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# Visual mismatch negativity elicited by magnocellular system activation

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**Abstract**

The processing of visual motion was tested by means of event related potentials recording (ERP) using a paradigm designed to produce a visual mismatch negativity effect. The stimuli were unattended and presented in the peripheral visual field (outside the central 15°). The standard stimulus consisted of an up/down motion sequence, whilst the deviant stimulus of a down/up motion sequence. Significant ERP differences between the standard and deviant conditions were found in 8 out of 10 adult subjects already in 80 ms and prevailingly in interval 145–260 ms from the initial stimulus presentation. The results demonstrate that the magnocellular information undergoes processing capable of detecting differences in the sequence of unattended peripheral motion stimuli.

*Keywords:* Visual mismatch negativity; ERPs; Motion-onset; Dorsal stream visual attention

## 1. Introduction

Unattended processing of information within the auditory sensory cortex, including the ability to detect changes in information, can be revealed by recording of the human electroencephalographic activity in so called mismatch negativity (MMN) paradigm. The test subject is exposed to a series of standard stimuli, which are occasionally replaced by a different—"deviant" stimulus. It has been shown that the auditory sensory cortex produces a more negative deflection of the transient event related potentials (ERP) at about 200–300 ms after the presentation of the mismatch (deviant) stimulus than of the standard stimulus. Furthermore, this effect has been shown to be independent of the subjects' attention. This ability to differentiate sensory information content without attention is used as an example of pre-attentive parallel sensory processing in the brain (Näätänen, Gaillard, & Mäntysalo, 1978, for an overview see Näätänen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001).

The MMN effect is most likely a result of neuronal activity associated with the short-term retention of stimulus related information (also known as the echoic memory trace) rather than system refractoriness (habituation) (Jacobsen, Horenkamp, & Schröger, 2003). Such a task requires an adaptive causal system with memory storage and independence on the attention.

The visual systems dealing with both parallel and temporal processing aspects of vision have been searched for MMN like responses (vMMN) with controversial results (e.g., Nordby, Brønnick, & Hugdhal, 1996; Nyman et al., 1990; Stagg, Hindley, Tales, & Butler, 2004; Tales, Newton, Troscianko, & Butler, 1999, for a comprehensive overview see Pazo-Alvarez, Cadaveira, & Amenedo, 2003). It is known that visual processing is conducted along two streams, the ventral and the dorsal streams, incorporating different cortical structures, analyzing different visual features, and playing different roles in visual perception and action (Goodale & Milner, 1992; Ungerleider & Desimone, 1986). The magnocellular pathway and the dorsal stream, sometimes referred to as the "where" pathway, are optimised to "vision for action". That might be advantageous to a system that is thought to be responsible for pre-attentive detection of fast changes in the visual field.

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To test this hypothesis, we performed vMMN experiments with motion-onset visual evoked potentials (M-VEPs) (Kuba & Kubová, 1992) and explored the dorsal stream for detection of changes (Kremláček, Kubová, Chlubnová, & Kuba, 2001). We found that the dorsal stream was able to detect differences in motion direction without attention of the subject and to produce MMN like responses. These results were confirmed by Pazo-Alvarez, Amenedo, and Cadaveira (2004) who additionally showed that the vMMN to motion direction change was independent of the subject's attention and system's refractoriness.

In the current study, we have further explored the dorsal stream to investigate whether its pre-attentive processing is restricted to detecting the motion direction or whether it also has an ability to detect more complex information such as changes in the sequence of the motion.

## 2. Methods

### 2.1. Subjects

A group of 10 healthy adult subjects participated in the experiment. There were seven women and three men aged 25–49 years. They had no ophthalmologic or neurological abnormalities. Informed consent was obtained from each subject once the test procedure had been explained to them. The study was approved by the Ethical Committee of the Faculty of Medicine in Hradec Králové.

### 2.2. Stimuli

The stimuli consisted of low contrast (10%) horizontal sinusoidal gratings: with a low spatial frequency (0.1 c/deg) outside the central 15° of the field and high spatial frequency (1 c/deg) inside the central 5°. The stimuli were generated by means of our own developed stimulus generator available free of charge (Kremláček, Kuba, Kubová, & Vít, 1999).

The test paradigm was specifically designed to elicit the MMN and was based on a similar study by Tales et al. (1999). It involved presenting a standard stimulus 88% of the time and a random deviant stimulus 6% of the time. In order that the subjects paid no attention to these stimuli, they were given the task of responding to a target random stimulus that was presented in the central visual field 6% of the time. The subjects had to press a handheld button whenever the target stimulus appeared.

The standard and deviant stimuli were presented as fast motion (50 deg/s) in the peripheral visual field. The standard stimulus consisted of 100 ms of upward motion followed by 100 ms of downward motion. The discriminative information was provided by reversing the sequence in the deviant stimulus, i.e., 100 ms of downward motion was followed by 100 ms of upward motion. The inter stimulus interval was 600 ms of stationary pattern (the stimulus onset asynchrony was 800 ms). Fig. 1 illustrates the spatial temporal parameters of the stimuli.

Separate use of the standard and deviant stimulus evokes the same sensory response because the M-VEPs are not specific to motion direction (Maurer, Heinrich, & Bach, 2004; verified also in our own experiments with inverted motion sequence—unpublished data).

The stimuli were presented on a 21″ computer monitor ViewSonic with a frame rate of 70 frames per second. The screen subtended a visual field of 42° × 30° at a 0.5 m viewing distance. The mean stimulus luminance was 17 cd/m$^2$.

### 2.3. Recording

The ERP acquisition was performed in a darkened, sound attenuated, electromagnetically shielded room with a background luminance of 1 cd/m$^2$. The subjects sat in a comfortable dental chair with a neck support to reduce muscle artefact and were instructed to fix on the centre of the stimulus field. Correct fixation was checked via a CCD camera located in the test room.

Responses were recorded from six unipolar electrode derivations, selected with the experience of similar previous studies. The active electrodes were positioned at $F_Z$, $C_Z$, $P_Z$, $O_Z$ and two lateral temporo-occipital locations placed 5 cm to the right and to the left of $O_Z$ ($O_R$ and $O_L$, respectively). The right earlobe ($A_2$) served as a reference. The signal amplifier had a bandwidth of 0.3–100 Hz (Contact Precision Instruments—PSYLAB, System 5). The responses were sampled at a rate of 500 Hz and selectively averaged off-line in a personal computer.

Each subject underwent four recording sessions each consisting of 170 stimulus presentations; 150 standard, 10 deviant and 10 target. Ten responses from each of the three stimuli were recorded. The pseudorandom selection of ten standard responses was determined in advance and remained fixed for all sessions. The recorded standard response preceded the deviant stimulus by at least three and at most six standard stimuli. The purpose was to keep the time from the standard stimulus to the following deviant one as short as possible (to assure similar habituation) and simultaneously the time from the deviant to standard stimulus as long as possible (to keep the standard condition truly standard).

As a result of the off-line processing, 40 single sweeps ERP were averaged for each stimulus condition. Before signal averaging the DC component was removed. The DC level was specified as the mean value of the first 15 samples (30 ms), of each sweep. The averaged signal was digitally filtered by a low pass filter with a cut-off frequency of 30 Hz.

### 2.4. Analysis

Statistical analysis of the recordings was based on the differences in the ERPs recorded from the standard and deviant stimuli. PC1 method (Achim, 1995) was used to assess the difference between standard and deviant ERPs (the vMMN) in the time interval between 30 and 400 ms

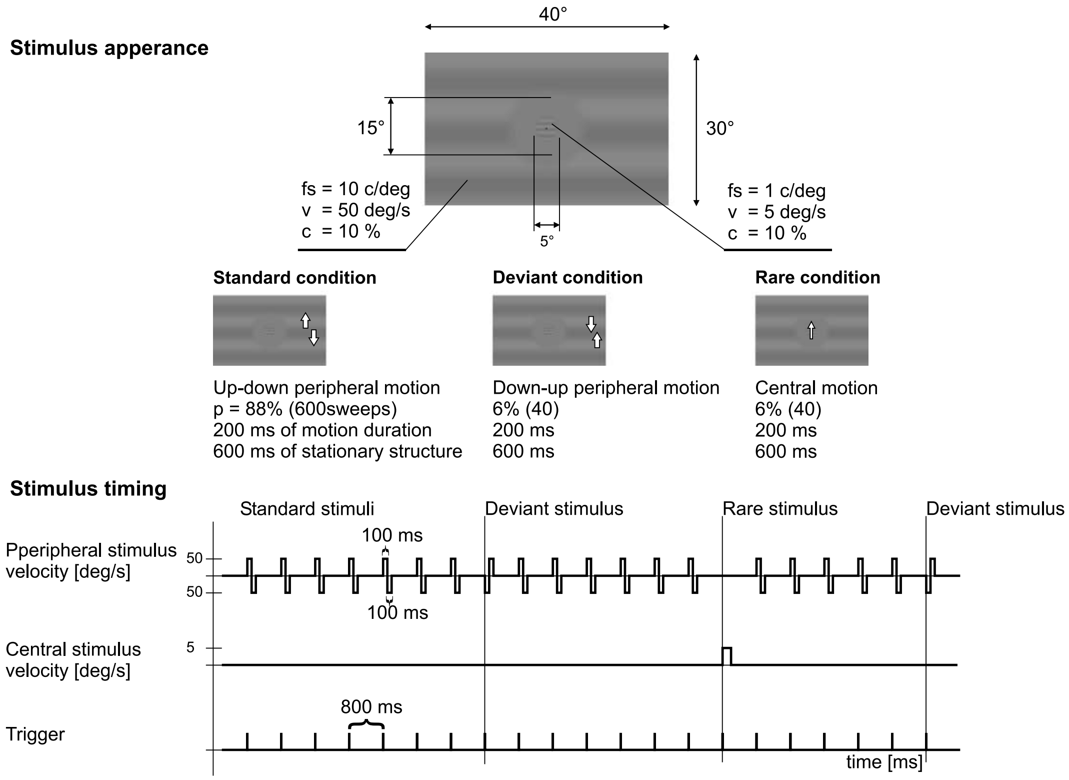

Fig. 1. Stimulus design and properties. The stimulus appearance is illustrated in the upper part of the figure and symbolic representations of the motion are depicted in the middle of the figure. The white arrows represent the direction of motion and their order. The standard condition comprised motion of a peripheral stimulus (horizontal grating outside the central 15° of the visual field) initially moving upwards with a velocity of 50 deg/s for 100 ms and then moving downwards with the same velocity for a further 100 ms. The pattern remained stationary for a period of 600 ms between stimuli. The other stimulus conditions are similarly depicted. The stimulus timing diagrams in the lower part of the figure illustrate the sequence of events in this study.

from stimulus onset. The method uses Principal Component Analysis to extract the first principal component of the vMMN and then it tests component projections (weights) among subjects by the Student's *t* test. This technique was adopted to avoid multiple statistical comparisons. In case of significant difference the exact timing was determined by point-wise tests of the mean of each ERP (paired *t* test). A significance level of 5% ($p = 0.05$) was used for all the statistical tests. The validity of the PC1 results was verified by criterion of critical length of consequent significant differences (at least 7 successive significant changes on the level of 0.05 for 8 subjects) (Guthrie & Buchwald, 1991).

## 3. Results

Nine subjects had reproducible responses and all demonstrated a vMMN response. One subject did not have reproducible sensory part of responses and was excluded from further evaluation. The grand average response for each condition and recording site are illustrated in Fig. 2. The responses from the occipital region had a more complex shape than those recorded from unidirectional motion-onset VEPs in previous studies (Kremláček et al., 2001). The typical motion-onset N160 negative peak was preceded by an additional negative peak at 110 ms. The difference, caused by the stimulus design, was the same for standard and deviant condition. For the target condition the response contained a dominant positive P300 peak, with a latency of 375 ms; with the maximum amplitude response occurring at the $P_Z$ and $C_Z$ active electrode sites.

The PC1 test and criterion of critical length of consequent significant differences demonstrated significant differences in the ERPs recorded from the standard and deviant conditions for each recording site. The statistical significance is illustrated in Fig. 2. The point-wise *t* test showed that the significant changes were clustered in the time interval between 145 and 260 ms from the initial stimulus onset.

## 4. Discussion

A fundamental question regarding the vMMN component of the motion-onset ERP is whether it is caused by adaptation. During our experiments, the sequence of opposite motion direction stimuli bore the discriminative information and so we excluded the possibility of long-term motion adaptation by the stimulus design. Consequently no subject reported any motion after-effect illusion.

Direction specific short-term motion adaptation has been shown to be a property of the macaques' mediotemporal (MT) neural circuits. The time course of this adaptation and recovery is relatively rapid, 64 ms of adaptation is

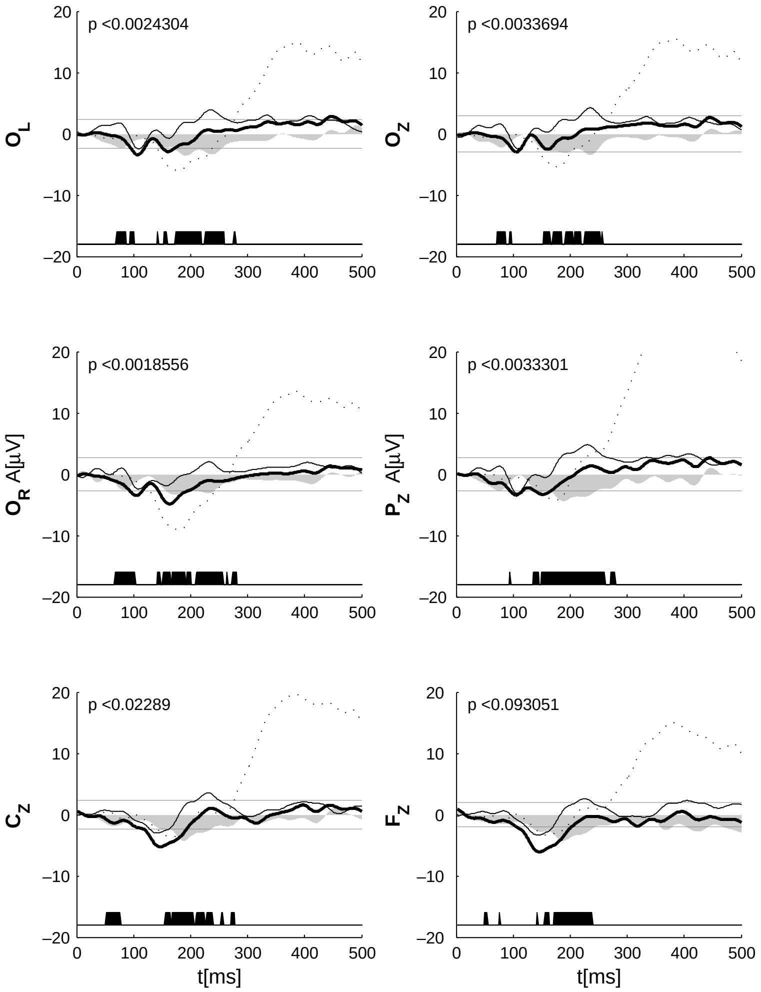

Fig. 2. Group average responses (9 subjects). The group averaged ERPs recorded from the electrodes at $O_L$ (5 cm left of $O_Z$), $O_Z$, $O_R$ (5 cm right of $O_Z$), $P_Z$, $C_Z$ and $F_Z$ are depicted for the standard condition (thin lines), deviant condition (bold lines) and target condition (dashed thin lines). The recording positions are identified on the vertical axis of each panel. The statistical significances of the differences between the ERPs from the standard and deviant conditions are shown in the left upper corner of each panel. The timing of the significant differences determined by the point-wise *t* test is illustrated by the black ticks in the lower part of each panel. The two horizontal lines adjacent to the 0 μV represent the ±2.5 standard deviation for the differences between the standard and deviant ERPs during the interval between 0 and 30 ms. The grey patches illustrate when the difference between the ERPs exceeded the ±2.5 standard deviation confidence interval.

diminished within 200 ms of rest (Priebe & Lisberger, 2002). In our experiment, we had 100 ms of motion in each of two directions, interspersed by at least 600 ms of a stationary pattern, so it is unlikely that there was any short-term adaptation. Furthermore, there was no direction change between the offset of the standard stimulus and the onset of the deviant stimulus—downward motion (see the Fig. 1), so if there had been any motion direction adaptation, it should have led to a decrease in the ERP response to the deviant stimulus, and not the enhancement that was observed.

It has also been shown that a later motion-onset VEP peak (P2 with a latency of 230 ms at Cz) is adapted by temporally specific mechanisms—global phasic adaptation, which are directionally non-specific (Hoffmann, Unsold, & Bach, 2001). Because of P2's directional insensitivity and the equal temporal changes in our standard and deviant stimuli, this adaptation could not have been the cause of the observed vMMN behaviour either.

Adaptation can be understood to be an active process of a neural system trying to discount the ambient information and increase awareness of novel stimuli (Barlow, 1990). Such mechanism could be responsible for the Mismatch Negativity phenomena; however, it is not adaptation causing the motion after-effect, the short-term MT adaptation or global phasic motion-onset VEPs adaptation.

Because each subject's attention was focused on the central stimulus and this was checked through monitoring, another explanation for the ERP difference could be that the peripheral stimuli drawn distributed covert attention. Such process would, however, need a pre-attentive mechanism capable of distinguishing between the standard and deviant conditions what supports non-attentional processing. Furthermore, an attentional switch is followed by the frontal positive deflection P3a (Garcia-Larrea, Lukaszewicz, & Mauguiere, 1992; Squires, Squires, & Hillyard, 1975). This component is present for the rare stimuli but it was not observed in our results for the deviant ones (see the Fig. 2). The P3a absence provides another evidence for the non-attentional processing of the peripheral stimuli. Therefore we can conclude that the motion-related ERP amplitude changes were recorded as a result of alteration in the sequence of motion directions without allocated attention and without any evidence of adaptation.

Similar experiments with pattern and motion-onset stimuli found significant ERP differences at a latency of 145–165 ms (Pazo-Alvarez et al., 2004) in the occipito-temporal area. For motion-reversal stimuli significant differences were found at a latency of 200–250 ms (ffytche, Guy, & Zeki, 1995) in a similar region. The findings of the current study support these results when they demonstrate the vMMN effect in the time period from 145 to 260 ms for each recording site. The reason that we found significant differences at all recording sites, rather than just in the occipital-temporal area, are probably mainly because the P2 component of the motion-onset VEP is of non-striate origin and has a fronto-central distribution (Kremláček & Kuba, 1999; Schellart, Trindade, Reits, Verbunt, & Spekreijse, 2004). It is probable that modulation of P2 component results into vMMN of similar spatial properties. This hypothesis, however, remains to be verified by a brain mapping technique. Furthermore, the peripheral position of the standard and deviant stimuli further enhances the projection of the motion-onset response to the central recording sites (Kremláček, Kuba, Chlubnová, & Kubová, 2004).

The determination of a cortical net responsible for vMMN generation was not the subject of this experiment and straightforward suggestion that it might be within the dorsal stream, because the vMMN was triggered by magnocellular system activation, is not the only possible explanation. The reason is that the ventral and dorsal streams are largely interconnected (Ungerleider, Courtney, & Haxby, 1998) and in the time of vMMN (145–260 ms after stimulus presentation) all visual areas were probably activated (Bullier, 2001). Also from imaging studies it is known that not only the stimulus features but the task can determine activated areas, e.g., motion-discrimination activates the middle fusiform gyrus or the inferior temporal sulcus—parts of the ventral stream (Orban et al., 1998).

In addition to the 'late' vMMN response we also observed an early difference (peaking at 80 ms) between the ERPs to standard and deviant stimuli. This change was observed in all derivations; however, it was only significant for the right occipito-temporal derivation (see the Fig. 2). Similar findings were also reported by Pazo-Alvarez et al. (2004) on page 1984, when they obtained a significant difference in the occipito-temporal regions at a comparable time, at about 70 ms after their stimulus onset. Their explanation was unclear, since they reported that the early peak was dependent on the position of the stimulus in the visual field, while between the standard and deviant condition there was no change in this sense.

We assume that this early difference might be an integral part of the vMMN. First, we used a different vMMN paradigm to Pazo-Alvarez, yet observed similar early changes. Second, early processing of motion stimuli is reported to peak at about 71–75 ms in the MT or MST areas (Buchner et al., 1997; ffytche et al., 1995) and third, the earliest interactions of two concurrent pattern-onset stimuli first appear in the medio-temporal region at 80 ms (Vanni et al., 2004).

## 5. Conclusion

The results of previous vMMN experiments suggest that there is a pre-attentive processing of motion direction events (Kremláček et al., 2001; Pazo-Alvarez et al., 2004). However, a sufficient mechanism needed for detection of these events can be a simple direction sensitive integrative process.

In this study, we have shown that the stimuli predominantly activating the dorsal stream can be processed not only by means of motion direction, but also as a sequence of two directions of motion. This suggests that the neural networks treat these sequences as events or that there is a temporal representation of a 'visual rhythm'. Such representation is subject of a pre-attentive learning independent of the attention and influencing the detection of the events and their processing.

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