

**ELECTROPHYSIOLOGICAL CORRELATES OF MEMORY-
BASED VISUAL CHANGE DETECTION IN HUMANS**

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Abstrakti

Ärsykepoikkeamatilanteessa (oddball) toistuvasti esitetty ärsyke (standardi) korvataan satunnaisesti poikkeavalla ärsykkeellä (deviantti), jolloin ainakin kuuloaistipiirissä syntyy poikkeavaan ärsykkeeseen poikkeavuusnegatiivisuusvaste (MMN). Tämän tutkimuksen tarkoitus oli selvittää, onko visuaalisessa aistipiirissä auditorista poikkeavuusnegatiivisuutta (MMN) vastaava vaste, ja mikäli on niin millainen ärsyke voi synnyttää sen. Herätevasteet mitattiin koehenkilöiden päänahan pinnalta keskiviivan elektrodeista, koehenkilöiden kuunnellessa kuunnelmaa ja keskittyessä auditoriseen tehtävään. Kokeissa esiintyi satunnaisessa järjestyksessä oddball-tilanne, deviant-alone-tilanne sekä tilanne, jossa standardeja ja deviantteja esiintyi yhtä paljon. Tutkimuksessa käytettiin kahta erilaista ärsykeparia, joista toinen stimuloi verkkokalvoa yksityiskohtaisesti (shakkiruudukko) ja toinen kokonaisvaltaisesti (värivalot). Tässä tutkimuksessa ei löytynyt auditorista MMN-vastetta vastaavaa visuaalista vastetta, mutta molemmissa kokeissa syntyi varhainen positiivinen muistipohjainen herätevaste (ERP) oddball tilanteessa. Nämä erot standardin ja deviantin välillä eivät syntyneet deviant-alone-tilanteessa, jossa standardit poistettiin sarjasta. Täten tämän tutkimuksen mukaan visuaalinen aistipiiri rekisteröi eroja automaattisesti jo hyvin varhaisella latenssilla, mutta on mahdollisesti mekanismiltaan erilainen kuin auditorinen aistipiiri.

Avainsanat: Herätevaste (ERP); Poikkeavuusnegatiivisuus (MMN); Muutoksen havainnointi; Ihminen; Visuaalinen; Varhainen vaste

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Abstract

In the oddball condition a frequently presented stimulus (standard) is occasionally replaced by a different stimulus (deviant) when at least in the auditory modality mismatch negativity (MMN) response is elicited to the deviant one. The aim of this study was to clarify if there is visual counterpart to auditory MMN, and if so what kind of a stimulus is able to elicit it. Event-related potentials (ERPs) were recorded from the human scalp from midline electrodes while the subjects listened to a story and concentrated to an auditory task. Three stimulus conditions, the oddball-condition, a deviant-alone condition and a condition in which standard and deviant stimuli were shown equally often, were presented in random order in the experiments. Two different kinds of stimulus pairs were used in this study, one of which stimulated the retina specifically (chessboard figure) and the other universally (color light). The visual counterpart to auditory MMN was not found in this study while early positive-going memory based response was elicited in both experiments in the oddball condition. This response did not emerge in the deviant-alone condition, in which standards were removed from the series. Thus, according this study the visual modality detects changes automatically very early but the mechanism may be different from the auditory modality.

Keywords: Event-related potential (ERP); Mismatch negativity (MMN); Change detection; Human; Visual; Early response

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1. Introduction

Mismatch negativity (MMN) is a component of event-related potential (ERP) (Näätänen, 1992), first isolated from the auditory N2 wave by Näätänen, Gaillard and Mäntysalo in 1978. It is normally elicited in a passive oddball condition, in which a repeated standard stimulus is randomly replaced by a deviant one while subject's attention is directed away from the stimuli (Näätänen, 1990). Deviant stimulus elicits a pre-attentive negative brain response at a latency of about 100-250 ms from stimulus onset (Näätänen, 1992). According Näätänen (1990, 1992) this suggests that MMN is a pre-attentive automatic brain mechanism for acoustic change detection. In most cases the largest MMN amplitudes are reached frontally, but its amplitude can be enhanced by decreasing deviant stimulus probability. MMN which is elicited in the passive oddball condition should be pre-attentive but if the subject's attention switches to the deviant stimulus it elicits P3a ERP component. (Näätänen, 1990, 1992.)

According to Näätänen (1990, 1992) MMN is a memory based process, meaning that no stimulus per se generates MMN, but rather it is generated by the comparison process between the current input (deviant) and the past input's (standard) memory trace. However, there is also another explanation for MMN called refractoriness according which MMN is elicited when in the course of the oddball condition the neurons responsive to standard stimuli become refractory because of the repeated stimuli and the short inter-stimulus-interval (ISI). In contrast, the neurons responsive to deviant stimuli remain responsive because of the long ISI between them. (Näätänen, 1990, 1992). However, this explanation is not supported as much as the memory-trace explanation which is supported by many studies. For example, MMN is not only elicited when the stimulus intensity or ISI is increased, but also when they are reduced (Näätänen, Paavilainen, Alho, Reinikainen, & Sams, 1989; Ford & Hilyard, 1981; Näätänen, 1992). Furthermore MMN is not elicited in a deviant-alone condition, in which deviants are shown alone without intervening standard stimuli (Näätänen et al., 1989). There is also an alternative control procedure to test the memory trace hypothesis called an equal probability condition developed by Jacobsen and Schröger (2001). This condition aims to eliminate neural refractoriness by presenting deviant stimulus among

other stimuli all with same frequency, which is same as deviant stimulus's in the oddball condition, and with same ISI as in the oddball condition. Therefore none of them is more refractory than the other and refractoriness is eliminated. (Jacobsen & Schröger, 2001.)

The first MMN was found in the auditory modality (Näätänen et al., 1978) but there are also studies searching its visual counterpart, visual mismatch negativity (vMMN) (Pazo-Alvarez, Cadaveira & Amenedo, 2003). However, the results of vMMN studies are inconsistent. Some studies have not found the visual counterpart for auditory MMN (Nyman, Alho, Laurinen, Paavilainen, Radila, Reinikainen, Sams & Näätänen, 1990; Csibra & Czigler, 1990). Of those that have found vMMN, some support the memory trace explanation (Astikainen, Ruusuvirta, Wikgren & Korhonen, 2004; Horimoto, Inagaki, Yano, Sata & Kaga, 2002; Czigler, Balázs & Winkler, 2002; Pazo-Alvarez, Amenedo & Cadaveira, 2004; Fu, Fan & Chen, 2003), while the study of Kenemans, Jong and Verbaten (2003) supports the refractoriness explanation. Still others have found vMMN but have left the explanation open (Alho, Woods, Algazi & Näätänen, 1992; Cammann, 1990; Tales, Newton, Troscianko & Butler, 1999; for a review, see Pazo-Alvarez et al., 2003). Moreover, many studies have methodological limitations, such as the primary task having also been presented in the visual field (Czigler et al., 2002; Pazo-Alvarez et al., 2004; Fu et al., 2003; Tales et al., 1999; Kenemans et al., 2003), the primary auditory task having cued the visual changes (Alho et al., 1992; Camman, 1990; Horimoto et al., 2002), or lack of a control procedure for the memory trace explanation (Horimoto et al., 2002; Alho et al., 1992; Cammann, 1990; Tales et al., 1999; see Pazo-Alvarez et al., 2003).

On the other hand, there are also studies according which the human brain seems to be able to process visual information and auditory change already before 100 ms from stimulus onset. For instance, the study of Ruusuvirta and Huotilainen (2004) reveals that the human brain detects auditory change within 56 ms from stimulus onset. Furthermore, according to Foxe and Simpson (2002) visual input starts activating the occipital cortex at a latency of 56 ms from stimulus onset and according to Wyss, König and Verschure (2003) 66 % of the information about visual stimuli is available for processing within 20 ms from stimulus onset in the mammalian brain. Therefore, it seems that visual change detection might already take place before 100 ms from stimulus onset.

Although many studies have researched vMMN they have not been trying to clarify its characteristics. It is known that auditory MMN has specific characteristics, such as that it is a memory based change detection process, occurring as a negative response at a latency of 100-250 ms from stimulus onset, independent of attention and elicited by any discriminable change in sound (Näätänen, 1990, 1992). These issues are not clear with vMMN. It is difficult to prove vMMN to be a counterpart for acoustic MMN or clarify the nature of visual change detection process if its characteristics are not known. Therefore, it is important to try to clarify these issues. The first aim of this study is to clarify whether there is visual counterpart for auditory MMN and if not what characteristics the visual change detection process has. The hypothesis is that there is visual MMN or at least memory based change response. The second aim is to clarify what kind of a stimulus is able to elicit this memory based change detection response. In the first experiment the retina is stimulated specifically by a chessboard figure and in the second experiment the retina is stimulated universally by red and green color lights. The prediction is that at least the color light stimuli should be able to elicit memory based change response because in previous vMMN studies it has elicited MMN-like responses (Pazo-Alvarez et al., 2003).

2. Experiment 1

2.1 Methods

Subjects. Ten native Finnish-speaking subjects, five male and five female, reporting normal vision (with correction if necessary) and hearing participated voluntarily in this study. Their age ranged from 20 to 33 years, with mean age being 24.4 years. An informed consent was obtained from the subjects before participation in the study.

Stimuli and procedure. The visual stimuli were presented on a computer screen in the form of a 10.5x10.5 cm chessboard of sixteen squares. Black and white squares

changed their places in the standard and deviant stimuli. The stimuli were shown to the subjects on a white screen, 90 cm distance in front of them.

There were three stimulus conditions in the experiment: the oddball condition, the deviant-alone condition and a condition in which standard and deviant stimuli were shown equally often. In the oddball condition standards were repeated at 510-ms onset-to-onset intervals and were randomly replaced by deviants. In the deviant-alone condition standards were omitted from the series and only deviants were shown randomly at the same inter-stimulus-interval (ISI) as in the oddball condition. There were 900 standards and 100 deviants per condition. In the third condition the standards and deviants were both shown equally often at 510-ms onset-to-onset intervals. This condition will not be analyzed here. The order of the conditions was random.

During recordings the subjects were seated in a comfortable chair in dim light. As a primary task the subjects were instructed to count all the words beginning with the letter /y/ in the story they heard from the speaker, and to fix their gaze on the black spot 5.5 cm under the stimuli. The story was an oral narrative in Finnish which included also musical elements. It was independent of the visual stimuli, offering no cue for them. After every stimulus condition the subjects were asked the number of words beginning with the letter /y/ to control the primary task.

EEG recordings. The electroencephalogram (EEG) was recorded with Ag/AgCl electrodes at the midline electrodes Fz, Cz, Pz and Oz (Jasper, 1958). Linked left and right mastoids were used as the reference electrode. All recording electrodes' impedances were less than 10 k Ω . The signals from the electrodes were amplified, digitally band-pass filtered from 0.1 to 200 Hz (12 dB per octave roll off) and sampled at 500 Hz.

Data analyses. Single EEG-sweeps, from 100 ms before to 510 ms after stimulus onset, were corrected by their baseline, which was 50 ms before stimulus onset. All the sweeps whose amplitude difference from peak to peak exceeded 100 μ V were discarded for a control of artifacts such as eye movements. One subject's Oz ERPs had to be removed because there was too much noise in the data. The remaining sweeps were averaged separately for deviants and for standards immediately preceding deviants. The

averaged sweeps were digitally low-pass filtered with a 30 Hz cut-off (12 dB per octave roll off). After that the sweeps were corrected to start from zero.

In statistical analysis the oddball standard sweep was first compared to oddball deviant sweep and second to deviant-alone sweep at every time point with paired t-test (two-tailed). When determined at which latency standard and deviant sweeps significantly differed from each other, deviant-alone sweep was compared to standard sweep at these same latencies to see if the difference between standard and deviant is really memory based. Standard and deviant were also compared to each other at a latency of 250-300 ms from stimulus onset to see if there has been attention switch toward the visual changes.

2.2 Results and Discussion

Standard and deviant ERPs significantly differed from each other at quite early latencies of 19-47 ms at Fz, $t(9) = 2.29-3.30$, $P < 0.05$, at 19-37 ms at Cz, $t(9) = 2.44-3.21$, $P < 0.05$, and at 17-33 ms at Pz, $t(9) = 2.32-2.73$, $P < 0.05$. However, at Pz significant differences between standard and deviant ERPs could be seen at a MMN latency of 100-250 ms from stimulus onset, at 117-133 ms, $t(9) = 2.26-2.30$, $P < 0.05$, and at 187-199 ms, $t(9) = 2.28-2.46$, $P < 0.05$.

The ERPs to deviant-alone did not significantly differ from the ERPs to standard at a latency of 19-47 ms at Fz, $t(9) = 0.41-1.34$, $P > 0.05$, at 19-37 ms at Cz, $t(9) = 0.53-0.79$, $P > 0.05$ and at 17-33 ms at Pz, $t(9) = 0.15-0.99$, $P > 0.05$. However, the ERPs to deviant-alone significantly differed from the ERPs to standard at a latency of 117-133 ms at Pz, $t(9) = 5.78-5.94$, $P < 0.05$ and at 187-195 ms at Pz, $t(9) = 2.60-3.63$, $P < 0.05$.

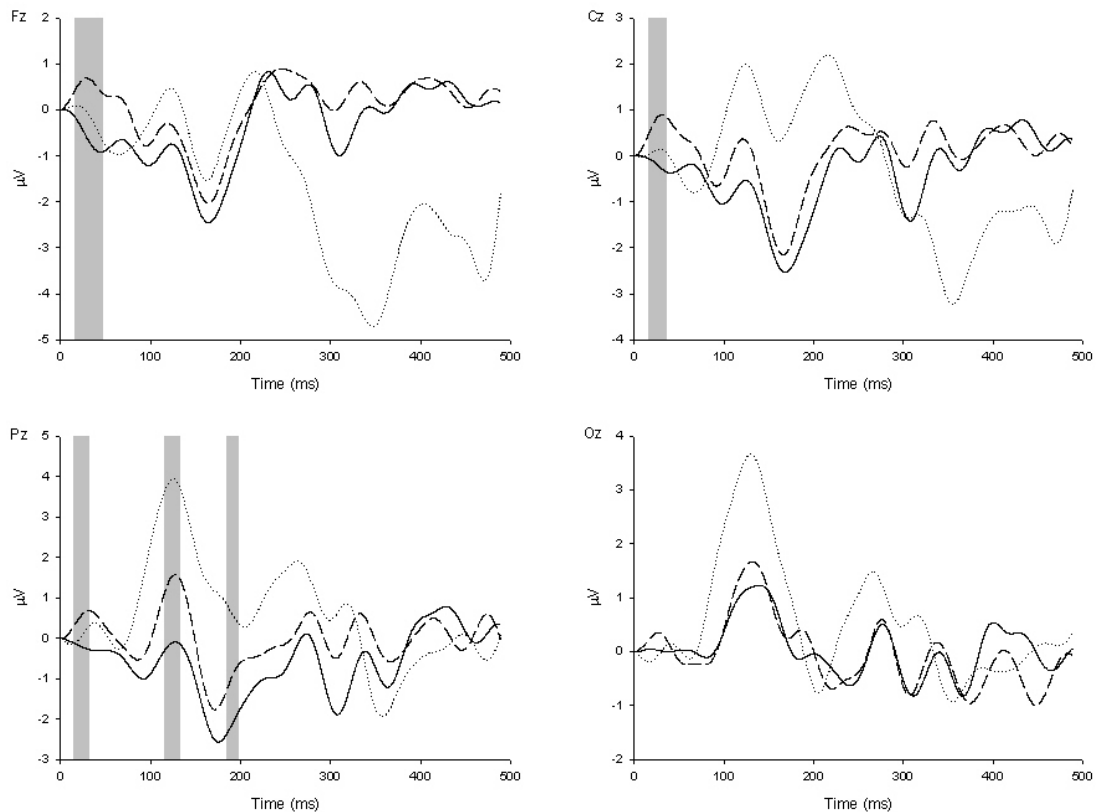


Figure 1. Grand-averaged ERPs to standard stimuli (solid line), deviant stimuli (dashed line) and deviant-alone stimuli (dotted line) at different scalp sites. Significant difference ($P < 0.05$) between standard and deviant stimuli is marked with gray. Note: the scaling is not same in every picture.

It seems that the subjects did not switch their attention towards the visual stimuli, because P3 wave could not be seen at any channel in this data. Standard and deviant ERPs did not significantly differ from each other at a latency of 250-300 ms from stimulus onset at any channel, $t(8-9) = 0.01-2.08$, $P > 0.05$.

In Experiment 1 it could be seen that the chessboard elicited quite an early standard-specific positive ERP sweep at a latency of 19-47 ms at Fz, 19-37 ms at Cz and 17-33 ms at Pz. This may indicate early memory based visual detecting of change. Most clearly it can be seen in Figure 1 at Fz that deviant and deviant-alone curves are going in different directions at a latency of 19-47 ms from stimulus onset, meaning that they are qualitatively different from each other and refractoriness can not explain differences. In contrast in same figure but at Pz at a latency of 117-133 ms from stimulus onset deviant and deviant-alone are going in same direction while deviant-alone makes just bigger

curve which possibly reflects refractoriness. However, there could not be seen a memory based ERP sweep at a MMN latency of 100-250 ms from stimulus onset.

3. Experiment 2

3.1 Methods

Subjects. Seventeen other native Finnish-speaking subjects, five male and twelve female, reporting normal vision (with correction if necessary) and hearing participated voluntarily in this study. Their age ranged from 18 to 34 years, and mean age was 23 years. An informed consent was obtained from the subjects before participation in the study.

Stimuli and procedure. The visual stimuli were flashing green and red led lights in the outer corners of the glasses the subjects were wearing during the experiment. In approximately half of the subjects the red light was deviant and the green light was standard, and in the rest of the subjects the green light was deviant and the red light standard.

In the experiment there were the same three stimulus conditions as in the first experiment, but the inter-stimulus-interval was now 500-ms.

During recordings the subjects were seated in a comfortable chair in dim light. The primary task was otherwise the same as in the first experiment, but the subjects did not need to fix their gaze on a certain spot.

EEG recordings, data analysis and statistical analysis were conducted the same way as in the Experiment 1.

3.2 Results and Discussion

In Experiment 2 standard and deviant ERPs significantly differed from each other at a latency of 35-47 ms at Cz, $t(16) = 2.13-2.36$, $P < 0.05$, at 87-105 ms at Pz, $t(16) = 2.21-2.56$, $P < 0.05$, and at 87-111 ms at Oz, $t(16) = 2.25-3.90$, $P < 0.05$.

The ERPs to deviant-alone stimulus did not significantly differ from the ERPs to standard at a latency of 35-47 ms at Cz, $t(16) = 0.39-0.54$, $P > 0.05$, at 87-105 ms at Pz, $t(16) = 0.01-0.58$, $P > 0.05$, and at 105-111 ms at Oz, $t(16) = 1.37-2.06$, $P > 0.05$.

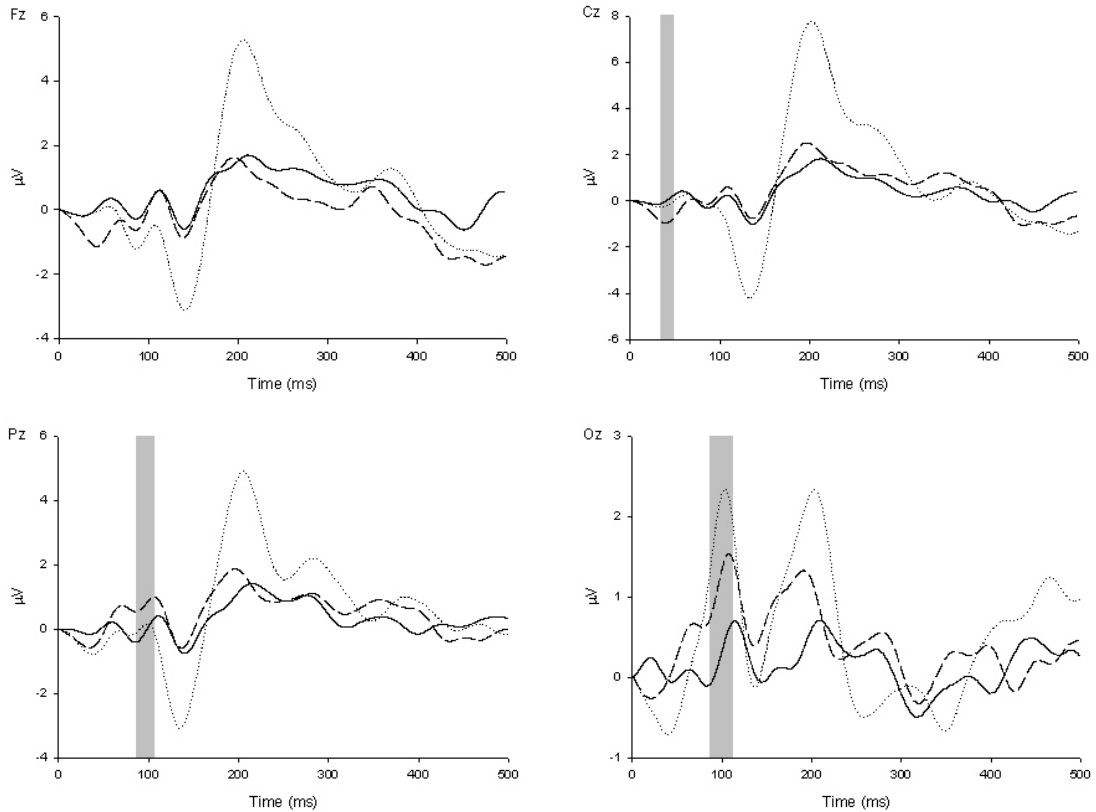


Figure 2. Grand-averaged ERPs to standard stimuli (solid line), deviant stimuli (dashed line) and deviant-alone stimuli (dotted line) at different scalp sites. Significant difference ($P < 0.05$) between standard and deviant stimuli is marked with gray. Note: the scaling is not same in every picture.

In this data P3 wave could not be seen at any channel. Standard and deviant ERPs did not significantly differ from each other at a latency of 250-300 ms from stimulus onset at any channel, $t(16) = 0.02-0.94$, $P > 0.05$. This indicates that the subjects did not switch their attention towards the visual changes.

Thus, it could be seen in Experiment 2 that the color light stimulus could elicit standard-specific positive ERP sweeps at quite early latencies at Cz and Pz. The most MMN-like wave can be seen at Figure 2 at Fz where at a latency of 200-300 ms from stimulus onset the response to deviant stimulus is more negative than the response to

standard one. However, the difference between them is not significant. The responses at Cz at a latency of 35-47 ms from stimulus onset and at Pz at a latency of 87-105 ms from stimulus onset may indicate early memory based visual change detection. For example, it can be seen very clearly in Figure 2 at Pz that deviant and deviant-alone curves are going in different directions at a latency of 87-105 ms from stimulus onset, meaning that deviant and deviant-alone are qualitatively different from each other and refractoriness can not explain differences. In contrast the response at Oz at a latency of 87-111 ms from stimulus onset possibly reflects refractoriness because deviant and deviant-alone curves are going in same direction while deviant-alone makes just bigger curve.

4. General Discussion

The visual counterpart to auditory MMN was not found in this study while the results suggest that visual change detection in the human brain may be reflected by early positive-going memory based response. Positively displaced ERPs were elicited selectively as a response to deviant stimuli and not to deviant-alone stimuli. In other words, the positive response to deviant which was elicited in the oddball condition was not elicited in the deviant-alone condition, a control procedure for testing a memory trace hypothesis, in which standards were removed from the series. Therefore, it seems that these positive ERPs were elicited as a response to change, not as a refractory response. These standard-specific responses to deviant stimuli indicate that the visual change detection process may indeed be memory based. In addition, the results suggest that the human brain could be able to process visual change very fast. Both experiments' stimuli could elicit very early positive standard-specific ERP responses selectively to deviant stimuli at a latency range from 17 ms to 47 ms from stimulus onset. This might suggest that a timing of visual processing might be faster than thought before and also different from auditory processing.

Significant differences between standard and deviant stimuli could be seen quite clearly at Pz in both experiments with a chess-board stimulus, stimulating the retina

specifically, and with color light stimulus which stimulates the retina universally. Also it can be seen that color light stimulus is processed as different from standard at Oz, Pz and Cz, but chess-board stimulus at Pz, Cz and Fz. Even though, a memory based change response did not emerge at Oz which is the first cortical processing level of visual information. It raises the question whether the memory based visual change response is generated already before or after the occipital cortex. If the response is generated after the occipital cortex the visual processing areas in the brain might explain it. The occipital cortex includes first cortical processing levels of visual information processing in the brain and it is therefore possibly able to recognize universal difference, such as a difference between red and green light, but not been able to recognize specific difference such as changing chess-board's squares. Furthermore the visual information of color is processed in the area V4 at the occipital cortex (Bartels & Zeki, 2000) which may explain why the detection of difference between red and green light could be seen as a difference between standard and deviant stimulus at Oz. However, the chess-board stimulus elicited clear differences between standard and deviant stimulus not until at the parietal lobe. This lobe is specialized to spatial information processing (Sack, Hubl, Prvulovic, Formisano, Jandl, Zanella, Maurer, Goebel, Dierks & Linden, 2002), meaning that it is specialized for example to recognize where the objects are. This may explain why the parietal lobe recognized so easily the difference when chess-board's black and white squares changed their places. On the other hand, the other possibility is that the memory based change response would be generated already before the occipital cortex. That would mean that already the sub cortical structures, for instance the thalamus, would be able to detect change. However, this issue would need to be studied further, for example with invasive animal studies, to clarify if the sub cortical structures would be able to process visual change detection and exactly what sub cortical structures would be involved in this process.

As hypothesized the color stimulus elicited memory based response quite easily while the difference between standard and deviant stimuli was quite difficult to elicit with the chess-board stimulus. The possible explanation is that the difference between the chess-board's deviant and standard stimuli was small and eye movements may fade the change. That is, standard and deviant stimulus does not necessarily stimulate the

nervous system exactly the same way repeatedly because of subject's eyes movements. Therefore, standard and deviant might not elicit so different representation from each other to the nervous system. As a result, the change effect might in other words fade.

Previous visual MMN studies have shown inconsistent results about existence and the underlying mechanism of vMMN, while all of them have reported the response to deviant been negative. Even though, this study indicates that the response to deviant stimulus could be positive it supports the memory trace explanation and in that way is line with Astikainen et al. (2004), Horimoto et al. (2002), Czigler et al. (2002), Pazo-Alvarez et al. (2004) and Fu et al. (2003). In fact it seems like the response to deviant stimuli would not necessary be negative because also Shinozaki, Yabe, Sutoh, Hiruma and Kaneko (1998) have reported positive response to deviant stimuli in the oddball condition in the somatosensory modality.

After all, this data does not offer full support for the visual change detection process being analogous for auditory MMN. Auditory MMN has specific characteristics such as it is a memory based change detection process, occurring as a negative response at a latency of 100-250 ms from stimulus onset, independent of attention and elicited by any discriminable change in sound (Näätänen, 1990, 1992). Although this kind of response was not found in this study the most MMN-like wave can be seen in Figure 2 at Fz where at a latency of 200-300 ms from stimulus onset a response to deviant stimulus is more negative than a response to standard one. However, the difference between them is not significant. In contrast, this study suggests that the visual change detection process might be much faster than that, occurring already at a latency range of 17-47 ms from stimulus onset. Fast processing of visual stimulation gets support from Foxe and Simpson (2002) and Wyss et al. (2003). According to Foxe and Simpson (2002) visual input starts activating the occipital cortex at a latency of 56 ms and the dorsolateral frontal cortex at a latency of 80 ms from stimulus onset. They also suggest that the activity in the occipital cortex could represent activation from V1 but also from other visual areas (Foxe & Simpson, 2002). Furthermore according to Wyss et al. (2003) 66 % of the information about visual stimuli is available for processing within 20 ms from stimulus onset in the mammalian brain. The results of this study suggest that also visual change detection would take place before 50 ms from stimulus onset. This result is in

line with the gamma-band electroencephalogram study of Ruusuvirta and Huotilainen (2004) according which the human brain can detect deviant sounds as rare in comparison to standard sound within 56 ms from stimulus onset. These results support the possibility that the human brain would be able to process visual information and detect change very fast. In fact, if this change detection process is this fast, it raises the question again, whether this change detection process would already take place in the sub cortical structures.

The results of this study were obtained from two experiments in which the primary task reliably directed the subjects' attention away from the visual stimuli, because P3 waves could not be seen in ERP. It is also noteworthy that the primary auditory task was presented asynchronously, offering no cue for the visual stimuli. That is, the responses were elicited to visual stimuli and not to the primary task. Both of these two experiments showed parallel results and the sample was sufficient, meaning the results should be reliable.

Altogether, the visual counterpart to auditory MMN was not found in this study while the results suggest that visual change detection in the human brain may be reflected by early positive-going memory based response. This memory based response might be elicited by both specifically and universally retina stimulating stimuli. Thus, it seems that the visual modality detects changes automatically very early but the mechanism may be different from the auditory modality.

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