealed in both UVF and LVF[19,20], there was few studies exploring the attentional difference between the two visual fields. The neural mechanism of the attentional asymmetry between the UVF and LVF remains unknown.

The aim of the present study is to determine the electrophysiological asymmetries between the UVF and LVF for both early and late ERP components, and to investigate asymmetries in the attentional modulation of the evoked potentials between the UVF and LVF.

1 Material and methods

1.1 Subjects, stimuli and procedure

Sixteen postgraduate and undergraduate students (6 females) ages from 19 to 25 years were studied. All subjects were right-handed and had normal or corrected-to-normal vision. Stimuli were presented in white on a black background using a computer-controlled video monitor 70 cm from the subjects' eyes. A green fixation cross (0.4×0.4°) appeared in the center of the monitor during the experiment. Three types of stimuli were used (Fig. 1). Each stimu-7lus (2.6×2.6°) contained a vertical bar (0.3×2.6°) intersecting a horizontal bar (2.6×0.3°). The junction of the two bars was located in the middle of the horizontal bar for the target stimulus (Fig. 1(a)) and 0.6° to the left or right of the horizontal bar for the non-target stimulus (Fig. 1(b) and (c)). The stimulus was presented on the vertical meridian, 4.8° above or below the fixation point (center-to-center). The stimulus presentation duration was 50 ms. Interstimulus intervals (ISI) were randomized between 550 and 950 ms.

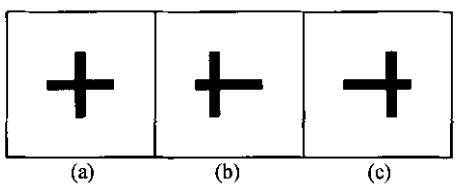

Fig. 1. Stimuli used in the present experiment. (a) Target; (b) and (c) non-target. Subjects were required to respond explicitly to the target presented in the attended hemifield.

For each subject, 32 blocks of 100 trials were performed. In each block, there were 20 trials of target stimuli (10 in the UVF and 10 in the LVF) and 80 trials of non-target stimuli (40 in the UVF and 40 in the LVF). The stimuli were presented randomly for both types (target/non-target) and location (UVF/LVF). Subjects were instructed to maintain fixation throughout each block and were told that their eye movements were monitored. The attended hemifield (UVF or LVF) was indicated before each block started. For half of the blocks, subjects were told to pay attention to the UVF, and for the other half, to the LVF. Subjects were required to press a button with the left or right thumb when they detected a target stimulus in the attended hemifield. Both accuracy and speed of responses were emphasized equally. The order of the blocks and the response of left/right thumb were counterbalanced across subjects. Subjects received one practice block for each of the two conditions (attending to the UVF and attending to the LVF) before the ERP recording began.

1.2 Electrophysiological data recording and analysis

The electroencephalogram (EEG) was recorded using an EEG/ERP system (NeuroScan Inc.) with 29 channels in the standard 10-10 System (FP1, FP2; F7, F3, Fz, F4, F8; FT7, FC3, FC4, FT8; T7, C3, Cz, C4, T8; TP7, CP3, CPz, CP4, TP8; P7, P3, Pz, P4, P8; O1, Oz, and O2). Horizontal and vertical electro-oculograms (EOGs) were also recorded. The EEG was physically referenced to the left mastoid and was then off-line re-referenced to the average of the left and right mastoid. Impedance of each electrode was below 5 kÙ. EEG data were digitized on-line at a sampling rate of 500 Hz. After acquisition, a 0.1—40 Hz band pass filtering was applied off-line. Each epoch of the EEG was from 200 ms of pre-stimulus to 800 ms of post-stimulus. The baseline for ERP measurements was the mean voltage of the 200 ms pre-stimulus interval. The EEG to only non-target stimuli (without explicit response) was analyzed for minimizing movement-related artifacts of finger response. Trials contaminated by eye blinks or muscle potentials at any electrode or by incorrect behavioral responses were excluded from the ERP averages. To minimize the contribution of differential eye movements during recording to the ERP results, the HEOG and VEOG were inspected carefully off-line, and trials with detectable ocular deflections (about 10% of the trials overall) were rejected. The HEOG and VEOG were then averaged separately over stimulate-up and simulate-low trials, and the results indicated that in each condition the eye deviation from fixation was <0.3°.

Behavioral and ERP data were analyzed with repeated-measure analyses of variances (ANOVAs) within subjects. For behavioral data there was only one factor: Visual Field (UVF vs. LVF). For the ERP data, four-way ANOVAs were analyzed for the peak amplitude and peak latency of the N1 component (at O1, O2, P7, and P8 sites), and for the mean amplitude of the P1 (at O1, O2, P7, and P8 sites), N2 (at C3, C4, CP3, and CP4 sites) and P3 (at CP3, CP4, P3 and P4 sites) components. The factors were Visual Field, Attention (Attended vs. Unattended), Hemisphere (Left vs. Right)

and Area (Occipital vs. Temporal for P1 and N1, Central vs. Central-parietal for N2, and Central-parietal vs. Parietal for P3).

2 Results

2.1 Behavioral data

Both reaction time and response accuracy did not differ between the UVF (515 ms, 89.2%) and LVF (521 ms, 90.7%) stimuli ($F(1,15)=2.169$ and 0.819 respectively; both Ps > 0.1).

2.2 ERP data

The grand average ERPs elicited by the non-target stimuli under the four conditions (i.e. UVF/attended, UVF/unattended, LVF/attended, and LVF/unattended) are shown in Fig. 2. The P1 (80—130 ms) and N1 (140—200 ms) components were both quite different for the upper and lower field stimuli. While the lower field stimuli elicited a small P1 (with the maximum over the lateral occipito-temporal areas), the upper field stimuli elicited a much larger P1 (with the maximum over the occipital area). The N1 component was prominent over the occipital area for the lower field stimuli, and over the temporal area for the upper field stimuli. The upper and lower field stimuli elicited similar N2 (250—290 ms) components over the lateral central-parietal areas and P3 (350—470 ms) components over a broad area, which were both more evident under the attended conditions. The ERP amplitudes and latencies are listed in Table 1.

ANOVAs showed a significant main effect of Visual Field on P1 amplitude ($F(1,15)=29.197$, $p<0.001$). The amplitude of P1 was much larger for the upper field stimuli than for the lower field stimuli. In addition, a significant Visual Field × Area interaction ($F(1,15)=25.461$, $p< 0.001$) suggested different distributions of P1 between the UVF and the LVF. Further analysis showed that, for UVF, the P1 was much larger over the occipital than the temporal area ($F(1,15)=35.126$, $p<0.001$), whereas for LVF, the amplitude of P1 between areas was similar ($F(1,15)=3.090$, $p>0.05$). The P1 component was modulated by spatial attention, where the attended stimuli elicited much larger P1s ($F(1,15)=21.271$, $p<0.001$). Moreover, a significant Attention × Visual Field interaction ($F(1,15)=5.749$, $p<0.05$) was found, suggesting that the attentional effect on P1 differed between the UVF and LVF. In contrast to the large attentional effect in the UVF (attended-unattended: 0.74 μV; $F(1,15)=19.388$, $p<0.001$), the attentional effect in the LVF was weaker (attended-unattended: 0.34 ì V; $F(1,15)=9.325$, $p<0.01$).

The lower field stimuli elicited significantly larger N1 than the upper field stimuli ($F(1,15)=132.170$, $p<0.001$). Also, a significant Visual Field × Area interaction ($F(1,15)=79.455$, $p<0.001$) was found, suggest-

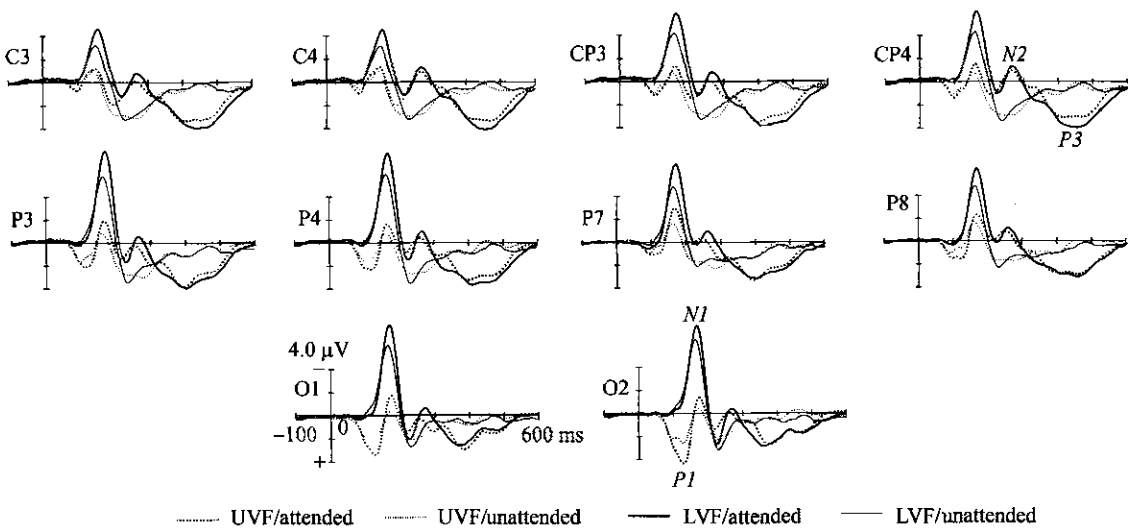

Fig. 2. Grand average ERPs waveforms (n=16) elicited by non-targets. Separate waveforms are plotted for trials in which the non-targets were present in the attended UVF (thick dotted line), the unattended UVF (thin dotted line), the attended LVF (thick solid line) and the unattended LVF (thin solid line).

Table 1 Amplitude and latency of ERP components under different conditions[a)]

	Electrodes	Attended UVF	Unattended UVF	Attended LVF	Unattended LVF
P1 amplitude (80—130 ms)	P7	0.92 ± 0.26	0.57 ± 0.24	0.14 ± 0.18	–0.28 ± 0.17
	P8	1.41 ± 0.34	0.72 ± 0.26	0.00 ± 0.25	–0.18 ± 0.23
	O1	2.60 ± 0.41	1.81 ± 0.41	–0.12 ± 0.28	–0.57 ± 0.29
	O2	3.24 ± 0.49	2.14 ± 0.46	–0.40 ± 0.46	–0.72 ± 0.36
N1 amplitude	P7	–3.42 ± 0.50	–1.91 ± 0.43	–7.11 ± 0.58	–5.06 ± 0.49
	P8	–3.14 ± 0.61	–2.06 ± 0.35	–6.67 ± 0.62	–5.00 ± 0.45
	O1	–2.34 ± 0.66	–0.89 ± 0.41	–8.34 ± 0.67	–6.46 ± 0.56
	O2	–2.23 ± 0.69	–0.99 ± 0.40	–8.16 ± 0.81	–6.82 ± 0.68
N2 amplitude (250—290 ms)	C3	0.13 ± 0.74	2.98 ± 0.68	–0.54 ± 0.78	2.83 ± 0.42
	C4	–0.65 ± 0.77	2.12 ± 0.51	–1.00 ± 0.88	2.59 ± 0.55
	CP3	0.31 ± 0.73	3.00 ± 0.60	–0.52 ± 0.77	2.46 ± 0.44
	CP4	–0.66 ± 0.76	2.80 ± 0.70	–1.00 ± 0.87	2.32 ± 0.54
P3 amplitude (350—470 ms)	CP3	2.99 ± 0.66	0.58 ± 0.34	3.36 ± 0.69	0.48 ± 0.26
	CP4	2.71 ± 0.55	0.70 ± 0.37	3.25 ± 0.61	0.60 ± 0.23
	P3	3.11 ± 0.56	0.64 ± 0.30	3.42 ± 0.61	0.83 ± 0.28
	P4	2.88 ± 0.49	0.49 ± 0.32	3.26 ± 0.56	0.67 ± 0.24
N1 latency	P7	171 ± 4	160 ± 3	168 ± 2	161 ± 2
	P8	172 ± 5	163 ± 3	167 ± 2	162 ± 2
	O1	176 ± 4	172 ± 3	168 ± 2	162 ± 2
	O2	180 ± 4	173 ± 3	166 ± 2	162 ± 2

a) For P1, N2 and P3, mean amplitudes (mean ± S.E; μV) were measured; for N1, peak amplitude (mean ± S.E; μV) and peak latency (mean ± S.E; ms) were measured.

ing different distributions of N1 between the UVF and LVF. Further analysis showed that, for UVF, the N1 was larger over temporal area ($F(1,15)=11.209$, $p<0.01$), whereas for LVF, the N1 was larger over the occipital area ($F(1,15)=11.971$, $p<0.01$). Like P1, the N1 amplitude was much larger under the attended than unattended condition ($F(1,15)=23.799$, $p<0.001$). No attentional difference was shown between the UVF and LVF ($F(1,15)=1.250$, $p>0.2$). In addition, N1's latency was earlier for the LVF stimuli than the UVF stimuli ($F(1,15)=10.143$, $p<0.01$) and was earlier for the unattended stimuli than the attended stimuli ($F(1,15)=12.474$, $p<0.01$). No significant Attention × Visual Field interaction on N1 latency was found ($F(1,15)=1.131$, $p> 0.3$).

Unlike P1 and N1 components, N2 and P3 components did not show significant difference between the UVF and LVF in amplitude (N2: $F(1,15)=1.798$, $p>0.1$; P3: $F(1,15)=1.270$, $p>0.2$). The attended stimuli elicited much larger N2 and P3 than the unattended stimuli (N2: $F(1,15)=23.616$, $p<0.001$; P3: $F(1,15)=24.897$, $p<0.001$), and these attentional effects resulted in no significant difference between the UVF and LVF (N2: $F(1,15)<1$, P3: $F(1,15)=2.230$; both Ps >0.1).

3 Discussion

While the behavioral performance showed no difference corresponding to the upper and lower field stimuli, significant electrophysiological differences were found in the distribution and amplitude of P1 and N1, the latency of N1, and the attentional modulation effect of P1.

The lower field stimuli elicited a laterally-distributed, much smaller P1 and a wider, much larger N1 than the upper field stimuli. Similar findings were also obtained in a previous study by Gunter *et al.*[20]. Since the representations of the UVF and LVF are widely separated in the extrastriate cortex[4,5] from where P1 and N1 are believed to be generated[21], we suggest that these ERP differences on P1 and N1 are based on the difference in

the cortical representation of the two vertical hemifields. However, two recent studies by Di Russo *et al.*[18,19] did not find significant difference for P1 and N1 amplitudes between the UVF and LVF. The inconsistency of these findings might be accounted for by the different stimuli and paradigms used in these experiments. In particular, stimuli were presented on the vertical meridian in our and Gunter's studies but in the visual quadrants in Di Russo's studies. According to the retinotopic organization principle, different locations of the visual field would map to different extrastriate areas of the brain. We suggest that the different stimulus positions and different cortical representations may play an important role in the different evoked brain potentials between our and Di Russo's studies.

In addition to the larger peak amplitude, N1 also exhibited shorter peak latency for the lower than for the upper field stimuli. This is consistent with a previous ERP study[22], and supports the greater sensitivity of human visual system to lower field stimuli than to upper field stimuli. This LVF precedence fits well with the anatomical findings that receptors and retina ganglion cells are denser in the upper than the lower hemiretina of humans[23].

In contrast to the early ERP components (P1 and N1), the late ERP components (N2 and P3) showed little difference between the UVF and LVF. The N2 and P3 components, which were mainly distributed over relatively higher levels of brain cortex, might reflect higher cognitive processes in this experiment, such as stimuli identification and/or decision[24,25], where little upper/lower specificity would be expected. Moreover, the N2 and P3 were much more prominent under the attended condition than under the unattended condition, suggesting that unattended information might be largely filtered out before reaching later cognitive processes (stimulus identification and/or decision). Considering the early and late ERP components together, we suggest that the electrophysiological asymmetries between the UVF and LVF occur mainly in the early stage of visual information processing and in the low levels of brain cortex.

In addition to the above electrophysiological differences, more interestingly, our study found that attentional modulation differed between the UVF and LVF. Specifically, the enhancement of amplitude in the P1 component induced by spatial selective attention was more pronounced for the UVF than for the LVF. One possible explanation of the smaller P1 attentional modulation in LVF may be due to the smaller P1 amplitude in LVF than in UVF. But this possibility alone can not explain both the P1 and N1 results, since no attentional difference in the N1 component was detected, which also exhibited different amplitude across hemifields. A more plausible explanation is that the different attentional modulation of P1 reflects the attentional asymmetry between the two vertical hemifields. There was no such attentional difference in N1, N2 and P3 components, suggesting that the attentional asymmetry occurred only in early stage of information processing. Considering the equally good behavioral results across hemifields, we proposed that the lesser attentional effect in the LVF may reflect LVF superiority on attention. That is, attention might be more efficient in LVF than in UVF when performing the same task. This speculation is in agreement with a previous behavioral study[12] in which attentional superiority was found in the LVF, with the LVF showing a greater attentional resolution. The attentional superiority of LVF, together with the greater sensitivity to LVF stimuli, suggests a preference for LVF information in humans.

Finally, in our study, sustained attention to the upper and lower visual fields generated enhanced P1 and N1 components, which is consistent with previous studies[26]. However, the peak latency of N1 for attended stimuli was a little longer than that for unattended stimuli. This result is different from previous studies[26], in which spatial attention did not affect the latencies of the early ERP components. It is a question for further study.

In conclusion, the present study provides clear electrophysiological evidence for the different visual processing between the UVF and LVF. The asymmetry was present not only in the distributions, amplitudes, and latencies of early ERP components but also in the attentional modulation of early visual activity. Our data suggest that the electrophysiological asymmetry between the UVF and LVF mainly occurs in the early stage of visual information processing, and the attentional asymmetry might reflect an attentional superiority for the LVF.

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References

1. Hellige, J. B., Hemispheric asymmetry for visual information processing, Acta. Neurobiol. Exp., 1996, 56: 485—497.
2. Previc, F. H., Functional specialization in the lower and upper visual fields in humans: Its ecological origins and neurophysiological implications, Behav. Brain Sci., 1990, 13: 519—575.
3. Skrandies, W., The upper and lower visual field of man: Electrophysiological and functional differences, Prog. Sens. Physiol., 1987, 8: 1—93.
4. Felleman, D. J., Van Essen, D. C., Distributed hierarchical processing in the primate cerebral cortex, Cereb. Cortex, 1991, 1: 1—47.
5. Sereno, M. I., Dale, A. M., Reppas, J. B. *et al.*, Borders of multiple visual areas in human revealed by functional magnetic resonance imaging, Science, 1995, 268: 889—893.
6. Payne, W. H., Visual reaction times on a circle about the fovea, Science, 1967, 155: 481—482.
7. Riopelle, A. J., Bevan, W., The distribution of scotopic sensitivity in human vision, Am. J. Psychol., 1952, 66: 73—80.
8. Rubin, N., Nakayama, K., Shapley, R., Enhanced perception of illusory contours in the lower versus upper visual hemifields, Science, 1996, 271: 651—653.
9. Bilodeau L, Faubert J, Isoluminance and chromatic motion perception throughout the visual field, Vision Res., 1997, 37: 2076—2081.
10. Danckert, J., Goodale, M. A., Superior performance for visually guided pointing in the lower visual field, Exp. Brain Res., 2001, 137: 303—308.
11. Genzano, V. R., Di Nocera, F., Ferlazzo, F., Upper/lower visual field asymmetry on a spatial relocation memory task, Neuroreport, 2001, 12: 1227—1230.
12. He, S., Cavanagh, P., Intrilligator, J., Attentional resolution and the locus of visual awareness, Nature, 1996, 383: 334—337.
13. Altpeter, E., Mackeben, M., Trauzettel-Klosinski, S., The importance of sustained attention for patients with maculopathies, Vision Res. 2000, 40: 1539—1547.
14. Goldstein, A., Babkoff, H., A comparison of upper vs. lower and right vs. left visual fields using lexical decision, Q. J. Exp. Psychol. A, 2001, 54A: 1239—1259.
15. Zhou, W., King, W. M., Attentional sensitivity and asymmetries of vertical saccade generation in monkey, Vision Res., 2002, 42: 771—779.
16. Portin, K., Vanni, S., Virsu, V. *et al.*, Stronger occipital cortical activation to lower than upper visual field stimuli. Neuromagnetic recordings, Exp. Brain Res., 1999, 124: 287—294.
17. Naito, T., Kaneoke, Y., Osaka, N. *et al.*, Asymmetry of the human visual field in magnetic response to apparent motion, Brain Res., 2000, 865: 221—226.
18. Di Russo, F., Martínez, A., Sereno, M. I. *et al.*, Cortical sources of the early components of the visual evoked potential, Hum. Brain Mapp., 2001, 15: 95—111.
19. Di Russo, F., Martínez, A., Hillyard, S. A, Source analysis of event-related cortical activity during visuo-spatial attention, Cereb. Cortex, 2003, 13: 486—499.
20. Gunter, T. C., Wijers, A. A., Jackson, J. L. *et al.*, Visual spatial attention to stimuli presented on the vertical and horizontal meridian: An ERP study, Psychophysiology, 1994, 31: 140—153.
21. Clark, V. P., Fan, S., Hillyard, S. A., Identification of early visual evoked potential generators by retinotopic and topographic analyses, Hum. Brain Mapp., 1995, 2: 170—187.
22. Miniussi, C., Girelli, M., Marzi, C. A., Neural site of the redundant target effect electrophysiological evidence, J. Cogn. Neurosci., 1998, 10: 216—230.
23. Curcio, C. A., Allen, K. A., Topography of ganglion cells in human retina, J. Comp. Neurol., 1990, 300: 5—25.
24. Renault, B., Ragot, R., Lesevre, N., Remond, A., Onset and offset of brain events as indices of mental chronometry, Science, 1982, 215: 1413—1415.
25. Schapkin, S. A., Gusev, A. N., Kuhl, J., Categorization of unilaterally presented emotional words: An ERP analysis, Acta. Neurobiol. Exp., 2000, 60: 17—28.
26. Mangun, G. R., Neural mechanisms of visual selective attention, Psychophysiology, 1995, 32: 4—18.

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