

Late Divergence of Target and Nontarget ERPs in a Visual Oddball Task

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Summary

Different mental operations were expected in the late phase of intracerebral ERPs obtained in the visual oddball task with mental counting. Therefore we searched for late divergences of target and nontarget ERPs followed by components exceeding the temporal window of the P300 wave. Electrical activity from 152 brain regions of 14 epileptic patients was recorded by means of depth electrodes. Average target and nontarget records from 1800 ms long EEG periods free of epileptic activity were compared. Late divergence preceded by almost identical course of the target and nontarget ERPs was found in 16 brain regions of 6 patients. The mean latency of the divergence point was 570±93 ms after the stimulus onset. The target post-divergence section of the ERP differed from the nontarget one by opposite polarity, different latency of the components, or even different number of the components. Generators of post-divergence ERP components were found in the parahippocampal gyrus, superior, middle and inferior temporal gyri, amygdala, and fronto-orbital cortex. Finding of late divergence indicates that functional differences exist even not sooner than during the final phase of the task.

Key words

Intracerebral recording • Oddball task • Visual evoked potentials
• Mental counting • Memory

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Introduction

Scalp-recorded event-related potentials (ERPs) elicited during the so-called “oddball” task have been employed for decades as a useful tool for studying the processes of cognition. In the oddball task the subject responds by button pressing and/or mental counting only to the infrequent “target” (T) stimulus, which is presented randomly and repeatedly among frequent “nontarget” (NT) stimuli. The electrophysiological response to the targets is compared with that to the nontargets and the difference is taken as a measure of the differences in underlying brain processes (Sutton *et al.* 1965). As a rule, these ERPs are composed of several components, which differ in amplitude, latency, and/or polarity. The early or exogenous ERP components are thought to express the stimulus identification processes (Jewett *et al.* 1970, Grönfors 1993). On scalp recording these components are referred to as P100, N100, and P200. The later or endogenous ERP components are considered to be associated with cognitive processes. One of the most studied endogenous ERP components is the P300 or P3 wave, the largest positive-going peak occurring after the exogenous components within a time window of 250-500 ms. Subsequent research showed that this component occurs in two main variants, P3a and P3b (Polich 1998, Comerchero and Polich 1999). These variants differ in latency and amplitude distribution.

According to recent interpretation (Polich 2007), the P3a originates from stimulus/driven frontal attention mechanisms during task processing, whereas P3b originates from temporal-parietal activity associated with attention and appears related to subsequent memory processing. It has also been suggested that the P300 may be related to updating internal models about context and environment, which is triggered by event-related changes in theta rhythms reflecting self-motion (Shin 2011), thus supporting the view that cognition may be tightly interlocked to motor activity.

The assessment of differences between the target and nontarget ERPs is usually based on the amplitude and latency differences in the components. The differences between the T and NT responses occur in exogenous components if the triggering stimulus situation is complex (Luck and Hillyard 1994). On the other hand, the P300 components always differ in the T and NT responses representing a key differential sign (Hillyard *et al.* 1971, O'Donnell *et al.* 1997). In the nontarget response the P300 component either does not appear at all or exhibits smaller amplitude (Kok 1997).

From the behavioral point of view the oddball task consists of a sequence of brain operations, which include the detection of the stimulus, decoding its significance, decision "what to do", execution of the instructed movement, and/or counting the T stimuli. The difference between the T and NT tasks in principle consists in motor response and counting of stimuli in the target trials and doing nothing in the nontarget ones. Searching for the spatiotemporal relationship between these operations using registration of the ERP is in scalp recording difficult because of large summation of the electrophysiological signals. The intracerebral recording is far more suitable in this respect. For example, in a number of cortical and subcortical brain structures generators of the P3-like wave were found using intracerebral electrodes (McCarthy *et al.* 1989, Baudena *et al.* 1995, Halgren *et al.* 1995a, b, 1998, Brázdil *et al.* 1999, 2003, Rektor *et al.* 2003, 2005, 2007, Sochůrková *et al.* 2006, Damborská *et al.* 2009). Intracerebral recording disclosed also brain sites with different temporal characteristics of the P3-like component in the visual oddball task: one type related to the stimulus, other type related to the movement, and yet another type without any obvious relationship to these events (Roman *et al.* 2005). Another study reports on the modality specific P3-like component elicited in certain brain sites (Halgren *et al.* 1995b). With the help of

intracerebral recording, generators of late evoked potentials similar to P3-like component were also found in Contingent Negative Variation paradigm in cortical as well as subcortical sites (Bareš *et al.* 2003). Intracerebral recording methods were also employed in studies using different response conditions in which the existence of task-specific P3-like potential generators (Brázdil *et al.* 2003) and of Contingent Negative Potential generators (Bareš *et al.* 2007) was proved.

The description of spatiotemporal characteristics of intracerebral ERP components may provide relevant data for understanding of organization and functional principles of cognitive networks (Brázdil *et al.* 2003, Kukleta *et al.* 2003, Roman *et al.* 2005, Damborská *et al.* 2006, Rektor *et al.* 2007). The oddball paradigm seems to be very useful in this respect, as it consists of sequence of partial functions both in target and nontarget variants. These functions are believed to be associated with the sequence of ERP components and thus the point of divergence (DP) between the target and nontarget ERPs found in a given brain site can be considered as a demonstration of the beginning of a functional divergence. In accordance with this interpretation the onset of the P3-like component could be considered as one example of such divergences. While there are many intracerebral studies aimed at the P3-like component in the visual oddball task, only two of them concerned also components of longer latency. In lateralized visual oddball intracerebral studies (Clarke *et al.* 1999a, b) patients exhibited late (>600 ms peak latency) ERP components with slow/broad morphology in response to target stimuli that, in turn, were either absent or of smaller amplitude to nontarget stimuli. These components were typically negative-going and followed behavioral motor responses. They were pervasive, and polarity reversals were present in the insula/operculum region. Authors interpreted them as reflecting activity from secondary somatosensory cortex.

In the current study we searched for the divergence points of the target and nontarget ERPs in very late phase of the visual oddball task with mental counting. We supposed that even in the time window exceeding the latency of the P3-like component, differences between the target and nontarget ERPs should appear, thus giving rise to such late divergences, because different mental operations are expected in this phase.

Table 1. Investigated brain structures.

Patient	Electrodes (left/right)	Contacts (left/right)	Structures
1	5/2	28/13	AMY', PHG', FG', STG', MTG', ITG', FOC', RG' PHG, ITG, CG, A6
2	5/4	25/16	AMY', HIP', PHG', STG', MTG', ITG', OG' AMY, HIP, PHG, MTG, OG
3	4/1	27/15	AMY', PHG', FG', MTG', ITG', CG', DLPFC', WTL' HIP, BG, WFL
4	1/6	15/26	HIP', PHG', BG', WFL' AMY, HIP, FG, STG, MTG, ITG, CG, OG, DLPFC, MFG
5	1/1	14/14	AMY', HIP', BG', WTL', WFL' AMY, HIP, BG, WTL, WFL
6	6/4	24/17	AMY', HIP', STG', MTG', OG', MeFG' AMY, HIP, MTG, CG, RG, MFG, IFG, WFL
7	1/3	12/29	AMY', HIP' HIP, PHG, STG, DLPFC, FOC
8	1/3	13/28	AMY', PHG', BG', STG', MTG', WTL', WFL' AMY, HIP, BG, STG, MTG, ITG, WTL, WFL
9	0/6	0/41	AMY, HIP, PHG, FG, STG, MTG, ITG, FOC, RG, MeFG, MFG
10	0/4	0/27	AMY, HIP, STG, MTG, WTL
11	0/6	0/36	HIP, FG, STG, MTG, ITG, CG, A4, A5, IPL, MT, WTL, WPL
12	4/5	15/26	HIP', MTG', CG', DLPFC', A8', A9', A10' HIP, MTG, CG, DLPFC, MFG, A8, WTL, WFL
13	7/0	41/0	AMY', HIP', STG', MTG', CG', DLPFC', FOC', A9', WFL'
14	3/0	29/0	AMY', PHG', FG', BG', MTG', ITG', WTL'

Number of the patient; number of electrodes implanted in the left and right hemispheres; number of contacts exploring sites in the left and right hemispheres; anatomical structures investigated: AMY – amygdala, HIP – hippocampus, PHG – parahippocampal gyrus, FG – fusiform gyrus, BG – basal ganglia, STG, MTG, and ITG – superior, middle, and inferior temporal gyri, CG – cingulate gyrus, DLPFC – dorsolateral prefrontal cortex, FOC – fronto-orbital cortex, OG – orbital gyri, RG – rectal gyrus, MeFG, MFG, and IFG – medial, middle, and inferior frontal gyri, A 4, 5, 6, 8, 9, and 10 – Brodmann's areas 4, 5, 6, 8, 9, and 10, IPL – inferior parietal lobule, MT – mesencephalic tegmentum, WTL, WFL, and WPL – white matter of the temporal, frontal, and parietal lobes, symbol (') indicates structures of the left hemisphere.

Materials and Methods

Subjects

Fourteen patients (3 women) aged from 20 to 45 years were employed in the study. All subjects suffered from medically intractable epilepsy and were candidates for surgical treatment. They all were under antiepileptic drug therapy, which was determined by clinical considerations. During the period of diagnostic examination by intracerebral EEG recording, the doses of medicaments were reduced to allow seizures to develop spontaneously. They had normal or corrected-to-normal vision and all but one (Patient No. 6) were right-handed. The subjects gave us their informed consent to the

experimental protocol that had been approved by the Ethical Committee of Masaryk University.

Paradigm

A visual oddball task with mental counting was performed. The patients were sitting comfortably in a moderately lighted room and were focusing the centre of a monitor situated at about 100 cm from their eyes. Yellow capital letters X (target, T) or O (nontarget, NT) appeared repeatedly on white background in random order as experimental stimuli. Each stimulus presentation lasted 200 ms and the interstimulus interval varied randomly between 2 and 5 seconds. The target stimuli were five times less frequent than the nontarget ones. The

subjects were instructed to press a microswitch button with the dominant hand as quickly as possible, whenever a T stimulus appeared, to mentally count the T stimuli, and to ignore the NT stimuli.

Data acquisition

Electrical activity was recorded during the task simultaneously from various brain sites by means of standard Micro Deep semi-flexible multicontact platinum electrodes. Having a diameter of 0.8 mm, each electrode carried 5-15 contacts 2.0 mm long separated by constant intervals of 1.5 mm. Strictly for diagnostic reasons, intracerebral depth electrodes were implanted to the patients; and structures of the frontal, temporal, and parietal lobes were examined (Table 1). Every patient received from 2 to 10 such electrodes exploring either or both hemispheres. Long electrodes examined both lateral and mesial cortical regions. The electrodes were placed using the methodology of Talairach *et al.* (1967) and their position was afterwards verified by magnetic resonance imaging with electrodes in situ. The registration was made with the help of a 64-channel Brain Quick EEG system (Micromed). All the recordings were monopolar with respect to a reference electrode attached to the right processus mastoideus. The impedances used were less than 5 k Ω . The EEG signal was amplified with a bandwidth of 0.1-40 Hz at a sampling rate of 128 Hz. One of the channels recorded the button pressing and yet another channel recorded the presentation of the experimental stimuli. We did not do electrooculography, because in contrast to the scalp recordings artefacts caused by eye movements and blinking are considered to be negligible in depth recordings.

Analysis

The signal analysis was made offline with the help of ScopeWin software providing us 44 channels for simultaneous recordings. The recordings from lesions and epileptogenic zones and the trials with artefacts were rejected offline with visual inspection made by experienced person. Switching the button in response to a nontarget stimulus or its omission in response to a target one were considered as errors. In each subject all artefact-free trials with correct responses were used for calculation of average curves. Excluding of different number of trials explains the interindividual variability in number of trials used (29-58 T trials, 198-331 NT trials). Peristimulus EEG periods (from -300 to +1500 ms from the stimulus onset) were averaged separately for T and

NT responses using the stimulus onset as a trigger. The statistical significance of ERP components was computed between the mean amplitude observed during the baseline region (from -600 to -100 ms from the stimulus onset) and the mean value computed as a mean from the neighbourhood of each point (170 ms length) after stimuli using a non-parametric Wilcoxon Rank Sum (Signed Rank) test for paired samples.

Records from one contact of each multicontact intracerebral electrode implanted in a particular anatomical structure were included into the analysis selecting the largest one from ERPs. In such selected contacts the amplitude differences between the target and nontarget records were assessed using a cluster-based permutation test (Maris and Oostenveld 2007). In every contact, clusters of time samples whose absolute t-value was larger than 97.5th quantile of T-distribution were computed in the poststimulus EEG period (from 0 ms to +1500 ms from the stimulus onset). Monte-Carlo estimates of the permutation p-values for each cluster were calculated on 1000 random partitions of the data set and compared with a critical alpha-level of 0.05. We disclosed brain regions with an initially almost identical course of the target and nontarget ERPs followed by a clear-cut divergence. The onset of such divergence was identified as the starting time point of the first statistically significant cluster in the post-stimulus period. To assess the portion of ERPs, attributable to movement-related potentials, we investigated the character of the relationship between the latency of a particular target post-divergence ERP component and the reaction time using the method already applied for classification of P3-like waves (Roman *et al.* 2005).

Results

The performance of subjects during the task was very good not seeming to be substantially influenced by their illness and medication (only 1.3 \pm 1.7 % of all responses were incorrect; mean patient's SRI varied between 457 \pm 34 ms and 644 \pm 78 ms, median 525 \pm 63 ms). Total number of explored brain regions was 152; ERPs were found in 102 regions, which make 67 % of explored regions. In assessing the number of ERP components, their polarity, latency and amplitude, various regions generating several types of ERP were identified: 1) regions that generated different ERPs to target and nontarget stimuli (22 brain regions); 2) regions that generated the target and nontarget ERPs exhibiting clear-cut divergence after initially almost identical curves

(41 brain regions); 3) regions that generated target and nontarget ERPs with almost identical course but statistically significantly different amplitudes in some of their components (20 brain regions); 4) regions generating ERP only to target but not to nontarget stimuli (9 brain regions); 5) regions generating almost identical ERPs to target and nontarget stimuli (10 brain regions).

In accordance with the aim of the current study, only ERPs from group 2) were further analyzed. In this group ERPs were arbitrarily divided into two subgroups according to the latency of their divergence. The first subgroup (early divergence) included ERPs diverging sooner than 420 ms after the stimulus onset and the second subgroup (late divergence) included ERPs diverging later

than 420 ms after the stimulus onset (see Figure 1 and Table 2).

ERPs exhibiting the early divergence were found in nine patients in 25 brain regions (15 in the frontal lobe, 8 in the temporal lobe, and 2 in the parietal lobe). The mean latency of the point of divergence was 346 ± 35 ms from the stimulus onset. ERPs exhibiting the late divergence were found in six patients in 16 brain regions (13 in the temporal lobe and 3 in the frontal lobe). The mean latency of the point of divergence was 570 ± 93 ms from the stimulus onset. Statistical testing showed significant amplitude differences in post-divergence section of all the early and late diverging ERPs (cluster-based permutation test).

Table 2. Early and late divergences of the target and nontarget ERPs.

EARLY				LATE			
Patient (Contact)	Struct.	Latency ms	% RT	Patient (Contact)	Struct.	Latency ms	% RT
1(C'6)	ITG	280	49	1(A'1)	AMY	440	77
1(F3)	CG	360	63	1(B'2)	PHG	536	93
1(F11)	Area 6	368	64	1(B2)	PHG	568	98
1(O'2)	FOC	320	56	1(C'2)	PHG	640	111
3(G'2)	CG	312	66	1(T'3)	STG	640	111
4(G1)	CG	352	67	2(B'5)	ITG	616	96
5(X14)	BG	312	55	2(C'2)	PHG	488	76
6(D'4)	STG	344	68	2(C3)	FG	552	86
6(G2)	CG	392	78	3(C'14)	MTG	448	95
6(O'6)	OG	376	75	3(B'3)	PHG	800	169
6(O6)	IFG	416	83	4(A9)	MTG	664	126
6(T'1)	STG	368	73	4(C10)	ITG	624	119
6(B9)	MTG	328	65	4(X'1)	PHG	592	112
6(G10)	MFG	336	67	5(X'10)	BG	544	95
11(B4)	HIP	320	67	9(O11)	FOC	520	89
11(B9)	MTG	344	72	9(P1)	MeFG	440	75
11(G2)	CG	312	65				
11(R5)	Area 5	344	72				
11(B14)	ITG	408	85				
11(G11)	IPL	376	79				
11(T3)	STG	400	84				
12(F'3)	Area 8	360	61				
13(G'1)	CG	288	56				
13(O'8)	DLPFC	312	61				
14(X'15)	BG	328	72				

MFG – middle frontal gyrus, MeFG - medial frontal gyrus, IFG – inferior frontal gyrus, FOC – fronto-orbital cortex, OG – orbital gyri, DLPFC – dorsolateral prefrontal cortex, STG – superior temporal gyrus, MTG – middle temporal gyrus, ITG – inferior temporal gyrus; IPL – inferior parietal lobule, CG – cingulate gyrus; BG – basal ganglia, AMY – amygdala, FG – fusiform gyrus, PHG – parahippocampal gyrus, HIP – hippocampus, Area 5, Area 6, Area 8 – Brodmann's areas; symbol (') indicates structures of the left hemisphere, the divergence point latency is given in ms and in % of patient's mean reaction time (% RT).

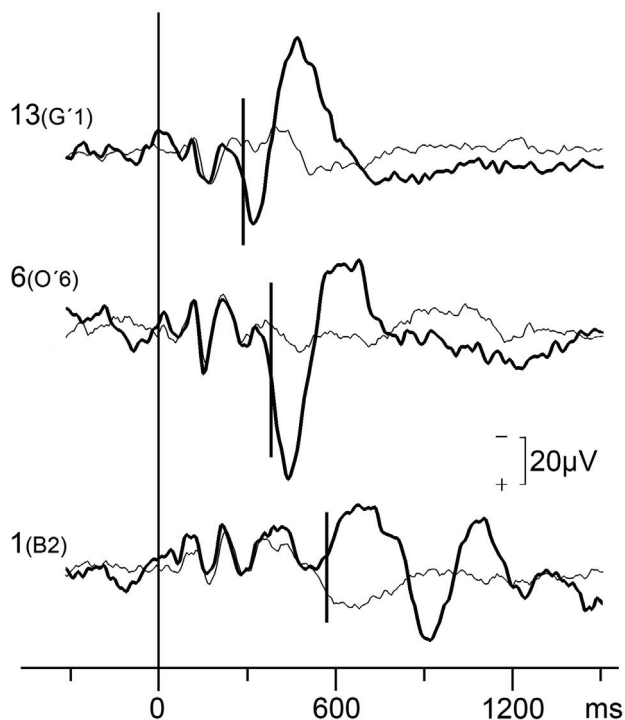


Fig. 1. Selected examples of early (288 ms and 376 ms), and late (568 ms) divergences of ERPs elicited in response to target (thick curve) and nontarget (thin curve) stimuli. Curves are labelled with patient number and recording contact (13G'1 – cingulate gyrus, 6O'6 – orbital gyri, 1B2 – parahippocampal gyrus); vertical line at zero point indicates the stimulus onset; short vertical lines indicate the divergence points of target and nontarget ERPs (i.e. the starting time point of the first statistically significant cluster calculated in the post-stimulus period using the cluster-based permutation test); symbol (') indicates structures of the left hemisphere.

The relationship between the divergence point latency and the reaction time can be assessed from the values presented in the Table 2. It is evident that the late divergence appeared shortly before, after, or approximately at the moment of the button pressing (in average at 102 ± 23 % of the mean reaction time).

Figure 2 shows all of the late diverging ERPs. Six of them were found in the right and ten of them in the left hemispheres. No clear-cut preponderance of ERPs exhibiting the late divergence was observed in any anatomical structure; however, most of these ERPs exhibited signs of local generation of post-divergence components in structures of temporal lobe. One example of local generation for each type of response is presented in Figure 3. Phase reversals of target post-divergence components were found in the amygdala (1A'1), fronto-orbital cortex (9 O11), and parahippocampal gyrus (1B2); phase reversals of nontarget components were found in the amygdala (1A'1), parahippocampal gyrus (1B2), and

middle temporal gyrus (4A9). Relative decrease of amplitude by 36 ± 16 % in adjacent contacts of the same electrode was observed on target post-divergence components in the parahippocampal gyrus (1B'2, 1C'2, 2C'2, 3B'3, and 4X'1), superior (1T'3), middle (3C'14 and 4A9), and inferior (2B'5 and 4C10) temporal gyri. Relative decrease of amplitude by 39 ± 13 % in adjacent contacts of the same electrode was observed on nontarget post-divergence components in the parahippocampal gyrus (1B'2, 1C'2, 2C'2, and 4X'1), middle (3C'14) and inferior (2B'5 and 4C10) temporal gyri. Thus, generators of the target late post-divergence components were found in the amygdala (in 1 out of 16 explored regions), parahippocampal gyrus (in 6 out of 10 explored brain regions), fronto-orbital cortex (in 1 out of 4 explored brain regions), superior temporal gyrus (in 1 out of 11 explored brain regions), middle temporal gyrus (in 2 out of 16 explored brain regions), and inferior temporal gyrus (in 2 out of 9 explored brain regions), generators of the nontarget late post-divergence components were found in the same anatomical structures with the exception of the superior temporal and the fronto-orbital cortex.

From the records presented in Fig. 2 it is evident that clear-cut components were observed in the post-divergence section of not only all target but also of most nontarget late diverging ERPs. The post-divergence section of the target ERP was unequivocally different from the nontarget one exhibiting opposite polarity, different latency, or even different number of the components (see Table 3). The peak latency of the first post-divergence component varied between 516 and 968 ms (mean 695 ± 140 ms) in the T response and between 576 and 1128 ms (mean 725 ± 145 ms) in the NT response. The number of post-divergence ERP components varied between one and three in the T response and was significantly higher than the number of post-divergence ERP components in the NT response, which varied between none and two ($p < 0.001$, Student's paired *t*-test). From 32 target post-divergence ERP components (Table 3) only two were time-locked to the button pressing (superior temporal gyrus, fusiform gyrus), seven were time-locked to the stimulus onset (amygdala, parahippocampal gyrus, superior temporal gyrus) and 23 had ambiguous relationship to both these events (amygdala, parahippocampal gyrus, fusiform gyrus, middle and inferior temporal gyri, basal ganglia, fronto-orbital cortex, and medial frontal gyri).

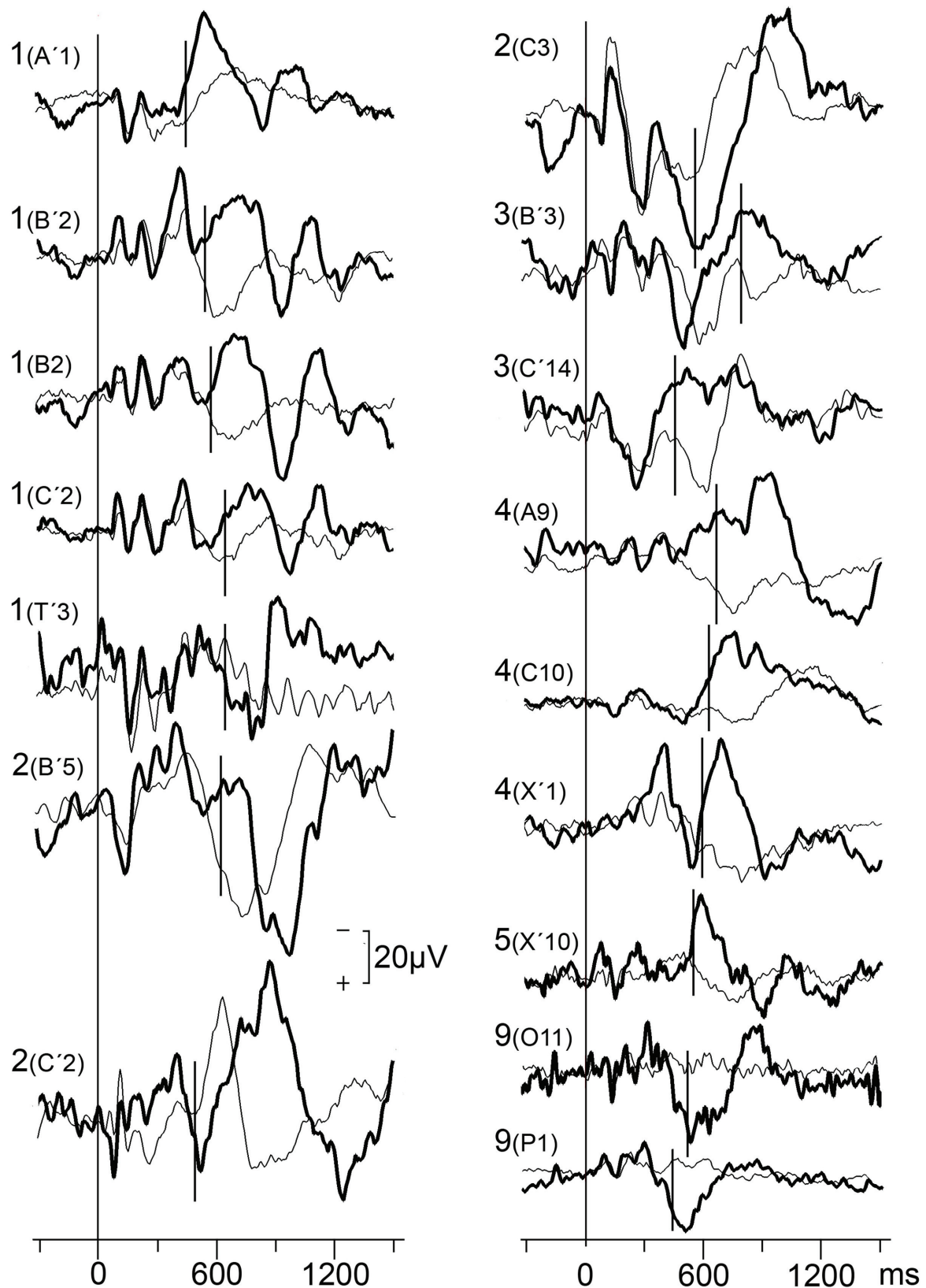


Fig. 2. Late divergence of the ERPs elicited in response to target (thick curve) and nontarget (thin curve) stimuli. Curves are labelled with patient number and recording contact; vertical line at zero point indicates the stimulus onset; short vertical lines indicate the divergence points of target and nontarget ERPs (i.e. the starting time point of the first statistically significant cluster calculated in the post-stimulus period using the cluster-based permutation test); symbol (') indicates structures of the left hemisphere.

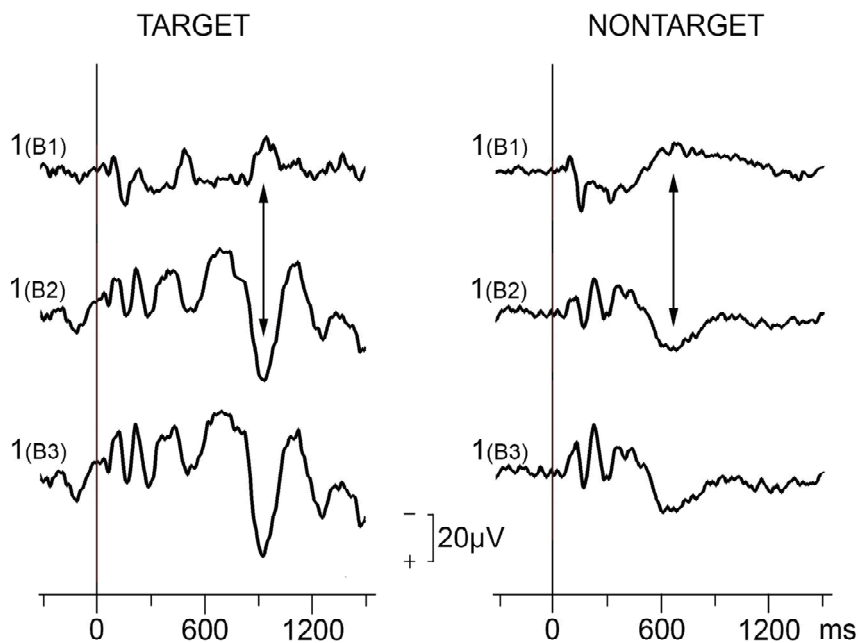


Fig. 3. An example of post-divergence ERP components. **Left section:** records from consecutive contacts of an electrode passing through the right parahippocampal gyrus (phase reversal between B1 and B2) in the target response; **Right section:** records from the same contacts in the nontarget response. Vertical line at zero point indicates the stimulus onset. Records from 1(B2) contact are also presented in Figure 1 and Figure 2.

Table 3. Polarity and latency of the target and nontarget late post-divergence components.

Patient (Contact)	Structure	Target		Nontarget		
		Post-divergence components		Post-divergence components		
1(A'1)	AMY	N528 ^a	N992		N704	
1(B'2)	PHG	N736	P928 ^a	N1088 ^a	P576	
1(B2)	PHG	N688	P920	N1112 ^a	P656	
1(C'2)	PHG	N752	P952 ^a	N1112	P600	N856
1(T'3)	STG	P773 ^b	N904 ^a			
2(B'5)	ITG	P968			P728	N1072
2(C'2)	PHG	P523	N864	P1240	N600	P776
2(C3)	FG	P568 ^b	N944		N824	
3(C'14)	MTG	N752			P600	N776
3(B'3)	PHG	N828	P1211			
4(A9)	MTG	N936	P1360		P744	
4(C10)	ITG	N752			N1128	
4(X'1)	PHG	N680 ^a	N1200		P792	
5(X'10)	BG	N584	N882		P744	
9(O11)	FOC	P531	N835			
9(P1)	MeFG	P516				

AMY – amygdala, PHG – parahippocampal gyrus, FOC – fronto-orbital cortex; STG – superior temporal gyrus, MTG – middle temporal gyrus, ITG – inferior temporal gyrus; FG – fusiform gyrus, BG – basal ganglia, MeFG – medial frontal gyrus, N – negativity, upward deflection, P – positivity, downward deflection; symbol (') indicates structures of the left hemisphere, ^a component time-locked to the stimulus, ^b component time-locked to the button pressing.

Discussion

Our results demonstrated the existence of the target and nontarget event-related potentials initially

almost identical in course and then divergent, with the point of divergence manifesting in the very late phase of the visual oddball task. The question arose as to whether these late divergences could be related to the differences

in motor demands between T and NT tasks. Certain factors suggest otherwise. The motor system activities that precede execution of movement include decision-making, action planning, and formation of a motor command. As the results of this study showed, the DP occurred shortly before, after, or at the moment of pressing the button. Thus, all of the pre-movement activities occurred during the period when the two EEG responses were following almost identical courses. Further, post-movement activity cannot be excluded from considerations of factors leading to the divergence. However, such involvement may only be partial because only negligible portion of ERP components was time-locked to the button pressing. The ERPs attributable to movement-related potentials were found in superior temporal and fusiform gyri.

Memory mechanisms are involved in the various steps of the task from beginning to end. They start with cognitive discrimination of the stimuli and continue with selection of the correct response, i.e. the decision as to whether to move or not and whether to count or not, in order to follow the instructions for the experiment. The next important step associated with memory processes involves counting the target stimuli. When counting, one must recall the result of the previous calculation, then do the calculation, which consists of adding "one" to the recalled number, and then store the new result in the memory.

Our results showed that majority of the generators of the late post-divergence ERP components were observed in structures known to participate in memory processes. Due to the fact that recording sites were selected according to diagnostic concerns, and many regions potentially engaged in the task were not explored, the possibility to use this result for functional interpretations is limited. Thus, it still remains in question as to whether the late post-divergence ERP components could represent mental counting processes or other processes, for instance those associated with so-called closure of the whole response (disengagement from the just finished decision, engagement to the consecutive one).

Our results also showed a predominance of targets over nontargets in terms of the number of late post-divergence ERP components. The higher number of late post-divergence ERP components indicated in the T variant suggests higher demands on memory functions in the T response. This interpretation is also in accordance with the results of the visual oddball studies without

mental counting (Clarke *et al.* 1999a, b), where only single target components are reported in different brain sites during the very late phase of the task. Unlike in present study no counting process was performed after target stimulus presentation in these studies, which could lead there to decreased number of late target ERP components.

In a paradigm where two different stimuli are presented and two different tasks are required it is not surprising that the ERPs diverge (for further details, see Brázdil *et al.* 2003, Rektor *et al.* 2007). Of more interest in the current study is the finding that the divergence point in several brain sites was observed so late in the course of the EEG response. In these responses, the targets and nontargets revealed an almost identical course of ERPs until this very late DP, thus suggesting that the stimuli were being processed equally in these brain sites for a very long time. It seems paradoxical that during the period, in which the stimuli have already been distinguished, while the subject must be aware of different demands and the motor response has already been planned and in some cases even executed, some sites in the brain keep responding almost identically. However, in the light of the previous demonstration of brain sites with task-relevant EEG activity almost identical during the whole oddball task (Kukleta *et al.* 2003); this finding does not appear so illogical. Evidently, as well as the specific electrical activities elicited in the oddball task, there are also activities that are common to the T and NT responses. As regards the processes underlying the non-specific activities, they could include consciousness and sustained attention, since these functions are required for both T and NT responses.

Extensive literature on event-related potentials in target detection tasks shows that the target and nontarget electrophysiological responses may diverge after sensory potentials had been elicited, giving rise to a post-divergence ERP component, well-known as the P300 component (see Polich 2007). This occurs after the initial phase of ERPs in which the stimulus is being detected and discriminated. This component represents the cognitive functions involved in the orientation of attention, contextual updating, response modulation, and response resolution. In scalp recordings it consists mainly of two variants, P3a and P3b (Courchesne *et al.* 1975, Squires *et al.* 1975, Knight 1984, Donchin and Coles 1988, Comerchero and Polich 1999, Polich 2007), which differ in their scalp topography and temporal

characteristics. The P3a exhibits a frontal/central scalp distribution and a relatively short peak latency, while the P3b exhibits a parietal scalp distribution and relatively long peak latency. In this context the early post-divergence components presented in present study could correspond to the P3a-like and P3b-like waveforms.

The differences between EEG responses are generally viewed as reflecting differences between underlying functions engaged in the tasks. By the same logic, differences between the late post-divergence ERP components described in the current study (see Fig. 2 and Table 3) appear to embody different brain processes in the late phase of the target and nontarget task variants. These processes might be associated with the different closure of the task. It is not clear, however, to what extent these differences are associated with different demands on memory engagement in relation to the request for counting the target stimuli. These late post-divergence ERP components generated in the

parahippocampal gyrus, superior, middle and inferior temporal gyri, amygdala, and fronto-orbital cortex represent a finding that was previously missing in the whole interpretation of ERP from visual oddball task with mental counting.

Conflict of Interest

There is no conflict of interest.

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