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Visual mismatch negativity to elementary stimulus features

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Table of contents

List of publications that the dissertation is based upon

Czigler, I., & Sulykos, I. (2010). Visual mismatch negativity to irrelevant changes is sensitive to task-relevant changes. Neuropsychologia 48, 1277–1282.

Sulykos, I., & Czigler, I. (2011). One plus one is less than two: visual features elicit non-additive mismatch-related brain activity. Brain Research 1398, 64–71.

Sulykos, I., & Czigler, I. (2014). The visual mismatch negativity is sensitive to illusory brightness changes. Brain Research 1561, 48–59.

Sulykos, I., Kecskés-Kovács, K., & Czigler, I. (2015). Asymmetric effect of automatic deviant detection: The effect of familiarity in visual mismatch negativity. Brain Research, 1626, 108-117.

Foreword

Understanding the history of visual mismatch negativity (vMMN) is an appropriate way of understanding the current vMMN research. The reason is that empirical sciences are fundamentally conservative; except for the “scientific revolutions”, changes are gradual and slow. The origin of a theory determines the basic concepts and methods in the long run.

The vMMN originated in MMN, an acoustic ERP component. The discovery of MMN is traditionally assigned to a paper published by Risto Näätänen and colleagues in 1978 (the citations of this paper are over 1900). In this study, rare and frequent stimuli were delivered in a dichotic stimulation paradigm. The participants’ task was to respond to the rare stimuli delivered in the attended ear. The ERPs to the rare and frequent stimuli differed in not only in the attended, but also in the non-attended channel. This negative difference (registered to stimuli in the non-attended channel) was named later as mismatch negativity (MMN). The stimulus sequence was termed as oddball sequence; in the oddball sequence, the rare and frequent stimuli were termed as deviant and standard, respectively. Additionally, the paradigm was termed as a passive one, because the standard and deviant were (intentionally) a part of the non-attended stream of the experimental stimulation. In short, the paradigm is called “passive oddball paradigm”, and became the basic paradigm of the MMN research.

In the subsequent years numerous standard-deviant differences were investigated, many of them beyond the elementary feature changes; and highly sophisticated designs were applied to discover the cognitive functions reflected by the MMN (for an introduction of the development of the MMN research, see Winkler, 2007). At the millennium, the most elaborated account was the predictive model based on automatic detection of sequential regularity. In this theory, the MMN is described as an error signal elicited by any deviation between the predicted and the current event. The prediction is based on the sequential rule established by the stimulation. The function of the error signal is to update the model of the environmental stimulation. It is important to emphasize that the process occurs automatically[1] with or without attentional processes. Any repetitive

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[1] The relationship between vMMN and attention and the exact definition of automatic processes in the vMMN literature will be detailed in section 1.4.

pattern in the stimulation can be considered as a sequential rule. In the simplest case, the pattern is the repetition itself (i.e., a sequence of identical stimuli). However, the pattern can be so complex that it is basically independent from elementary feature changes.

Research on vMMN began around the millennium. The initial concept underlying the first vMMN research was to test the existence of MMN as such in the visual modality (the viability of this concept will be discussed later).

The first explicitly vMMN study was published in 1999 by Tales and her colleagues (Tales et al., 1999). The standard and deviant were the appearances of bar patterns in the upper and lower visual half-fields. The singletons were white bars on black background with or without black line along their midlines. The task-field was between the bars, in the center of the visual field. It was a square outline presented continuously during the stimulation. From time to time, the frame filled with a square. This was the target. The participants' task was to respond to the target with a button press. With this design, vMMN was elicited by the deviant. (Later, this design was applied numerous times.)

The second significant vMMN paper was published by Czigler and his colleagues in 2002 (Czigler et al., 2002). The stimuli were full-screen, colored grating patterns. The standard differed from deviant in the color of the pattern. The task was to respond to size changes in a fixation cross in the center of the visual field by pressing a button. In this experiment, vMMN was elicited by color deviancy. (The study also applied a so-called equiprobable sequence for the first time which is probably the reason why the study is the most cited research report in the vMMN literature; the condition will be discussed later.)

The third milestone in the vMMN research was an extensive review by Pazo-Alvarez and her colleagues in 2003 (Pazo-Alvarez et al., 2003). The authors systematically reviewed 20 papers related to the vMMN. Their conclusion showed the feasibility of a visual counterpart of the auditory MMN, and delineated the future directions of vMMN research.

Since then, the average number of publication per year has grown as well as the number of labs investigating the vMMN. At present, there are more than 150 vMMN research reports and 8 reviews. In the publications, the theoretical approach and the basic methods are similar to that of the MMN research. However, there are important differences between the MMN and vMMN. The modality of the stimulation is an obvious difference, and all the additional differences can be deducted from this fundamental distinction. All of them presented a challenge for researchers on vMMN. They had to reevaluate some characteristics of the initial acoustic paradigm, and adapt the concepts to the visual domain.

Differences in the visual and auditory attention require different designs for controlling attention, and different approaches in testing the limitation of the automatic processes underlying vMMN (for a review see Czigler, 2007).

Differences in the visual and auditory feature representation and object formation cause differences in the experimental stimuli and spatio-temporal attributes of the stimulation (for a review, see Winkler and Czigler, 2012 and Czigler, 2014).

Differences in the sensory memory and the perceptual attributes of the visual and auditory systems cause differences in the hypothetical cognitive processes and underlying mechanism of vMMN (for a review, see Kimura et al., 2011, Kimura, 2012, and Stefanics 2014).

1. Introduction

1.1. Visual mismatch negativity

1.1.1. Theoretical background

The most recent general review of the vMMN was written by Stefanics and his colleagues in 2014. The review presents the “state of the art” theory of vMMN with a selection of research reports as empirical evidences. Furthermore, the review took the vMMN component into the wider perspective of cognitive neuroscience. According to the review, the processes underlying the vMMN are an integral part of the visual perceptual system. As an afferent stream of processes it carries information about the mismatch (hence the name) between the predicted and the current event. The prediction is an efferent signal from higher visual areas. The prediction involves the attributes of the event (e.g., elementary features, feature conjunction, or category) and the (subjective) probability for the occurrence of the event (based on a cognitive model acquired by the environmental stimulation). The signal of the current event is an afferent one from lower level visual areas (e.g., V1) carrying information about the attributes of the event (the probability of the event is obviously one). So, the mismatch process compares the information of afferent and efferent streams. The comparison process generates either a match or a mismatch signal. The signal modulates the process at higher levels by modulating the prediction. This way the mismatch signal is an error signal weakening the validity of the predictive model. The match signal is a confirmatory signal strengthening the same model.

The argument is in line with the general theory of predictive coding (Friston, 2010). According to the theory, the neural system is a hierarchically organized neural network of local backward and forward loops. At each level, the network is comprised of representation cell and error cell populations. The error cells get information from representation cells at higher and lower levels. The higher level representation cells yield information about the expected environmental stimulation based on the former experience (both short- and long-term). The lower level representation cells carry information about the attributes of the current event. The error cells compare the (representation of the) expected stimulus with the (representation of the) current stimulus. In case of any deviancy, the error cells send signals to higher visual areas to modify the information of the representation cells. It is important to note that the feedback and forward loops occur multiple times during the formation of a perceptual experience resulting in more and more accurate representations. In that sense, the process not terminated just ended (probably when the adaptive response starts). A great example of that process is Bar's theory (Bar, 2004). The author argued that magnocellular information is processed faster yielding a coarse representation form. Then the coarse representation directs the further information processing of the parvocellular system.

The cognitive function of the vMMN is an adaptive reaction to the violation of the expectancy; that is to adjust the probability assigned to a certain event. Since the whole environment is comprised of individual events, the environmental model is basically the set of each expected event with the assigned probability (and of course their relation as a conditional probability). So, the function of the vMMN is to update the mental representation of the environmental model by adjusting the probability of each event. The mechanism of the adjustment is considered to be a bottom-up error signal; originating in the detection of the deviancy and flowing towards higher level areas[2].

The vMMN is regarded as an automatic process; taking place during all expectancy violation irrespective of whether the deviancy is within the attended or non-attended part of the visual scene. However, attention is a robust factor of the perception modulating all cognitive processes. Therefore, the search for a genuine vMMN (gvMMN) is consequently investigated in the non-attended or passive (oddball) paradigm. In the typical vMMN experiment, the participants do not respond to the stimuli of the oddball sequence. Furthermore, the aim of the experimental design goes one step further. In the appropriate design, the participants ignore entirely the vMMN-

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[2] It is important to mention that, although the vMMN is regarded as the prediction error signal itself, the case is a little bit more complicated. Actually the vMMN is an ERP component reflecting the prediction error signal. In other words, the vMMN is an indicator (or electrophysiological index) for the deviant-related processing of the stimulus and not the process *per se*. For the sake of simplicity, the doctoral thesis (and the vMMN literature as well) uses the two terms as synonyms.

related stimuli. To reach that aim, the design includes a so-called primary task. The only purpose of the task is to draw the participants' attention away from the experimental stimulation, so the recorded brain responses to the deviants and standards are attention-free. However, this method includes a caveat. Due to the modulating factor of attention, the data from vMMN experiments and (behavioral or ERP) data recorded in active conditions are hardly comparable.

1.1.2. VMMN as component

In short, the vMMN is regarded as a perceptual prediction error signal with the cognitive function of memory updating. The vMMN is a negative subcomponent on the ERP elicited by the deviant relative to a control (i.e., standard) stimulus (see Figure 1.1). The typical emergence of the vMMN is between 120 and 400 ms after the onset of the deviant event. The range is surprisingly wide; however, there is a pattern in the vMMN latency and the experimental condition. Elementary feature changes and simple sequences elicit typically earlier vMMN with latency in between 120 ms and 250 ms. Complex changes and more sophisticated sequences elicit later vMMN with latency in between 200 and 400 ms. Furthermore, several studies reported two subsequent vMMNs. It is typical when the deviancy occurs at elementary feature level and complex stimulus attributes level at the same time (e.g., emotional expression deviancy, but the standard and the deviant are the same person). As well as the vMMN-latency, the scalp distribution of the component also shows wide variability. The maximum of the component is typically over posterior areas. However, within this area, various scalp distributions may occur: bilateral and midline, parieto-occipital, temporo-parietal and occipital vMMN are equally reported. Probably the source of the vMMN generator highly depends on the deviancy. The source is where the deviancy is unraveled during the stimulus processing. Similarly to the case of double vMMN, multiple deviancies may activate more vMMN generators (the spatio-temporal attributes of the vMMN, with the relating studies, will be detailed in sections 1.2 and 1.3).

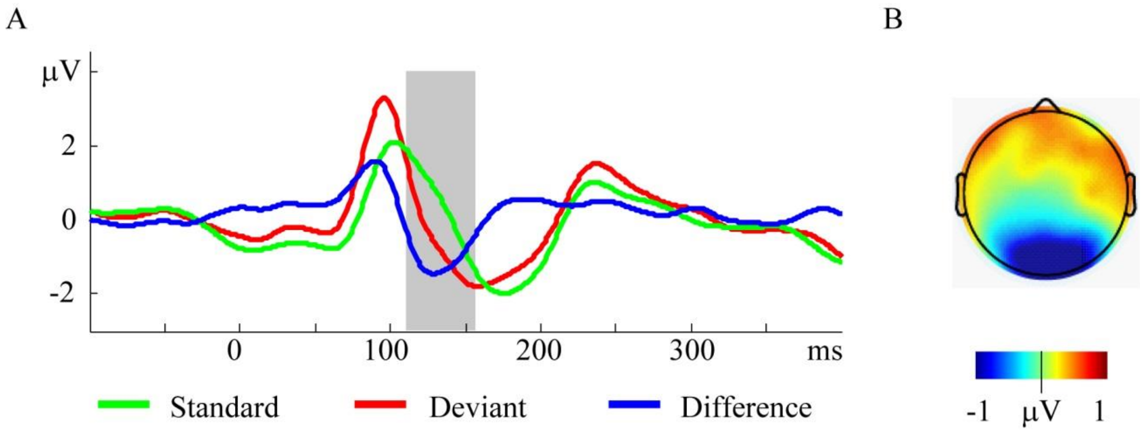

Figure 1.1. Emergence of a typical vMMN. (A) Event-related potentials and deviant-minus-standard difference potential. The grey area denotes the emergence of vMMN (B) Scalp distributions of the vMMN.

1.2. Paradigms and subcomponents

1.2.1. Oddball paradigm

The typical paradigm for investigating the vMMN is the passive oddball paradigm (see Figure 1.2A, top row). The oddball sequence consists of two stimulus types: standard and deviant. The deviant and standard differ from each other in certain stimulus attributes. The standard minus deviant difference or attribute is termed as *deviancy*. Besides the deviancy all other attributes of the standards and deviants are the same. In the simplest case, all the standards are identical (e.g., vertical, high-contrast bars), all the deviants are identical (e.g., horizontal, high-contrast bars), and the deviancy is an elementary feature (e.g., different orientation of high contrast bars). However, the deviancy can be either complex or categorical, such as a difference in the emotional expression of faces (sad vs. happy face). In this case, the common attributes of the standard and deviant are complex (e.g., all of them are faces) as well, and the stimuli (both standards and deviants) differ from each other from trial to trial in physical attributes (different identity, but all of them express happy or sad emotion).

Besides the deviancy, the second difference between the standard and deviant is their global frequency within the stimulus sequence. The presentation of the standard is much more frequent, between 70 and 95 per cent. The rest of the stimuli are the deviants with a frequency between 5 and 30 per cent. Due to the higher frequency of the standards, they are repeated many times (between 1 and 10) before any deviants are presented. It is highly important whether the position of the deviant in the sequence is random or not. In the typical experimental condition the position of the deviant is intentionally (pseudo)randomized. This fact can cause the probability of the subsequent event, whether it is a deviant or a standard, to be deducted from the global frequencies (e.g., 10 per cent frequency is equal with 0.1 probability). Because of this, the terms frequency and probability are commonly used as synonyms, but this convention is valid only if the presentation of the deviant is random. If not, the (local) probability of each single deviant matters.

In the case of the deviant, the low probability causes low predictability in every single deviant event; therefore, the occurrence of each deviant is unexpected. The term expectancy (or predictability) is used as mental representation of the probability of a certain event. According to that logic, the occurrence of the standard is expected. So, the oddball sequence is a model of a calculable environment (where most events are expected due to the high probability) with a few exceptions (i.e., low probability events).

1.2.2. Problems with oddball control

The difference between the ERPs to the standards and to the deviants reflects the difference between the brain electric responses to expected and unexpected (or surprising) events. The difference is commonly calculated by subtracting the ERPs to the standard from the ERPs to the deviant. This is because the standard serves as a contrast to enhance the surprise effect of the deviant. The subtraction results in a negative difference which is the polarity of the vMMN. However, this negative difference contains other subcomponents that are independent of the surprise effect. The experimental contrasts unraveling the genuine vMMN (gvMMN) among other subcomponents of the deviant-related brain electric response are one of the biggest challenges in the vMMN research. The solution is to filter out the effects using an appropriate control condition (cf. Luck, 2005). In that sense, the vMMN research is rather a discovery of the caveats of the original oddball paradigm. Up to now, there are several known ERP effects contaminating the gvMMN. The first one is elicited by the physical differences of the compared stimuli. As an example, face stimuli elicit a characteristic component (N170; Bentin et al., 1996) which component is absent in case of other complex objects such as houses. For this effect, I will use the descriptive term of *stimulus-effect* (see Figure 1.2B). The solution is that the compared stimuli should be identical (face with face, house with house). The second ERP effect is caused by stimulus repetition: the standards (i.e., repeated stimulus) elicit smaller ERP relative to the deviants (i.e., stimulus change). For this effect, I will use the term *repetition-effect*. The solution is to compare the deviant with a similarly changing control stimulus. Third, frequent presentation of the same stimulus causes a gradually decreasing ERP. The effect is called *frequency-effect.* The modulation of the exogenous components (generally N1 component) is called stimulus specific adaptation (SSA). The solution is to equalize the frequencies of the deviant and control stimuli during the sequence. It is worth mentioning that the repetition and the frequency effects are not orthogonal, since repetition causes larger frequency in the sequence (see above). Finally, the experimental factor of gvMMN (i.e., surprise) should be absent (or diminished) in the case of the control stimulus. That is, the expectancy of the control stimulus should be higher than the expectancy of the deviant. It is important to mention that the above terms have different names in cognitive neuroscience (O'Shea, 2015). In the following, the terms I use are descriptive, i.e., without any reflection of putative physiological reference.

1.2.3. Reverse control

The most prevalent control in the vMMN research is the *reverse control* (see Figure 1.2A, middle row). The reverse control is an additional oddball sequence where the roles of the standard and of the deviant stimuli are reversed. That is, the same stimulus is standard in the oddball sequence and deviant in the reverse control sequence. The difference wave (i.e. vMMN) is calculated as a subtraction of the deviant from the reverse control standard (and vice versa). This method filters out the stimulus-effect; however, the frequency-related effect probably remains in the vMMN. The use of the reverse control is commonly used in the vMMN research; the list of the studies using such control is almost identical to the whole list of the vMMN papers. Furthermore, reverse control is especially useful when the equiprobable control (see below) cannot be used (e.g., the experimental stimuli have binary nature).

1.2.4. Equiprobable control

At present, the best control condition meeting the above requirements is the *equiprobable sequence* (see Figure 1.2A, bottom row) developed by Schröger and Wolff (1996) and Jacobsen and Schröger (2001). The equiprobable sequence is comprised of 3 to 11 different stimuli. The stimuli are presented with equal frequencies, and these frequencies are the same as that of the deviant in the oddball condition. The stimuli are delivered in a random order. Similarly to the oddball sequence, the stimuli are identical in all characteristics except one. The common attributes of the stimuli are the same as the common attributes of the oddball sequence (e.g., all of them are tilted grey bars in the center of the screen). The distinctive feature dimension of the stimuli is the same dimension of the deviancy in the oddball sequence (e.g., the orientation of the bars). One of the stimuli is physically identical to the deviant of the oddball condition. That stimulus is the control stimulus for the deviant. Since the critical feature randomly changes trial by trial, there will be no expectancy relating to that feature. Furthermore, since the frequencies of the deviant and control are equal, there will be no frequency-related response attenuation. Since both control and deviant change relative to the previous stimulus, there will be no repetition-related effect. Since the control and deviant are physically identical, there will be no exogenous ERP difference (i.e., stimulus-effect).

The deviant-minus-control difference shows the genuine vMMN reflecting the prediction error signal. The control-minus-standard difference includes both the repetition- and frequency–related effects. The difference is called refractoriness (or N1 modulation) in the vMMN literature; however, the stimulus-specific adaptation (SSA) term is more appropriate. The sum of SSA and gvMMN is the traditional vMMN (tvMMN) obtained by deviant-minus-standard subtraction.

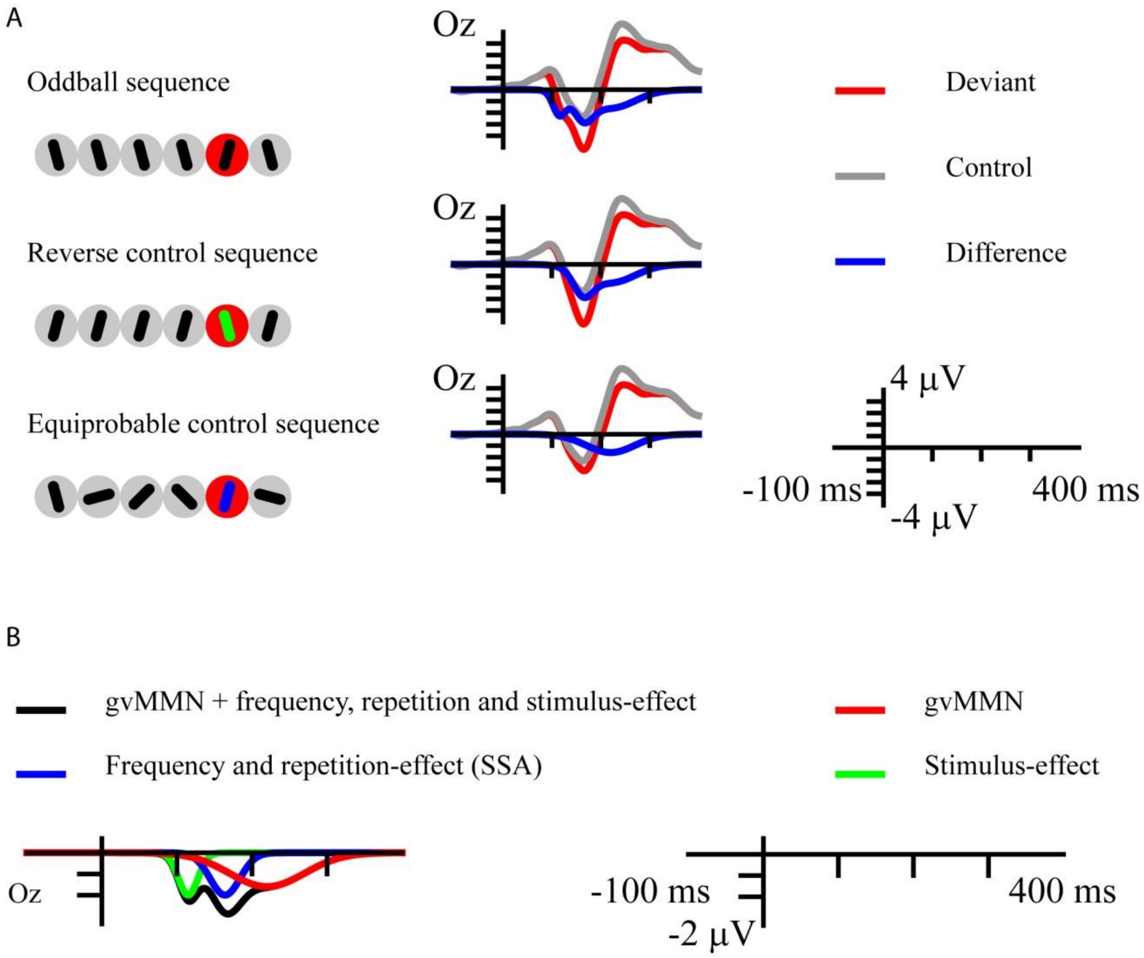

Figure 1.2. Prevalent paradigms in the vMMN research. A: common stimulus sequences eliciting the vMMN (left column) and hypothetical ERPs obtained in the different sequences (middle column). B: subcomponents emerging with the contrast of the different control sequences.

The first study which applied the equiprobable paradigm in the visual modality was published by Czigler et al. (2002). In this study, the stimuli were colored checkerboard patterns. The colors of the equiprobable sequence were pink, purple, turquoise, yellow, green and red (the latter two were the colors of the oddball sequence). VMMN was obtained with both deviant-standard and deviant-control contrasts; however, the two difference waves were slightly different: the traditional vMMN had midline scalp distribution with a 140 ms latency, and the gvMMN had right-side dominance a bit earlier (slow shift; 120 ms latency). The authors’ interpretation of the results was that the SSA per se is not responsible for the deviant-standard difference; instead, the vMMN is an outcome of memory comparison.

Because of the spectral nature of the orientation (i.e., continuous variation of possible orientations), the orientation is an especially appropriate feature for studying the gvMMN effect. Kimura et al. (2009) used a single light grey bar with black background at central position. The orientations of the bars were 0, 36, 72, 108, and 144 degrees in the equiprobable sequence, and all orientations were both deviant and standard in separate oddball sequences (both equiprobable and reverse controls). They obtained gvMMN (deviant-minus-control) in the 200-250 ms latency range, and the bilateral scalp distribution showed right hemispheric dominance. The control-minus-standard comparison (i.e., SSA) revealed an earlier difference in the 100-150 ms range, and the scalp distribution was symmetric bilateral. Obviously, the deviant-minus-standard (traditional vMMN) was the sum of the two difference waves. The authors interpreted the results as the decomposition vMMN's two subcomponents. The earlier one corresponds to the refractoriness effect (SSA) as N1 decreasing, and the later one corresponds to the genuine vMMN reflecting clear memory effect. The results were replicated later with a pattern of bars around a central task (Kimura and Takeda, 2013). Astikainen et al. (2008) used a design similar to that of design Kimura et al. (2009), but they switched the luminance of the figure-background (the stimulus was black and the background was grey). They obtained a genuine vMMN at left lateral, posterior electrode sides with 195 ms latency. The SSA was more extended at the whole posterior areas (same latency range). File et al. (submitted) also investigated the SSA and gvMMN during orientation deviancy. The stimuli were a texture of line segments delivered in the lower part of the visual field. The ERPs elicited by the deviant and the control stimuli were quite similar, therefore SSA fully explained the deviant-minus-standard difference (the tvMMN was a slow shift between 100 and 200 ms post-stimulus with an occipital maximum). In the same study, File et al. also tested windmill patterns. Windmill patterns elicited an occipital double tvMMN at 150 and 270 ms. Relative to the tvMMN, the gvMMN was smaller in the earlier range, but similar in the later range. The authors argued that the early difference reflects SSA, and the later vMMN is a gvMMN. Chang et al. (2011) used stimuli similar to those in the classic study by Tales et al. (1999). The equiprobable stimuli were patterns of three or more white bars in an arrangement similar to the oddball stimuli. The deviant stimuli elicited a double gvMMN (occipital, at around 150 and 300 ms) with equiprobable contrasts. Furthermore, only the early negativity (i.e. SSA) emerged in the control-minus-standard difference wave.

The usefulness of equiprobable contrast was confirmed in complex stimuli as well. The complex stimuli were mostly human faces, and the deviancy was the emotional expression. Astikainen et al. (2013) applied pictures from the stimulus set of Picture of Facial Affect (Ekman and Friesen, 1976). The standard was a neutral expression; the deviant was either a happy or a sad expression. The equiprobable sequence included all three faces with equal (33.3 per cent) frequencies. Unfortunately, the authors did not compare the deviant with the control; instead, they subtracted the neutral from the emotional expressions in both conditions separately. Thus, the difference waves were contaminated by the ERP effect of physical differences (i.e., stimulus-effect; e.g., neutral vs. happy). With this method, the vMMN (180 ms) preceded the SSA (170 ms; however, the 'SSA' probably reflected the physical differences). Li et al. (2012) also used pictures of faces. The standard was a neutral face; the deviant was a sad face. The equiprobable sequence consisted of additional emotional expressions (happy, fear, surprise). With the right method, the SSA (310 ms) preceded the gvMMN (360 ms; right temporo-parietal maximum). The results are quite consistent with the equiprobable contrast. In the case of an elementary feature, the latency of the SSA is between 100 and 200 ms, and the latency of gvMMN is between 200 and 400 ms post-stimulus. Complex stimuli elicited a later component; however, the order of the components was similar: the SSA preceded the gvMMN. With equiprobable control, the scalp distribution of the gvMMN shifted toward right parieto-occipital areas.

1.2.5. Other paradigms

Another approach of gvMMN research is based on specific sequential rules. One of the most elegant solutions is the alternating sequence, where the deviant violates the pattern of the alternation. Czigler et al. (2006) delivered colored checkerboards in a regular RRGGRRGG sequential pattern; where the R stands for red-black, and the G stands for green-black checkerboard. The deviant event was an irregular third repetition of either color. This design ruled out the stimulus and frequency effects. Furthermore, according to the repetition-effect, the third repetition should elicit a smaller ERP than the second repetition. In contrast, the ERP was more negative to the third repetition relative to both the second repetition and the first alternating stimulus. The negativity emerged between 200 and 270 ms with midline occipital scalp distribution. The authors argued that since a low level repetition effect can be ruled out by the condition, the effect should reflect gvMMN. The result was later replicated by Kimura et al. (2012) in a similar experiment. The authors used happy (H) and sad (S) faces instead of colored checkerboards, and the sequence was also different: it was an HSHS alternating sequence. Here, the deviant event was the rare repetition of the same emotional expression. The irregular repetition elicited right occipital gvMMN at 300 ms post-stimulus.

Stefanics and his colleagues (2011) used patterns of colored circles around a central task. The stimuli were delivered pairwise with longer inter-stimulus-interval (ISI) between the pairs and shorter ISI within the pairs. The color of the pairs was identical, but the color changed on a pair-by-pair basis. This was the conditional probability rule: the color of the second stimulus was the same as the color of the first stimulus. The deviant event was when the color of the second stimulus differed from the first one. This deviation elicited a gvMMN with 250 ms latency above occipital areas.

Probably the most elegant solution is Kimura and his colleagues (2010) study. The authors compared 20 per cent frequency rare stimulus in two conditions. In the first one, the stimuli were delivered in a regular AAAAB pattern. Therefore, the probability of the rare stimulus was one, although the frequency was 20 per cent. In the second condition (oddball sequence), the position of the rare stimulus was random, so the probability was 0.2 (cf. with the argument in section 1.2). The design filtered out the three known subcomponents on the deviant-related ERP. The authors found larger vMMN (250 ms latency; occipital distribution) in the oddball sequence, but only if the stimulus onset asynchrony (SOA) was 160 ms. With longer SOA (480 ms and 800 ms) the size of the two difference waves were similar. In sum, the results of sequential regularity studies are quite consistent: the gvMMN’s scalp distribution restricted to occipital areas, and its latency limited into a narrow range between 200 and 300 ms.

Kimura and Takeda (2014) used self-generated stimuli to induce obvious prediction. According to the ideomotor and common coding theory of voluntary action control (Hommel et al., 2001), self-initiated action predicts its behavioral consequence. So the predictability (probability) of an event is independent from the global frequency of the stimulus. The participants generated visual stimuli by pressing buttons with either hand. Both actions generated a grey bar against black background, but the orientation of the bar depended on the laterality of the hand (e.g., left hand generated vertical, right hand generated horizontal bar). The participants were trained to press the button according to an oddball sequence (i.e., frequent left hand and rare right hand at random positions or vice versa). Due to the temporal pattern of the voluntary actions the self-generated stimuli were delivered as an oddball sequence. However, the probability of each event was one, since the action perfectly predicts the current stimulus. The irregular event in the stimulus sequence was when the stimulus deviated from the predicted one (e.g., left hand generated horizontal bar instead of a vertical one). The ERPs elicited by predicted frequent and infrequent stimuli differed in an earlier range. This negative difference was interpreted as SSA. The ERPs elicited by predicted frequent and unpredicted rare differed in two ranges. The earlier component was similar to the SSA effect in the other condition; the later one was interpreted as gvMMN.

1.2.6. Summary

The list of the studies which used sophisticated experimental paradigms showed that the deviant-standard difference contains the gvMMN. That is, the mechanism underlying the vMMN is not restricted to SSA, predictive processes are also involved. However, the weight of the SSA and gvMMN may differ depending on the experimental stimuli. In the following section I will give a short description of the stimuli used in the vMMN research.

1.3. Stimuli and representations

The topic of this section is the description of the attributes of the vMMN eliciting events. In the following paragraphs, I detail the experiments and the obtained results in the case of several features and stimuli. Figure 1.3 summarizes the experimental stimuli used in the vMMN research. As the figure shows, the vMMN-eliciting stimuli are not restricted to elementary features; the vMMN is also sensitive to highly complex stimulus sets.

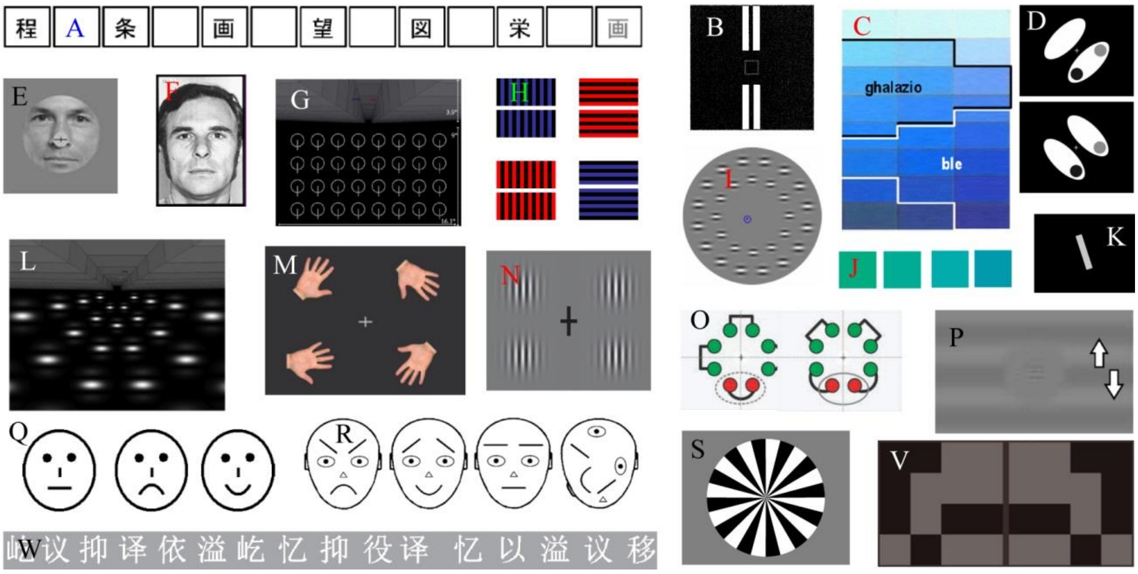

Figure 1.3. An overview of the experimental stimuli used in the vMMN research. The pictures come from the following studies. A: Fujimura et al. 2013; B: Tales et al., 1999; C: Athanasopoulos et al. (2010); D: Müller et al., 2013; E: Kecskés-Kovács et al., 2013; F: Astikainen and Hietanen, 2009; G: Czigler et al., 2013; H: Winkler et al., 2005; I: Takács et al., 2013; J: Mo et al., 2011; K: Kimura et al., 2009; L: Sulykos et al., 2013; M: Stefanics and Czigler, 2012; N: Farkas et al., 2015; O: Müller et al., 2009; P: Kremláček et al., 2006; Q: Zhao and Li, 2006; R: Kreegipuu et al. 2013; S: Maekawa et al., 2005; V: Kecskés-Kovács et al., 2013; W: Wang et al, 2013.

1.3.1. Elementary features

The vMMN can be elicited by all known elementary feature deviancies (luminance, orientation, spatial frequency, movement direction, duration, shape, and color).

Kimura and his colleagues (2010a, 2010b) used patterns of bright and dark disks (with black background) surrounding a central task. In both studies, they obtained a midline vMMN between 150 and 250 ms. Stagg and her colleagues. (2004) used bright and dark bars in a similar arrangement to that in Tales et al.'s study (1999). The vMMN was a slow shift at around 300 ms, and had a maximum at the O2 location. It is important to mention that in these studies it was not just the increase in luminance elicited the vMMN, but also the decrease in luminance (see the refractoriness issue, the previous section).

One of the most frequently used features in the vMMN research is stimulus orientation. Orientation deviancy has been investigated in the following stimulus types: a central bar (Kimura et al., 2009; see Figure 1.3K; Astikainen et al., 2008), patterns of line segments (Kimura and Takeda, 2013; Bodnár, submitted; File, submitted), patterns of Gabor patches (Takács et al., 2013; see Figure 1.3I; Farkas et al., 2015; see Figure 1.3N), and square gratings (Jack et al., 2015). The vMMNs typically appeared in two latency ranges: between 100 and 150 ms, and between 200 and 250 ms. Sometimes a double vMMN emerged in both ranges. The earlier one is commonly linked to the SSA (cf. Kimura et al., 2009), the later one is considered to be a gvMMN. According to the scalp distribution, the amplitude maximum appeared over the occipital midline areas, typically when the stimuli were high spatial frequency patterns, and they stimulated the whole visual field (Takács et al., 2013; Farkas et al., 2015). A parieto-occipital bilateral maximum with right-side dominance appeared in Kimura et al., 2009, Jack et al., 2015, Kimura and Takeda, 2013.

Spatial frequency was investigated with two stimulus types. The first type is the single and double bars along the vertical midline; delivered simultaneously in the upper and lower hemi-fields (see Figure 1.3B). The first study which used such stimuli was already mentioned earlier (Tales et al., 1999). All of the studies followed can be considered a replication of the original study (Chang et al., 2011; Hedge et al., 2015; Kenemans et al., 2003; Tales et al., 2008; Stagg et al., 2004). Despite the fact that the experimental designs were quite similar (not just the stimuli, but the timings and the primary tasks were also the same), the obtained vMMNs varied in a wide range. Sometimes a double vMMN appeared (Stagg et al, 2004; Chang et al, 2011, Tales et al, 2008), in other studies, there was a slow shift between 150 and 400 ms. In the case of a single vMMN, the latencies varied from 100-150 (Kenemans et al., 2003) through 200 ms (Stothart et al., 2015; Kazanina, 2013) to 300 ms (Hedge et al., 2015). The second frequent stimuli in the spatial frequency domain are the windmill patterns with different number of vanes (Maekawa et al., 2005, 2013, 2011, 2009; File, submitted; Bodnár, submitted; see Figure 1.2S). In these studies, the elicited vMMNs were fairly consistent: a double vMMN with midline occipital scalp distribution; the peak latency of the earlier difference is between 150 and 200 ms, and the peak latency of the later vMMN is between 250 and 300 ms.

The aim of movement direction deviancy research was to investigate the activity in the magnocellular system. As a general rule, the standard and deviant had opposite motion directions. For investigating transversal motion, low spatial frequency horizontal sinusoid gratings with vertical motion (Kremláček et al., 2006; see Figure 1.2P; Hosák et al., 2008; Urban et al, 2008; Pazo-Alvarez et al., 2004) or vice versa (Kuldkepp et al., 2013) were applied. Furthermore, Kremláček et al. (2013) used sinusoidal circular patterns, and the motions were expanding and contracting radial motions. In these studies, vMMNs were quite similar: midline scalp distribution and between 150 and 200 ms post stimulus (typically 170 ms).

Shape deviancy was investigated by using the deformation of a circle (Clery et al., 2012, Bottari et al., 2014). The circle was presented during the ISI (surrounding a central task). The deviant and standard events were continuous transitions of the circle to an ellipse along the vertical and horizontal axes. In both study a bilateral vMMN was obtained with 210 ms latency.

Up until now, there has been only one study reporting a duration-deviant-related vMMN (Chen et al., 2010). The stimulus was a single red disk, and the standard and deviant durations were 200 ms and 120 ms, respectively. For that stimulation, a bilateral vMMN emerged at 370 ms post-stimulus with a right-side maximum.

Color is a special case of the elementary feature, because it has a dual nature. At the lower level, the processing of color depends on the weighted mixture of the 3 wavelength (low, middle, and high). At the higher level, the category dependent representations organize the wavelengths into chunks according to the color categories (red, green, blue, etc.).

The investigation of color deviancy follows this duality. Czigler and his colleagues used colored-black checkerboards (Czigler et al., 2006) or square wave gratings (Czigler et al., 2002, 2006, 2007) as stimuli to investigate the deviant-related processing of color as elementary feature. The obtained vMMNs were quite consistent: 150 ms peak latency and occipital midline maximum.

Another approach compared the vMMN obtained in within-color (e.g., light and dark blue) category and between-color (e.g., green and blue) category conditions (implicating that larger differences elicit larger vMMN). In the Clifford et al. (2010) study, the stimuli were two colored squares in the same (upper or lower) hemi field, arranged along the midline, above or below a central task. The standard pattern comprised of one color. The deviant pattern comprised of two colors: the square closer to the center had the same color as the standard, and the peripheral square had a different color. The two colors were either within-or between-category (light blue – dark blue or light blue – light green, respectively). Slow negative shifts emerged in both conditions above the left occipital regions which were interpreted as a vMMN. Importantly, the vMMN was larger within than between category in both hemi-field stimulation conditions. Mo et al. (2011; see Figure 1.3J) used bilateral squares colored symmetrically and asymmetrically as standard and deviant, respectively. The deviant color pattern comprised of the same (light blue - light green) or different color categories (light blue - light green), and the deviant color appeared on either side. In terms of the vMMN, the region of interest was the bilateral occipito-temporal regions at around 160 ms post-stimulus. When the deviancy appeared on the left side, the within-category and between-category vMMNs were similar. However, when the deviancy appeared on the right side, the between-category vMMN was larger. The pattern of results is in accordance with the right hemispheric dominance of language processing responsible for color labels. Zhong et al. (2015) used a similar design with an important difference. They compared the brain electric responses of two groups: training and naïve groups. The training group learned a new color category before the EEG recording; the naïve group did not participate in such training. For the novel category, right hemi field stimulation elicited a vMMN in the training group but not in the naïve group. Furthermore, no vMMN was obtained during left hemi field stimulation in both groups. The effect of the linguistic relativity principle is strongest when cultures with different language-specific categories are compared. Thierry et al. (2009) reported a cross-cultural vMMN study. The stimuli were green and blue disks against middle-grey background. The deviancy was color luminance; i.e., the deviant and standard were the light and dark versions of the same color. The Greek language strictly separates the two shades of blue with different terms: the lighter one is called *ghalazio* and the darker one is called *ble*. In contrast, the English have one term for blue color. The light and the dark greens have a uniform label in both the Greek and English languages. Therefore, in the English group both deviancies were within-category, and in the Greek group one (green) was within- and one (blue) was between-category. In the Greek group, the vMMN was larger to the blue color deviancy than to the green one. In the English group, the two vMMNs were similar. These findings were extended by Athanasopoulos et al. (2010, see Figure 1.3C). They tested three groups: English speakers, Greek speakers with long stay in the UK, Greek speakers with short stay in the UK (the latter two were bilinguals). Thus, the cultural exposure to the English language gradually decreased along the three groups. The magnitude of the vMMN negatively correlated with the cultural exposure in the blue condition, whereas no correlation was found in the green condition. The study demonstrated the top-down modulation of the deviant-related processing of elementary features.

1.3.2. Between simple and complex stimuli

Results from color vMMN studies support that the vMMN is sensitive to the early level of perceptual integration. Winkler et al. (2005; see Figure 1.3H) investigated perceptual integration and vMMN with a different approach: they studied the pre-attentive binding of stimulus features. The stimuli were color-black square wave gratings characterized by orientation (horizontal and vertical) and color (green and red). Two combinations of the orientations and colors were frequent (45 per cent each); those were the standards. The deviants were the remaining infrequent combinations (5 per cent each). So the standard and deviant differed in neither feature per se, but only in the combination of the two of them. For these infrequent combinations, a midline vMMN was obtained with 130 ms peak latency. (It is worth mentioning that the relatively early vMMN followed, and not preceded, the also early N1 component.)

Two studies (Müller et al., 2009, 2013) investigated the sensitivity of the processes underlying vMMN to object-related deviancies. In the first study (Müller et al., 2009, see Figure 1.3O), the stimulus pattern comprised of 8 disks arranged along the angles of an imaginary octagon. The neighboring disks were connected pairwise with black lines which resulted in four separate objects (i.e., each comprised of two disks; cf. Scholl, 2001). The color of the disks was identical (red or green) during the standard event. During the deviant event, two disks were different (the other color) relative to the standard. The position of the deviant disks as well as the grouping of the disks changed in every stimulus presentation (trial by trial). The two deviant disks were either in the same object or in two different objects (these were the experimental conditions). In both conditions, a double vMMN was elicited with 220 ms and 265 ms latencies. Both vMMNs had bilateral distribution with right-side dominance. Furthermore, the magnitude of the second vMMN was larger in the same object condition. In the second study (Müller et al., 2013; see Figure 1.3D), the stimulus pattern comprised of two white, parallel oblique (45 degree) ellipses and two dark or light (or both) grey disks. The background color was black. The two disks were within the same or within two ellipses; that is, the pattern comprised of two ellipses with one disk each, or one ellipse containing both disks (and the other was empty). The two patterns were the standard and deviant (with reverse control). Therefore, during the oddball sequence the object-assignment of the disks (or the object identity) changed. Both object-related deviancies elicited similar vMMNs: 250 ms latencies and parieto-occipital scalp distributions.

1.3.3. Higher-order representations

Astikainen and Hietanen (2009; see Figure 1.3F) delivered greyscale pictures from the Pictures of Facial Affect (Ekman and Friesen, 1976) in a central position against black background. The neutral expression was always in the role of the standard. Happy and fearful emotional expressions were the deviants. Thus, the deviancy was the appearance of an emotional expression on the faces. The face identities changed on a trial-by-trial basis varying the low-level (orientation, luminance) as well as the high-level (age, gender) attributes of the stimuli. For both deviancies, a double vMMN was obtained with 170 and 300 ms latencies. Unfortunately, the authors recorded the EEG at occipital channel locations instead of parieto-occipital ones where presumably the maximum is the face-related vMMN. As an example, in a similar experiment, Astikainen et al, (2013) found a bilateral (double) vMMN with right-side maximum at 130 ms and 170 ms at parietal locations. The experiment also contained an equiprobable control filtering out the later vMMN. Kimura and his colleagues (2012) used an alternating sequence of happy and fearful faces. The irregular repetition elicited vMMN in both conditions between 300 and 400 ms. The fearful-vMMN was bilateral (with a PO8 maximum) and larger compared to the smaller and midline (a POz maximum) happy-vMMN. Interestingly, the same deviancy elicited a smaller vMMN when the faces were delivered in an inverted position. Stefanics and his colleagues (2012) presented four different faces (from Pictures of Facial Affect, similarly to Astikainen et al., 2009) in the periphery around a central task. They obtained a double vMMN in both conditions with 200 and 300 ms latencies; however, the magnitude and scalp distribution differed in the two conditions: the fearful-vMMN was larger with a right, parieto-occipital distribution, while the happy-vMMN was smaller with a left-side distribution. In Gayle et al.'s (2012) design, the pictures were colored, and the deviancies were happy and sad (instead of fearful). Both deviancies elicited vMMNs emerged between 200 and 300 ms with right parieto-occipital scalp distributions; and again, the negative emotion resulted in a larger vMMN. Li et al. (2012) investigated the emotional-expression-related vMMN in a different culture: the face stimuli were Asian as well as the participants. The deviant was a sad expression against a neutral expression as the standard; and the design also contained an equiprobable control sequence. Both gvMMN and SSA emerged at 150 and 300 ms, and the gvMMN was larger at around 170 ms.

Zhao and Li (2006) used schematic faces (similar to emojis; see Figure 1.3Q). As before, the standard was neutral and the deviants were happy or sad faces. The vMMN was similar to the face picture studies. Both deviancies elicited vMMN between 150 and 350 ms, and the vMMN was larger for the sad deviant. The results were replicated by Xu et al. (2013) and Chang et al. (2010). The latter study also included the inverted version of the faces. The 180 degree rotation of the faces resulted in a smaller vMMN. In Kreegipuu et al. (2013; see Figure 1.3R) study, the negative emotion deviant was anger instead of sadness. Despite the differences, the results were similar: a bilateral vMMN between 150 and 350 ms with larger amplitude to angry faces. The anger superiority effect was also investigated by Lyyra and his colleagues (2014). They delivered four faces at the corners of the display (a similar design to that in Stefanics et al., 2012). The standard comprised of four identical faces (angry or happy). The deviant was similar to the standard with one exception: one of the faces expressed the other emotion. This difference was labeled as threatening (happy to angry) or non-threatening (angry to happy) changes in the experimental stimulation. The vMMN (300 ms peak latency) was larger for the threatening changes. Lyyra and his colleagues (2014) investigated the face-specific vMMN with a similar design but different stimuli. Here, scrambled and normal faces were delivered as standard and deviant (or vice versa). Both changes elicited vMMN with 250 ms latency, although the vMMN elicited by the decomposition of a face was smaller.

It is worth emphasizing several consistencies in the pattern of the results. First, in most cases, the scalp distributions are parieto-occipital bilateral with left-side dominance.

Second, the temporal patterns of the vMMNs are also similar: a double vMMN with peak latencies at around 180 ms and 350 ms. The earlier one may reflect changes in low-level features, such as the shape of the mouth. This is particularly true when the models were identical during the stimulation (e.g., Zhao and Li, 2006; Xu et al., 2013; Chang et al., 2010; Kreegipuu et al., 2013). In this case, the SSA (as an additional factor) also cannot be ruled out. (There was no reverse control in the experiment.) Third, emotional expression with negative valence elicited a larger vMMN. According to the evolutionary psychology approach (cf. anger superiority effect), the negative emotions have higher value relating to the survival. However, this post hoc interpretation is hard to test as hypothesis with the tool of vMMN. Up until now, there have been two face-related vMMN studies in the literature investigating features other than emotional expression. The first deviancy (Kecskés-Kovács et al., 2013; see Figure 1.3E) was gender identity; i.e., the stimuli were female and male faces. A double vMMN was obtained to the deviancy with 200 and 300 ms latencies; both had bilateral scalp distributions with a maximum on the left side. The second deviancy was orientation. Wang et al. (2014) delivered upward or inverted faces as standards, and the deviant was the same face rotated with 90 degrees. Both conditions elicited a vMMN, and the vMMN was larger for normal than inverted faces.

The face is the most relevant but not the only body part in terms of self-valence and detailed mental representation. The human hand is also an important and overlearned human body part (cf. “I know him like the back of my hand.”). Stefanics and Czigler (2012, see Figure 1.3M) investigated the deviant-related response to changes in the laterality of the hands. The stimuli were delivered in a similar design to that of Stefanics et al. (2012); however, here the stimuli were homogenous patterns of right or left hands. The orientation of the hands changed trial by trial, so the orientation could not be used as information about the laterality of the hands. A vMMN was obtained to both rare left and rare right hands with 200 ms latency, and an additional vMMN emerged to the right hand deviant at 410 ms post stimulus. The asymmetry between the vMMNs was explained as a result of a stronger mental representation of the right hand. The interpretation was supported by the correlation between the vMMN magnitude and the (Edinburgh) handedness score.

The second commonly used complex stimulus type contains letters and words. This is reasonable a reasonable choice. Similar to face-stimuli, letters are also overlearned stimuli; therefore, the mental representations of such stimuli are also detailed. Consequently, significant parts of stimulus processing occur automatically.

Wang et al. (2013; see Figure 1.3W) delivered Chinese characters according to an oddball sequence. The characters differed trial by trial. The common attribute of the standard was the pronunciation, all standards were homophones. The deviant differed in pitch contour. The deviation elicited a double vMMN with 200 ms and 300 ms peak latencies; the earlier had a left parieto-occipital, the later had a right temporo-parietal distribution. Fujimura et al. (2013, see Figure 1.3A) used Japanese kanji characters with emotional content. In the first experiment (Fujimura et al., 2013), the characters changed trial by trial; the standard had neutral meaning, while the deviant had positive or negative valence. A double vMMN (bilateral distribution; peak latencies: 250 and 400 ms) was obtained to the rare appearance of the emotional content. In the second experiment, the standard had positive or negative meaning, and the deviant was (emotionally) incongruent with the standard. Here, the standards were identical during the sequence. Again, a double vMMN emerged, with a bilateral parieto-occipital distribution but with different latencies (150 and 230 ms). According to the authors interpretation, the early (150 ms) vMMN reflects physical differences between the oddball stimuli, and the later one reflects the deviation in the emotional contents (thus, the later component corresponded to the later vMMN in experiment 1).

The third higher-order representation form in the vMMN research is connected to the spatial statistics of the environment. During the perceptual learning, the frequent correlations in the environment acquired a stable and detailed mental representation resulting in a specific perceptual category.

Kecskés-Kovács and her colleagues (2013, see Figure 1.3V) used black and white matrices (similar to a checkerboard pattern) against dark grey background. The matrices formed either a symmetrical or a random pattern. Both stimuli were standard and deviant in separate conditions. The rare random pattern embedded in a sequence of symmetrical patterns elicited a bilateral (left-side dominance) vMMN with a 290 ms latency. Importantly, no vMMN was obtained in the reverse condition; i.e., when the stimulus sequence consisted of mostly random patterns. The pattern of the results emphasizes the role of the standard in the vMMN experiments. The repetitive presentation of the symmetrical pattern acquired symmetry as a perceptual category, so the deviancy from the pattern (i.e., the appearance of a random pattern) elicited a vMMN. In the case of the standard random pattern, no categorical representation was formed for the stimuli, since there is no such thing as a ‘randomness’ category. The lack of representation of the stimuli was investigated in a backward mask vMMN experiment (Czigler et al., 2007).

Durant and her colleagues (submitted) investigated the relationship between spatial statistics and vMMN via testing orderliness deviancy. Here, the orderliness means the global similarity of Gabor patches in terms of orientation. Ordered patterns comprised of similarly (but not identically) orientated Gabor patches. Disordered patterns comprised of highly variable orientated Gabor patches. The mean orientation of the Gabor patches changed trial-by-trial. A midline vMMN with 200 ms latency was obtained to the disordered deviant; i.e., when the standard was the ordered pattern. No vMMN was obtained, when the standard was the disordered pattern. The interpretation of the results was similar to the previous one, ordered patterns acquired perceptual category in contrast with the disordered pattern.

In a study by Czigler and his colleagues (2014; see Figure 1. 3G), the pattern comprised of circles with or without an additional vertical line (similar to a lollipop drawing; Treisman and Gelade, 1980). The standard was a homogenous pattern (e.g., all drawings were circles). The deviant was a heterogeneous pattern; it contained both drawings in a 16/84 ratio (e.g., 16 per cent of the pattern were lollipops, 84 per cent were circles). The positions of the two types of drawings changed trial by trial within the pattern. A vMMN was obtained in both conditions; however, the vMMN was larger and earlier for the lollipop deviant (254 ms) than the vMMN for the circle deviant (286 ms).

1.3.4. Summary

Despite the high variation of the listed studies, the obtained results are quite converging. The vMMN responds to a wide variety of visual features. The features included all elementary and several higher-order features, such as perceptual category, language-related category, object-related grouping, and emotional content of facial expression. So the mechanism underlying the vMMN is not restricted to a particular level of the visual system. Instead, the vMMN is sensitive to the mental representations of various levels of the hierarchy. It is important to mention that, the higher level was only tested with highly familiar (i.e., overlearned) categorical representations, so it is not clear whether less familiar complex stimuli elicit vMMN (cf. Kaliukhovich and Vogels, 2014). The spatio-temporal attributes of vMMN follow the hierarchical organization of the visual system. As the deviancy becomes more and more abstract, the obtained vMMN shifts toward parieto-temporal areas and the latency elongated. That is, where vMMN is generated, the deviancy is detected. The emergence of a double vMMN is another good example for that. A certain part of the stimuli deviated in a low-level feature, and then the global perception of the stimulus also changed (high-level feature), which elicited a subsequent vMMN. The argument implicates that low-level deviancies modulate the global perception of the stimulus. Emotional expression of a schematic face can be changed by mirroring the curve of the mouth (Zhao and Li, 2006; Xu et al., 2013; Chang et al., 2010). Deviation in a feature of the object changes the whole object perception (Müller et al., 2009, 2013). So bottom-up processes modulate the mental representation at higher levels, and the vMMN is sensitive to such modulation. Besides the afferent stream, the effect of the efferent stream was also demonstrated in several vMMN studies. The color deviancy is a great example for demonstrating that. Simple luminance changes elicited different vMMNs in case of different colors (Thierry et al. 2009), and the effect was modulated by long-term learning processes (Athanasopoulos et al., 2010). Similarly, face perception modulated the vMMN elicited by orientation deviancy (Wang et al., 2014). Besides the vertical connections (bottom-up, top-down), the vMMN studies support the process of horizontal connections in the visual system. Winkler et al. (2005) found an interaction between the processing of color and orientation. In sum, the mechanism underlying the vMMN exists at many levels of the hierarchical network of the visual system. This is in accordance with the predictive coding theory of vMMN. That is, it is an error signal modulating the environmental model at multiple levels of the hierarchical system.

1.4. Task and attention

The second section argued that the vMMN is part of the predictive system by adjusting the internal model of the environment. The third section showed that the vMMN is sensitive to both lower- and higher-order visual representations, so it is a general process in terms of mental representation as well. The take-home message of the section was that the interactions of representations modify the vMMN-related processes via feedback loops. However, the memory processes are not the only significant factor modifying the deviant-related processes. Task-related processes are also involved. The theoretical prerequisite of the vMMN is the automatic manner of stimulus processing. Therefore, the third investigated characteristic of vMMN in the literature is the independence of the vMMN from attentional processes. At present, two approaches exist. The first one applies inattentional paradigms; i.e., in which no attentional processes are directed to the incoming stimulation. The second one directly measures the effect of attention on the vMMN by comparing the vMMNs elicited during various attentional load conditions.

1.4.1. Inattentional paradigms

Change blindness is a robust example of non-attentional conditions. The term refers to the lack of conscious detection of a change which occurs in the visual scene when the change is separated with a short blank interval (Rensink, O'Regan, & Clark, 1997). The first change blindness vMMN-study was reported by Czigler and Pató (2009). The authors delivered a short train of standards with one deviant embedded in the sequence at random positions. The standard and deviant were horizontally or vertically lengthened grid patterns above and below a central task. In the half of the session, the participants were asked to fill out a questionnaire about the task-irrelevant stimulation. The data of the participants who reported conscious detection of the peripheral change were discarded from the experiment. Naïve participants were informed about the nature of the change, and they continued with the second half of the session. Both unconscious and conscious conditions elicited a vMMN (although, the vMMN was larger in the second part). Change blindness was tested with natural scenes as well. Lyyra and his colleagues (2014) delivered scenes from the movie *Star Trek*. The deviant and standard scene differed in one object (an actor from the scene), and the possible differences were the color (of the uniform), the place of the appearance (or disappearance) of the object. The paradigm was an active one; participants had to search for the differences during the stimulation. However, after the successful detection, a new sequence was delivered. Therefore, the brain electric response to the change had been always recorded while the participants were not aware of the given change. The authors obtained vMMN with a relatively short ISI (100 ms).

A second prominent example of inattentional paradigms is the attentional blink phenomenon (Raymond et al., 1992). In the attentional blink paradigm, two targets and several non-targets are delivered for a short duration without ISI (rapid serial visual presentation, RSVP). The time spent (or the number of non-targets) between two targets is a critical point in the phenomenon. When the temporal window is (approximately, depending on the given paradigm) between 200 and 700 ms the detection of the second target dramatically drops. Berti (2011) applied the attentional blink paradigm in a vMMN experiment. Stimuli were delivered according to a combination of an oddball sequence and RSVP. According to the RSVP paradigm, the stimuli successively appeared for 100 ms duration without blank periods in between the stimuli. Stimulus sequences comprised of a short train of 16-24 stimuli. The stimuli were letters (non-targets) or numbers (targets). Deviants were non-targets with a slightly different position. In the sequence, the position of the first target (T1) was between 6 and 10, after which a second target (T2) or a position deviant (D) appeared after 3 or 7 stimulus (i.e., during the attentional blink window). Forty per cent of the trials were T1-T2, and 40 per cent of the trials were T1-D stimulus pair. In the remaining 20 per cent, nor T2 neither D was presented. Although the behavioral data support the existence of an attentional blink in the applied temporal window, vMMNs were obtained in both conditions; therefore, vMMN can be elicited during the attentional blink.

The third inattentional paradigm in the vMMN literature is the binocular rivalry (for a review, see Blake and O’Shea, 2009). In a binocular rivalry experiment, different images are presented to the eyes. The two images do not integrate during perception; instead, the perceptual experience is one of the two images, but not both of them (in contrast to double vision). The perceived image (i.e., the dominant eye) changes from time to time; however, the identity of the dominant eye remains unconscious. Jack et al. (2015) used binocular rivalry stimuli: orthogonal grid patterns were delivered to the two eyes. The task was a behavioral response according to the perceived orientation (implicating the side of the dominant eye). The deviant was a sudden reverse of the stimuli between the two eyes. It is important to mention that neither the identity of the dominant eye nor the occurrence of the eye-swap deviant became conscious during the stimulation, so there was no difference in the perceptual experiences caused by internal or external eye swap. Even so, the deviant elicited a double vMMN with 110 ms and 380 ms latencies.

In sum, converging evidences support the notion that the vMMN is indeed an automatic process in terms of being independent from the conscious detection of the vMMN-related stimuli. However, the question remains whether it is independent from the task set or there is an interaction between the task-related and task-unrelated processes.

1.4.2. Task difficulty

There are a few VMMN studies investigating the independence of the perceptual or working memory load from the vMMN-related processes. By doing so, the studies recorded vMMN in various task-difficulty conditions. Heslenfeld (2003) was the first who investigated the task-related modulation of vMMN. The task-irrelevant stimuli were the same as in the study of Tales et al. (1999). The central task was a visuo-motor tracking of a square moving along the horizontal axis. The task has three difficulty levels defined by the speed and frequency of direction changes of the motion of the target. The elicited vMMNs were independent of the task difficulty in terms of magnitude or latency. Pazo-Alvarez et al. (2004) obtained similar results with motion direction deviancy and a working memory task. The task irrelevant stimuli were peripheral sinusoidal gratings. The task-relevant stimuli were colored numbers delivered at central location. There were two difficulty levels: the easier one related only to the number, the harder one related to the combination of both color and number. As before, the vMMNs were similar in both conditions. The results were replicated by Kremláček et al. in 2013. Here, the movement directions were expanding and contracting motions of a circular sinusoid pattern. The task had three difficulty levels: gazing to a fixation point (no task), response to a target number, and response to a set of target numbers. VMMNs emerged in all three conditions and the obtained vMMNs were similar. In contrast to the former studies, Kimura and Takeda (2013) reported a significant effect of task difficulty on vMMN. The stimulus pattern comprised of a central target and peripheral line segments. The target was a grey disk, and the task was the perceptual discrimination, i.e., the detection of luminance change of the target. In the task, three difficulty levels were defined by the magnitude of the luminance change. The task-irrelevant changes on the periphery were in the orientation of the line segments. The traditional (deviant-minus-standard) vMMN was not modulated by task difficulty; however, with the equiprobable contrast, the latency of the gvMMN was longer in case of the most difficult task. Therefore, the gvMMN is not fully independent from the primary task. The difference between the results of the present and the previous study is the application of the equiprobable control. May be the SSA is fully independent from the primary task, and the robust effect masks the gvMMN-effects. The studies support the notion that although the vMMN is modulated by the primary task, the effect is not a robust one. Similar results can be obtained by the overview of different primary tasks and different attentional conditions in literature.

1.4.3. Task Types

Although the vMMN is an automatic process, it is not fully independent from attentional processes. The primary task may modulate the gvMMN as well as the SSA; furthermore, other attention-related component also can emerge in the vMMN latency range (e.g., N2pc). Therefore, the primary task is just as important characteristic of a vMMN experiment as the sequence or the stimuli. The following section details the applied primary tasks in thematic order. The order of the listing follows the strength of attentional control of the primary task. This order partially overlaps with the chronological order of the studies reflecting the development of the vMMN-design.

1.4.3.1. Cross-modal task

The first approach is the visual counterpart of the acoustic design: the task-relevant and task-irrelevant stimuli are delivered in different modality; i.e., in acoustic and visual modalities, respectively. In parallel with the visual stimulation, a story is played for the participants. The task is to silently count the words beginning with a certain sound (Astikainen et al., 2013, 2008; Astikainen and Hietanen, 2009, Gayle et al., 2012), or to reply to 40 questions about the story after the EEG recording (Maekawa et al., 2013, 2011, 2005; it is worth mentioning that the acoustic task complemented the three stimulus oddball task, see below). Another task-related acoustic stimulation was a tone sequence delivered asynchronously with the visual stimulation (cross-modal). The participants had to discriminate between the tones with a button-press (cross-modal delayed response task; Zhao and Li, 2006; Chang et al., 2010, Chen et al., 2010, Fisher et al., 2010).

In contrast to the auditory modality, cross-modal primary task has a poor control of attention in the visual modality. The reason is the different nature of the two modalities. In natural conditions, visual attention and gaze direction connect together. So it is really hard not to see what one looks at.

1.4.3.2. Three stimulus active oddball paradigm

In the three stimulus active oddball paradigm, the sequence is comprised of a frequent standard, an infrequent deviant, and also an infrequent target. In some studies, task-irrelevant stimuli appear at the same spatial location as the target. Furthermore, all three stimuli have common attributes, i.e., all of them are windmill patterns (different number of vanes; Maekawa et al., 2005, 2013, 2011), colored objects (different shape, square; Thierry et al., 2009) letters (different color; Fujimura et al., 2013, Wang et al., 2013), faces (with spectacles, Kimura et al., 2012; or scrambled faces, Kreegipuu et al., 2013). In other studies of three stimulus oddball paradigm the target and the task-irrelevant stimuli appear at separate locations. Typically, the target has a central position and the other two stimuli are delivered in the periphery. In many studies of this kind, the target and the task-irrelevant stimuli are in a different category. In the simplest case, the task is to detect the stimulus (Chang et al., 2011; Hedge et al., 2015; Kenemans et al., 2003; Tales et al., 1999, 2008; Stagg et al., 2004) or motion (Amanedo et al., 2007, Kremláček et al., 2006). In a more complex case, the task is to discriminate motion direction (Kuldkepp et al., 2013), shape (cross vs. circle; Mo et al. 2011; Clifford et al. 2010), duration (Berti and Schröger, 2004, 2006) a numerical feature (even or odd; Amanedo et al., 2007, 2004; larger or smaller than five; Lorenzo-Lopez et al., 2004).

The problem with same-position three stimulus oddball is similar to the cross-modal paradigm. The non-targets are just as well attended as the targets. The different position design avoids this problem. However, in this case, the onset of a stimulus induces an automatic orientation reaction, even at the task-irrelevant positions; so it is impossible not to attend to the appearance of a new object in the visual field.

1.4.3.3. Task relevant and irrelevant features of the same object

In studies by Kimura and his colleagues (Kimura et al., 2009, 2010), the experimental stimulus was defined by a task-related and the task-unrelated feature. The stimulus was a central bar, the task-related feature was the shape of the bar's endpoint (square or rounded), and the task-irrelevant feature was the orientation of the bar. In Müller et al. (2013) the task was to detect whether the luminance of two disks was the same or not.

The advantage of the paradigm is the simultaneous emergence of task-related and –unrelated features at different positions. However, the object-related attention studies (Duncan, 1984) showed that attention is connected to the object as a whole. All features belonging to the same object are the subjects of the attentional processes.

1.4.3.4. Continuous target

In this paradigm, the task is to detect the infrequent (3-20 seconds) change of an object (usually in the center of the visual field) and to respond (usually with speeded response; i.e., reaction time) to the change. The change is a short disappearance of the target (Bottari 2014, Clery et al, 2012), orientation-change (Czigler et al., 2004, 2007, 2006; Stefanics et al., 2012a,b; Farkas et al., 2015; Kecskés-Kovács et al., 2013; Wang et al., 2016; Winkler et al., 2005), or size-change (Müller et al., 2009; Czigler et al., 2002; Berger and Arendt, 2014; Kimura et al., 2010 a,b; Quian et al., 2014; Wang et al, 2014; Czigler and Pató, 2009).

The continuous presentation of the target stimulus and the unpredictable changes almost fulfill the requirements of the strict attentional control. However, the relatively rare changes of the target allow the participants to monitor the task-irrelevant stimuli immediately after the change of the target.

1.4.3.5. Continuous task

So far, the most advanced primary task regarding the strict attentional control has been a visuo-motor tracking task. The task involves the tracking of central objects doing pseudorandom motion (Heslenfeld, 2003; Takács et al., 2013; Bodnár et al., submitted, File et al., submitted). In another approach, the tracking task is a simple video game, and the task is maneuvering a spaceship among other spaceships (Kecskés-Kovács et al., 2013, Sulykos et al., 2013).

In this case, the task demands the continuous monitoring of the target(s). Therefore, for now, this is the best solution for the control of attentional processes. The only caveat of the task is the presence of excessive eye-movements decreasing the signal to noise ratio of the ERP data.

1.5. Research questions of the thesis

1.5.1. Thesis study 1

The aim of the study was to test the effect of a task set on the deviant-related processing of elementary feature changes. The primary task was a feature change detection task in the center of the visual field. The task-irrelevant stimuli were patterns of colored line segments surrounding the central task. In the congruent conditions, the task-relevant and irrelevant changes were restricted to the same feature dimension (both changes occurred in color or in orientation). In contrast, in the incongruent conditions, the changes occurred in different feature dimensions (color-task and orientation deviancy or vice versa).

The hypotheses were both related to behavioral performance to the task-relevant stimuli and ERP data to task-irrelevant stimuli. The hypotheses were as follows:

Behavioral data: As per the non-spatial contingent capture principle (stronger distractor effect of stimuli sharing the characteristics with the target; Folk et al., 2008) we expected slower RT in congruent conditions relative to incongruent conditions.

ERP data: Based on existing theories we had two contradicting hypotheses. On the one hand, we expected a smaller vMMN in the congruent conditions relative to incongruent conditions. This hypothesis was based on both the competition theory (Sussman et al., 2003) and the load theory of selective attention (Lavie, 2005); that is, the attended channel takes priority over the unattended channel in the distribution of processing-resources. On the other hand, we expected a larger vMMN in the congruent conditions relative to incongruent conditions (i.e., the direction of the relationship between the vMMNs’ magnitudes is reversed), since the more effective distractors are considered to be more salient, and the more salient deviancy is considered to elicit enhanced vMMN (e.g., Berger and Arendt, 2014).

1.5.2. Thesis study 2

In the second study we investigated the horizontal connections between deviant-related processing of elementary feature changes. In other words, we investigated whether the deviant-related processing of elementary feature changes depends on or is independent from that of another elementary feature change. In this particular study, the elementary features were orientation and spatial frequency. The deviant and standard differed in either one or both features. We compared the vMMNs obtained in the double-deviant condition with the arithmetical sum of the two vMMNs obtained in the other two, single-deviant conditions (additive model). The identical negativities are the valid estimation of the additive model, reflecting independent processes.

Since the study was rather an explorative research than a confirmatory one, our hypotheses were twofold. That is, both non-additive (super or sub-additive) and additive responses were expected. In the case of additive results, the data support the independent theory. In contrast, the non-additive results favor the dependent theory.

1.5.3. Thesis study 3

In the third study, vMMN’s sensitivity was tested to illusory brightness changes. The experimental stimuli were concentric patterns inducing Craik -Cornsweet-O’Brien (CCOB) illusion (Craik, 1966; Cornsweet, 1970; O’Brien, 1958). In the concentric patterns, from the center to the periphery, three equiluminant grey annuli and four Cornsweet-edges alternated in a manner similar to a concentric sine-wave. The Cornsweet-edges induced different (illusory) brightness experience of the grey annuli; the middle annuli seemed brighter or darker than the flanking ones depending on the characteristics of the Cornsweet-edges. Besides the experimental condition, two additional control conditions were introduced. The first tested the perceptual experience of real contrast changes caused by luminance differences between the stimuli (i.e., the grey annuli). The perceptual experience of brightness was matched between the real and illusory conditions in each participant by adjusting the luminance of real contrast stimuli. The second control condition tested the ERP-effect of changing the characteristics of the Cornsweet-edges. In the illusory condition, such changes induced brightness changes; however, in this control condition, the same physical changes induced no visual illusion. In all three conditions, the stimuli were delivered according to the passive oddball paradigm causing illusory or real brightness changes or physical changes without brightness changes.

We had three hypotheses, each related to one of the sequences. First, we expected the emergence of vMMN in the illusory condition, since probably the perceptual experience organizes the deviant-related processing. Second, we expected no vMMN in the third (only Cornsweet-edge) condition, since the perceptual (and physical) changes were negligible in an inattentional paradigm. Third, we expected vMMN in the real contrast condition, since luminance deviancy has been reported to elicit vMMN. We have no a priori hypothesis about the relationship between the vMMNs obtained in the real contrast and illusory conditions. The comparison of the vMMNs might reveal the common temporal characteristics of the two mechanisms.

1.5.4. Thesis study 4

In the fourth study, we investigated the familiarity effect on vMMN. The stimuli were patterns of familiar N and unfamiliar reversed N stimuli. The stimuli were delivered according to a passive oddball paradigm with reverse control (i.e., both stimuli were both standard and deviant in separate conditions). With these stimuli, we induced double deviancy. On the one hand, the physical difference between the stimuli was the orientation of the line segments which is an elementary feature change. On the other hand, the elementary feature change induced change in the familiarity of the stimulus which is a high level difference. So the standard and deviant differed in both orientation of the line segments and the familiarity of the pattern. We introduced an additional control experiment in which we kept the low-level deviancy (orientation changes) without the higher-order familiarity effect. In this condition, the pattern did not include the vertical lines forming the familiar and unfamiliar letter characters.

In general, we expected asymmetrical results in the familiarity condition and symmetrical results in the non-familiarity condition. That is, we expected different vMMNs (in terms of latency or magnitude) in the first and similar vMMNs in the second condition. However, the direction of asymmetry was not determined. Two competitive approaches might result in inverse directions. Faster processing of familiar stimulus (Wolfe, 2001) might result in faster deviant-related processing (i.e., an earlier vMMN to the N deviant). However, the faster processing of familiar stimuli is based on a more stable memory representation. According to the predictive coding theory (Stefanics, 2014), the memory trace of familiar stimulus is carried out by the representation cells; and this representation is acquired by the standards. In that case, we predicted a longer vMMN for the familiar stimulus.

2. Visual mismatch negativity to irrelevant changes is sensitive to task-relevant changes (Thesis study 1)[3]

Event-related potentials (ERPs) were measured in response to frequent (standard) and infrequent (deviant) task-irrelevant bar patterns. The constituent bars of the deviant patterns had either different orientation or different color than the bars of the standard. The task was the detection of either the orientation or the color change of a centrally presented shape. The deviant minus the standard ERP difference produced posterior negativity and was identified as visual mismatch negativity (vMMN). On the one hand, vMMN to orientation deviancy had smaller amplitude in the task demanding detection of the orientation change, and vMMN to color deviancy had smaller amplitude in the task demanding the color change. On the other hand, irrelevant deviancy influenced the task-performance. Reaction time (RT) to the orientation change of the target shape was longer in sequences with orientation change in the background, whereas RT to color change was longer in sequences with color change in the background. This interaction suggested that there was competition between the processing of irrelevant stimuli that share characteristics of task-related changes and target-related processing.

2.1. Introduction

It is not unusual that environmental changes have important consequences, even if these changes are unrelated to the ongoing behavior. Therefore, attention attracted by such events has adaptive value. In contrast, involuntary attention to the irrelevant stimulation may distract the performance during the ongoing task. Stimulus saliency is an important determinant of attentional capture by irrelevant stimulation (Theeuwes, 2004). However, as some results show, irrelevant stimuli sharing the characteristics of task-related stimuli capture attention more effectively. The top-down effects of task characteristics are emphasized by the “contingent capture” (Folk, Leber, & Egeth, 2008; Folk, Remington, & Johnston, 1992; Kumada, 1999; Lamy, Leber, & Egeth, 2004) and

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[3] Czigler, I., & Sulykos, I. (2010). Visual mismatch negativity to irrelevant changes is sensitive to task-relevant changes. Neuropsychologia, 48(5), 1277–82.

“dimensional-weighting” (Müller, Heller, & Ziegler, 1995; Müller, Reimann, & Krummenacher, 2003; Schubö & Müller, 2009) accounts, and results of both spatial and temporal attentional tasks support these theories (for the limit of the effect see Poiese, Spalek, & Di Lollo, 2008). Task-relevant stimulation may also influence the processing of task-irrelevant stimuli. The load theory of selective attention (Bahrami, Lavie, & Rees, 2007; Lavie, 2005) is an example of such directional influence. According to a large body of results, the larger the processing demand of the relevant event, the narrower is the attentional focus. Therefore, processing of irrelevant stimuli is attenuated at higher task load. In behavioral studies, the effect of target processing on irrelevant stimuli is inferred from the changes in target-related performance (e.g., reaction time (RT) differences in the presence of various irrelevant stimuli). Unlike such indirect measures, event related brain potentials (ERPs) provide more direct evidence on the influence of target stimuli characteristics on the processing of irrelevant events. In this study, we investigated the relationship between the processing of relevant and irrelevant changes. The visual characteristics of target-related changes and the changes of the visual background texture varied, and the visual mismatch negativity (vMMN) ERP component was recorded. VMMN is elicited by infrequently presented (deviant) stimuli within the sequence of frequent ones (standard). VMMN emerges in response to deviant features (such as color, spatial frequency, orientation, and movement direction), deviant conjunction of features, deviant objects, and violation of sequential rules. Deviant stimuli elicit vMMN even if such changes are irrelevant and remained unnoticed (Czigler & Pato, 2009; for a review see Czigler, 2007). Behavioral effects of irrelevant novel and deviant stimulation on task-related processing and the ERP correlates of the processing of such irrelevant stimulation are well documented in the auditory (Escera, Alho, Winkler, & Näätänen, 1998; Schröger & Wolff, 1998) and in the visual modality (Berti & Schröger, 2001, 2006; Grimm, Bendixen, Deouell, & Schröger, 2009; Kimura, Katayama, & Murohashi, 2007). Similar results were reported as intermodal (Corral & Escera, 2008) effects. RT in trials related to such stimuli was usually longer, and deviant stimuli in such studies elicited the auditory MMN component. In this study the deviants had no cue-function. Irrelevant deviant stimuli either immediately preceded the task-relevant change (near change), or there were standard stimuli between the irrelevant deviant and the target change (far change). Two task conditions were used. Participants responded to either the orientation change or the color change of a continuously presented shape. Bar patterns were presented on the background in oddball sequences. Under the two deviant conditions, either the orientation or the color of the bars was infrequently different from the standard. As predicted by the “contingent capture” principle, irrelevant change is expected to have a larger effect on the RT in “congruent” conditions (e.g., orientation task and an orientation deviant). However, to the best of our knowledge, there are no vMMN data available on the interaction between task-related and unrelated physical characteristics of stimulation. Regarding task-related effects on vMMN, only the task difficulty was investigated. As a function of this variable, Heslenfeld (2003) reported no change in the deviant-related posterior negativity; however, in an fMRI study using a design similar to the vMMN studies, and during a difficult tracking task, Yucel, McCarthy, and Belger (2007) reported decreased brain oxygen level dependent activity (BOLD) in the posterior cortex in response to irrelevant deviants. In this study, the effect of task difficulty was determined as the RT difference between the two tasks. The saliency of the two kinds of deviant stimulation was assessed indirectly, as an inference from the RT to target changes. A shorter RT to one of the task-related changes (orientation or color) is considered as a more salient change in the background. If the effect of irrelevant change is determined by the saliency of the deviants, asymmetric RT effects are expected; a deviant characteristic that elicits shorter RT is expected to be a more effective distractor. If an effect similar to the “contingent capture” principle holds for a given situation, a symmetric effect is expected, i.e., RTs increase in sequences with similar distractors, irrespective of the saliency of the stimulus change.

2.2. Methods

2.2.1. Participants

Participants included 24 paid students (10 females; mean age: 22.0 years, SD: 2.2 years). They had normal color vision and normal or corrected-to-normal visual acuity. Written consent was obtained from every participant. Due to the large number of artifacts, the data from three additional participants were discarded.

2.2.2. Apparatus and procedure

2.2.2.1. Irrelevant stimuli

The irrelevant stimuli were patterns of oblique line segments. This pattern was seen as a textured background on the screen. The lines were dispersed on an LCD screen except for the central part (a circular area with the diameter of 8.8◦ of the visual arch from a 120-cm viewing distance). The lines had 0.38◦ lengths (30 pixels), and 1-pixel thickness. The screen was dark grey (0.7 cd/m^2) and the color of the line segments was either yellow-green (128, 179, 0 RGB; 8.7 cd/m^2) or turquoise (0, 179, 128 RGB; 9.2 cd/m^2). The line segments deviated from the horizontal direction by 20◦, 50◦ or 80◦. The patterns were presented for 70ms with 350ms (±10 ms) SOA (75-Hz refresh rate), and seen as a textured background. There were two deviant stimulus conditions. In the Color deviant condition, one of the line colors was standard ($p = 0.85$), the other was deviant ($p = 0.15$). The lines had a 20◦ orientation. In the four blocks of the Color condition, there were two blocks with yellow-green and two blocks with turquoise deviants. In the Orientation deviant condition, for 12 participants, the 20◦ and 50◦ lines were shown; for the other 12 participants, the 20◦ and 80◦ lines were presented[4]. In two blocks, the 20◦ orientation was deviant; in the other two blocks this orientation was standard. There were 800 stimuli per block.

Deviancy	**Orientation**		**Color**	
	Near	**Far**	**Near**	**Far**
Task				
Orientation	367 (10.1)	364(10.2)	360(11.0)	360(11.4)
Color	422(13.2)	417(11.2)	428(11.2)	431(12.8)

Table 1. Mean reaction time (ms) in the Orientation and Color tasks in sequences with orientation and color deviancy. Near: RT preceded by a deviant stimulus; far: RT is preceded by at least four standards (S.E.M. in parenthesis).

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[4] In the initial analysis, we compared the results from 50◦ and 80◦ orientation deviancy conditions. The magnitude of the deviancy had neither RT nor ERP effects; therefore, we collapsed the data for both groups.

2.2.2.2. Relevant stimuli

The relevant stimuli appeared in the center of the screen (task-field) as shapes with three lines in a rectangular/diagonal arrangement. This pattern was 0.21◦ (horizontal and vertical) in size and had a 5-pixel thickness. The pattern was continuously present. In the Color task, the color of the shape alternated between yellow-green and turquoise. In the Orientation task, the slant of the line segments alternated. The interval between the two alternations was random, within the 16- to 22-s range. The task was to indicate the color or the orientation change. The participants pressed a response button ("as fast as possible") whenever they detected the change. Such changes did not appear simultaneously with the onset of the line pattern. However, the task-relevant changes were preceded by a deviant stimulus either by 200ms ("near" change) or by 1440ms ("far" change). The appearance of a deviant did not serve as a cue for target change, and only 13% of the targets were preceded by a deviant. The Color and Orientation tasks were orthogonal to the Color and Orientation deviant conditions, i.e., there were two blocks with each deviant–task combinations. The order of the stimulus blocks was counterbalanced within the sample.

2.2.3. Measurement of brain electric activity

EEG recordings were taken (DC-200 Hz, sampling rate 1000 Hz,Synamps2 amplifier, NeuroScan recording system) with Ag/AgCl electrodes placed on 61 scalp locations (modified 10–20 international system) using an elastic electrode cap (EasyCap). Two electrodes were attached to the mastoids. The reference was on the right mastoid, but it was re-calculated for the average mastoid activity. 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. The vertical EOG was recorded with a bipolar configuration between electrodes placed above and below the right eye. EEG signals were stored on a magnetic disk, filtered offline (0.15–30 Hz, 24 dB) and epochs of 600 ms, starting 100ms before the stimulus onset, were averaged separately for the standard and deviant stimuli. Trials with an amplitude change exceeding ±70_V on any channel were rejected from further analysis. To identify change-related activities, ERPs produced in response to standard stimuli were subtracted from ERPs for deviant stimuli with the same physical characteristics. These difference potentials were than averaged for the two blocks of the same Deviance × Task combinations. VMMNs were identified on the deviant minus standard difference potentials, as detailed in section 2.3, and measured as the mean values of 8-ms epochs around the largest negativity at Oz from the group average of difference potentials. ANOVAs were calculated using Deviancy (orientation, color), Task (orientation, color) and two-electrode localization as factors. To compare the distribution of the difference potential (vMMN) with the distribution of exogenous activity (a posterior negativity), the amplitude values were scaled (McCarthy & Woods, 1985). When appropriate, after ANOVA, the Greenhouse–Geisser correction was used.

2.3. Results

2.3.1. Behavioral results

RT in the Orientation and Color tasks under the Orientation and Color deviant conditions are shown in Table 2.1. RTs were analyzed separately for the “near” and “far” changes (Distance factor). As determined by three-way ANOVA (Task × Deviancy × Distance), the significant main effect of Task [$F(1,23 = 98.5$, $p < 0.0001$, $\varepsilon = 0.80$)] showed that the RT was shorter in the Orientation task. Furthermore, as the significant Task × Deviancy interaction [$F(1,23 = 9.56$, $p < 0.005$, $\eta 2 = 0.30$)] indicated, RT in the Orientation task was shorter in sequences with color deviancy, whereas RT in the Color task was shorter in sequences with that particular orientation deviancy. No other main effect or interaction was significant, i.e., the Distance factor had no influence on the RT. Error rate was low; the range was 0.5–3.7. By ANOVA, we did not observe main effects or interactions.

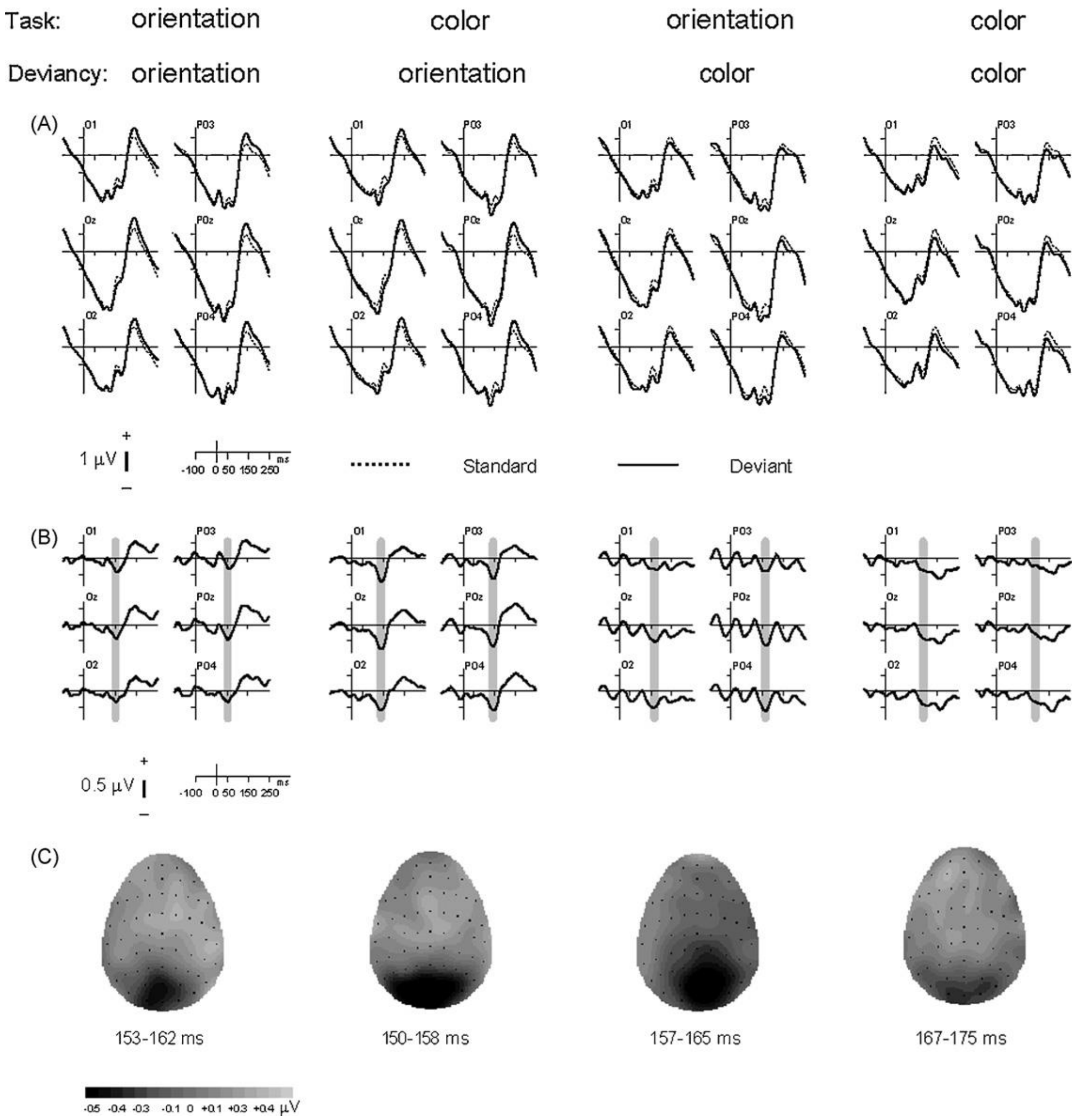

Figure 2.1. (A) Group average event-related potentials to the standard, orientation deviant, and color deviant stimuli in the Orientation and Color tasks. (B) Difference potentials (deviant minus standard) for the orientation and color deviancies in the Orientation and Color task. (C) Difference potential voltage maps to the orientation deviant and color deviant in the Orientation and Color tasks. The values under the maps correspond to the vMMN latency ranges in the four deviant/task conditions.

2.3.2. Event-related potentials

Figure 2.1 shows the ERPs (A), the deviant minus standard difference potentials over the occipital (O1, Oz, O2) locations (B), and the voltage distribution of the vMMN (C). In the event-related activity, the negativity with the 130-ms peak was followed by positivity with a peak latency of 250 ms. In the orientation-related difference potentials, clear negativity emerged with 153- and 143-ms peak latencies in the Orientation and Color tasks, respectively. The negativity was less clear for color deviancy. In order to investigate the reliability of the negative component, in the first step, within the 130–190ms range we measured the latencies of the smallest negative value of the ERPs to the standard, and the largest negative value of the ERPs to the deviant within the 130–190ms range at Oz location. The average of the two values was considered as the latency of the deviant-related negativity (vMMN). (This value closely corresponded to the negative peak on the difference potentials in both task conditions; 166 and 170ms in the Orientation and Color task, respectively.) In the next step, we measured eight consecutive amplitude values (1-ms epochs) around this latency values. These amplitude values were compared to zero in the t-tests. All comparisons were significant at $p < 0.05$ level. As shown in the voltage maps (Figure 2.1C), deviant-related negativity concentrated over the occipital and parieto-occipital locations. For ANOVAs with mean amplitude (8-ms epochs around the mean latency values) and latency values, we used a 2×3 grid of electrodes for Posteriority (parieto-occipital, occipital) and Laterality (left, central, right) factors. The other factors were Task and Deviancy. Peak latency values of the negative components are shown in Table 2.2. As the ANOVA showed, the shorter latency for the orientation deviant was reflected by the significant deviant main effect [$F(1,23 = 36.1$, $p < 0.001$, $\eta2 = 0.99$)]. The task effect on the deviance related negativity is reflected by the significant Task×Deviancy interaction [$F(1,23 = 11.0$, $p < 0.01$, $\eta2 = 0.32$)]. The latency for the orientation deviant was shorter in the Color task, whereas the latency for the color deviancy was shorter in the Orientation task. The latency for the color deviant was shorter on the left side than on the midline and on the right side, while the latency for the orientation deviant increased on the left side. This difference is reflected by the significant Deviancy×Laterality interaction [$F(2,46 = 7.2$, $p < 0.01$, $\varepsilon = 0.99$, $\eta2 = 0.24$)]. Mean amplitude values of the posterior negativity are shown in Table 2.3. In the ANOVA, the Task×Deviancy interaction was significant [$F(1,23 = 4.54$, $p < 0.05$, $\eta2 = 0.17$)]. This effect was due to the larger amplitude of the orientation deviancy in the Color task, and the larger amplitude of the color deviancy in the Orientation task. Furthermore, we obtained a significant Task × Posteriority [$F(1,23 = 6.33$, $p < 0.05$, $\eta2 = 0.22$)] interaction. In the Orientation task, the negativity was larger over the parieto-occipital locations, whereas in the Color task it was larger over the occipital locations. In the latency range following the negative difference potential, the ERP for the orientation deviant was more positive, whereas for the color deviant, it was less positive than the standard ERP (Figure 2.1B). However, this positivity/negativity was unaffected by the task factor[5]. To investigate whether the difference potential only reflects the amplitude change of exogenous activity, we compared the vector-scaled values of the ERPs to the standard, deviant and the difference potentials obtained using ANOVA. In the first analysis, the difference-related values were measured at the latencies of the maximal amplitudes of the negativities, and the amplitudes of the exogenous potentials were measured in same latency ranges. In the second analysis, the difference potential amplitudes were identical to those of the previous measure, but the exogenous potentials were measured at their amplitude maxima. In both analyses, the factors were the Component (standard, deviant, and difference), Deviant (orientation, color), Task (orientation, color), Posteriority (parieto-occipital, occipital) and Laterality (left, midline, standard). In the first ANOVA, we obtained a significant Component × Posteriority interaction [$F(2,46 = 4.55, p < 0.05, \varepsilon = 0.51, \eta2 = 0.16)$]. The Component × Task × Posteriority interaction was also significant [$F(2,46 = 4.90, p < 0.05, \varepsilon = 0.52, \eta2 = 0.18)$]. Scaled values of the difference potentials were lower for the difference potentials over the occipital locations, and this difference was larger in the Color task. Similar results emerged from the second ANOVA; the Component × Posteriority [$F(2,46 = 15.61, p < 0.001, \varepsilon = 0.50, \eta2 = 0.40)$] and the Component × Posteriority × Task [$F(2,46 = 4.77, p < 0.05, \varepsilon = 0.50, \eta2 = 0.17)$] interactions were significant.

Deviancy	**Orientation**			**Color**		
	Left	**Midline**	**Right**	**Left**	**Midline**	**Right**
Task						
Orientation	157 (5.2)	151(5.3)	153(6.1)	147(5.7)	141(5.6)	142(6.3)
Color	164(6.3)	166(5.5)	164(5.4)	173(6.1)	179(6.8)	182(6.8)

Table 2.2.Mean latency (ms) of the negative difference potential in the Orientation and Color tasks in sequences with orientation and color deviancy on the left side, midline and right side (S.E.M. in parenthesis).

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[5] The apparent increase of the negativity at 250ms (249–252ms latency range) in the color task/color deviant condition, in comparison to the orientation task/color deviant was non-significant. In an ANOVA for the color deviant conditions with factors of Stimulus, Task, Posteriority and Laterality we obtained only Stimulus, Posteriority and Laterality main effects [$F(1,23 = 7.76, p = 0.01, \eta2 = 0.25)$; $F(1,23 = 45.95, p < 0.05, \eta2 = 0.21)$; $F(2,46 = 3.42, p < 0.05, \varepsilon = 0.91, \eta2 = 0.13)$, respectively].

Deviancy		**Orientation**			**Color**	
	PO3	**POz**	**PO4**	**PO3**	**POz**	**PO4**
Task						
Orientation	-0.3 (0.10)	-0.4(0.16)	-0.3(0.18)	-0.4(0.13)	-0.6(0.16)	-0.6(0.16)
Color	-0.5(0.15)	-0.5(0.16)	-0.5(0.15)	-0.2(0.19)	-0.2(0.20)	-0.2(0.19)
Deviancy		**Orientation**			**Color**	
	O1	**Oz**	**O2**	**O1**	**Oz**	**O2**
Task						
Orientation	-0.4 (0.10)	-0.4(0.14)	-0.3(0.15)	-0.5(0.13)	-0.5(0.12)	-0.5(0.13)
Color	-0.6(0.14)	-0.6(0.14)	-0.5(0.14)	-0.3(0.15)	-03(0.15)	-0.3(0.12)

Table 2.3. Mean amplitude (microvolt) of the negative difference potential in the Orientation and Color tasks in sequences with orientation and color deviancy on the left side, midline and right side, over the posterior parietal (PO3, POz, PO4) and occipital (O1, Oz, O2) locations (S.E.M. in parenthesis).

2.4. Discussion

Behavioral (RT) and ERP (vMMN) results showed that the effects of task-related changes and background changes are not independent. The RT was longer in sequences when the change in the background texture was similar to the target-related change. According to the RT data shown here, the orientation change was more salient than the color change, but the effects of the background change were similar in both background-related tasks. This pattern of results was similar to the “contingent capture” (Folk et al., 1992, 2008; Kumada, 1999; Lamy et al., 2004), “dimensional weighting” (Müller et al., 1995, 2003; Schubö & Müller, 2009) principles with two qualifications. First, in our study, we obtained a sustained interaction of relevant and irrelevant stimuli, i.e., RT increases were not restricted to trials where the background deviance preceded the target change. To explain the pervasive effect of the otherwise irrelevant deviancy, one can speculate that the background change characteristic to the sequence in the task set was categorized as “not all orientation/color changes are significant”. Second, in the Color task condition the irrelevant and relevant stimuli had identical colors (yellow-green and turquoise), while in the Orientation task condition the relevant and irrelevant orientation changes were different. As the larger effect of relevant change on the vMMN in the Orientation task condition shows, task set effects were not specific to a particular value of a stimulus dimension, instead these effects extends to a stimulus dimension. This result corresponds to the “dimensional-weighting” theory (Müller et al., 1995, 2003), and within this framework our results support recent findings reported by

Schubö and Müller (2009). These authors obtained attention-related ERP components (N2pc) to irrelevant singletons sharing the dimension of task-related singletons (irrelevant color singletons in a search task for relevant color singleton, and irrelevant orientation singleton in a search task for relevant orientation singleton), even if the color or the orientation was different from the color or orientation of the target. In our study rare changes in the background texture (deviant stimuli) elicited a posterior ERP component. We identified this posterior negativity (difference potential between the ERPs of the deviants and standards) as vMMN. The distribution of the vMMN had a different main latency and scalp distribution than the exogenous components. Therefore, the emergence of the negativity cannot be explained by frequency-related habituation of the ERPs to the standard. The vMMN for the orientation change was observed in other studies (Astikainen, Lillstarng, & Ruusvirta, 2008). In the Astikainen et al. (2008) study bars were presented at the center of the visual field, whereas in the present study, the oblique line segments were texture constituents of the stimulus background. The shorter latency of the present study was somewhat shorter than the vMMN latency reported by Astikainen et al. (2008). Thus, the change of the line segments of the background texture seems to be particularly effective in eliciting the vMMN. This possibility is supported by the higher sensitivity of vMMN to the color contrast in our study. In a previous experiment (Czigler, Balázs, &Winkler, 2002), only larger color contrast elicited vMMN. The latency of the difference potentials of the present study was shorter, than the latency of the attention-related posterior negativity (selection negativity, posterior N2; e.g., Anllo-Vento & Hillyard, 1996; Czigler & Csibra, 1992; Schubö & Müller, 2009). The vMMN was smaller in the "congruent" conditions, i.e., in conditions with similar task-related and background changes. In these conditions, the RT was longer. Accordingly, in the "congruent" conditions, the set for the task-related change inhibited the mismatch-generating process. These results are in contrast to the findings reported by Martinez-Trujillo and Treue (2004) in monkeys, and Saenz, Buracas, and Boyton (2002) in humans. In those studies, the attended stimulus feature facilitated the processing of irrelevant stimuli that shared target characteristics. However, there is an obvious difference between the designs of those studies and this one. In our studies, the relevant and irrelevant stimulus changes were either similar or different. In those studies, they reported facilitatory effects; the stimuli were similar, but the irrelevant stimuli did not change. In studies investigating the relationship between relevant and irrelevant changes, ERP results were similar to the ones presented here. In an auditory MMN study, Sussman, Winkler, and Wang (2003) reported diminished frequency-related MMN, but no decrease in amplitude for duration-related MMN in a dichotic task with a frequency discrimination requirement. They argued that due to top-down effects, feature-specific resources were used for the task-related discrimination; therefore, decreased capacity for irrelevant discrimination in the task dimension (frequency) remained. There was no such bias in dimensions other than that of the task; therefore, automatic change detection was more efficient in duration discrimination. Unfortunately, no behavioral data were available for compatible and incompatible stimulus sequences from this study. In line with our results, the explanation offered by Sussman et al. (2003) also holds true in the visual modality. As an important extension, our RT data showed that the influences are mutual. The locus of task characteristics (top-down influences) on the detection of irrelevant deviancy is indicated by the relatively early and modality-specific vMMN difference. However, in the case of RT differences, a later locus (e.g., the elevation of response threshold) is equally likely. As the results of the this study show, the interaction between the relevant and irrelevant environmental changes is highly specific and connected to particular stimulus features or stimulus dimensions, instead of a general saliency factor. In a broader framework, the results can be considered as a manifestation of competition for processing resources (Desimone & Duncan, 1995).

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3. One plus one is less than two: visual features elicit non-additive mismatch-related brain activity (Thesis study 2) [6]

In a passive oddball task (performing in a video game), participants were presented with sequences of either standard stimuli or patterns containing deviant orientation, deviant spatial frequency or both deviant orientation and spatial frequency. Orientation deviants presented to the lower half of the visual field elicited a posterior negative component with a peak latency of 130 ms. Spatial frequency deviants elicited a similarly negative component that was later followed by another negative component. Activity elicited by the double deviant stimulus was identical to activity elicited by the orientation deviant alone. The subtraction difference of the peak latency and scalp distribution of the deviant minus the standard difference potentials were unequal to those of the exogenous event-related potential (ERP) components and were therefore considered visual mismatch negativities (vMMNs). The non-additivity of the feature-related responses is interpreted as sensitivity of the implicit change-detection system to deviant events rather than an exclusive sensitivity to individual features. Deviant stimuli presented to the upper half of the field elicited responses with positive polarity, but this activity was less pronounced than the vMMN. Polarity reversal of the response to upper half-field stimulation suggests that the origin of the activity lies in retinotopic areas. Because of the emergence of a mismatch component with positive polarity, we propose that the term visual mismatch negativity (vMMN) be replaced with the more general term visual mismatch response (vMMR).

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[6] Sulykos, I., & Czigler, I. (2011). One plus one is less than two: visual features elicit non-additive mismatch-related brain activity. Brain Research, 1398, 64–71.

3.1. Introduction

Events violating regularities of environmental stimulation will elicit brain activity even when those events have no immediate relevance. This brain activity can be recorded as either electric or magnetic mismatch negativity (MMN) in the auditory (for review, see Kujala et al., 2007; Näätänen et al., 2007), visual (for review see Czigler, 2007) and somatosensory (e.g. Shinozaki et al., 1998) modalities. Brain activity elicited by irrelevant but irregular events is usually investigated with the passive oddball paradigm. In this paradigm, stimuli with rare deviant features (such as pitch, tone intensity, color and orientation) are presented in sequences of frequent identical (standard) stimuli, during which the participants attend to task-related stimuli or their attention is diverted from the standard and deviant in other ways. In our study, we presented two deviant features in the visual modality and asked whether processing of these two features is independent or common. One goal of this research was to answer the question of whether separate, feature-related mechanisms are responsible for visual mismatch negativity (vMMN), or whether vMMN is generated by a unified mechanism that is sensitive to regularity violation per se. In the auditory modality, some results suggest independent MMNs in response to various stimulus features. These studies reported additive MMN (Schröger, 1995, 1996; Takegata et al., 1999) and magnetic mismatch field (Levänen et al., 1993) to stimulus features such as pitch, intensity, stimulus duration, location and deviant inter-stimulus interval. However, in other cases, the sum of MMNs in response to individual features was larger than the MMN elicited by double-deviant stimuli (Czigler and Winkler, 1996) or additivity hold, albeit only in case of specific electrode locations (Paavilainen et al., 2003; Wolff and Schröger, 2001) or combination of features (Takegata et al., 2001). Furthermore, in the case of triple-deviant stimuli, sub-additivity was recorded (Paavilainen et al., 2001). It should be noted that sub-additivity of the mismatch response to stimuli violating two (or more) deviant features does not prove that the individual deviant features are treated as integrated units (as opposed to a set of isolated features). It is possible that feature violations are indeed processed separately, but that sub-additivity reflects saturation (or limited temporal accuracy) of the MMN-generating mechanism. However, as studies using the auditory modality have shown, a deviant event violating two different regularities (e.g., pitch and duration) elicits only one MMN, even when the detection of these two regularities is separated by 100 ms (Czigler and Winkler, 1996). Furthermore, violation of regular stimulus duration and a sequential regularity rule elicits two distinct MMNs (Winkler and Czigler, 1998). It seems that the larger MMN amplitude resulting from double deviants is due to the more frequent detection of more prominent irregular events (Horváth et al., 2008). In the present study we investigated deviance-related activity in response to two visual stimulus features (orientation and spatial frequency of Gábor patches) presented to either the lower or upper half of the visual field. Typical feature-related vMMN is elicited by the lower half of the field (Czigler et al., 2004), indicating that the activity source is a retinotopic part of the visual cortex, most likely the prestriatal areas (Pazo-Alvarez et al., 2004). With the present study, we sought to provide further evidence supporting this idea.

3.2. Results

3.2.1. Behavioral results

By two-way ANOVA (with factors Half-field and Deviancy) no significant effects were found (group averaged RT and HIT rates were 551±5.7 ms and 89.9±2.1%, respectively).

3.2.2. ERP results

As shown in Figure 3.1 (A and B), stimulating the lower half of the field elicited a positive–negative–positive ERP sequence, whereas stimulating the upper half elicited a negative–positive–negative sequence. The three exogenous components were labeled C1, C2 and C3, even though their latencies differed somewhat from those reported by Jeffreys and Axford (1972). The mean latencies for the standards at the three conditions for C1, C2 and C3 at the lower-half field stimulation were 97, 153 and 244 ms, respectively, and 101, 169 and 262 ms for upper-half field stimulation. The peak latencies of the ERP components are shown in Table 3.1. Figure 3.1 (A and B) also shows the difference potentials of the standard subtracted from the deviant. These difference potentials were markedly different for lower- and upper-half field stimuli.

For lower-half stimulation, the difference potentials were negative, with the largest peak amplitude at occipital locations, whereas for upper half-field stimulation, the difference potentials were positive with broader and more anterior scalp distribution. For the frequency deviant/lower half field stimulation the difference potentials had two negative peaks, whereas the five other conditions each had a single peak. Average amplitudes and peak latencies of the deviant-related components are presented in Table 3.2. Emergence of the deviant-minus-standard difference was reliable in the six t-tests (two half-field, three types of deviancy each) in the earlier range of difference potentials, $t(11)= 5.67–3.79$, $p<0.0001–0.003$ (Bonferroni criterion). For the later latency range at lower-half field stimulation/spatial frequency deviancy, a test showed the difference was also significant, $t (11)=2.49$, $p<0.05$.

3.2.2.1. Additivity effect

First, we investigated the possibility of different scalp distributions for the modeled and observed double deviant lower-half field stimuli. Accordingly, vector-scaled values were tested by ANOVA with the factors being Latency range, Additivity, Anteriority and Laterality. There was no significant interaction between Additivity and the distribution-related Anteriority and Laterality factors. Thus, in the analyses of additivity, the non-scaled values were used. The main effects of Additivity and Latency range were significant, $F(1,11)=8.9$, $p<0.05$, $\eta2=0.45$ and $F(1,11)=29.6$, $p<0.001$, $\eta2=0.73$, respectively. These results can be attributed to the smaller activity of the observed double-deviant brain response relative to the modeled response (i.e., the sub-additivity of the deviants). The other significant main effect revealed the generally smaller amplitudes at the later range. Figure 3.1 (C) illustrates the estimated (modeled) and observed (actual) double-deviant difference potentials at lower-half field stimulation. Additivity of the responses to upper-half field stimulation was tested by ANOVA with the factors of Additivity, Anteriority and Laterality. In this case, the analysis on vector-scaled values showed significant Laterality main effect, $F(1,11)=6.2$, $p<0.05$, $\eta2=0.30$, Additivity × Anteriority, $F(2,22)=5.6$, $\varepsilon=0.56$, $p<0.05$, $\eta2=0.34$, and Additivity × Laterality, $F(2,22)= 3.9$, $\varepsilon=0.75$, $p<0.051$, $\eta2=0.26$, interactions. These interaction effects reflect the distribution difference between the observed double deviance (midline parieto-occipital) and the additive model (right centro-parietal), whereas the Laterality main effect was due to the smaller effect over the left side.

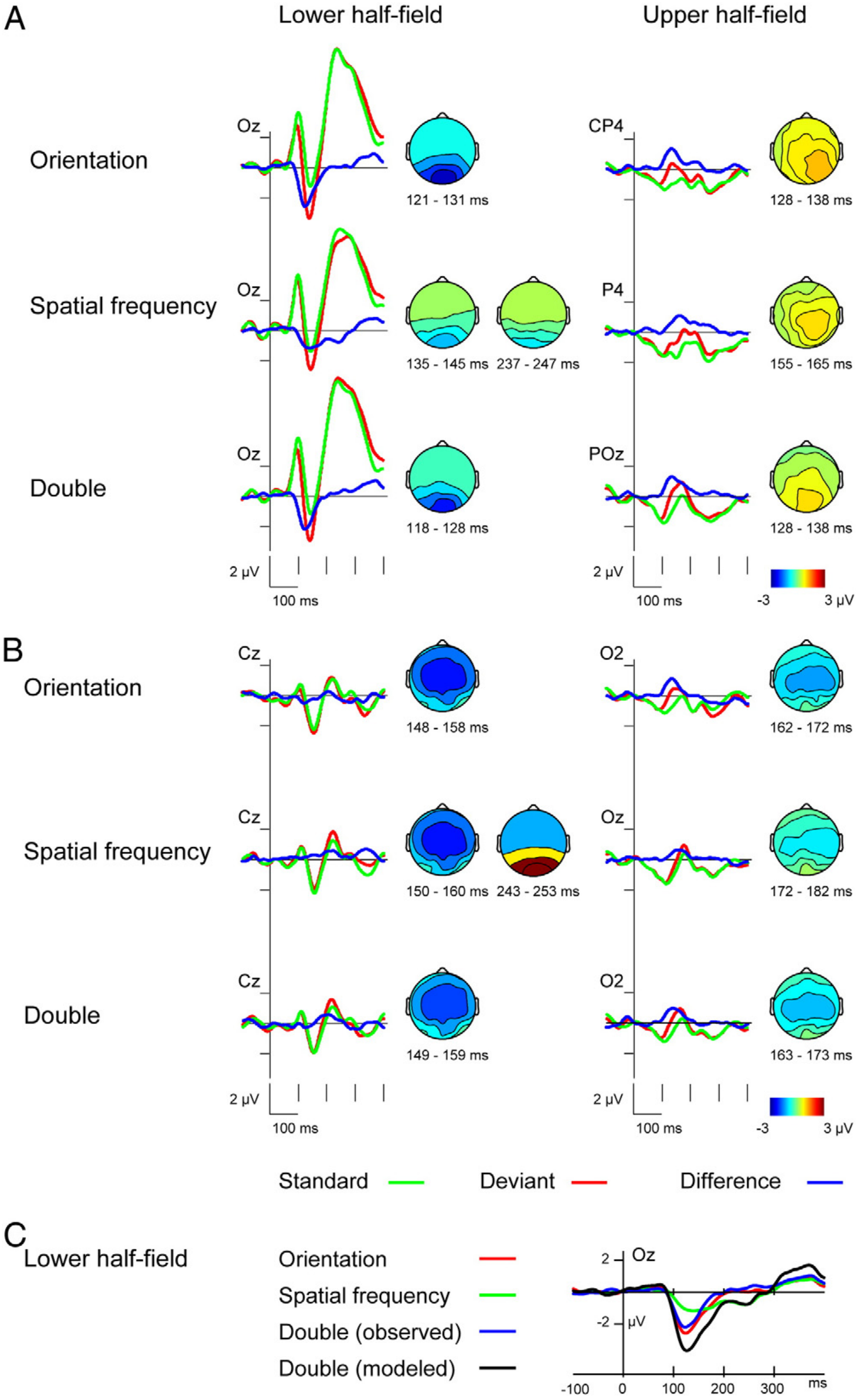
A
Lower half-field
Upper half-field
Orientation
Spatial frequency
Double
Oz
CP4
P4
POz
121 - 131 ms
128 - 138 ms
135 - 145 ms
237 - 247 ms
155 - 165 ms
118 - 128 ms
128 - 138 ms
2 µV
100 ms
-3
3 µV
B
Orientation
Spatial frequency
Double
Cz
O2
Oz
148 - 158 ms
162 - 172 ms
150 - 160 ms
243 - 253 ms
172 - 182 ms
149 - 159 ms
163 - 173 ms
2 µV
100 ms
-3
3 µV
Standard
Deviant
Difference
C
Lower half-field
Orientation
Spatial frequency
Double (observed)
Double (modeled)
2
Oz
-2
µV
-100
0
100
200
300
ms

Figure 3.1 – Event-related activity and deviant-standard difference potentials at the location having the amplitude of the largest difference potentials (A) and exogenous C2s (B). Voltage maps show latency ranges of amplitude analyses. Deviant-related activity in the orientation, spatial frequency and double deviant conditions, and the additive model (orientation plus frequency difference potential) is shown on C.

2.2.2. Exogenous potentials

In general, the three exogenous ERP components had opposite polarities for lower- and upper-half field stimuli. Furthermore, the latency values of these components differed, with latencies being generally shorter with lower-half field stimulation than forupper-half field stimuli (Table 1). For validation we compared these latency differences by t-test for each deviant condition (Component × Deviancy, 9 comparisons in total). Using the Bonferroni criterion, only C2 latency differences were deemed significant, t(11)=5.63–3.88, p<0.001–0.003.

Deviancy	**Orientation**		**Spatial frequency**		**Double**	
Half-field	**Lower**	**Upper**	**Lower**	**Upper**	**Lower**	**Upper**
C1	99 (2.9)	104(4.9)	97(4.0)	103(4.9)	96(4.7)	98(3.7)
C2	153(3.0)	166(3.8)	154(2.9)	174(4.0)	153(3.2)	169(4.1)
C3	242(4.8)	266(7.5)	248(5.3)	257(5.3)	243(4.5)	263(5.0)

Table 3.1. Mean peak latencies (ms) of the exogenous components (S.E.M. in parenthesis).

3.2.2.3. Comparison between exogenous components and difference potentials

To investigate the possibility of a distribution or latency difference between the exogenous components and the difference potentials, we used ANOVA to compare the vector-scaled amplitude values and the peak latencies of C2 and the earlier negativity. For these ANOVA tests the factors were as follows: Component (C2, difference potential), Deviancy (orientation, spatial frequency and double), Anteriority and Laterality, with the latter factors (calculated from a 3×3 grid including the following electrodes: C3, Cz, C4, P3, Pz, P4, O1, Oz, O2) used only for distribution analyses.

3.2.2.4. Scalp distribution

In the case of lower-half field stimulation, the Component× Anteriority, $F(2,22)=7.25$, $\varepsilon=0.54$, $p<0.01$, $\eta 2=0.39$, and Deviance× Laterality, $F(4,44)=3.29$, $\varepsilon=0.68$, $p<0.05$, $\eta 2=0.23$, interactions were deemed significant. The former interaction reflects the more posterior distribution of the deviant-related activity (in comparison to C2), whereas the latter effect reflects larger amplitudes over the midline. For upper-half field stimulation we observed a significant Laterality main effect, $F(2,22)=7.19$, $\varepsilon=0.82$, $p<0.01$, $\eta 2=0.39$, and significant Component × Anteriority, $F(2,22)=4.71$, $\varepsilon=0.57$, $p<0.05$, $\eta 2=0.30$, and Anteriority × Laterality, $F(4,44)=3.36$, $\varepsilon=0.57$, $p<0.05$, $\eta 2=0.23$, interactions. The Component × Anteriority interaction reflects the more anterior maximum of the deviant-related activity (in comparison to C2), whereas the other two effects reflect the right parieto-occipital distribution of the components.

Deviancy		**Orientation**		**Spatial frequency**		**Double**	
Half-field		**Lower**	**Upper**	**Lower**	**Upper**	**Lower**	**Upper**
vMMR early	**Amplitude**	-2.55 (0.46)	1.34 (0.27)	-1.18 (0.31)	0.99 (0.22)	-2.18 (0.50)	1.27 (0.22)
	Latency	130 (2.9)	132 (3.0)	136 (4.2)	163 (3.8)	129 (3.4)	138 (4.1)
vMMNR late	**Amplitude**			-0.78 (0.31)			
	Latency			241 (4.1)			

Table 3.2. Mean amplitude (μV) and peak latencies (ms) of the mismatch responses at lower and upper half-field stimulations (S.E.M in parenthesis).

3.2.2.5. Latency

In an ANOVA we compared C2 and difference potential latencies at lower-half field stimulation. The main effect of Component was significant, $F(1,11)=29.1$, $p<0.001$, $\eta 2=0.73$, showing generally a shorter difference potential latency. A similar test with upper-half field stimulation yielded significant Component, $F(1,11)=35.9$, $p<0.001$, $\eta 2=0.77$, and Deviancy, $F(2,22)=32.9$, $\varepsilon=0.89$, $p<0.001$, $\eta 2=0.75$, main effects, as well as a significant Component × Deviancy interaction, $F(2,22)=12.1$, $\varepsilon=0.90$, $p<0.001$,

$\eta 2=0.52$. The Component effect was similar to the lower-half field stimulation (that is, with shorter difference potential latency). According to the Tukey HSD tests, the Deviancy and Component × Deviancy effects were due to the smaller latency difference in the spatial frequency condition. C3 latency and the latency of the later difference potential component were compared only for the spatial frequency deviant at lower-half field stimulation conditions. The resulting t-test revealed a shorter peak latency, $t(11)= 14.1$, $p<0.001$, of deviant-related negativity relative to the latency of the exogenous C3.

3.3. Discussion

Deviant and standard stimuli elicited different ERPs. At lower half field stimuli this difference is typical of the vMMN component described previously (e.g., Astikainen et al., 2008; Czigler and Sulykos, 2010; Kimura et al., 2009 for orientation deviancy; and Heslenfeld, 2003 for spatial frequency deviancy). The main finding of the present study is the clear subadditivity of event-related brain activity to the violation of regularities in the case of two visual features, spatial frequency and orientation. The earlier deviant-related activity to lower half field stimuli was observed as a negativity (vMMN), with a mean latency of 130–140 ms to both the orientation and the spatial frequency deviants. The summed activity of the two individual deviant-related components was much larger than the vMMN to the double deviant. Furthermore, the later negativity to the spatial frequency deviant (with a mean latency of 241 ms) was clearly absent for the double deviant. Accordingly, the difference potentials for the orientation and the double deviant conditions were similar. The absence of the later vMMN at the double deviant argues against saturation as an interpretation of sub-additivity. Whereas the similar vMMN amplitudes in the orientation and double-deviant conditions can be explained by a saturation effect, the missing later vMMN cannot be interpreted in this fashion. The absence of the later mismatch-related activity to the double deviant can be interpreted as a hierarchical dependence of deviance-related pre-attentive mechanisms. This is similar to the processes involved in attentive target detection. In both auditory (e.g., Hansen and Hillyard, 1983) and visual (e.g., Smid et al., 1997; Wijers et al., 1989) modalities, feature related components (N1/processing negativity, selection negativity) were smaller or absent when another feature with more effective processing indicated a non-target stimulus. Accordingly, it seems that the processes responsible for generating vMMN are sensitive to deviant events as well as to separate deviant features. This finding confirms earlier auditory reports by Czigler and Winkler (1996), Paavilainen et al. (2001), Winkler and Czigler (1998), and Winkler et al. (1998). However the hierarchical relations among the automatic processing of various features are still debated. As an example Smid et al. (1997) reported context dependent relations between the task-related processing of color and shape, while the results found by Harter and Aine (1984) was interpreted as a feature-related serial processing of spatial frequency and orientation (i.e. spatial frequency is processed faster than orientation). As a conclusion the task-related treatment of the various features could be considered stimulus, task and context dependent with some fixed, feature related exception. Similar conclusion was drawn by Garner (1974) who investigated the selective attention to a specific feature in the context of another task-irrelevant feature. Garner (1974) defined two types of relations between simultaneously appearing feature dimensions. Two features are separable (e.g. color and shape), if the processing of such features does not interfere, while the processing of integral dimensions (e.g. lightness and saturation) is mutually dependent. In the present study separable dimensions (spatial frequency and orientation) were investigated. A study investigating integral dimensions would be a test of the generality of the present findings1. Another obvious line of research to investigate the feature-related hierarchical relations is the magnocellular–parvocellular subdivision of the visual system. To date, the majority of vMMR research has focused on parvocellular features, but there is evidence for motion-related vMMR, a deviance-related activity of the magnocellular system (e.g. Kremláček et al., 2006; Pazo-Alvarez et al., 2004). It would therefore be valuable to investigate possible interactions between vMMRs generated in the magnocellular and parvocellular systems. It is also important to investigate the extent of interactions between the mechanisms underlying the feature-related vMMRs; forasmuch in the auditory modality, there is a temporal limit of these interactions (Winkler et al., 1998). Another novel finding of our study is the emergence of positive deviance-related activity to upper-half field stimuli. In some previous studies (Clifford et al., 2010; Czigler et al., 2004; but see Berti, 2009; Amenedo et al., 2007), only lower-half field stimuli elicited vMMN. Compared to the vMMN to the lower-half field stimulation, the mismatch-related positivity (vMMP) of the present study is a less defined component. However, the stimulus location dependence of the mismatch related components makes the term “visual mismatch response” (vMMR) more appropriate for describing the deviance effects than the term “visual mismatch negativity”. One simple but reasonable explanation for the difference between our results and previous studies is the possibility of larger sensitivity to the deviant features in our task. In addition to the polarity difference, distribution of the vMMR to upper-field stimulation also differed from the vMMR to lower-field stimulation (i.e., more anterior), indicating that the mismatch responses are generated in retinotopic areas (Czigler et al., 2004). In a recent study using sLORETA method of cortical three dimensional distribution of current source density (Pascual- Marqui, 2002), Kimura et al. (2010a) localized orientation related vMMN into the pre-striatal (BA19) and prefrontal (BA47 and 11) areas. Attempts to localize the precise source of vMMR to other features and feature conjunctions are another possible line of future researches. As an alternative interpretation of the deviant-related activity, larger responses to infrequent stimuli can be attributed to the refractoriness of exogenous activity that is specific to the features of the standard stimuli (Berti and Schröger, 2006; Kenemans et al., 2003; Kimura et al., 2006; Mazza et al., 2005; for a discussion of a similar controversy in auditory modality see e.g. Näätänen et al., 2005; May and Tiitinen, 2010). However, some studies of change-related visual activity showed that refractoriness cannot adequately explain the emergence of deviant-standard differences. Rare visual stimuli elicited distinct posterior activity only when frequent (standard) stimuli were in the sequence (Astikainen et al., 2008; Czigler et al., 2002). Furthermore, both stimulus omission (Czigler et al., 2006b) and irregular repetition of stimuli (Czigler et al., 2006a; Kimura et al. 2010b) elicited vMMR. Several aspects of the present study also seem contradictory to the refractoriness explanation. First, peak latency of the earlier vMMR preceded the C2 exogenous component. Second, in the case of spatial frequency/lower-half field stimulation the second posterior negativity emerged together with a positive exogenous component (i.e., ERP was less positive to the deviant). Third, obvious distribution differences were found between the exogenous components and the vMMRs in cases of both visual fields. Therefore, even if selective refractoriness contributes to the deviant-standard difference, we consider reported effects to be genuine mismatch-related activity. In conclusion, stimuli with two features different from regular stimulation elicit a mismatch-related activity that is identical to the earliest mismatch-related activity to stimuli violating only a single feature. Thus, with regard to visual mismatch responses, one plus one is less than two.

3.4. Experimental procedures

3.4.1. Participants

Paid students (6 male and 6 female) of a combined mean age of 22±2.3 (SD) years with either normal or corrected-to normal visual acuity and with normal color vision participated in the experiment. Written informed consent was obtained from all participants. The study has been carried out in accordance with the Declaration of Helsinki. Due to a large number of artifacts, data from one additional participant were discarded.

3.4.2. Task-irrelevant stimuli

The irrelevant stimuli were greyscale images of Gaussian windowed sinusoidal gratings. Four variants of these Gábor patch-like images were constructed, with two values of orientation (0° and 90°) and two spatial frequencies (3 cycle/image and 7 cycle/image).The common parameters of the images were the Gaussian standard deviation (0.17-fold of image size), phase (320°) and trim-value (0.25). Twenty-four simultaneously displayed images were arranged along four imagined concentric semi-circles (with six images/semi-circle). Both the radius of the semi-circles and the diameter of the images increased exponentially (with a quotient of 1.6), approximating the cortical magnification factor (e.g., Leff, 2004). The radius of the smallest semi-circle was 16.8°, and the diameter of the smallest image was 0.8°. The stimulus duration was 80ms, the SOA was 560ms and the background was dark.

3.4.3. Task and task-related stimuli

The task-related stimuli were displayed on the part of the screen opposite to the task-irrelevant stimuli. The task itself was a simple video game, the aim of which was to maneuver a spaceship across a canyon. The center of the animation was the spaceship (i.e., the spaceship was fixed in a stationary position on the screen), whereas the obstacles (which comprised the target and non-target stimuli) moved toward the spaceship in the canyon, inducing illusory movement of the spaceship. The canyon (a tube with a rectangular cross-section) was sunk into the surface of a schematic planet, the surface of which was the horizon. The canyon was segmented by walls, each containing a colored door. Three door colors (red, green and blue) were used; two of the colored doors were targets, and a response button was assigned to each target. The task was to press the proper button upon appearance of the target and before the spaceship reached the wall (640 ms timeout, 8 trials per target in a block). The third color indicated the non-target door, which required no response. The color-button assignment was randomized among the blocks and indicated by two colored symbols on the left and right sides of the screen, visible throughout the block. No target appeared simultaneously with the task-irrelevant stimuli. Figure 3.2 shows a sample of the stimulus display.

3.4.4. Procedure

Participants were seated in a reclining chair 1.2m from a 17- inch LCD monitor (60-Hz refresh rate) in a dimly-lit, sound attenuated chamber. Task-irrelevant stimuli were either standards (p=0.82) or deviants (p=0.18). In each block there were 704 stimuli, 576 standards and 128 deviants. In the session, there were three sets of four stimulus blocks each: in four blocks, the infrequent stimuli had deviant orientation; in another four blocks, the infrequent irrelevant stimuli had deviant frequency; and in the remaining four blocks, both orientation and spatial frequency were deviant. Both values of orientation and frequency were standard (and deviant). In six blocks, the task-irrelevant stimuli appeared on the lower half of the visual field and in the other six blocks, they appeared on the upper half. The order of the blocks was counterbalanced across participants.

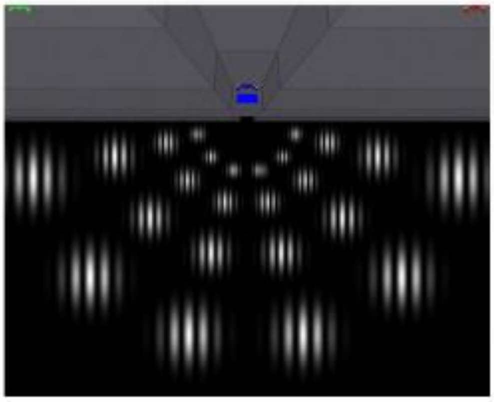

Figure 3.2. An example of the display. ERPs were recorded for stimuli in the lower half-field. The upper half-field presents the task

3.4.5. Measuring brain electrical activity

EEG was recorded (DC-70 Hz, sampling rate 1000 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 on the right mastoid with the reference recalculated (off-line) to linked mastoids, and 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 bandpass filtered offline, with cutoff frequencies of 0.1 and 30 Hz (24 dB slope). Epochs of 500 ms duration (including a 100-ms pre-stimulus interval) were extracted for each event and averaged separately for the standard and deviant stimuli. 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 ±70 μV on any channel were rejected from further analysis. Event-related potentials (ERPs) were averaged separately for the standard and deviant stimuli from the six conditions (orientation deviant, spatial frequency deviant and double deviant at upper and lower visual half-field stimulations). To identify change-related activities, ERPs from standard stimuli were subtracted from ERPs from deviant stimuli of the respective condition. Both orientations and both spatial frequencies were presented as standards and deviants;

therefore, the effects of physical differences were eliminated by this averaging and subtracting procedure. Deviance-related activity was considered to occur if the subtraction difference of the average amplitude of a 10-ms epoch around a peak of the deviant minus the standard difference potential was statistically significant. The t-tests were applied at the location having the amplitude of the largest difference potentials. Thereafter, channel matrices were defined as the regions of interest of the deviant-related components. For lower-half field stimulation the matrix involved the locations PO3, POz, PO4, O1, Oz and O2; for upper-half field stimulation, the matrix involved the locations CP3, CPz, CP4, P3, Pz, P4, PO3, POz and PO4. We investigated the possibility of anterior effects, but we obtained no significant deviance related activity. To compare deviant effects, mean amplitude values of the 10-ms (i.e., 11 data points) epochs of the difference potentials were compared by ANOVA, (with upper- and lower-half fields analyzed separately) using as factors of Deviancy (orientation and spatial frequency), Anteriority and Laterality, with the latter two factors calculated from the channel matrices. In this analysis, distribution differences were analyzed on the vector-scaled amplitude values (McCarthy and Wood, 1985). Though there were no significant differences between scalp distributions of the orientation and spatial frequency deviants in either half-field, difference potentials were summed (as the additive models of double deviants) for comparison with the difference potentials elicited by the double deviant. In this comparison, the ANOVA factors were Additivity (both modeled and observed double deviant), Latency band (both early and late negativities, but only for lower-half field stimulation), Anteriority and Laterality. We also investigated the peak latencies and scalp distributions of the exogenous components. Peak latencies were measured at the maxima of the components, while vector-scaled values were used to analyze distribution differences. ANOVA tests related to these exogenous components are described in the Results 3.2.2.2 and 3.2.2.3 sections. Where appropriate, the Greenhouse–Geisser correction was applied. Post-hoc analyses were calculated by the Tukey-HSD test. In the reported effects the alpha level was at least 0.05. Behavioral performance was measured as RT and HIT rates, and compared by two-way (Half-field, Deviancy) ANOVA. Where applicable, data are presented as the mean±SD.

Acknowledgments

This research was supported by the National Research Found of Hungary (OTKA 71600).

4. Visual mismatch negativity is sensitive to illusory brightness changes (Thesis study 3)[7]

The aim of the study was to investigate the sensitivity of the visual mismatch negativity (vMMN) component of event-related potentials (ERPs) to the perceptual experience of brightness changes. The percept could be based on either real contrast or illusory brightness changes. In the illusory condition, we used Craik-Cornsweet-O'Brien (CCOB) stimuli. CCOB stimuli comprised of grey, equiluminant areas and Cornsweet-edges that separated the areas. These specific edges, containing opposing darkening and lightening gradients modify the perceived brightness of the flanking areas. Areas next to the darkening part (of the edges) perceived darker while areas next to the lightening part perceived lighter. Reversing the gradients induces illusory brightness changes. The normal and reversed stimuli were delivered according to a passive oddball paradigm. In another condition (REAL condition), we used stimuli with real contrast difference. The perceived brightness of the stimuli applied in this sequence was fitted to the normal and reversed CCOB stimuli. In a third condition (CONTROL condition), we tested the ERP effect of the reversing of Cornsweet-edge. In this condition, the changes did not induce illusory brightness changes. We obtained vMMN with double peaks to both real and illusory brightness changes; furthermore, no vMMN emerged in the CONTROL condition. VMMNs fell in the same latency range in the two conditions; nevertheless the components slightly differed in terms of scalp distribution. Since the perceptual experience (i.e. brightness changes) was similar in the two conditions, we argue that the vMMN is primarily sensitive to the perceptual experience and the physical attributes of the stimulation has only a moderate effect in the elicitation of the vMMN.

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[7] Sulykos, I., & Czigler, I. (2014). Visual mismatch negativity is sensitive to illusory brightness changes. Brain Research, 1561, 48–59.

4.1. Introduction

The aim of the present study was to investigate, whether an electrophysiological index of automatic brain activity to visual events violating temporal-sequential regularities was sensitive to illusory perceptual changes, even if such changes were outside the focus of attention. The illusory change of luminance in this study was elicited by the Craik-Cornsweet-O'Brien (CCOB) brightness illusion (Cornsweet, 1970; Craik, 1966; O'Brien, 1958). The electrophysiological index we measured was the visual mismatch negativity (vMMN; for reviews see Czigler, 2007; Kimura, 2012). VMMN is a counterpart of the auditory mismatch negativity (for a review see Näätänen et al., 2007) and usually investigated in passive two-stimulus oddball paradigms. In this paradigm, within the sequence of frequently presented (standard) stimuli, infrequent (deviant) ones are presented in unpredictable sequential positions. The function of the standards is to acquire a model of the sequential regularity of stimulation, while deviants represent unpredictable changes. Deviant minus standard ERP-difference is considered as a prediction-error signal specific to sequential attributes of the environment (Kimura, 2012). VMMN is a negative ongoing ERP component (but see Sulykos and Czigler, 2011) over posterior areas and emerges in the 120–350 latency range after the stimulus onset. It is important to emphasize that the vMMN is considered as an automatic component at least in terms of that attention is not necessary to obtain vMMN (Berti, 2011; Kimura and Takeda, 2013; for a review see Czigler, 2007).

In the majority of studies vMMN was investigated by deviations in elementary stimulus dimensions such as color (Czigler et al., 2002), orientation (Astikainen et al., 2008; Kimura et al., 2009, 2010), motion direction (Pazo-Alvarez et al., 2004), spatial frequency (Heslenfeld, 2003) and contrast (Stagg et al., 2004). Nevertheless, the mechanism underlying vMMN is well beyond the simple, feature-specific change detection processes. First, visual (as well as auditory) MMN is elicited by infrequent conjunction of two features (Winkler et al., 2005). VMMN to feature conjunction shows that the memory system underlying vMMN is capable of registering bound features. Similar conclusion was drawn by a study of Sulykos and Czigler (2011). In this study, concurrent deviancies in two features elicited a sub-additive response compared to the sum of the vMMNs to single feature deviancies. Second, vMMN is impacted by object formation as reported by Müller et al. (2009, 2013). In the Müller et al. (2009) study, the standard patterns comprised of 8 equicolored (green or red) filled circles coupled by black thin lines. The bound circles were regarded as separated objects. In case of deviant patterns two of the circles were colored the alternative color. The two deviant circles belonged either to the same or to different objects. In the latter case, they registered a single vMMN to color deviancy. However, when the deviancies occurred within the same object, it elicited an additional vMMN at a later latency range. In the Müller et al. (2013) study, the stimulus pattern comprised of two white ellipses and two grey circles. The ellipses represented the objects. The grey circles were either in the same or in different ellipses. The assignment of the circles (whether the two circles belonged to the same or different objects) defined the difference between the standard and the deviant. They obtained vMMN to deviant assignment of the circles; therefore, repeatedly supported that vMMN is sensitive to object formation. Finally, vMMN is elicited by deviant categories of facial expressions (e.g. Stefanics et al., 2012), laterality of hands (Stefanics and Czigler, 2012), symmetry (Kecskés-Kovács et al., 2013a) and gender (Kecskés-Kovács et al., 2013b). In these studies, the deviant and standard stimuli did not differ in terms of a certain stimulus dimension. Instead, the deviant-standard difference manifested only at the level of category representation. The effect of categorization is not restricted to the process of complex stimulus pattern such as face or bilateral symmetry (for a detailed review about the categorization-effect, see Czigler, 2013). A few recent studies (Thierry et al., 2009; Clifford et al., 2010) pointed out that the vMMN to color-deviation (as an elementary feature change) is modulated by the category of the color. Clifford and her colleagues (2010) demonstrated that the same distance in color-space elicited larger vMMN if the standard and deviant colors belonged to different color-category (e.g. dark blue vs. light blue or green vs. light blue). Thierry et al. (2009) investigated the cross-cultural language effect on deviant-related processing of color. The Greek language differentiates between light (ghalazio) and dark (ble) blue while English language does not. Contrary to the blue, both languages use one word for the green color. The authors used light and dark shades of the colors (green and blue in separate conditions) as standards and deviants. In case of Greek speakers, they registered larger vMMN to blue condition than to green condition. That is, the vMMN was larger if the deviation occurred across color-categories (ghalazio and ble) than within the category (green). In case of English speakers, they obtained similar vMMNs in the two conditions. The authors argued that the cross-cultural effect was due to the differences in category representations, since the differences in language-labels reflect the differences in the mental structures of categories. Furthermore, category-representations affect the perceptual experience of the incoming stimulation even at the level of elementary feature changes (linguistic relativism; Whorf, 1956). As the above mentioned studies pointed out, these category-effects resulted in differences not just in the perceptual experience but in the process of automatic deviance-detection also (the results of cross-cultural effect were replicated by Athanasopoulos et al., 2010).

Based on the previous findings, we suppose that, the formation of conscious perceptual experience and the automatic deviance detection (vMMN) is affected by similar factors. As a consequence, we also suppose that cognitive processes underlying the vMMN and the cognitive processes underlying the perceptual experience are similar. Since similar cognitive processes probably result in similar representation forms, we presume that the representations underlying both responses (the vMMN and the perceptual experience) are also similar. In other words, the vMMN is primarily sensitive to the representation form correspond to the perceptual experience. This supposition does not contradict to the vMMN-literature since the perceptual experience is also sensitive to elementary features, binding of features, object formation and category-representation just as the vMMN. The aim of the present study was to investigate the presumption; i.e. to explore the relationship between the perceptual experience and the vMMN. To this end, we chose the field of visual illusions for generating the experimental stimuli. We had two main reasons for doing so. First, by using illusions, we are able to induce significant changes in the perceptual experience with negligible changes in the physical properties of the stimulus. Therefore, we can measure the automatic deviance-detection processes to changes in the perceptual experience with minimal (contaminating) effect of elementary feature change detection. Second, the constructive processes inducing illusory experience are presumably not identical to the ones responsible for feature binding, object formation or category-representation. Therefore, we can investigate the emergence of vMMN to the changes in the perceptual experience independently from the above mentioned processes.

As far as we know, in the vMMN-literature, there has been a single study using visual illusion (Flynn et al., 2009). Flynn and her colleagues applied Kanizsa-squares. When four concave circle sectors (‘packman-figures’) are arranged in a certain way, it induces illusory edges creating a Kanizsa square. In the applied three-stimulus paradigm, one of the deviant patterns was such Kanizsa-square (illusory deviant). The other deviant and the standard patterns comprised of other arrangements of the packman figures that did not induce illusory edges. They obtained vMMN to both the deviant and the illusory deviant stimuli at 170–190 ms latency range. Additionally, a fronto-central positive component was registered at around 350 ms after onset considered as P3a. Furthermore, under an attentionally loaded condition (the participants were requested to respond to infrequent changes at the center of the screen) the vMMN to both deviants decreased. They interpreted the data as evidence of attentional capture to the illusory deviant. Unfortunately, in the paradigm of the Flynn et al. (2009) study emergence of the illusion was confounded with a real physical change (i.e., the different orientation of the packman figures). In the present study we attempted to avoid this problem. The illusion that we applied was the CCOB brightness illusion. In the CCOB illusion, a 'Cornsweet-edge' (special pattern of luminance transition; for detailed description see Figure 4.4A and section 4.4) separating regions of equal luminance induces apparent perceptual brightness difference between the regions. Regions adjacent to the darker side of the border appear darker than the regions adjacent to the higher luminance part of the border (Figure 4.4A). Reversing the edge induces illusory brightness changes in the flanking areas, therefore, generating changes in the perceptual experience without the occurrence of real luminance changes.

There is no consensual account of the mechanisms generating CCOB illusion. In the literature both stimulus-driven (e.g. Davey et al., 1998; Grossberg and Todorović, 1988; Komatsu, 2006) and top-down (Purves et al., 1999, 2004) explanations are present. Furthermore, studies investigated the brain structures involved in the generation of the illusion reported equivocal findings also. Some neurophysiological data show that cells in the primary visual cortex (V1) are sensitive to local luminance change, but insensitive to CCOB stimuli (Hung et al., 2001; Roe et al., 2005) and similar pattern of results were obtained in several fMRI studies (Perna et al., 2005; Cornelissen et al., 2006; Boyaci et al., 2007). Contrary to these findings, Anderson et al. (2009) reported fMRI data showing that CCOB effects appeared even at the level of corpus geniculatum laterale. At the level of the neuronal mechanism underlying CCOB as well as on the theoretical level, diversity of explanations is considerable. We emphasize that in the present study we do not want to resolve these controversies.

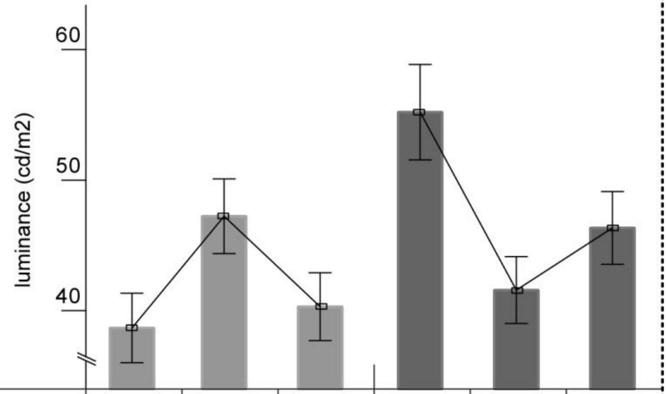
Instead, our aim is to explore the relationship between the perceptual experience and the vMMN. Our expectation is that the representation underlying the registration of violated environmental regularities and the representation underlying our perceptual experience are similar. To test the assumption, we applied an oddball sequence comprising of standard and deviant CCOB stimuli inducing infrequent illusory brightness changes. We expect vMMN to illusory brightness changes, since such changes evoke changes at the level of perceptual experience. To test the contribution of the Cornsweet-edge to the elicitation of vMMN to CCOB stimuli, i.e. the ERP-effect of the physical changes inducing the illusory changes, we added a CONTROL condition. In the CONTROL condition, standard and deviant patterns of Cornsweet-edges were presented without the experience of the brightness illusion. We expect that, such changes in the Cornsweet-edge will not elicit vMMN (since the changes in the Cornsweet-edges will not be significant enough to elicit vMMN), or the obtained difference wave will significantly differ from the one that will be obtained in the CCOB condition (since the perceptual experience to the Cornsweet-edge differs from the one that is evoked by the illusion). Finally, we introduced a third condition, where perceptual differences between the standards and deviants were similar to the ones in the CCOB condition. However, in this case, the stimuli actually differed in luminance (REAL condition). We expect the elicitation of vMMN to real luminance changes as well. The aim of this third condition was to directly compared vMMNs elicited by real and illusory changes. Since the perceptual experiences of real and illusory changes are similar, we expect similar vMMNs in the two conditions. Contrarily, differences of the two deviant-related responses may reveal that representations underlying the vMMNs to various stimuli are affected by the different stages of perceptual processing.

4.2. Results

4.2.1. Behavioral results

4.2.1.1. Psychophysical results

To test the effectiveness of the CCOB stimuli in eliciting the brightness illusion, we analyzed the results of the matching procedure. Based on the definition of the CCOB phenomenon (the equiluminant grey areas separated by a Cornsweet-edge are perceived differently in terms of brightness), the induced illusion is considered as efficient if the brightness judgments on the neighboring grey annuli were significantly different in both cases of CCOB stimuli. We compared the correspondent brightness judgment values with four paired t-tests; the results of the analysis are detailed in Figure 4.1. As the figure shows, the apparent brightness differences were in the expected direction at both stimuli. The differences were significant in every comparison. It is noteworthy to mention that the other aim of the psychophysical measures was to create the stimuli of REAL condition; in other words, the brightness judgments defined the contrast values of the REAL stimuli.



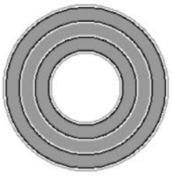
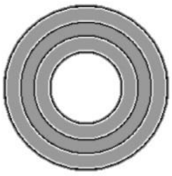
annuli	inner	middle	outer	inner	middle	outer
stimuli						
mean	38.68	47.24	40.31	55.21	41.58	46.34
s.e.m.	2.66	2.86	2.60	3.66	2.56	2.79
t-statistic	t(13) = 10.14 p < 0,01		t(13) = 5.40 p < 0,01	t(13) = 3.53 p < 0,01		t(13) = 3.15 p < 0,01

Figure 4.1 – Psychophysical results

Bars represents the group average of the brightness judgments, vertical lines show the standard error of mean. The attached table sums up the results of t-tests of the paired comparisons between the luminance values.

4.2.1.2. Performance in the primary task

Participants' performance in the detection task (the change of the fixation cross) was measured by means of reaction time and hit rate. We conducted one-way ANOVAs to reveal any possible statistical effect on both data types (the factor was condition with CCOB, REAL and CONTROL values). The ANOVA did not show any significant effect in either of the data types. Average performance and reaction time across the experimental blocks was 91 percent (standard deviation=11 percent) and 620 ms (standard deviation=160 ms) respectively.

4.2.2. Event-related potentials

4.2.2.1. Exogenous components

Figure 4.2 shows the event-related potentials to the standard stimuli in the three conditions. All types of stimuli (CCOB, REAL, CONTROL) elicited triphasic activities, each of which comprised of a positive (P1), a negative (N1) and a positive (P2) component. We used separate ANOVAs to compare the latency and amplitude values of the P1, N1 and P2 components. P1, N1 and P2 amplitudes were measured as the mean values of the 100– 180, 180–260 and 260–340 ms epochs, respectively, as highlighted in Figure 4.2 (the values are listed in Table 4.1). The factors were condition (CCOB, REAL, CONTROL), anteriority and laterality. The latter two factors were calculated from a matrix comprised of posterior electrode locations (P5, PO3, POz, PO4, P6, PO7, O1, Oz, O2 and PO8) by the following manner. The anteriority factor had two values: more anterior (P5, PO3, POz, PO4 and P6) and more posterior (PO7, O1, Oz, O2 and PO8) channel locations. The laterality factor had five values: left lateral (P5 and PO7), middle-left lateral (PO3 and O1), midline (POz and Oz), middle-right lateral (PO4 and O2) and right lateral (P6 and PO8).

In the range of P1, amplitude differences were found as significant condition x anteriority [$F(2,26)=5.70$, $p<0.05$, $\eta2 =0.30$, $\varepsilon=0.84$] and condition x laterality [$F(8,104)=3.53$, $p<0.05$, $\eta2 =0.21$, $\varepsilon =0.36$] interactions. However, these effects vanished when vector-scaled (McCarthy and Wood, 1985) values were entered into the ANOVA, i.e., the results did not reflect valid distribution differences. Instead, the interactions were due to the enhanced P1 at anterior right lateral channel locations in the CCOB condition (this assumption was confirmed by the Tukey HSD test). ANOVA on P1 latencies showed condition main effect [$F(2,26)=7.83$, $p<0.01$, $\eta2 =0.38$, $\varepsilon =0.81$] and condition x laterality interaction [$F (8,108)=4.57$, $p<0.01$, $\eta2 =0.26$, $\varepsilon =0.41$]. According to the Tukey HSD test, the significant effects were due to the longer latencies in the REAL and CONTROL conditions over midline and left posterior areas.

The latency difference continuously decreased toward the right lateral electrode locations and completely faded at the PO8 electrode location.

Analysis on the N1s amplitude revealed significant condition x laterality [F(8,104)=6.88, p<0.01, η2 =0.35, ε=0.31] interaction. The effect remained significant even if the data were vector-scaled [F(2,26)=6.86, p<0.01, η2 =0.35, ε =0.30], i.e., N1 distribution was different in the conditions. In the REAL and CONTROL conditions N1 had bilateral distribution, whereas N1 to CCOB stimuli had a wider and smoother distribution. Latency-analysis on N1 components revealed significant condition main effect [F(2,26)=10.20, p<0.01, η2 =0.44, ε=0.55]. N1 latency in the CCOB condition was generally shorter than the N1 latencies in the REAL and the CONTROL conditions. We entered the mean epoch values of exogenous components measured at the P2 range, however, we obtained neither main [F(2,26)=0.43] nor interaction (condition x anteriority: [F(2,26)=0.26]; condition = laterality: [F(8,104)=1.18]) effect reflecting differences among the conditions. A similar ANOVA on the latency of the P2 components resulted in no significant effects at all (condition: [F(2,26)=1,29]; condition = anteriority: [F(2,26)= 0.44]; condition x laterality: [F(8,104)=0.42]).

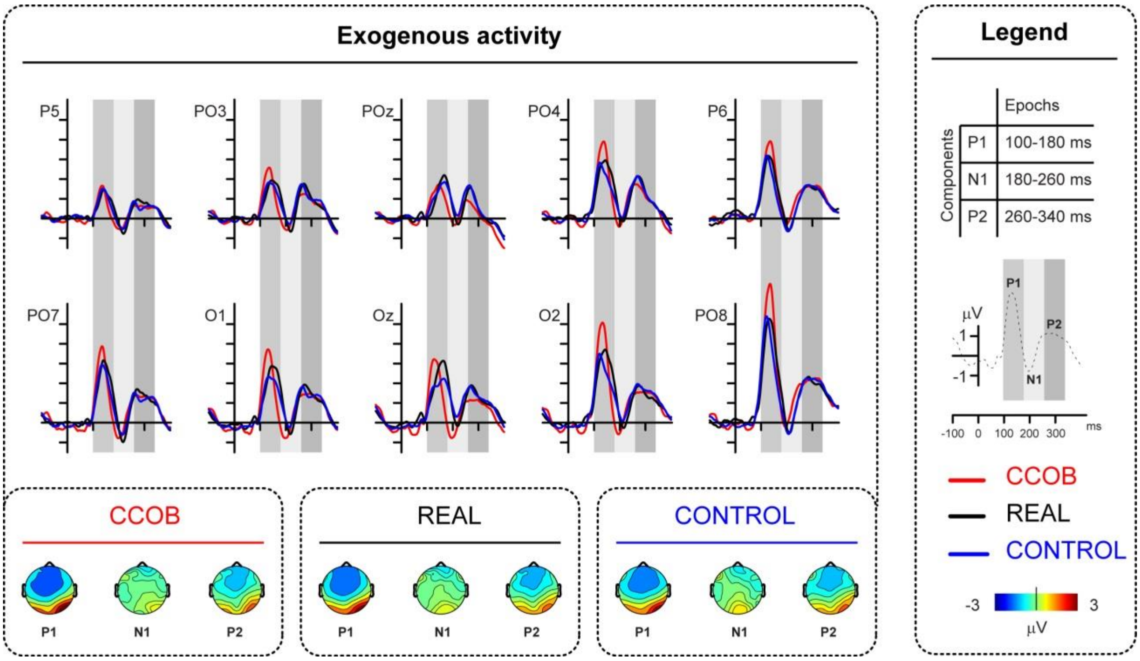


Figure 4.2. Exogenous activities. Exogenous activities recorded at posterior channel locations. The grey highlights show the latency ranges of amplitude analyzes. Voltage maps show the scalp distributions of the components at the highlighted ranges.

	P1	**N1**	**P2**

CCOB	**Amplitude**	2.23 (1.00)	0.31 (0.77)	1.19 (0.65)
	Latency	133 (6.4)	203 (12.2)	297 (16.2)
REAL	**Amplitude**	2.12 (0.86)	0.41 (0.87)	1.33 (0.53)
	Latency	145 (10.2)	214 (10.1)	290 (13.5)
CONTROL	**Amplitude**	1.90 (1.04)	0.53 (0.99)	1.33 (0.61)
	Latency	140 (8.7)	212 (11.2)	295 (14.7)

Table 4.1. Mean peak latencies and mean epochs of the exogenous components (s.e.m. in parenthesis) measured at 10 posterior electrode locations (P5, PO3, POz, PO4, P6, PO7, O1, Oz, O2 and PO8).

4.2.2.2. Deviant-minus-standard difference waves

Figure 4.3 depicts the ERPs to deviant and standard stimuli in the CCOB, REAL and CONTROL conditions, and the deviant minus standard difference potentials. As these difference waves show, in the CCOB and in the REAL conditions two posterior deviant-related negativities (DRN) emerged: one in an earlier (at around 200 ms) and another one in a later latency range (at around 300 ms). In the CONTROL condition no deviant-related activity appeared in the above mentioned ranges; the maxima of the deviant-standard differences were at 150 and 260 ms after stimulus onset. To validate the statistical significance of the deviant-standard differences, we performed six (3 conditions in the 2 ranges) separate ANOVAs on the mean epochs (maxima 720 ms) of ERPs. The factors were probability (deviant, standard), anteriority and laterality. The anteriority and laterality factors were calculated from a grid including the following electrode locations: PO3, POz, PO4, O1, Oz and O2. Anteriority factor comprised of two values: more anterior (PO3, POz and PO4) more posterior (O1, Oz and O2). Laterality factor had three values: left lateral (PO3 and O1), midline (POz and Oz) and right lateral (PO4 and O2). The comparison revealed significant probability main effects in both latency ranges in the CCOB [F(1,13)=5.74, p<0.05, η2 =0.30; F(1,13)=12.34, p<0.01, η2 =0.49] and REAL [F(1,13)= 6.65, p<0.05, η2 =0.34; F(1,13)=18.72, p<0.01, η2 =0.59] conditions. In the CONTROL condition, the main effects of probability [F(1,13)=2.81, p40.1; F(1,13)=2.00, p40.1] were not significant. Surface distributions of the four DRNs (early and late components in the CCOB and REAL conditions) are presented on Figure 4.4; Table 4.2 contains the mean amplitude and latency values of the four DRNs.

To investigate the DRNs across the two ranges and across the CCOB and REAL, we entered the mean epochs of the difference waves to a four-way ANOVA. The factors were condition (CCOB, REAL), range (early, late), anteriority and laterality. The analysis was repeated on vector-scaled data. Both analyzes pointed out significant condition x laterality interaction [F(2,26)=6.93, $p<0.01$, η2 =0.35, ε =0.96, and F (2,26)=5.92, $p<0.01$, η2 =0.31, ε =0.98, respectively]. Therefore, a genuine distribution difference appeared: DRNs were different between the two conditions and within the conditions the distributions were similar in the two latency ranges. In the CCOB condition both DRNs had left lateral maxima, while in the REAL condition, both DRNs were larger at the right side. We also investigated the possibility of DRN latency differences between the CCOB and REAL conditions, in separate ANOVAs for the two ranges and no significant effect of the conditions emerged.

	CCOB		**REAL**		**CONTROL**	
Epoch (ms)	180-220	280-320	180-220	280-320	130-170	220-300
Amplitude (μV)	-0.37 (0.38)	-0.49 (0.34)	-0.64 (0.61)	-0.52 (0.29)	-0.21 (0.31)	-0.21 (0.37)
Latency (ms)	201 (7.2)	303 (8.2)	201 (8.7)	303 (6.4)	153 (9.1)	260 (7.5)

Table 4.2. Mean epochs and peak latencies of the deviant-minus-standard difference waves (s.e.m. in parenthesis) measured six posterior electrode locations (PO3, POz, PO4, O1, Oz and O2).

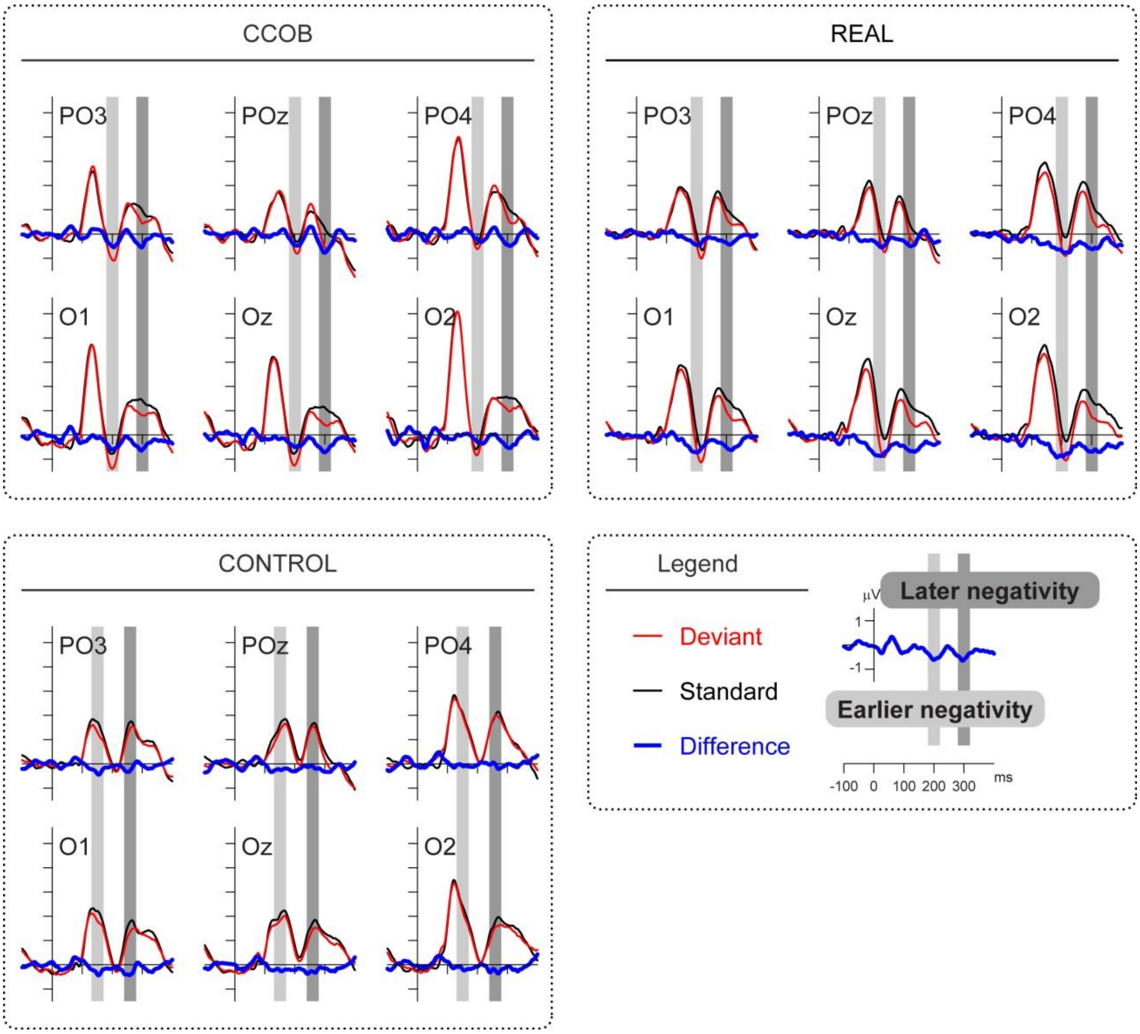


Figure 4.3. Event-related potentials. Event-related activities and deviant minus standard difference potentials. The grey highlights show the latency ranges of amplitude-analyzes.

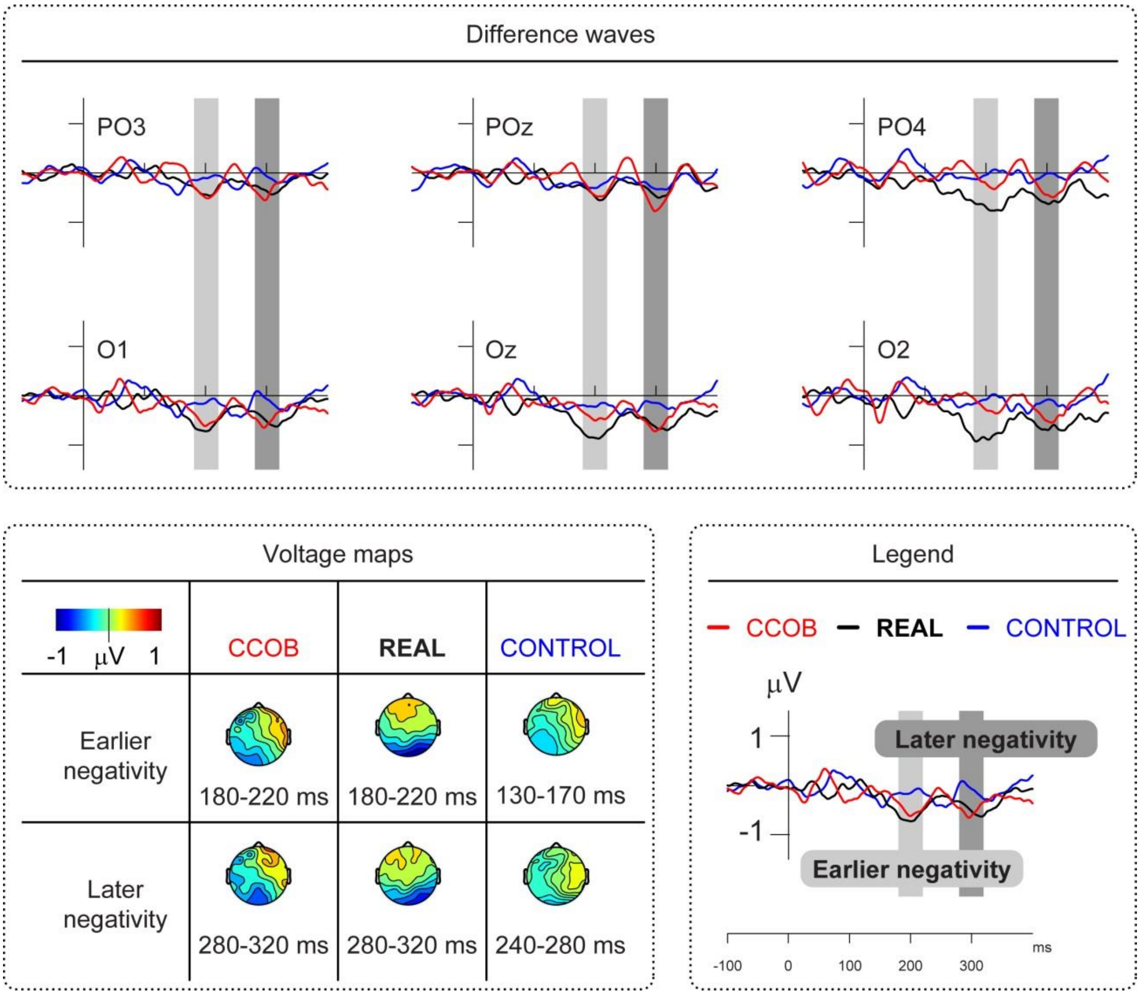


Figure 4.4. Comparison of difference waves. Deviant minus standard difference potentials in the three conditions. The grey highlights show the latency ranges of amplitude-analyzes. Voltage maps show the scalp distributions of the difference waves at the highlighted ranges.

4.3. Discussion

The main result of the experiment was the emergence of two consecutive DRNs both in the CCOB and REAL conditions. The maxima of the DRNs were at about 200 and 300 ms; all of them restricted to posterior scalp locations. Due to the latency and distribution the DRNs are considered as vMMNs (Czigler, 2007; Kimura, 2012). In the control condition, we obtained no significant deviant-related response. Consequently, the vMMNs in the CCOB condition cannot be attributed to the local changes at the Cornsweet-edges. Since the vMMN in the CCOB condition is not explicable by the physical properties of the CCOB stimuli the elicitation of vMMN was due to the other characteristic of the stimuli which is the generation of the brightness illusion. That is, the vMMN is sensitive to illusory brightness changes just as well as the perceptual experience. Contrary to the Flynn et al. (2009) study, we did not obtain P3a to illusory deviant stimuli. Therefore, the illusory changes were not salient enough to capture the participants' attention. The lack of the orientation-related related ERP component implicates that the conscious attention did not follow the detection of deviants; i.e. the task-irrelevant stimuli remained non-attended during the stimulation. Consequently, conscious attention is not a sufficient condition for the processing of illusory deviants i.e. the cognitive processes can be regarded as automatic ones. The present findings have three implications.

First, we obtained double deviant-related activities. This finding is not a unique phenomenon in the vMMN-literature (e.g. Astikainen and Hietanen, 2009; Müller et al., 2009; Sulykos and Czigler 2011; Kecskés-Kovács et al., 2013a). The emergence of the earlier vMMN was partially overlapped with the exogenous N1, while the later vMMN was elicited in the latency range of the P2 component. As for the earlier difference, it is possible that instead of a genuine vMMN, the negativity is an amplitude modulation of the N1 component (Kenemans et al., 2003; Kimura et al., 2009, 2010, for an extensive review in the acoustic modality, see May and Tiitinen, 2010). N1 decreases to the repetitive presentation of the standard while deviant stimuli stimulate fresh neural networks (a similar explanation is not probable in case of the later vMMN). In principle, this effect can be avoided by using equiprobable control stimuli (Kimura et al., 2009). Unfortunately, in our paradigm, application of such experimental control was impossible. However, some evidence indicates that the earlier difference was a genuine vMMN. First, one may expect different scalp distribution of the difference waves elicited by N1 modulation and by a genuine vMMN. However, the scalp distributions of the earlier and later vMMN were similar in both conditions. Furthermore, in case of selective N1 refractoriness, one may expect latency differences on vMMN in the CCOB and REAL conditions, since the N1 latencies in the two conditions were different. However, latencies of the two early vMMNs were not different.1 As another possible interpretation, the emergence of two successive vMMNs is a manifestation of a cascade of cognitive processes. Czigler (2007) delineated a multistage model underlying the vMMN.(for an advanced model, see Winkler et al., 2009). According to this approach (1) the vMMN subcomponents reflect different stages of deviant detection, and (2) under some conditions the different stages are more or less separated in time. This suggestion corresponds with the view that scalp-recorded vMMN is a resultant of hierarchically organized error signals (Winkler and Czigler, 2012). The adequate explanation of the finding (and the classification of the earlier vMMN) exceeds the scope of this study; however the riddle of double vMMNs is noteworthy, even if N1 adaptation may contribute to the effect.

The second implication concerns the identical vMMN latencies in the CCOB and REAL conditions. At first glance, the similarity suggests that the processing speed of the real and illusory contrast was equal. However, it is important to emphasize that vMMN latency is not a measure of the onset time of illusion per se. According to recent theories (Winkler et al., 2009; Kimura et al., 2011; Kimura, 2012; Winkler and Czigler, 2012) the cognitive processes underlying the vMMN serves as a predictive mechanism, expecting a regular event, and the vMMN is a correlate of the initial failure of memory match, and further processes to identify the deviant event. The similar vMMN-latencies reveal that the temporal patterns of such processes were similar in both conditions. The perceptual experience in the conditions was similar: the perceived brightness of the grey annuli infrequently changed. The results reveal that the similar percepts elicited similar vMMN in terms of the peak latency of the double vMMNs. The fact that the perceptual experience correlates with the temporal attributes of the vMMN supports the initial presumption. The perceptual (sub)processes and (consequently) the memory representation underlying the vMMN and the ones underlying the perceptual experience are fairly similar.

VMMN voltage distributions in the CCOB and in the REAL conditions were different; illusory brightness changes elicited left, real contrast changes elicited right lateralized vMMNs. Moderate differences in vMMN distributions to various visual dimensions (e.g. Sulykos and Czigler, 2011; orientation and spatial frequency) or features (Takács et al., 2013; oblique and cardinal orientations) were already reported. It seems that, the present results extended the findings to illusory feature-changes. However, in this sense, cautious interpretation is needed. In the Sulykos and Czigler (2011) and Takács et al. (2013) studies, the perceptual experience of feature-changes was different while in the present study, it was similar (real vs. illusory changes). So far, we argued that the perceptual experience and the vMMN are based on similar memory representations. Therefore, one may expect similar scalp-distributions for the two vMMNs just as we obtained similar vMMN-latencies. Nevertheless, the scalp-distribution and the latency of the vMMN reflect different aspects of the deviant-related response. (Furthermore, the temporal resolution of the ERP is much better than the spatial resolution). The latency of the vMMN reveals the temporal attributes of the deviant-related processing. In other words, the latencies of the vMMN give information about the subsequent stages of the deviant-related processing. In that sense, the cascades of stages of the cognitive processing are similar in both (REAL and CCOB) cases. The scalp-distribution shows the spatial summation of the scalp-recorded cortical activities in a given moment. Based on the scalp-distribution, we can infer to the loci of the multiple sources of the deviant-related brain response. Consequently, the scalp-recorded deviant-related brain response is probably generated by overlapped neural circuits, i.e. both similar and separate sources. The stimuli, per se, were different; therefore, the cortical networks what process the deviations could be also different. Differences between the (sub)cortical sources as well as the mechanisms that process the CCOB illusion and that process elementary feature of luminance intensity are still unclear (cf. Purves et al., 2004; Davey et al., 1998). As a tentative suggestion, we conceive that the distribution differences between the two conditions were caused by stimulus-related and processing-related effects together. The results reveal that although the cortical sources of vMMNs to different stimuli (partially) differ, the temporal patterns of the processing stages are similar when the perceptual experiences of the deviations are identical. The cortical sources of vMMNs based on various representation levels and modulated by various physical attributes of the stimulation could be a straightforward direction of the further studies.

Although the focus of the study was on the vMMN component, the pattern of the P1 and N1 exogenous components deserves a short discussion (we obtained no P2 differences). The maxima of the P1s were at the PO8 location, and we obtained P1 with the largest amplitude in the CCOB condition. Furthermore, in this condition the P1 latency was similar at all posterior locations. However, in the other two conditions (REAL, CONTROL), P1s' latencies increased as a function of distance from PO8 (i.e. the larger the distance from the PO8 the longer the latencies of the P1s). This pattern of results can be an averaging of artifacts. Since the magnitude of P1 was not the same in the conditions, the signal to noise ratio was not the same either. This difference was not salient at the maxima of the component, however, as the components decreased, the signal to noise ratio increased resulting a less synchronized signal. After the averaging procedure, the single trial activities summed as a lengthened response as seen in Figure 4.2 (c.f. Luck, 2005, chapter 2). The exogenous activity in CCOB condition separated in case of N1 components as well. We argue that this is another exogenous difference and not just the consequence of the P1 effect because of two reasons. First, latency difference (CCOB vs. the other two conditions) emerged at all locations (i.e. it was a latency main effect). Second, the scalp distributions were different among the CCOB and the other two conditions. These distinctions suggest that the N1 differences on ERPs, at least in parts, reflect valid difference in brain responses. The interpretation of the results is challenging since the literature investigating the Cornsweet-effect on exogenous potentials is limited and the stimuli per se were different across the conditions. We only adjusted a particular segment of the stimuli that were the perceived brightness of the grey annuli (CCOB vs. REAL) or the Cornsweet-edges (CCOB vs. CONTROL conditions). As a tentative suggestion, we suppose that the exogenous effects were caused by certain attributes of stimuli that are independent of the brightness illusion such as intensity (larger average brightness change relative to the background).

In summary, we obtained double vMMNs to illusory brightness changes. Emergence of vMMN cannot be attributed to the local effect of Cornsweet-edges as it was pointed out by the CONTROL condition. Therefore, the novel finding of the experiment is that the vMMN is sensitive to illusory brightness changes. We also obtained double vMMNs to matched luminance changes. The latencies of the vMMNs elicited by illusory and real, physical changes were similar. Contrarily, the scalp distributions of the two vMMNs were not fully identical. The results reveal that the cortical sources of vMMNs to different stimuli probably differ. However, the temporal patterns of the cognitive process are similar when the perceptual experiences of the deviations are similar. In other words, the processing stages (and the representational forms) of the deviant-related brain responses are similar in case of similar perceptual experiences; nevertheless, the neural circuits involved in such processing are slightly different. The results essentially support the initial presumption. The vMMN is primarily sensitive to the representation form correspond to the perceptual experience and the physical attributes of the stimulation has only a moderate effect in the elicitation of the vMMN.

4.4. Experimental procedure

4.4.1. Participants

20 paid students with either normal or corrected-to-normal visual acuity participated in the experiment. Six participants were disclosed from further analyzes due to the low signal to noise ratio (i.e. in the statistical analyses, data collected from 14 participants were used; 7 females, 7 males; mean age of 21.6 years, SD=1.82 years). Written informed consent was obtained from all participants before the experimental procedure. The study has been carried out in accordance with the Declaration of Helsinki, and approved by the United Ethical Committee of the Psychology Institutes in Budapest.

4.4.2. Stimuli and experimental design

The stimuli appeared on the center of a 17 in. LCD monitor (refreshing rate: 60 Hz), 1.2 m from the participants. The stimulus duration was 400 ms and the stimulus onset asynchrony (SOA) was between 692 and 748 ms (mean: 722 ms).

We tested the occurrence of vMMN in a passive oddball paradigm, i.e. stimuli were task-irrelevant and stimuli were delivered according to an oddball sequence. The global probability of the deviants was 0.2. In a sequence, there were 400 stimuli (320 standards and 80 deviants). The number of standards between 2 deviants varied between 2 and 6 (standard uniform distribution).

Three types of stimuli were used: CCOB, CONTROL and REAL. The stimuli eliciting the CCOB effect (upper-row on the right panel of Figure 4.5) consisted of 3 grey, equiluminant, concentric annuli and four Cornsweet-edges (the left panel of Figure 4.5 contains the luminance-values and sizes of the annuli and the edges). Cornsweet-edge has a specific pattern of contrast transition. The edge comprised of 2 opposing (one lightening and one darkening) luminance gradient that meet at an edge with maximum relative contrast. Two of the four Cornsweet-edges separated the grey annuli while the other two were the inner and the outer boundary of the CCOB stimuli. Such an arrangement of the grey areas and Cornsweet-edges induced a brightness illusion resulting in apparent luminance difference between the grey annuli. As Figure 4.5 shows, we used two kinds of CCOB stimuli by reversing the Cornsweet-edges. This manipulation caused double differences between the two CCOB stimuli: (1) real local luminance difference between the Cornsweet-edges and (2) apparent brightness difference between the grey annuli. Therefore, the two stimuli delivered in an oddball sequence resulted in infrequent illusory brightness changes together with real local luminance changes. These stimuli were used in the CCOB condition. The sizes of the CCOB stimuli were 2.44 deg in visual angle; the luminance of the grey annuli was 54,75 cd/m² (the left panel of Figure 4.5 contains the precise luminance values and the sizes of the annuli and the edges).

Stimuli of the other two conditions were designed to investigate the two changes of the CCOB sequences separately. Stimuli of CONTROL condition (CONTROL; middle row in right panel of Figure 4.5) consisted of contrast gradients identical to the Cornsweet-edges of CCOB stimuli. These stimuli served as a control for changes in the Cornsweet edges without the Cornsweet-effect. It is important to emphasize that the brightness perception of background (blue-violet, 0.1, 0.2, 0.5 RGB values, 5.85 cd/m²) was not (or not significantly) modulated by the Cornsweet-edges. This color was produced by a group of observers as a color resistant to the brightness illusions. The sizes of the CONTROL stimuli were identical to the CCOB stimuli. The luminances of the Cornsweet-edges varied between 0.45 cd/m² and 206.57 cd/m².

The stimuli of REAL contrast condition (REAL; lower row on right panel of Figure 4.5) consisted of three concentric grey annuli. The positions, the sizes and the brightness of the annuli corresponded to the grey annuli of the CCOB stimuli. However, contrarily to the CCOB condition, the brightness differences were due to real luminance differences between the annuli. The apparent brightness of the CCOB and the REAL stimuli was matched by each participant (see Contrast matching procedure). The sizes of the REAL stimuli were 2.29 deg. The average luminance values of the REAL stimuli are presented on Figure 4.1.

To avoid the ERP effect of differences in physical properties between the standards and deviants, we applied a reverse control method (c.f. Kujala et al., 2007), i.e. each of the six stimuli appeared in the roles of deviant and standard. Each sequence was repeated for gaining sufficient number of EEG epochs for averaging. There were 12 sequences in a 3 (condition) x 2 (reverse control) x 2 (repetition) arrangement [the total presentation number of the stimuli were 1280 (standards) and 320 (deviants) in each condition]. We randomized the order of the sequences for each session.

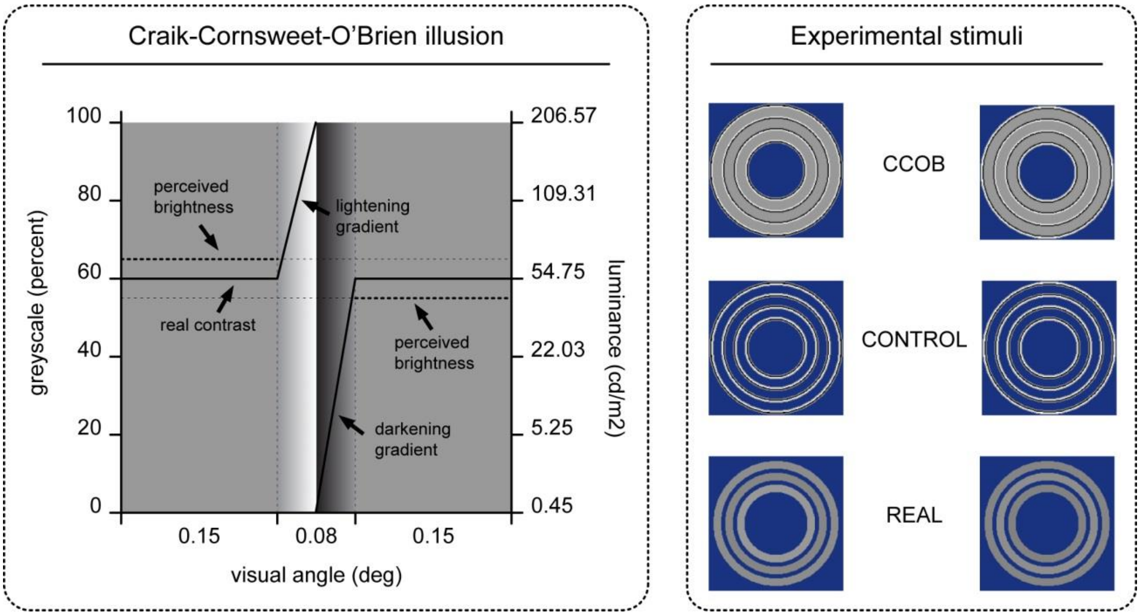


Figure 4.5. Illustration of Craik-Cornsweet-O'Brien illusion (left panel) and stimuli (right panel). Left panel: schematic illustration of the illusion. Solid line represents the real brightness values of the equiluminant areas and Cornsweet-edge in the function of size. Dashed lines show the border separating the edge (vertical lines) and a theoretical manifestation of the illusory brightness difference (horizontal lines). Right panel: experimental stimuli in the three conditions arranged row-wise.

4.4.3. Contrast matching procedure

To test the CCOB effect and generating stimuli for REAL condition, psychophysical measurement of CCOB stimuli preceded the EEG session with each participant. As a test stimulus, a CCOB stimulus was displayed on the left side of the monitor. The probe stimulus, one of the 3 grey annuli of REAL stimulus, was presented on the right side of the monitor. Participants adjusted the luminance value of the probe stimulus (using a gamepad) until it was matched to the perceived brightness of the corresponding annuli of the CCOB stimulus. The starting value of the test stimuli either exceeded (109.31 cd/m^2) or stayed beneath (22.03 cd/m^2) the real luminance of the grey annuli of CCOB stimulus (54.75 cd/m^2). The values of upward and downward adjustments were averaged.

4.4.4. Target stimuli

Participants were instructed to attend to a dark cross which was continuously presented at the center of the monitor. The fixation cross comprised of a shorter (0.41) and a longer (0.51) line. The fixation cross was continuously present, but the size of the vertical and horizontal lines changed infrequently, the shorter one became longer (0.51) and the longer one became shorter (0.41). The task was to respond to the changes by pressing a button. There were 15 changes within a block. The inter-target interval of such changes was 8.86–24.99 s (16.47 s in average). At the end of each block visual feedback was provided to the participants showing their current hit rate and reaction time.

4.4.5. Measuring and analyzing brain electrical activity

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 on the right mastoid. The average reference was off-line recalculated. 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 high-pass filtered offline, with a cutoff frequency of 0.1 Hz (24 dB slope). Epochs of 500 ms duration (including a 100 ms pre-stimulus interval) were extracted for all deviants and the standards that immediately preceded the deviants. 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 100 μV on any channel were rejected from further analysis. To avoid any possible ERP contribution of the physical differences between the standard and the deviants, we collapsed the ERPs to events with the ERPs to corresponding events of reverse sequences.

The data were analyzed by repeated measure ANOVA and paired t-test. Magnitude of ERPs was measured in terms of mean epochs. The peak latencies were measured with a sliding window algorithm. To investigate distribution differences of the ERPs, we rescaled the data (McCarthy and Wood, 1985). When appropriate, the Greenhouse–Geisser correction was applied. Post-hoc analyses were calculated by the Tukey-HSD test, the alpha level was 0.05. Effect size was characterized as partial eta-squared (η2).

Acknowledgment

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5. Asymmetric effect of automatic deviant detection: The effect of familiarity in visual mismatch negativity (Thesis study 4)[8]

The visual mismatch negativity (vMMN) component is regarded as a prediction error signal elicited by events violating the sequential regularities of environmental stimulation. The aim of the study was to investigate the effect of familiarity on the vMMN. Stimuli were patterns comprised of familiar (N) or unfamiliar (И) letters. In a passive oddball paradigm, letters (N and И) were presented as either standard or deviant in separate conditions. VMMNs emerged in both conditions; peak latency of vMMN was shorter to the И deviant compared to the vMMN elicited by the N deviant. To test the orientation-specific effect of the oblique lines on the vMMN, we introduced a control experiment. In the control experiment, the patterns were constructed solely from oblique lines, identical to the oblique lines of the N and И stimuli. Contrary to the first experiment, there was no significant difference between the vMMNs elicited by the two orientations. Therefore, the differences in vMMNs to И and N deviants are not attributable to the physical difference between the И and N stimuli. Consequently, the vMMN is sensitive to the familiarity of the stimuli.

5.1. Introduction

Since the beginning of cognitive psychology it is a well demonstrated fact that conscious recognition of environmental changes are restricted by a limited capacity mechanism, and this mechanism is closely connected to the construct called attention (e.g. Neisser, 1967;but for a qualification of this view see Lamme, 2003). As a demonstration of the limited capacity in vision, large environmental changes remain unnoticed if these events are outside the focus of attention (for a review, see e.g. Simons, 2000). However, as research on event-related potentials (ERPs) shows, non-attended stimuli violating regularities, either in the auditory or the visual modality, elicit

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[8] Sulykos, I., Kecskés-Kovács, K., & Czigler, I. (2015). Asymmetric effect of automatic deviant detection: The effect of familiarity in visual mismatch negativity. Brain Research, 1626, 108-117.

characteristic components, (auditory) mismatch negativity (MMN), and visual mismatch negativity (vMMN). (For reviews on MMN see e.g. Näätänen et al., 2007; for vMMN see Czigler, 2007; Kimura, 2012)Emergence of the mismatch components is an indirect evidence of the registration of regularities, otherwise deviation cannot be identified.

A recent study reported that an attribute of the automatic processes underlying vMMN is similar to search asymmetry, a well-documented finding of research on visual attention (Czigler et al., 2014). In many visual search tasks it is faster to find certain target stimuli among certain distractors than vice versa (for a review see Wolfe, 2001). Similarly, in the above mentioned vMMN study (Czigler et al., 2014), a particular deviant stimulus within the sequence of particular standard stimuli elicited vMMN with shorter latency than sequences with the reversed role of stimuli. The stimuli in this study were Q and O characters, i.e., a type of stimuli frequently used in studies of search asymmetry (e.g. Carrasco et al., 1998; Rosenholtz, 2001; Saiki, 2008; Spratling, 2012; Treisman and Souther, 1985). There is no generally accepted explanation of search asymmetry, and even in case of Q and O stimuli there are different explanations. According to the most frequent consideration, this kind of asymmetry is due to the low-level perceptual differences caused by the presence (or absence) of an additional feature (in this case, an additional vertical line on one of the circles; Treisman and Souther, 1985).

In other cases it is difficult to attribute the asymmetry to simple perceptual factors. Search asymmetry in some studies was connected to the familiarity vs. novelty of the target and distractor stimuli. Search for an unfamiliar target among familiar distractors is more efficient than search for a familiar target among unfamiliar distractors. A typical example of the familiarity-related search asymmetry is that it is faster to find mirror-imaged letters (e.g. И) among normal letters (N) than vice versa (e.g. Frith, 1974; Flowers and Lohr, 1985; Wang et al., 1994; Malinowsky and Hübner, 2001; see Wolfe, 2001 for other examples of the familiarity effect). It should be noted that various cases of search asymmetry cannot be explained by a unitary theory. While the asymmetry of the Q vs. O search is explained by the asymmetry of feature appearance vs. disappearance (Treisman and Souther, 1985), explanation of the familiarity-based asymmetry is less obvious. As Wang et al. (1994) demonstrated, in a visual search task, faster identification of the И target (among N distractors) was due to the faster processing of N distractors, and the slower detection of N target (among И distractors) was due to the slower processing of И distractors. That is, the more efficient processing was attributed to the familiarity of the distractor.

In this study, our aim was to investigate whether the stimulus-familiarity has an effect on vMMN as well, as was reported in visual search studies. To this end normal and reverse letters, more precisely, N and reversed N (И) were used. Interestingly, the expected direction of asymmetry of vMMN is disputable. On the one hand, at a superficial level one may expect that the direction of asymmetry would be identical in visual search and vMMN paradigms (i.e., faster search for N target and smaller vMMN latency to the И deviant). Indeed, in the previous study with Q and O stimuli we obtained results showing shorter vMMN latency to the Q deviant (Czigler et al., 2014). On the other hand, considering the theoretical interpretations of the search asymmetry (faster processing of a familiar stimulus), the expectation would be just the opposite. Following this reasoning, in the vMMN paradigm shorter vMMN latency is expected to the N deviants, because processing of the familiar letter is faster. However, one could also expect shorter vMMN latency for the И deviant. This is because a familiar stimulus acquired a more efficient memory representation, and the contrast between the deviant stimuli and the representation of the standard is more salient than the contrast in the opposite case. In spite of the apparently ad hoc flavor of this alternative, it is near the explanation of familiarity related search asymmetry. This is because in both cases the effects are due to the ‘less important’ (distractor and standard) stimuli. In the present study we tested the above mentioned alternatives.

In Experiment 1 we compare the effects of N and И deviants. However, dissimilarity can be due to the different orientations of the oblique line per se, therefore in Experiment 2 we investigate deviant effects without the vertical lines.

5.2. Results

5.2.1. Experiment 1

5.2.1.1. Behavioral results

According to the two-way ANOVA, participants' performance differed in the two tasks [$F(1,13)=27.451$, $p<0.01$, $\eta2 =0.679$]. Performance in the red-task (88.6%;

S.E.M=1.6%) was higher than performance in the green-task (81.6%; S.E.M=2.3%). Condition main effect as well as task x condition interaction was not significant.

5.2.1.2. Event-related potential results

Figure 5.1 shows the ERPs, the deviant minus standard difference potentials for the N and И deviant conditions and the scalp distributions of the differences in a 20 ms range around the average latency values of largest negativity, (measured at PO3, POz, PO4, O1, Oz and O2). The average peak latencies and mean amplitudes are listed in Table 5.1. We obtained neither latency nor amplitude difference on P1 to the standard N and И stimuli. However, standard И stimuli elicited larger N1 amplitude than the N stimuli over the right side, as reflected by the significant stimulus x laterality interaction [$F(2,26)=3.887$, $p<0.05$, $\varepsilon=0.952$, $\eta2=0.230$, and the significant results ($p<0.001$) of the Tukey HSD tests]. Furthermore, N1 latency was longer at the occipital locations as the anteriority main effect points out [$F(1,13)= 8.150$, $p<0.05$, $\eta2=0.385$]. No significant stimulus related effect appeared on the P2 amplitude. However, we found significant stimulus main effect on the latency values of P2 components [$F\ (1,13)=6.500$, $p<0.05$, $\eta2=0.333$].

As Figure 5.1 shows, in the difference potentials both the deviant N and the deviant И stimuli elicited a posterior negativity. Furthermore, as Figures 5.1 and 5.2 show, the latency of the negativity was longer for the N deviant (128 vs. 140 ms). This latency difference is reflected in the significant stimulus main effect [$F(1,13)=7.805$, $p<0.05$, $\eta2 =0.375$]. Contrary to the apparent difference, we obtained no significant amplitude effect on the range of the negative difference potential.

Comparing N1 latency and the latency of the difference potentials, in addition to the significant stimulus (N, И) main effect [$F(1,13)=8.792$, $p<0.05$, $\eta2=0.403$], component x stimulus interaction was also significant [$F(1,13)=6.250$, $p<0.05$, $\eta2=0.325$].

According to the Tukey HSD tests, the interaction (and main effect) was due to the shorter latency of the И-related negative difference ($p<0.05$ in all comparisons).That is, the latency of the difference potentials in the И-deviant condition was shorter than both N1s' latencies and N-deviant related negativity.

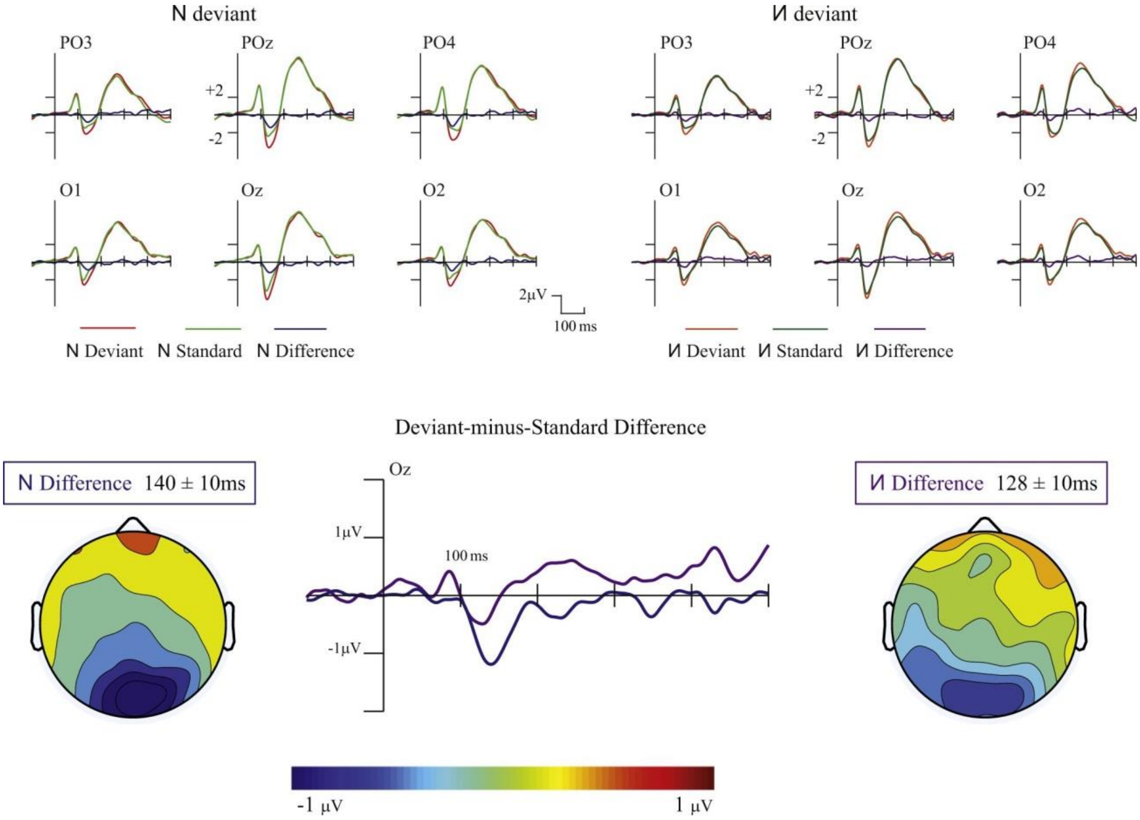

Figure 5.1. Experiment 1. Upper panel: event-related potentials and difference waves in the N and И conditions.

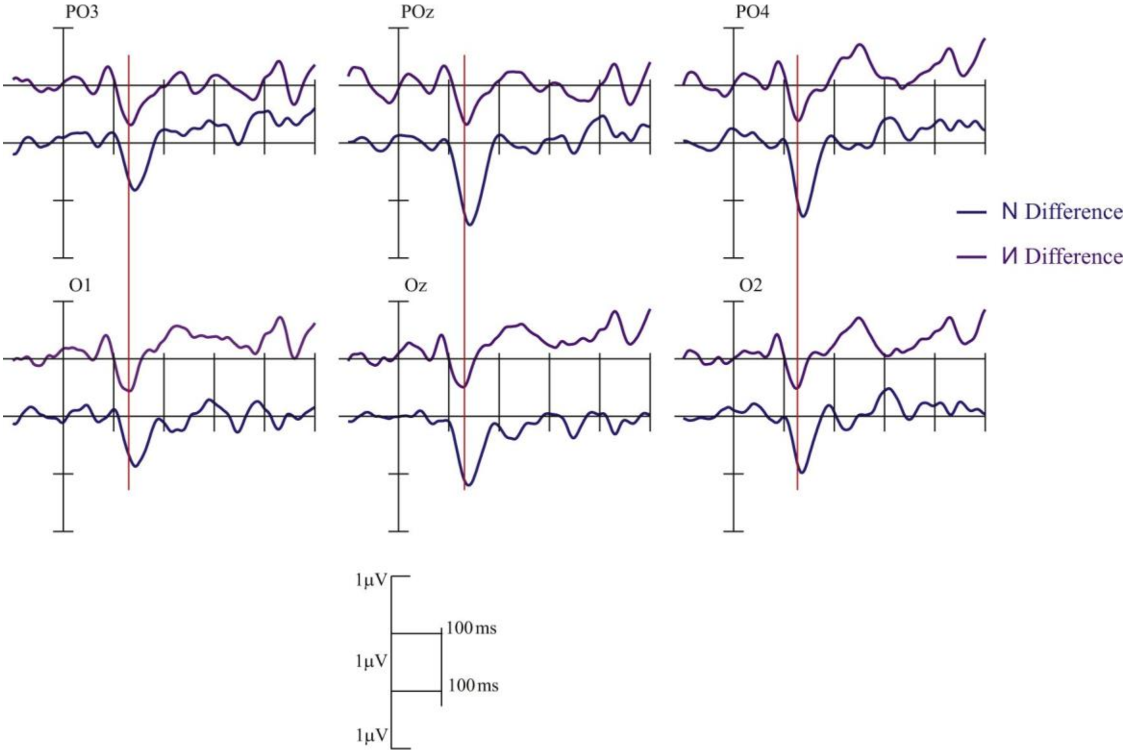

Figure 5.2. Experiment 1. Comparison of the deviant-related activities in the N and И conditions. Vertical lines denote the peak latencies of the difference waves in the И condition.

	Stimuli	P1	N1	P2	vMMN
Latency (ms)	**N**	91.0(6.3)	140.8(12.5)	261.1(12.5)	139.8(7.1)
	И	90.1(6.3)	141.3(13.0)	274.9(11.0)	127.9(6.5)
Amplitude (μV)	**N**	1.98(1.15)	-1.73(1.01)	5.17(1.95)	-1.03(0.66)
	И	1.79(1.18)	-2.06(0.95)	4.85(1.93)	-0.53(0.56)

Table 5.1. Experiment 1. Grand averages of peak latencies and mean epochs of the exogenous components (P1, N1, P2) and the vMMNs measured at six electrode locations (PO3, POz, PO4, O1, Oz and O2). S.E.M. in parenthesis.

5.2.1.3. Interpretation of the results

As the main result of this experiment, both the N and И stimuli elicited a deviant-related posterior negativity in the 100–180 ms latency range, but the peak latency of this negativity was shorter for the И deviant. One may say that the negativity can be attributed to the different stimulus-specific refractoriness of the deviant and standard stimuli (c.f. May and Tiitinen, 2010; Kimura et al. 2009, 2010; Kimura and Takeda, 2013). However, the significant component x stimulus interaction contradicts this possibility. In case of refractoriness of a unitary N1 component, the latency of the exogenous activity and the latency of the deviant-related negativity should be similar in both conditions. In fact the latency of the difference potential in the И condition was shorter than the latency of the other difference potential as well as both N1s' latencies. That is, the latencies of the deviant-related and exogenous activities were not similar in either of the conditions. Additionally, unlike the N1 component, the latency of the vMMN was similar at the PO and O locations. It should be noted that the interpretation of the latency difference as an argument against refractoriness is not without problem. Latency difference may arise as condition or stimulus dependent changes of latent components (Luck, 2005). As for the present study, emergence of the vMMN may influence the latency of the negativity. This case corresponds to our interpretation. However, one may say that N1 consists of various subcomponents with different refractoriness characteristic. In fact, some studies reported various posterior visual subcomponents in the N1 range (Di Russo et al., 2001; Hopf et al., 2002; Vogel and Luck, 2000). These subcomponents emerged as effects of attention, and their characteristics are unknown in a passive paradigm. Furthermore, no study reported different refractoriness effects on the subcomponents. Consequently, the obtained latency difference does not exclude with full confidence the possibility of stimulus-specific refractoriness. A stronger control of refractoriness is the equal probability procedure (comparison of the ERPs of the oddball deviant with ERPs elicited by identical stimuli from a sequence of a large variety of stimuli, with the same probability as the oddball deviant; Kimura et al., 2009, 2010). Unfortunately in case of binary stimuli like the N and И this procedure cannot be used. The ERP difference between the N and И deviants as a refractoriness effect of an N1 subcomponent is a possibility of familiarity-related N1 effect elicited by non-attended stimuli. So far there are no data showing such effects, but it is a testable possibility. In sum, the negativity is attributed to the emergence of vMMN, and we consider that the deviant И elicited this component earlier than the deviant N.

To interpret the vMMN-asymmetry in this study, it is necessary to clarify a more simple possibility, the perceptual anisotropy (the perception of the lines are directionally dependent) of the system underlying the vMMN (cf. Takács et al., 2013), i.e., the possibility that the sensitivity to oblique lines in forward and backward directions (/ and \) is different. This possibility has some support from the larger N1 to the N stimuli over the right posterior locations. To investigate the possibility of vMMN difference for the two deviant-standard relations, in Experiment 2, we presented oblique lines without the vertical lines of the N and И stimuli. Accordingly, in this experiment there was no familiarity difference between the two stimuli. Nevertheless, the physical differences between the standards and the deviants, i.e. the orientations of the oblique lines, were identical in Experiment 1 and Experiment 2.

5.2.2. Experiment 2

5.2.2.1. Behavioral results

According to the two-way ANOVA, participants' performance differed in the two tasks [$F(1,13)=41.321$, $p<0.01$, $\eta 2=0.761$]. Performance in the red-task (78.8%; S.E.M=1.9%) was higher than performance in the green-task (66.3%; S.E.M=1.9%). Condition main effect as well as task x condition interaction was not significant.

5.2.2.2. Event-related potential results

As Figure 5.3 shows, the stimuli elicited the canonical P1, N1 and P2 exogenous components. Table 5.2 contains the average peak amplitudes and the mean epochs of the components measured at six electrode locations (PO3, POz, PO4, O1, Oz and O2). Comparison of the amplitude of P1 components resulted in significant stimulus x anteriority interaction [$F(1,13)= 10.403$, $p<0.01$, $\eta 2 =0.445$] showing that the forward leaning lines (/) elicited larger P1 over the PO locations ($p<0.001$ in all Tukey HSD tests). No orientation-related effect appeared in regards to the N1's latency and amplitude, P2 latency was shorter for the backward leaning (\) stimuli [$F(1,13)=6.253$, $p<0.05$, $\eta 2 =0.325$ for the stimulus mean effect]. There was no P2 amplitude difference between the two orientations.

Deviant-related negativities emerged within the 100–180 ms latency range as shown in Figure 5.3. The amplitude and latency values of these negativities are listed in Table 5.2. The latency of the negativities were larger over the PO locations [$F(1,13)=5.081$, $p<0.05$, $\eta 2=0.281$ for the anteriority mean effect] and over the midline [$F(2,26)=6.364$, $p<0.01$, $\varepsilon=0.898$, $\eta 2 =0.329$ for the anteriority x laterality interaction]. More importantly, the two difference potentials (to backward and forward lines) were not different in terms of latency and amplitude values (Figure 5.4).

The latencies of the difference potentials were shorter than the N1 latencies (see Table 5.2). Accordingly, component main effect was significant [$F(1,13)=22.897$, $p<0.001$, $\eta 2=0.638$]. This main effect was qualified by the significant component x anteriority interaction [$F(1,13)=7.216$, $p<0.05$, $\eta 2=0.357$]. The interaction was due to the longer N1 latency at the PO locations.

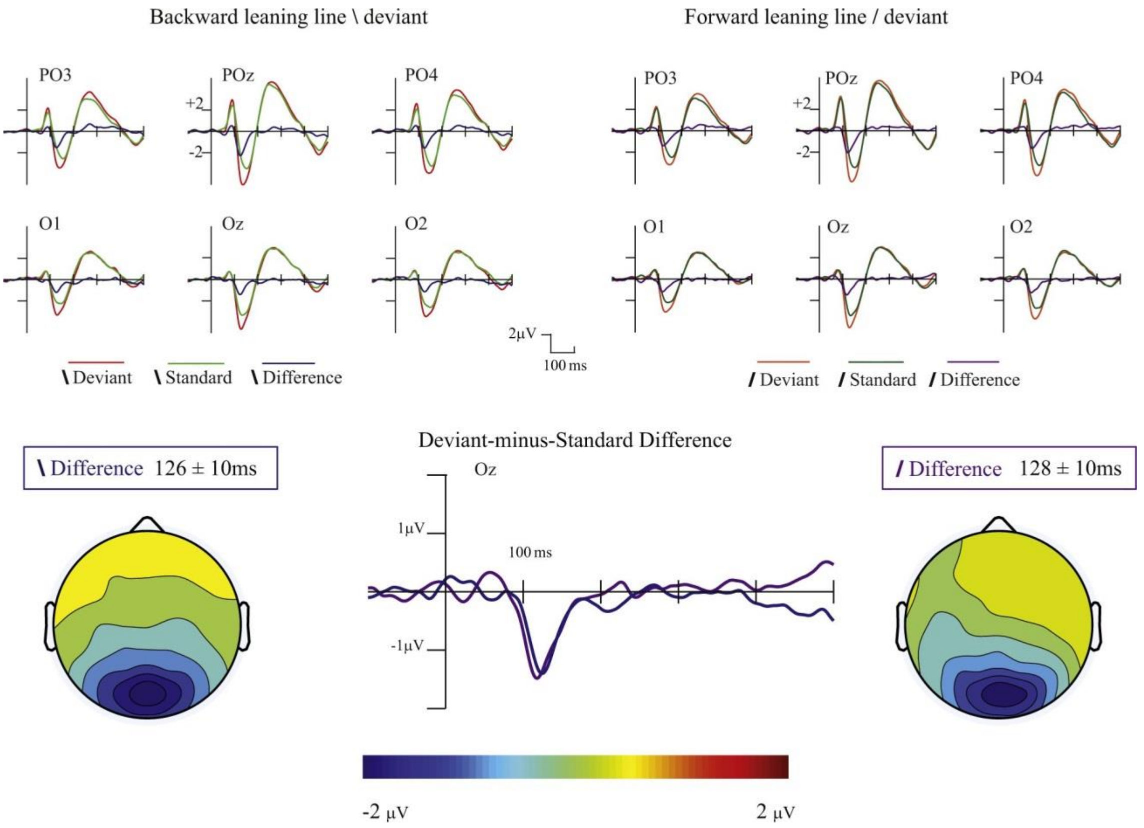

Figure 5.3. Experiment 2. Upper panel: event-related potentials and difference waves in the \ and / conditions. Lower panel: difference waves at Oz electrode location and scalp distributions of the deviant-related brain responses.

	Stimuli	**P1**	**N1**	**P2**	**vMMN**
Latency (ms)	\	84.4(5.5)	148.1(9.4)	248.9(12.5)	126.7(4.3)
	/	87.7(3.5)	146.4(10.1)	258.3(13.6)	127.2(11.4)
Amplitude (μV)	\	0.89(0.56)	-2.65(1.38)	2.97(1.28)	-1.19(0.48)
	/	1.09(0.71)	-2.66(1.29)	3.10(1.41)	-1.23(0.67)

Table 5.2. Experiment 2. Grand averages of peak latencies and mean epochs of the exogenous components (P1, N1, P2) and the vMMNs measured at six electrode locations (PO3, POz, PO4, O1, Oz and O2). S.E.M. in parenthesis.

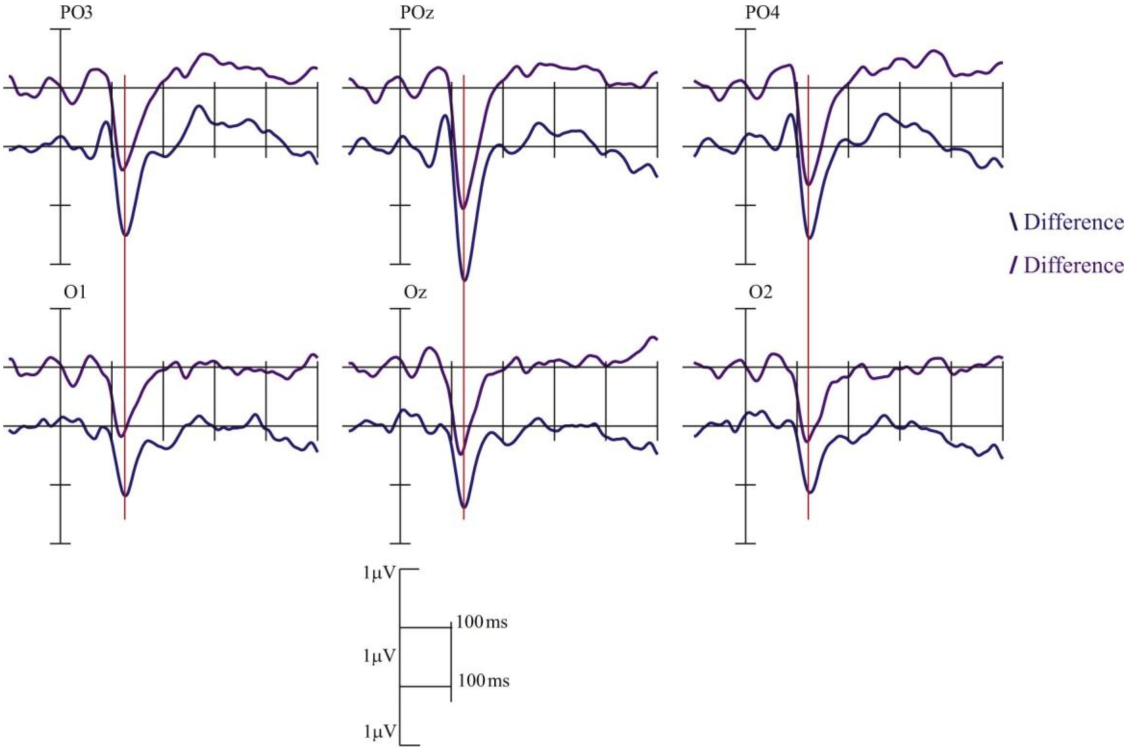

Figure 5.4. Experiment 2. Comparison of the deviant-related activities in the \ and / conditions. Vertical lines denote the peak latencies of the difference waves in both conditions.

5.2.2.3. Interpretation of the results

We obtained orientation-related differences on the exogenous components, but these differences were unrelated to the N1 component. Furthermore, the difference potentials were similar in the two conditions (i.e. to \ and / deviants). The latencies of the negative difference potentials were considerably shorter than the N1 latencies. We interpret the negative difference potentials as vMMNs, and these components were independent of the orientations of the deviants.

5.2.3. Comparison of Experiment 1 and 2

5.2.3.1. Behavioral results

Behavioral results of the two experiments were compared with an omnibus ANOVA. The factors were experiment, task and condition. The analysis revealed significant experiment [$F(1,26)=66.24$, $p<0.01$, $\eta2 =0.718$] and task main effects [$F (1,26)=68.30$, p<0.01, η2 =0.724] and experiment x task interaction [F(1,26)=5.46, p<0.05, η2 =0.174]. Performance was lower and performance-difference between the two tasks was higher in Experiment 2.

5.2.3.2. Event-related potential results

Comparing the two experiments, it is obvious that the deviant-related negativity was larger in Experiment 2 (-0.78 vs. -1.21). This observation is supported by the results of a mixed factor ANOVA (experiment as between group factor; line orientation, anteriority and laterality as within group factors) on the amplitude of the difference potentials. In this ANOVA we obtained significant main effect of experiment [F(1,26)=4.718, p<0.05, η2=0.154]. Comparison of the latency values of the difference potentials of the two experiments, a similar ANOVA resulted in a significant experiment main effect [F(1,26)=4.914, p<0.05, η2=0.159], showing the shorter latency in Experiment 2 (134 ms vs. 126 ms). The experiment x stimulus interaction approached the level of significance [F(1,26)=3.615, p=0.068, η2=0.122], showing a tendency that in contrast to Experiment 1, in Experiment 2 there was no difference between the two orientations.

5.3. Discussion

A typical result of the familiarity-related search asymmetry is that a mirror-imaged letter among normal letters is found faster than vice versa (e.g. Frith, 1974; Flowers and Lohr, 1985; Wang et al., 1994; Malinowsky and Hübner, 2001). In the present passive oddball study we obtained similar results, vMMN latency to the reversed character was shorter. Accordingly, relationship between search latency and vMMN latency was similar to the results of our previous study using Q and O stimuli (Czigler et al., 2014). In the introduction we raised that one may argue for the reverse results, i.e., shorter vMMN latency for the N deviant. This is because Wang et al. (1994) attributed the familiarity related search asymmetry to the faster processing of familiar stimuli, and in a typical visual search paradigm the number of distractors is larger than the number of targets (in a typical design the latter is only 1). Accordingly, if a familiar stimulus (N) is processed faster, shorter vMMN latency is expected for the N deviant. However, the results of the present study were just the opposite. Therefore, the above reasoning cannot be applied to the vMMN paradigm. Considering the standard stimuli of the vMMN paradigm as an analog of the distractors of the search task, and maintaining the claim that processing of familiar stimuli is more effective, the expected result is shorter vMMN latency in the И deviant condition. However, the question is obvious: in what way are the vMMN standard and the search task distractor similar? At first glance the situations in the two paradigms are different; in the vMMN paradigm there is no need of processing the standard stimuli when the deviant is presented. However, it is important to recall that vMMN emergence is a consequence of a comparison process; representation of regularity is stored in a memory system, and the representation of the incoming event is compared to this representation. This process requires the access of the representation of regularity. We suggest that retrieval of such representation is faster when the regular events are familiar. In other words, vMMN latency difference is due to the more efficient access to the memory representation of familiar events. This way, the identical direction of the visual search and the vMMN results is plausible.

ERP difference between the rare and frequent stimuli, especially in an earlier latency range is frequently attributed to a refractory effect (Kimura et al., 2009, 2010; Kimura and Takeda, 2013). Processing structures with specific sensitivity to a particular stimulus feature respond with diminished intensity to frequent stimulation, whereas rare events stimulate “fresh” networks of neurons. In the present study the latency of deviant minus standard difference did not correspond to the latency of the exogenous components. In Experiment1 N1 latency was similar to both N and И stimuli, whereas the latency of deviant minus standard difference potentials for the two stimuli was different. Therefore, the results of the present study are considered as a memory mismatch effect, instead of the manifestation of stimulus-specific refractoriness.

To control for the possibility of different effects of the two directions of the oblique lines, we conducted Experiment 2. In this control experiment the stimulus patterns consisted only from oblique lines. VMMN in the two experiments had different amplitudes and latencies, in Experiment 2 the latency of the difference potential was shorter and the amplitude was larger. As a post hoc explanation, the presence of the vertical lines in Experiment 1 diminished the deviant-standard differences in this experiment for two reasons. First, the vertical lines were identical in the N and И stimuli, therefore the net deviant-standard physical difference in Experiment 1 was smaller; second, presence of the vertical lines might impose a masking effect on the orientation difference. One may argue that task demand may influence vMMN, and the higher task demand of Experiment 2 had a masking effect on the line orientation effects. However, in vMMN studies investigating the effect of task demand no such results were obtained (Heslenfeld, 2003; Pazo-Alvarez et al., 2004), whereas Kimura and Takeda (2013) obtained increased latency (but not amplitude) at higher task demand. In the present study no longer vMMN latency appeared in Experiment 2.

In conclusion, the latency difference between the vMMNs elicited by N and И deviants was caused by the familiarity of the N stimulus. That is, vMMN, a correlate of automatic detection of the violation of sequential regularity is sensitive to the familiarity of stimulation.

5.4. Experimental procedures

5.4.1. Experiment 1

5.4.1.1. Participants

Participants were 14 paid students (4 female; mean age=21.9 years; range=19–24 years) from Budapest, Hungary. All had normal or corrected to normal vision. Participants were not familiar with the Cyrillic alphabet. Before the session they gave written informed consent. The study was accepted by the local committee of professional ethics and was carried out in accordance with the Declaration of Helsinki.

5.4.1.2. Stimuli and procedure

5.4.1.2.1. Task-irrelevant stimuli.

Stimuli were matrices of N or И characters (Figure 5.5). A matrix consisted of 8 columns and 4 rows (i.e. 32 characters). These stimuli were presented on a 17' LCD monitor (Samsung SyncMaster 740B) with 60 Hz refresh rate. The patterns were presented in the lower part of the display. The size of the whole stimulus pattern was 16.1 x 3.9 degree of visual angle from 120 cm. The luminance of the stimuli and the background were 36.67 cd/m² and 0.45 cd/m², respectively. The stimulus presentation time was 300 ms; the average inter-stimulus-interval (ISI) was 517 ms (range: 417–617 ms, even distribution). In the N-deviant condition 59 stimuli were N matrices, and 291 И matrices, in the И deviant condition the numbers were reversed. Within a session there were 2 N deviant and 2 И deviant conditions in random order.

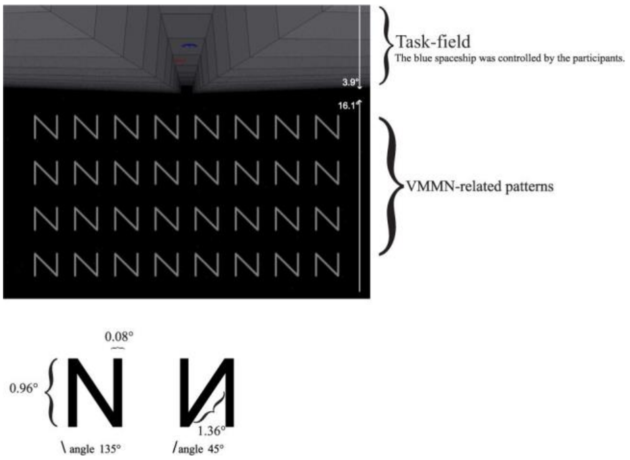

Figure 5.5. Experiment 1. Experimental stimuli. Upper panel: an example of the stimulus display. Lower panel: the physical characteristics of the task-irrelevant stimuli.

5.4.1.2.2. Task-related stimuli and primary task.

The only aim of the task, as in the majority of vMMN experiments, was to draw participants' attention away from the task-irrelevant stimulation. The task was a video game presented at the upper half of the screen (task-field, see Figure 5.5). The video game contains a stationary background and a few moving ‘figures’. The background was a canyon embedded into a planet. The ‘figures’ were dynamically moving spaceships displayed within the area of the canyon (this area termed as game-field; GF). The GF was segmented to 10 vertical and 19 horizontal units which defined the depth and the horizontal coordinates of the canyon. The spaceships moved along the 10 x 19 grid defined by the coordinates. The movements of the spaceships were either controlled by the participant (player-spaceship; PS; blue color) or an algorithm (task-spaceships; TSs; red or green colors). The task was to move the PS located at the top of the GF (10th vertical coordinate) to the left or to the right with a gamepad along the 19 points of the horizontal axis to avoid the red or to catch the green TSs. In each trial, a TS appeared at the end of the GF (1st vertical coordinate) at a random horizontal position (one of the 19 coordinates) with a random color. The probabilities of the red and green colors were 0.7 and 0.3, respectively. After the appearance, the TS started to move towards the top (10th vertical coordinate) to be caught (green) or to avoided (red) by the PS. The apparently continuous movement of the TSs comprised of little successive shifts. In each shift, the TS moved one coordinate vertically upwards (plus 1 vertical unit per step), and one coordinate horizontally. The horizontal movements (termed as vectors) could be -1 (moving to the left), 1 (moving to the right) or 0 (no horizontal movements). The horizontal coordinate was adjusted according to the vector with a probability of 0.3 or remained the same (p=0.7). The vectors were calculated by an algorithm differently in the case of red and green TSs. In case of red TS, the aim was to reduce the (horizontal) distance between the TS and the PS with a probability of 0.4. In case of green TS, the aim was just the opposite, and the probability was 0.3. Furthermore, the vector reversed (folded by -1) if the TS reach the edge of the GF (1st or 19th horizontal coordinate) or at the 4th vertical coordinate. In any other cases, the vector was the same as it was at the previous shift. The impact of the TS and PS (i.e. the performance in one trial) was calculated when the TS reach the 10th vertical coordinate. The duration of one shift was 116.67 ms, therefore one trial endured for 1166.67 ms (there was no inter-trial interval). In a block, there were 245 trials.

5.4.1.3. Measuring and analyzing the behavioral data

Participants' performance was expressed as percent values, separate for the two tasks. The number of successful avoids were divided by the total number of red spaceships, which yielded the red-performance. The numbers of successful collisions were divided by the total number of green spaceships, which yielded the green-performance. Performance was entered into a two way ANOVA with the factors of color (red and green) and stimulus (N and И deviant).

5.4.1.3. Measuring and analyzing the behavioral data

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5.4.1.4. Recording and measuring electric brain activity

Brain electric activity was recorded (DC -100 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 by using of an elastic electrode cap (EasyCap). The reference electrode was on the nose tip, and data was offline re-referenced to the average activity. Horizontal EOG was recorded with a bipolar configuration between electrodes positioned lateral to the outer canthi of the eyes. Vertical eye movement was monitored with a bipolar montage between electrodes placed above and below the right eye. The EEG signal was band-pass-filtered offline, with cutoff frequencies of 0.1 and 30 Hz (24-dB slope). Epochs with duration of 600 ms, including a 100 ms pre-stimulus interval, were extracted for each event and averaged separately for the standard and deviant stimuli. 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 7100 mV on any channel were excluded from further analysis. Event-related potentials were averaged separately for the standard and deviant stimuli in the two conditions. Epochs of standards and deviants were entered in the averaging process only if these stimuli were preceded by at least 3 standards. To identify change-related activities, ERPs elicited by standard stimuli were subtracted from ERPs elicited by deviant stimuli in the opposite condition (reverse control, c.f. Kujala et al., 2007), therefore physically identical stimuli were compared in the role of deviant and standard.

Exogenous components (P1, N1 and P2) and difference potentials were measured in a 2 x 3 grid of electrodes over the posterior areas (PO3, POz, PO4, O1, Oz, and O2). Peak latencies were measured with a sliding window algorithm (for detailed description of the algorithm, see Sulykos and Czigler, 2014). Amplitudes were measured by averaging the amplitude values of 20 ms epochs (11 data points) around the respective peak latency. These values were analyzed in three-way analyses of variance (ANOVA) with factors of stimulus (И, N), anteriority (PO, O) and laterality (left, midline, right). To compare the latency values of the exogenous components and the difference potentials, the factor of component was added. When appropriate, the Greenhouse–Geisser correction was used. Effect size is presented as partial eta-squared (η2). Post hoc comparison was calculated by Tukey HSD tests. Only results related to the purpose of the study are presented.

5.4.2. Experiment 2

5.4.2.1. Participants

Participants were 14 paid students (5 female) mean age=22.5 years; range= 19–26 years) from Budapest, Hungary. All had normal or corrected to normal vision. They have participated in event-related potential studies previously. Before the session they gave written informed consent to participate in the study. The study was accepted by the local committee of professional ethics and was carried out in accordance with the Declaration of Helsinki.

5.4.2.2. Stimuli and procedure

With two exceptions, all aspects of the stimulation (and the procedure) of Experiment 2 were identical to the ones used in Experiment 1. The first exception was the task-irrelevant stimuli applied. In Experiment 2, the patterns were constructed solely from oblique lines, identical to the oblique lines of the N and И stimuli. The second exception concerned the primary task. In Experiment 2, the game field was divided by 11 horizontal units (instead of 19), which resulted in larger horizontal movements of the task-spaceships.

5.4.2.3. Recording and measuring of behavioral data and brain electric activity

The parameters of the EEG-recording, the preprocessing of the EEG-signal and the statistical analyzes of the behavioral and ERP data were the same as the ones carried out in Experiment 1.

Acknowledgment

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6. Discussion

6.1. Discussion of the thesis studies

6.1.1 Thesis study 1

The aim of the first study was to test the modulatory effect of attentional processing of task-relevant stimuli on the deviant-related processing of task-irrelevant stimuli (and vice versa). The tool for measuring the former effect was the behavioral (RT) data; and the tool for measuring the latter effect was the ERP (vMMN) data. Both ERP and RT were collected during incongruent and congruent conditions. In the congruent conditions, the task-relevant and –irrelevant changes occurred in the same feature dimension (orientation or color). In the incongruent conditions, the two changes occurred in different feature dimensions.

The participants' performance was significantly worse in the congruent condition relative to the incongruent condition. That is, behavioral data showed a stronger distractor effect in the congruent conditions. The finding supports the contingent capture theory.

The ERP data results showed smaller vMMNs in the congruent and larger vMMNs in the incongruent conditions in the case of both orientation and color deviancies. When the task-related changes and task-unrelated changes occurred in the same feature, the automatic deviant-related processing of the feature (as reflected by the vMMN) was attenuated. The results support the competition theory (in contrast to the saliency hypothesis). Within the frame of the predictive coding theory, the results revealed the mechanism of the priority of the attended channel. Conscious representation of elementary features (those that are part of the task-set) modulated the processing of the same features during the automatic change detection processes. However, in contrast to other high level representations, in this case, the feedback attenuated the operation of the automatic process.

It is worth to mention that the ERP results seemingly contradict to the contingent capture theory. However (as it was mentioned earlier), behavioral and vMMN results cannot be compared directly because of additional processes such as the attention. Secondly, the vMMN is responsible primarily for memory updating and not for the inhibition of the processing of the unattended stimuli. So, contingent capture and competition theories explain different aspects of a complex cognitive phenomenon. In sum, the results revealed the vertical connections between task demands and automatic change detection system in the case of elementary feature changes.

Unfortunately, the lack of equiprobable control may limit the interpretation of the results. Without the experimental separation of frequency and repetition-related effects (i.e., SSA) and the prediction-related gvMMN, the relative weights of the subcomponents are not known. It is possible that the pattern of the results was due to the different SSAs in the congruent and incongruent conditions and not the different gvMMNs. However, SSA is regarded as a fully automatic process (Kovács, 2014). So, the attentional modulation of the SSA is less likely than the attentional modulation of the gvMMN (Kimura and Takeda, 2013). Nevertheless, future studies testing different aspects of the competition theory might consider including equiprobable paradigm.

6.1.2. Thesis study 2

The aim of the second study was to determine, whether the automatic deviant-related processing of two elementary features are independent or dependent processes. We used three conditions: two single deviant conditions and one double deviant condition. We estimated the vMMN in the double deviant condition with an additive model. The model was the arithmetical sum of the vMMNs obtained in the single deviant conditions. The model reflected the independent processes of the deviant-related processing of elementary features.

The vMMN elicited by the double deviant was significantly smaller than the sum of the two vMMNs elicited by the single deviancies (sub-additive response). According to the hypothesis, this means a dependent processing of orientation and spatial frequency. The study revealed horizontal connections between two low-level feature processing. (However, the direction of the connections is not clear: it can be mutually dependent or just a one-way direction.) The study can be considered as a first step in the mapping of the network of elementary feature deviancies. The importance of such basic results has a more general consequence. Elementary features are the bricks of complex stimuli; therefore, early integration of such features is an outset of the deviant-related response at high level attributes.

As the second aim of the experiment (the topic is unrelated to the main issues of the thesis), we investigated the effect of stimulus position. We systematically varied the stimulated hemi-field. The stimuli were delivered in the upper or lower hemi field, while in the opposite hemi field (task-field) a simple video game was presented as a primary task. The results were fairly consistent. Lower hemi-field stimulation elicited triphasic ERPs, and the deviant-minus-standard difference had negative polarity (vMMN). The obtained results were in accordance with many vMMN studies. However, when the stimuli were presented in the upper hemi field, both the ERPs and mismatch response reversed their polarities (and the latencies were somewhat later). The results have a theoretical and a practical implication. First, the error-signal is (at least for simple features) probably generated in retinotopic areas. This interpretation is in accordance with the vMMN literature (Czigler et al., 2004, Amanedo et al., 2007). Second, although whole-field stimulation was not tested, the simultaneous stimulation of both hemi fields may results in diminished ERP and vMMN responses; therefore, lower hemi field-stimulation is a feasible choice of the future vMMN studies.

The method of the primary task was innovative in the field. In the vMMN-research it was the first study to use a video game as a primary task. The obvious advantage of such primary task is the strict control of attention. Additionally, it also keeps the participants motivated for a longer time, i.e., in a state of higher arousal.

As in the case of the previous study, the paradigm has a caveat which is the lack of equiprobable control. Since the investigated variables are elementary features, the possibility of SSA effect is a feasible option. The interpretation is supported by the polarity-reversed vMMN. In both upper and lower hemi field conditions, the difference wave emerged as a larger response to the deviant which can be also interpreted as a response attenuation to the standard. Additionally, the peak latencies of the vMMNs correspond to the latency range of the SSA effect (i.e., between 100 and 200 ms, at the range of the exogenous N1 component). However, two findings contradict such conclusion. First, the second vMMN subcomponent elicited by the spatial frequency deviancy emerged as a decreased exogenous component (smaller positivity at lower half-field stimulation). Importantly, this second vMMN subcomponent is not observable in the double-deviant vMMN. It is unlikely that the spatial frequency deviancy elicits SSA only when it appeared as a single deviant. That is, probably all three vMMN included genuine vMMN. Second, the supposition that the SSA effect differently modulated the single and double deviancy is not plausible. This means that not just the vMMN, but also the SSA effect is a part of the vertical connections. However, it is advisable for future studies to include equiprobable control to narrow down the wide range of post hoc interpretations.

6.1.3. Thesis study 3

The aim of the third study was to test whether the vMMN is sensitive to illusory brightness changes. We used three conditions: an illusory condition and two control conditions. The illusory condition tested the vMMN's sensitivity to illusory brightness changes. The first control condition tested the vMMN's sensitivity to real contrast changes. The second control condition tested the ERP effect of physical changes in the illusory condition.

Both illusory and real contrast changes elicited double vMMNs. The latencies of the vMMNs were similar (or in a more accurate manner, statistically not different). However, the scalp distributions of the double vMMNs were different in the two conditions. In the illusory condition, the vMMNs had midline-occipital scalp distributions. In the real contrast condition, both vMMNs had right occipital maxima. In this area, the magnitudes of the vMMNs were larger than the vMMNs obtained in the illusory condition. Importantly, we obtained no vMMN in the second control condition (change in the Cornsweet-edges' characteristics without the brightness illusion). As a consequence, the vMMN obtained in the illusory condition was due to the illusory brightness changes and not the physical differences between the stimuli.

This important finding reveals the modulation effect of the high-level representations on low-level information processing. The high-level representation underlying the brightness illusion is supposed to be the consequence of long-term perceptual experience. In contrast, the low-level representation reflects only physical differences in the stimulation (which is overridden by the illusion). The case is similar to that of color perception. The perceptual categorization of color categories occurs only in high-level visual areas, such as V4. At the level of the V1, the representations correspond to the mixture of the three wavelengths. Similar to the color-category vMMN studies, the present study showed that vertical connections modulate the deviant-related processing of an elementary feature. However, the study goes one step further. The similar latencies in the two brightness conditions were an important (and unexpected) finding. That is, changes in the perceptual experience formed by the information flow followed similar cascade steps, irrespective of whether the experience is an illusory or a real one. The vMMNs were elicited at low-level processing steps and the high-level processing (i.e., the representation of illusion) modulated the low-level processing. The findings reveal the temporal characteristics of the vertical feedback connections.

Due to the binary nature of the stimuli, an equiprobable control condition was not used, so it is hard to separate the frequency-related SSA effect and the prediction-related gvMMN. One may say that the results can be explained by the SSA. Two observations contradict such an argument. First, although the latency of the early vMMNs overlapped with the range of the SSA-effect (i.e., to the latency of an exogenous N1 component), the later vMMN was too late for an SSA-effect. Even if there was a frequency-related ERP modulation, the SSA effect was probably restricted to the early vMMNs. This interpretation is in accordance with the literature (i.e., SSA and gvMMN are successive cascade processes). Second, probably higher SSA effect would be expected for real contrast change causing larger or earlier vMMN. In contrast, the latencies and the magnitudes of the vMMN are highly similar in the two conditions. The only significant difference between the conditions occurred at right occipital areas, where the magnitude of the real contrast vMMN was larger. Indeed, this difference can be caused by the SSA, but the interpretation only explains the differences in the scalp distributions in the two conditions and not the whole findings.

In sum, the pattern of the results supports the notion that high-level representations modulate the deviant-related processing of elementary feature changes via feedback connections.

6.1.4. Thesis study 4

The aim of the fourth study was to test the familiarity effect on the automatic deviant-detection of elementary feature changes. In the first condition, familiar and unfamiliar stimuli were delivered in an oddball sequence. In the second control condition, both standard and deviant were unfamiliar. The physical differences (i.e. orientation of the line segments) between the standards and deviants (i.e. changes during the oddball sequence) were the same in the two conditions.

In the familiar condition we obtained vMMNs for both the familiar and the unfamiliar deviant. Furthermore, we obtained the expected asymmetry between the two vMMNs. The latency of the vMMN to the unfamiliar deviant was shorter. In the non-familiar condition, we obtained similar vMMNs for both orientation deviances. The results favored the latter of the two contradicting hypotheses. The standard is an integral part of the comparison process underlying the vMMN. Moreover, in this case, the predictive mechanism underlying the vMMN is based on a stronger (more efficient) memory trace and better defined details of the expected visual attributes. During the comparison process, a more efficient prediction highlights the unattended changes in the environment. The results may reveal the importance of the standard stimulus in the vMMN research. Future research may focus more on the impact of the standard attributes setting the rules of the environmental stimulation.

The second observation is related to the latencies of the vMMNs in both conditions. We obtained single vMMNs instead of double vMMNs. As mentioned earlier, double vMMN probably reflects cascade processing of independent mechanisms and single vMMNs reflect unitary processing. Therefore, the processings of the two deviancies (the orientation and the familiarity) were not independent from each other. Either the high-level deviancy modulates the low-level deviancy or *vice versa*. Probably the former one is true; i.e., the familiarity effect modulates the deviant-related processing of orientation change. We have two reasons for that statement. First, based on the literature, the latencies of the vMMNs were too early for high-level processing. Second, the latencies of the vMMNs were similar to the ones obtained in the control condition using patterns of line segments.

Consequently, the vMMN is sensitive to the vertical connections between orientation-related and familiarity (letter)-related processes. This was probably executed through a feedback loop from higher visual areas (e.g., letter form area, Thesen et al., 2012) to the prestriatal cortex (Kimura et al., 2010). The results of the control experiment support such an interpretation. In this study, the elementary feature change was identical to the ones in the main experiment. In the control sequence, the obtained vMMNs were highly similar, almost identical to each other. That is, the orientation deviancy without the modulatory effect of familiarity elicited similar vMMNs. It is worth mentioning that in this study the attentional control was strict, so an attentional effect on the deviant-related processing of overlearned stimuli is not probable (c.f. Kovács and Vogels, 2014).

However, there are some caveats in the experiment. Due to the nature of the stimuli (binary stimulus types), the application of an equiprobable sequence was not possible. The main problem with the lack of the equiprobable control is that the contribution of frequency and repetition-related effects (in short: SSA) to the traditional vMMN is not known. That is, it is not known, whether the latency-asymmetry of vMMNs would have remained in the gvMMN (for a similar argument, see Kimura and Takeda, 2013). It is possible that, the SSA is fully responsible for the effect. The results partly support such an interpretation. The N1 component elicited by the standard N stimulus pattern was smaller than the N1 components of the other three ERPs (elicited by deviant N, standard reverse N, and deviant reverse N). Perhaps the frequent, familiar stimulus resulted in a stronger adaptation of the brain response in this case. Without further empirical data, the question remains open. An ideal test would be a task in which both standard and deviant are familiar in one condition (e.g., N and Z characters), and, similarly, both standard and deviant are unfamiliar in the other conditions (e.g., reversed N and reversed Z).

6.2. General discussion

The thesis studies encompass a wide range of parvocellular features: orientation (Study 1, 2 and 4), color (Study 1), spatial frequency (Study 2), and luminance (Study 3). In the case of orientation deviancy, both patterns of line segments (Study 1 and 4) and patterns of Gabor patches (Study 2) were used. The studies described vertical (Study 1, 2 and 4) as well as horizontal (Study 2) feedback loops. The vertical feedback loops are related to long-term memory processes (Study 3 and 4) and attentional processes (Study 1). The horizontal connection is related to the basic level of feature integration (Study 2). The studies used simple change detection tasks (Study 1 and 3) and two versions of a videogame (Study 2 and 4) as primary tasks. The stimuli were delivered either in the whole visual field (Study 1 and 3) or only in the lower visual hemi field (Study 2 and 4). The latencies of the obtained vMMNs were in the early range of 100-200 ms (Study 1, 2, and 4) and in the late range of 200-300 ms (Study 2 and 3). The maxima of the obtained vMMNs were consistently above the midline occipital areas in all Studies.

6.2.1. Predictive coding framework

Converging evidence from the four studies revealed the remarkable nature of the mechanism underlying the vMMN. Continuous interactions of feedforward and feedback loops are interwoven into a complex hierarchical network creating the visual system. The interactions constantly update the environmental model of the external stimulation and form the processing of the upcoming stimulus. The studies focused on the particular feedback loops modulating the deviant-related processing of the elementary features. The take-home message of the thesis studies is that the deviant-related processing of elementary feature changes depends not just on the input of the afferent signal; the efferent signal also has a huge impact on the vMMN.

The interpretation is in accordance with the temporal characteristics of the vMMN. The latencies of the earliest vMMNs are around 120 ms, and it can emerge as late as 400 ms after the stimulus onset (more accurately, the deviant event). Even the earliest vMMN is far beyond the first-cycle processing of the efferent (bottom-up) stream. Rousselet and his colleagues (2004) reviewed the processing sequence of stimulus attributes in terms of latency, brain area, and receptive field. The efferent stream reaches the TE at around 130 ms even in the case of the most complex stimulus. Regarding the vMMN, there is more than enough time for the feedback loops to connect to the processing cycle. As the thesis studies showed, this is the case: feedback loops are, indeed, involved in the deviant-related processing.

Nevertheless, the conclusion of the thesis goes one step further. Comparing the effects of the afferent and efferent streams (i.e., top-down and bottom-up processes), probably the latter is the larger factor in the complex sub-processes underlying the generation of the error signal. The third study showed that the deviant-related processings of illusory and real brightness changes are highly similar in relation to the spatio-temporal characteristics of the vMMN. This finding is only possible if the change-detection process is initiated at the low level of visual processing. In that sense, the interpretation is in accordance with the results of the so-called color-vMMN studies (Mo et al., 2011; Clifford et al., 2010; Thierry and Athanasopoulos, 2009; Athanasopoulos et al., 2010).

Similarly, the fourth study showed that the familiarity of a letter character modulated the early processing of orientation deviancy. The results also fit with the vMMN-literature. Takács and his colleagues (2013) reported more effective deviant-related processing of cardinal relative to oblique orientations (c.f. oblique effect). Another study (Wang et al., 2014) used upward and inverted faces as experimental stimuli, and the deviancy was the orientation of the faces. The authors obtained a larger vMMN to the more familiar upward faces compared to inverted faces. Thus, the weight of the top-down processes is probably larger than the weight of the bottom-up processes in the forming of the perceptual experience.

As mentioned earlier, the efferent stream includes the standard's features accompanied by the expectancy; and the deviant's features are carried by the afferent stream. Therefore, the attributes of the standard are just as (or more) important as the attributes of the deviant. Earlier studies underestimated the significance of the standard, and focused on the deviant's attributes and on the deviancy itself. Only a few studies reported experimental results regarding the memory trace of the standard's attributes (Kecskés-Kovács et al., 2013; Durant et al., submitted). Furthermore, in those studies, the interpretations were rather post hoc interpretations than hypotheses. It can be a viable approach for future studies to embrace the significance of the standard in the vMMN theory; and to emphasize the standard's role in the acquisition of the environmental model. Studies focusing on the standard's role might yield novel findings about the environmental model underlying the vMMN.

The second consequence is related to the elementary features. Most of the vMMN studies use a single object (white oblique bar) against neutral background (e.g., homogenous grey) as experimental stimulation. Although, the object can be complex (such as face, hands, or letters), the applied stimulation is far from the varicolored diversity of the natural scenes. The reason behind the minimalist choice of experimental stimulus-sets is practical. It is way easier to control the stimulation and systematically manipulate the experimental variables (e.g., deviancy) when the attributes of the stimuli are restricted to a few, well-defined features. However, the low ecological validity in the experiments may have more covert costs than apparent gains. The visual system is not optimized for the processing of isolating floating objects. Figure-background separation, filtering out the behaviorally relevant characteristics of the environment, emphasizing the edges and contours are all fundamental tasks that the visual system is designed for. Designing the experimental stimuli (and the stimulus sequence) while considering the special attributes of the visual system would be an advisable (and challenging) direction for future studies (for inspiration, see Lyyra et al., 2014; Czigler et al., 2013, Müller et al., 2013, Sysoeva et al., 2015). A recent experiment (Czigler et al., in preparation) demonstrated a promising approach in the vMMN research. In the majority of the vMMN studies the events are a sudden appearance of a stimulus (i.e., onset). In contrast, in this study, the event was created by the partial disappearance of a stimulus pattern. The standard-deviant difference was the part of the object that vanished. The deviant event can be interpreted as a changing in the object identity due to the change in the covered parts which is a common phenomenon in the visual world. A vMMN emerged to this deviancy. So the mechanism underlying the vMMN is sensitive to a change in the object identity induced by hiding the different part of the object.

The thesis studies focused on an additional visual-specific characteristic. In the four studies, the deviant-related processing of elementary feature changes was modulated by feedback loops. Although the limit of the phenomenon (i.e., the generalization of the results) is not known, together with other results (e.g., Athanasopoulos et al., 2010), it seems a valid supposition that there is a general mechanism. In other words, the visual system always uses any available information during the stimulus processing. This is also true when the stimulation is delivered in the unattended part of the visual field. In that sense, using laboratory stimuli may result in artifacts or at least may limit the generalization of the data.

Secondly, in the case of any elementary feature change, the possibility of additional high-level processing is a plausible option. So the careful evaluation of the experimental stimuli in terms of additional higher-order processes is an advisable direction for further studies. As an example, Kimura and Takeda (2013) used identical tilted line segments surrounding a central task. The stimulus pattern can be interpreted in two-ways. First, it can be a texture (similar to the first and third thesis study) which overlapped with the central task. Second, it can be interpreted as eight separate objects presented in the periphery. Since object-related (figure) and texture-related (background) processing is highly different, the interpretation of the data is ambiguous.

6.2.2 The connection between SSA and gvMMN

As already mentioned earlier, a caveat of the thesis-studies is the lack of the equiprobable control. In defense of the thesis studies, in the vMMN literature, only ten papers reported results from an equiprobable sequence (out of 150 papers). Furthermore, in the third and fourth study, the application of such control was not possible due to the stimuli of choice. The possibilities of the contribution of the SSA effect to the results were detailed during the reevaluation of each study. In sum, although the results might be slightly modulated by the SSA-effect, the main interpretation of the results remained unaffected.

The interpretation yields a question. What is the functional significance of the SSA, and what is the relationship between the SSA and gvMMN? In the literature, there is a consensus about the functional significance of the gvMMN; however, no similar consensus exists about the SSA. The probable reason is that for a long time, the vMMN (and auditory MMN) researchers considered SSA to be a systematic noise. However, the predictive coding framework treats SSA as a component of the predictive system. According to the theory (e.g., Stefanics, 2014), the SSA probably reflects the memory representation (or memory trace) acquired by the repeated presentation of the standard. Therefore, the SSA reflects the functioning of the representation cells. In that sense, the SSA is inextricably intertwined with the gvMMN as complement aspects of the same process. As a consequence, the gvMMN is always accompanied by the SSA. Therefore, the use of equiprobable control is should be a common method in the vMMN research.

The relative weights of the two sub-processes are presumably not constant. First, it is improbable that the same SSA and gvMMN operate in the case of a single white bar and in the case of face stimuli. Second, the more complex the stimulus, the more impact the prediction has, because there is richer contextual information.

A similar conclusion comes from fMRI experiments. There is evidence that SSA (or repetition suppression) can be modulated by the prediction induced by the probabilities present in environmental stimulation (Summerfield et al., 2008). By using the fMRI adaptation method (Grill-Spector and Malach, 2001), they conducted an experiment varying the expectation of alternating and repeating stimuli (in a similar design to that of Stefanics et al., 2011). They found a stronger SSA for the expected repetition compared to the unexpected one. Since then, the expectation effect (the fMRI counterpart of the vMMN) on the SSA has been investigated in many studies with inconsistent results. Kaliukhovich and Vogels (2014) found no expectation effect in the inferior cortex of macaque to non-face objects (single unit method). The results have been both supported (Kovács et al., 2013) and also contradicted (Mayrhauser et al., 2014) in the case of humans. Kovács and his colleagues (Kovács et al., 2013, 2012; Grotheer and Kovács, 2015) found an expectation effect to human face. Similarly, Larsson and Smith (2012) obtained an expectation effect to faces, but only in the full attention condition; without attention, the expectation effect diminished. Grotheer and Kovács (2014) found EE to Roman alphabet letters. Kovács and Vogels (2014) argued that probably only attended, familiar stimuli are able to elicit expectation effect.

The vMMN research extends the results of the fMRI experiments. The expectation effect, that is, the vMMN, can be obtained even if the participants do not attend to the stimulation. The differences in the results can be deduced from the differences in the experimental methods. The temporal resolution of the ERP experiments is much finer than the temporal resolution of the fMRI experiments. A plausible explanation is that the fMRI sums up many more sub-processes, and some of the sub-processes are probably stronger than a weakened expectation effect. The other sub-processes mask the early expectation effect.

6.2.3. Future directions in the methodology of vMMN research

Although theoretically the use of equiprobable control is reasonable, the general lack of such control draws the attention to a fundamental problem in the vMMN research; the lack of a standardized method. The problem is far beyond the stimuli and the stimulus sequence. This issue involves the relationships between the experimental stimuli and the primary task.

The most salient example of the stimulus variety is orientation as an elementary feature. Although the stimuli, in general, are fairly consistent (bar or line segments), the number (single bar or bar pattern), the location (central or peripheral), and the size of the stimuli varied within wide range. As mentioned earlier, the stimulus pattern might modulate the interpretation of the results. That is, the same pattern can be interpreted as a group of individual objects or a homogenous texture. The distinction is not just theoretical - texture-related and object-related processes are highly different. Similar is the case with the location of the stimulus. Due to the nature of visual attention, the location of the gaze and the focus of attention overlap. Therefore, spatially overlapping stimuli (in this case, task-related and –unrelated stimuli) are probably equally attended. Since attention is a robust factor modulating either high-level or low-level stimulus processing, its contribution to the results cannot be ruled out.

The size of the stimulus is another uncontrolled variable. This is because the stimulus size defines the receptive field. The receptive field correlates highly with the hierarchical level of the visual system. That is, the larger the receptive field, the higher the level the stimulus processing requires within the visual system. Furthermore, the resolution of the eye is not homogenous across the visual space. It is strong within 2 degrees in the center, and exponentially decays toward the periphery. In sum, the experimental stimulus influences the obtained results even if the deviancy is orientation deviancy. A study by File and his colleagues (submitted) is a significant example for that issue. The authors investigated the relative weight of gvMMN and SSA in case of two stimulus types. In their Experiment 1, the stimuli were patterns of line segments delivered in the lower visual half-field with a video game in the upper half-field. In Experiment 2, the stimuli were windmill patterns, and the primary task was a central visuo-motor tracking task. In Experiment 1 SSA fully explained the standard-minus-deviant difference. In Experiment 2 the difference wave separated into two subcomponents. Therefore, the relative contribution of the gvMMN and SSA is highly different depending on the experimental stimulus. It is important to mention that the (post hoc) interpretation does not contradict the main finding of the experiments. Instead it just switches the focus from elementary features to the stimulus as a whole. That is, it is more important to talk about a stimulus pattern than about elementary features. This is in accordance with the thesis studies. Even in the simplest cases, feedback loops modulate the deviant-related processing of elementary feature changes. Therefore the stimulus is always processed as a whole, and it cannot be reduced to elementary features. It is possible that the lack of such a fundamental process is the reason behind the high variability of the vMMN results. The investigating of the motion direction processing can be a promising alternative for the solution of the problem. The processing of global motion is restricted to a certain module (MT or V5). Therefore, the deviant-related processing is mostly unaffected by other elementary features processing resulting in a higher signal-to-noise ratio and lower inter-subject variability.

In the literature, no systematic research is known that/which compared the different elementary features in terms of inter-subject variability. However, three observations yield converging evidence in favor of motion direction deviancy. First, the motion-related vMMN studies showed the most consistent results. Second, Kremláček et al. (2004) carried out a systematic investigation on motion visual evoked potential (vEP), and found low inter-subject variability. Third, the individual vMMNs elicited by motion deviancy also showed the lowest inter-subject variability (unpublished results from our laboratory).

6.2.4. VMMN and (clinical) application

The pragmatic approach in the vMMN research focuses on the application of the vMMN irrespective of the neural mechanisms underlying the vMMN. So the pragmatic approach considers the vMMN to be a diagnostic tool for measuring differences between individuals or subgroups. The approach is most prevalent in the clinical domain. Kremláček and his colleagues (2016) in a recent review summarize the findings on the clinical application. In general, the vMMN is smaller for patients with schizophrenia and schizoaffective disorder (Csukly et al., 2013; Farkas et al., 2015, Urban et al., 2008, Neuhaus et al., 2013) as well as for patients with mood disorders

(Chang et al., 2010, Chen et al., 2010; Maekawa et al., 2013; Qiu et al., 2011). This direction of vMMN research is promising since it allows identifying the neuro-markers in the patients. An additional gain of such a direction is the evolving of the vMMN as a diagnostic tool. For now, the clinical approach inspired the design of a new experimental paradigm. The paradigm is called optimum paradigm. The optimum sequence consists of identical standards and different types of deviants. All deviants differ from the standard in one attribute, but the deviancy is different in each deviant type. That is, multiple deviant (color deviant, orientation deviant, spatial frequency deviant, shape deviant etc.) are delivered in a common sequence. The standards and deviants alternate during the sequence in a SDSDSD manner. The frequency of the deviant stimuli per se is 50 per cent; however, the frequency of the deviant feature or deviant event is kept below 10 per cent. Quian and his colleagues (2014) compared the vMMNs elicited in a traditional oddball condition and elicited in an optimum condition. They found highly similar vMMNs in both conditions in the case of color, orientation, duration, shape, and size (i.e., spatial frequency) deviancies. The real advantage of the optimum paradigm is that that it is cost-effective. In this special case the data collection is five times faster than in a traditional oddball paradigm. In sum, the optimum paradigm is a promising direction in the application domain, since the same data can be obtained much faster.

6.3. Conclusions

The aim of the doctoral thesis was to reveal the nature of the deviant-related processing in the case of elementary feature changes. The hypotheses were formulated in accordance with the work frame of the prevalent theory in the vMMN research. The predictive coding theory claims that the vMMN reflects the operation of the error signal. The trigger of the generation of the error signal is the mismatch between the predicted and the actual event. The prediction of the event is acquired by the sequence of the standards following a regular temporal pattern, and it contains the general probability of the event and also the attributes of the event. The predicted attributes are not restricted to a certain stimulus feature, it contains several parallel attributes. The attributes are represented at multiple levels of the hierarchical system. The representation of the attributes of the deviant stimulus can mismatch on each level separately (or all of them together).

The question of the thesis was whether multiple deviancies elicit independent processes or the internal connections within the visual system might modulate the mismatch process. The general conclusion of the thesis favors the latter one. Even in the case of elementary feature changes, parallel representations of the stimulus modulate the deviant-related processing. The thesis investigated various connections, including both higher and lower order representations. In sum, the doctoral thesis demonstrated that the vMMN elicited by elementary feature changes is sensitive to both the vertical connections originating from higher-order organizational levels and the horizontal connections of lower-order organizational levels. The doctoral thesis may partly fill the gap between the vMMN-studies investigating the vMMN sensitivity to higher-order organized stimuli (e.g.: faces, hands) and the ones investigating the vMMN sensitivity to elementary feature changes (e.g.: orientation, color). It seems that the perceptual and memory processes underlying the vMMN are integrated between and within the hierarchical levels. The findings support the presumption that the mental models underlying the vMMN are hierarchically organized, but function as an integrative system.

7. References

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