Mismatch negativity does not show evidence of memory reactivation in the visual modality

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ABSTRACT

The possibility of reactivation of the memory representation underlying visual mismatch negativity (vMMN) was investigated in a modified passive roving-standard paradigm. Stimuli (arrays of Gábor patches) were presented in sequences with blank interval between the sequences. The first member of each sequence was identical to the standard of the previous sequence, while the second stimulus had different orientation therefore the second stimulus was considered as deviant. In a control condition the stimuli of the previous sequence had random orientations. Event-related potentials (ERPs) in response to the deviants were compared to ERPs in response to the (physically identical) second stimulus of the control sequences. The comparison showed emergence of a positive component at an early (98-132 ms) latency range elicited by deviants. This component is interpreted as an index of increased sensitivity to rare changes in sequences dominated by identical stimuli rather than a component specific to violation of sequential regularity. Consequently, contrary to the findings in the auditory modality, the first stimulus of the sequence did not reactivate the memory representation underlying the vMMN, since subsequent deviant elicited no vMMN.

KEYWORDS

visual mismatch negativity, change positivity, reactivation, roving-standard paradigm

INTRODUCTION

The behavioral value of an event is often defined by the context in which the event is embedded. Therefore, organizing environmental stimulation along invariant characteristics increases the effectiveness of the processing of both the regular context and the events that are different from the regularity. An automatic mechanism underlying such function can be investigated by examining the mismatch negativity (MMN) components of event-related brain potentials (ERPs) both in the auditory (MMN; for reviews see Winkler, 2007; Schröger, 2007) and in the visual (vMMN; for review see Czigler, 2007) modalities. MMN is commonly investigated in oddball paradigms composed of frequent and infrequent stimuli in pseudorandom order. The function of the frequent stimuli (standard) is to represent a sequential regularity which is, in that simple case, frequency or repetition. Presentation of a rare stimulus (deviant) different from the frequent one in some feature values violates the sequential rule. In other words, the incoming stimulus mismatches to the predicted one. This mismatch elicits an event-related potential component (MMN), observable as the difference between ERPs in response to the deviant and the standard. In the visual modality, the polarity of such a difference potential is typically negative (but see Sulykos and Czigler, 2011), it has parieto-occipital maximum, and peaks at around 140 – 350 ms after the onset of the deviant event. Besides the sensitivity to violation of regularity, the other defining feature of vMMN is that it emerges to non-attended stimuli. Visual MMN is obtained even if the registration of the eliciting stimuli is not correlated with conscious perception or explicit report (Berti, 2011; Czigler and Pató, 2009).

Visual MMN is distinguished from another automatic, change-related ERP component, the change positivity (Fu et al., 2003; Kimura, 2005, 2006; Wang et al., 2003). As Kimura et al. (2006) pointed out, this component is also related to memory processes. Furthermore, it is independent of attentional processes. Unlike vMMN that has been recorded to single deviant features as well as to deviant conjunctions of features and also to the violation of complex sequential regularities (Winkler et al., 2005; Czigler et al. 2006), change positivity was investigated so far only to the change of single visual features. In short, vMMN is an index of brain processes initiated by events violating an automatically established representation of sequential regularities.

The mechanism underlying vMMN requests the active maintenance of regularity representation. However, a given regularity is relevant only in a specific environmental context; in the simplest case in the context in which the regularity has been established (Ritter et al., 2002). Consequently, context changes of the visual environment may deactivate the representation of regularity. Context change can be introduced by an unusually long break between two stimulus sequences (Gaeta et al., 2001, Winkler et al., 2001). However, after such a break an event representing the previously established regularity (i.e., corresponding to the previous context) may reinstate the validity of the regulation (Ritter et al., 2002). Such effect is termed as “reactivation phenomenon” (see Winkler and Cowan, 2005 for a review), and was first reported by Cowan et al. (1993). In this auditory study, stimulus sequences of nine pure tones were presented, and the sequences were separated by silent intervals of 11-15 sec. There were two types of sequences. In deviant sequences one of the nine tones had deviant frequency, and the standard sequences consisted of nine identical tones. In the deviant sequences the deviants were either in position 1, 2, 4, 6 or 8. After the silent interval, position 1 deviant elicited no MMN, while position 2 deviant did. Since a single standard cannot establish sequential regularity, this result shows that the previously established regularity was preserved. Furthermore the lack of mismatch response to position 1 deviant revealed that during the silent period this memory representation became inactive. However, the first standard of the sequence reactivated the preserved regularity, i.e., it served as a reminder.

In the present study, we investigated the possibility of reactivation effects on vMMN using a modified roving-standard paradigm, similar to the methods used in an auditory study that have reported reactivation effects (Ritter et al. 2002). The stimuli were arrays of Gábor patches. The critical feature of the task-irrelevant stimulation was the deviant orientation of the Gábor patches. In a previous study orientation deviancy of such stimuli resulted in clear vMMN (Sulykos and Czigler, 2011). In position 1 the orientation of the Gábor patches was identical to the standard of the previous sequence (reminder), in position 2 the Gábor patches had different orientation (deviant). The appropriate controls for deviant effects were delivered in a control condition (Winkler et al., 2002). In this condition, the standards were replaced by randomly oriented stimuli. Nevertheless, the first and second stimuli of the second members of the sequence-pairs were identical to the stimuli of a reactivation sequence.

In case of similar reactivation processes in the auditory and visual modalities, a visual stimulus identical to the standard of the previous sequence is expected to reactivate the representation of regularity established in the previous sequence, and accordingly, the second “deviant” stimulus is expected to elicit vMMN. To test this possibility ERPs into the deviant stimuli of the reactivation condition were compared to the ERPs of the second stimuli of the control condition. In the control condition the previous sequence did not establish any sequential regularity.

MATERIAL AND METHODS

Participants (5 female and 7 male, mean age = 21.5 years, SD = 2.4) signed an informed consent form prior to the experimental session. All of the participants had normal or corrected-to-normal vision. The study was conducted in accordance to the Declaration of Helsinki.

Participants were seated in a reclining chair 1.2 m from a 17 inch monitor (75 Hz refresh rate) in a dimly lit, sound-attenuated chamber. The primary task was designed as a simple video game. Participants used a gamepad controlling a spaceship to maneuver among other spaceships in, and along, a canyon. The task was to avoid the red spaceships and to catch the green ones (the color of the controlled spaceship was blue; see Figure 1B). The video animation appeared on the upper half of the visual field, while vMMN related stimuli were presented to the lower half of the visual field. Test stimuli were Gábor patch grayscale images (Gaussian-windowed sinusoidal gratings with 3 cycles / image). These stimuli were presented in six various orientations (0°-150°, in 30° steps). Within a stimulus-pattern there were 21 patches, arranged along four semicircles (see Figure 1B). Both the radius of the semicircles and the diameter of the images increased exponentially (with a quotient of 1.5), approximating the cortical magnification factor (e.g. Leff, 2004), i.e., the patches were smaller near to the center of the screen, and the size of the patches increased exponentially towards the periphery.

The radius of the smallest semicircle was 1.4 deg, and the diameter of the smallest image was 1 deg. The background was dark.

The task-irrelevant stimuli were clustered into sequences (Figure 1A). Each sequence contained 14 stimuli. Series of 30 sequences created a block, a session included 12 blocks. The stimulus onset asynchrony (SOA) was 690 ms within the stimulus sequences, while the sequences were separated by a 4750 ms blank interval. The duration of the stimulus presentation was 80 ms.

The orientations of the within-sequence stimuli varied according to the experimental conditions[1]. In the *reactivation condition*, every sequences (except the first one of each block) started with a *reminder* identical to the standards of the previous sequence. The reminder was followed by a *deviant* stimulus which differed from the reminder in orientation (the difference was 30°). After the deviant, 12 identical stimuli (standards) were presented to establish a new sequential regularity. The orientation of these standards was randomly selected from the remaining 4 orientations (6 possible orientations minus the reminder and deviant orientations). In the *control condition*, pseudo-random sequences of 14 stimuli were presented. The first and second stimuli of a given sequence were not presented in the previous sequence.

Please insert Figure 1 about here

EEG was recorded (DC-30 Hz, sampling rate 500 Hz; Synamps2 amplifier, NeuroScan recording system) with Ag/AgCl electrodes placed at 61 locations (according to the extended 10-20 system) using an elastic electrode cap (EasyCap). The common reference electrode was placed on the right mastoid; the ground electrode was attached to the forehead. The horizontal EOG was recorded with a bipolar configuration between electrodes positioned lateral to the outer canthi of the two eyes. Vertical eye movements were monitored with a bipolar montage between electrodes placed above and below the right eye. The EEG signal was low-pass filtered offline with a cutoff frequency of 1 Hz (24 dB/octave slope); the signal was then re-referenced to the average activity. Epochs of 500 ms in duration (including a 100 ms pre-stimulus interval) were extracted for each event and were averaged separately for each condition and sequence position. The mean voltage during the 100 ms pre-stimulus interval was used as the baseline for amplitude measurements, and epochs with an amplitude change exceeding ±50 μV on any channel were excluded from further analysis.

Statistical analyses were carried out in two steps. In the first step point-by-point t tests were calculated at posterior locations on the reactivation *minus* control difference potentials. In the second step, based on the t-tests, a channel matrix was defined (P1, Pz, P2, PO3, POz, PO4, O1, Oz, O2) as the region of interest (ROI). Within this matrix mean amplitude values were calculated for epochs of +/- 4 ms (5 data points) around the maximum differences of ERPs between the reactivation and control conditions, and these values were entered into ANOVAs. The factors were Condition (reactivation, control), Posteriority (parietal, parieto-occipital, and occipital areas) and Laterality (left, midline, right). Behavioral performance was measured in a two-way ANOVA with the Condition (reactivation and control) and Task (rate of avoidance of the red ships and rate of catch the green ones) as the factors. When appropriate, the Greenhouse-

Geisser correction was applied. Partial eta-squared (η^2) presented the explained variance of the effect.

RESULTS

There were no performance differences between the reactivation and control conditions: a two-way ANOVA with factors of Condition and Task (avoidance vs. catch) resulted no significant Condition main effect or interaction. The main effect of Task was significant [$F(1,11)=176.1$, $p<0.001$, $\eta^2=0.94$]. Accordingly, participants avoided the red targets at a higher rate (92.4 %) than the rate at which they caught the green targets (72.9%).

Figure 2 shows ERPs that were elicited by the second stimuli of the reactivation and control conditions. As the figure shows, ERPs have three major components: P1, N1 and P2 with approximately 90, 125 and 250 ms peak latencies, respectively.

Reactivation effect was expected as a negativity to position 2 stimulus of the reactivation condition (deviant after the reminder), in comparison to ERPs to position 2 stimulus of the control condition. However, in the vMMN range (140-350 ms) no such negative difference emerged at the first step of analysis. Instead, the deviant minus control difference potential was positive in an earlier latency range. The early positivity was proved to be significant at Pz, P2, P4, PO3, POz, PO4, O1, Oz, O2 electrode locations. The amplitude maximum of the positivity was at the POz location, with 112 ms peak latency. Table 1 shows the amplitude and latency values of the P1 and the difference potential.

The latency of the difference potential was longer than the latencies of the P1 components. In an ANOVA with factors of Condition (control, difference), Anteriority and Laterality, the main effect of Condition was significant [$F(1,11)=50.8$, $p<0.001$, $\eta^2=0.82$]. In a similar analysis with deviant and difference as values of Condition factor, the main effect of Condition was also significant [$F(1,11)=32.6$, $p<0.001$, $\eta^2=0.75$]. However, by comparing P1 latencies of ERPs to deviants and control stimuli, we obtained no latency difference. Concerning the mean amplitude values of the ERPs in the latency range of the P1 component (86-94 ms), three-way ANOVA with the factors of Condition (deviant, control), Anteriority and Laterality showed neither Condition main effect nor any interaction with the Condition factor. On the contrary, a similar analysis on mean amplitude values at a later latency range (108-116 ms: 8 ms epoch around the peak latency of the difference potential) revealed significant Condition main effect [$F(1,11)=11.2$, $p<0.01$, $\eta^2=0.50$]. Furthermore, there was a distribution difference between the P1 and the difference potential. The amplitude values of P1 were calculated by averaging the non-scaled (Urbach and Kutas, 2002) mean epoch amplitudes of P1 components belonging the two conditions. Using a three-way ANOVA with the factors of Component (P1, difference), Anteriority, and Laterality, we compared this average to the mean epoch amplitudes of the difference potentials over the parieto-occipital and occipital locations. According to the ANOVA, Anteriority main effect [$F(1,11)=27.57$, $p<0.001$, $\eta^2=0.71$] and Component x Anteriority interaction was also significant [$F(1,11)=6.17$, $p<0.05$, $\eta^2=0.36$]. This interaction was due to the parieto-occipital P1 maximum and the even distribution of the difference potential over the posterior locations.

Please insert Figure 2 and Table 1 about here

DISCUSSION

ERPs were measured to deviants preceded by a stimulus identical to the standard of the previous sequence. ERPs to these deviants were compared to ERPs elicited by control stimuli. Emergence of vMMN, a negative shift to deviants in the 120-320 ms latency range was expected as an evidence of reactivation effect. Contrary to the expectancy, no vMMN was elicited by the deviant. Instead, this comparison resulted in a positive deflection in an earlier, 98 – 132 ms latency range. This finding is different from that obtained in the auditory modality (Cowan et al., 1993; Ritter et al., 1998, 2002; Winkler et al., 1996). Accordingly, in the visual modality, presenting a stimulus corresponding to the previously established regularity did not engender any brain activity specific to violation of sequential regularities. The lack of reactivation effect can be interpreted in at least two different ways. First, it is possible that the representation of regularity decayed during the blank interval. Along these lines, in the present paradigm decay period would be shorter than the 12 sec, reported by Maekawa et al. (2009). The stimuli of the two studies were quite different, we used more stringent control of attention, and it is possible that the representation of regularity in our roving-standard paradigm was different from the representation in an oddball paradigm. Second, assuming the maintenance of the regularity representation, the lack of a mismatch response could be due to the unsuccessful reactivation of the “dormant” regularity representation. A recent observation supports the latter interpretation. Kimura et al. (in preparation) delivered trains of six successive bar stimuli. The first stimulus of a train was either an orientation deviant or the standard of the previous sequence. The authors found that the first position deviant elicited a vMMN even after a 5 sec blank interval. This result shows the possibility of preserved active mental representation for at least 5 sec. In our study the inter-train intervals were approximately equivalent to 5 sec, and the deviant feature dimension was similar either (i.e., orientation); thus it is reasonable to assume that the representation of regularity was similarly preserved in our case. Accordingly, contrary to studies in the auditory modality, the type of reminder (a single repetition of the standard of the previous sequence) in this roving-standard paradigm was inappropriate for reinstating the context in which the sequential regularity representation had been established.

Nevertheless we observed different processing of deviant and control stimuli in position two, as reflected by the positive deflection on the deviant-related ERPs. This positivity resembles to the change positivity reported in some studies (e.g., Fu et al., 2003; Kimura et al., 2005, 2006; Wang, 2003). Most of the “change positivity studies” applied sequentially presented stimulus pairs (S1 – S2 paradigm). Stimuli were identical or different in task-related and/or task-unrelated stimulus features. Change and no-change trials appeared with equal probability, therefore the presentation of S1 did not predict S2 characteristics. Change positivity emerged to stimuli with different task-independent features, i.e., as a difference between feature change vs. feature repetition. The situation in our reactivation paradigm was different. In both conditions (reactivation and control) the first and second members of the sequences were different from each other. While in the reactivation condition the stimulus change was preceded by 12 stimuli identical to the first stimulus of the new sequence (plus the blank period) and in the control condition, the sequence preceding the blank consisted of stimuli with mixed orientations. Therefore, unlike in the change positivity studies, the emergence of positivity was due to the characteristics of a set of antecedent stimuli. Considering the positivity obtained our study as “change positivity”, it is worth to note that this activity seems to be sensitive to previous environmental stimulation’s characteristics. In other words, processes underlying change positivity might also involve the representation of dominant feature-values of the situation. Additionally this memory representation was preserved during the 5 sec blank interval. Temporal limitation of change positivity as well as its sensitivity to the characteristics of environmental stimulation is a poorly investigated domain of automatic change detection studies. Presumptions requested to regard the component as change positivity exceeded the feasible interpretations based on the present results. Instead, as an alternative (and more plausible) explanation of the recent data we suggest that the appearance of the early positivity is due to a global difference between the two conditions. Reactivation condition was dominated by stimulus repetitions, while the Control condition was dominated by changing stimuli. In the context of repetitive stimulation a stimulus change is a more salient event than a similar change in a constantly changing environment. According to this view the early positivity is regarded to be the manifestation of the increased sensitivity.

One may attribute the early difference to the modulation of the P1 component. One of the possibilities of the modulating effect is the stimulus-specific habituation. However, in the present design the second member of a sequence was preceded by a stimulus with different orientation, and the first stimulus was preceded by a longer blank period. Furthermore, none of the second stimuli appeared in the previous sequence in either of the two conditions. As a second modulating effect, P1 amplitude is sensitive to spatial attention (e.g. Mangun et al., 1998), but in the present study there was no difference in spatial attention between the conditions. The deviant minus control difference (i.e., emergence of the positive difference potential) could also be attributed to a slight P1 latency difference between the two conditions. Contrary to this possibility, in the range of P1 amplitude maximum there was no significant latency difference between the two conditions. Finally, the scalp distribution of the P1 and the difference potential was not identical. Consequently, it might be reasonable to suggest that the early positivity is regarded as a genuine component rather than a consequence of amplitude or latency modulation of the exogenous components.

In summary, we did not obtain data indicative of reactivation effect in the present study Results supported neither that the memory representation underlying vMMN became inactive nor that this representation was reactivated by the reminder. The potential reasons of the null results might derive from the inappropriate reminder applied to reactivate the context in which the sequential regularity representation had been established. Investigating the appropriate reminder specific to the visual domain is a feasible way to obtain reactivation effect. Then again, it is possible that the representation of regularity in a roving-standard paradigm was different from the representation in an oddball paradigm. Investigating the reactivation phenomenon in an oddball design could be another way to find similarities between the auditory mismatch negativity and its visual counterpart. Nevertheless, a positive component is obtained to stimulus-changes embedded in environment constructing mainly from repetitive stimulus. This component is regarded as an index of enhanced sensitivity of change-detection processes.

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FOOTNOTE

[1] We also conducted a third condition. In this ‘interference’ condition the blank interval of the reactivation condition was replaced by the presentation of six Gábor-patch patterns with pseudo-random orientation. The results of this condition did not result in any additional finding, except that the first of the six random stimuli elicited a posterior negativity. This negativity can be considered as the aggregate of vMMN and the increased exogenous activity to a stimulus free of feature-specific refractoriness.

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Table 1. Latency (ms) and amplitude values (μV) of the P1 component and the difference potential. (S.E.M in parenthesis)

		P1		Difference potential
		Deviant	Control	
Latency	POz	93.7 (3.0)	90.8 (3.2)	115.3 (4.5)
	Oz	82.87 (6.2)	78.3 (6.0)	111.5 (4.7)
Amplitude	POz	2.6 (0.5)	2.3 (0.5)	0.8 (0.2)
	Oz	0.9 (0.7)	0.5 (0.6)	0.6 (0.2)

FIGURES

Figure 1

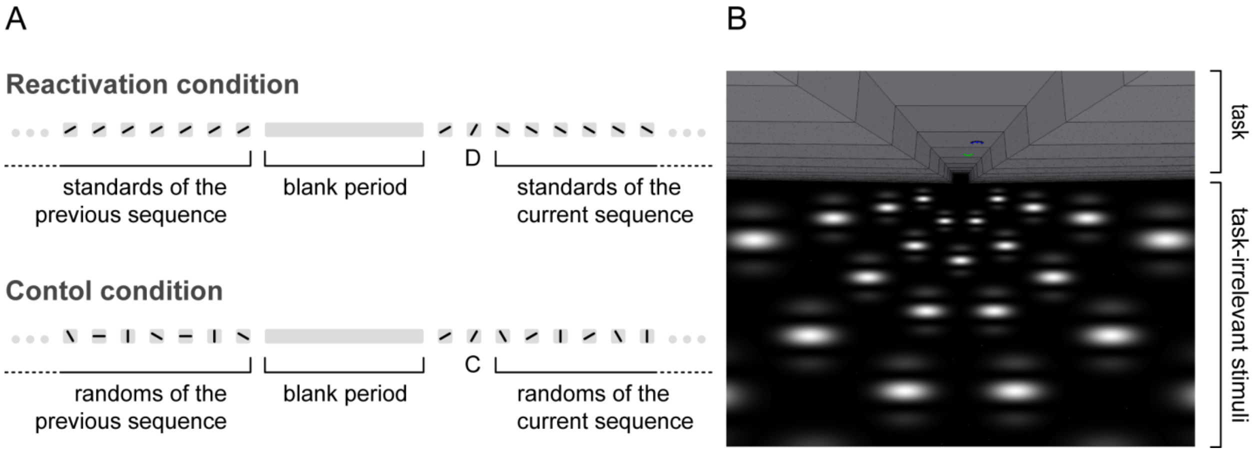
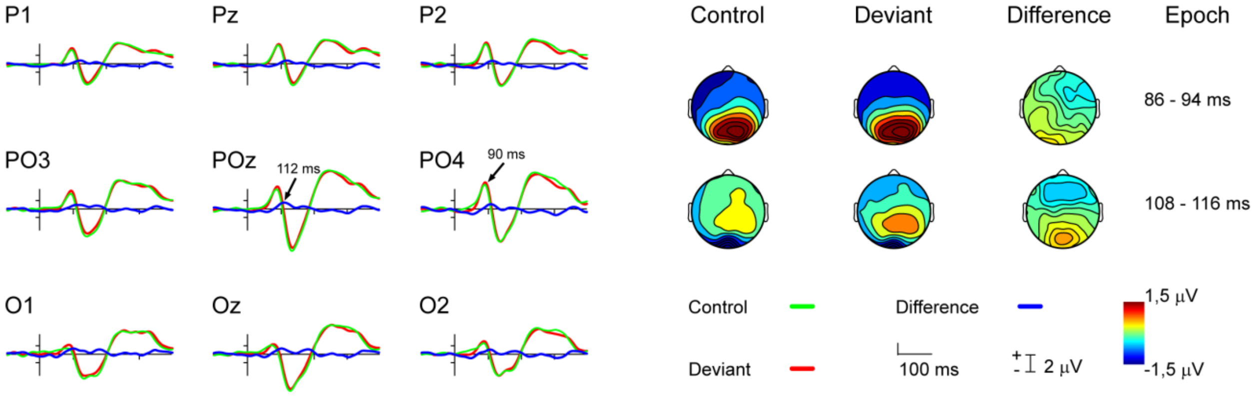


Figure 2



LEGENDS OF FIGURES

Figure 1

Experimental paradigm and stimuli. (A) Schematic illustration of experimental paradigm. Tilted bars symbolize the orientations of stimulus-patterns. D: deviant stimulus; C:

control stimulus for deviant; (B) An example of the display. ERPs were recorded for stimuli appeared at lower visual half-field. Upper half-field presented the task.

Figure 2

ERPs and deviant minus control difference potential registered at posterior channels. Voltage maps depict the mean amplitude values of latency range around the maxima of exogenous (upper row) and difference (lower row) potentials.