DOCTORAL DISSERTATION

DOMONKOS FILE

# INVESTIGATING THE UNDERLYING MECHANISMS OF VISUAL MISMATCH NEGATIVITY

UNIVERSITAS BUDAPESTINENSIS DE ROLANDO EÖTVÖS NOMINATA

16 35

2019

# [1]ADATLAP

## a doktori értekezés nyilvánosságra hozatalához

I. A doktori értekezés adatai

II. A szerző neve: File Domonkos
MTMT-azonosító: 10049900
A doktori értekezés címe és alcíme: Investigating the underlying mechanisms of visual mismatch negativity
DOI-azonosító[2]: 10.15476/ELTE.2019.147
A doktori iskola neve: ELTE PPK Pszichológiai Doktori Iskola
A doktori iskolán belüli doktori program neve: Kognitív Pszichológia
A témavezető neve és tudományos fokozata: Czigler Istvám, PhD, DSc
A témavezető munkahelye: MTA TTK Kognitív Idegtudományi és Pszichológiai Intézet

III. II. Nyilatkozatok

1. A doktori értekezés szerzőjeként[3]

a) hozzájárulok, hogy a doktori fokozat megszerzését követően a doktori értekezésem és a tézisek nyilvánosságra kerüljenek az ELTE Digitális Intézményi Tudástárban. Felhatalmazom az ELTE PPK Pszichológiai Doktori Iskola hivatalának ügyintézőjét Barna Ildikót, hogy az értekezést és a téziseket feltöltse az ELTE Digitális Intézményi Tudástárba, és ennek során kitöltse a feltöltéshez szükséges nyilatkozatokat.

b) kérem, hogy a mellékelt kérelemben részletezett szabadalmi, illetőleg oltalmi bejelentés közzétételéig a doktori értekezést ne bocsássák nyilvánosságra az Egyetemi Könyvtárban és az ELTE Digitális Intézményi Tudástárban;[4]

c) kérem, hogy a nemzetbiztonsági okból minősített adatot tartalmazó doktori értekezést a minősítés (dátum)-ig tartó időtartama alatt ne bocsássák nyilvánosságra az Egyetemi Könyvtárban és az ELTE Digitális Intézményi Tudástárban;[5]

d) kérem, hogy a mű kiadására vonatkozó mellékelt kiadó szerződésre tekintettel a doktori értekezést a könyv megjelenéséig ne bocsássák nyilvánosságra az Egyetemi Könyvtárban, és az ELTE Digitális Intézményi Tudástárban csak a könyv bibliográfiai adatait tegyék közzé. Ha a könyv a fokozatszerzést követőn egy évig nem jelenik meg, hozzájárulok, hogy a doktori értekezésem és a tézisek nyilvánosságra kerüljenek az Egyetemi Könyvtárban és az ELTE Digitális Intézményi Tudástárban.[6]

2. A doktori értekezés szerzőjeként kijelentem, hogy
a) az ELTE Digitális Intézményi Tudástárba feltöltendő doktori értekezés és a tézisek saját eredeti, önálló szellemi munkám és legjobb tudomásom szerint nem sértem vele senki szerzői jogait;
b) a doktori értekezés és a tézisek nyomtatott változatai és az elektronikus adathordozón benyújtott tartalmak (szöveg és ábrák) mindenben megegyeznek.

3. A doktori értekezés szerzőjeként hozzájárulok a doktori értekezés és a tézisek szövegének plágiumkereső adatbázisba helyezéséhez és plágiumellenőrző vizsgálatok lefuttatásához.

Kelt: a doktori értekezés szerzőjének aláírása

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[1] Beiktatta az Egyetemi Doktori Szabályzat módosításáról szóló CXXXIX/2014. (VI. 30.) Szen. sz. határozat. Hatályos: 2014. VII.1. napjától.

[2] A kari hivatal ügyintézője tölti ki.

[3] A megfelelő szöveg aláhúzandó.

[4] A doktori értekezés benyújtásával egyidejűleg be kell adni a tudományági doktori tanácshoz a szabadalmi, illetőleg oltalmi bejelentést tanúsító okiratot és a nyilvánosságra hozatal elhalasztása iránti kérelmet.

[5] A doktori értekezés benyújtásával egyidejűleg be kell nyújtani a minősített adatra vonatkozó közokiratot.

[6] A doktori értekezés benyújtásával egyidejűleg be kell nyújtani a mű kiadásáról szóló kiadói szerződést.

EÖTVÖS LORÁND UNIVERSITY
FACULTY OF EDUCATION AND PSYCHOLOGY

**Domonkos File**

# INVESTIGATING THE UNDERLYING MECHANISMS OF VISUAL MISMATCH NEGATIVITY

DOCTORAL SCHOOL OF PSYCHOLOGY
Head of the Doctoral School: Zsolt Demetrovics, PhD, DSc
COGNITIVE PSYCHOLOGY PROGRAM
Head of the Program: Ildikó Király, PhD
Supervisor: Prof. István Czigler, PhD, DSc

Committee:
Chair: Ildikó Király, PhD
Secretary: Katalin Oláh, PhD
Internal opponent: Ferenc Honbolygó, PhD
External opponent: László Balázs, PhD
Members: Anett Ragó, PhD
János Horváth, PhD,
Andrea Kóbor, PhD
Karolina Janacsek, PhD

Budapest, 2019

# TABLE OF CONTENTS

# ACKNOWLEDGEMENTS

First and foremost, I am really greatful to my supervisor, István Czigler, for providing constant theoretical and technical support during my doctoral years. I am also very thankful to my rewievers, László Balázs and Ferenc Honbolygó for spending their time reading the thesis and providing valuable feedback and comments. Their contribution significantly improved the quality of my work.

Also, I would like to say thank for every member of my research group; István Sulykos, Krisztina Kecskés-Kovács, Flóra Bodnár, Petia Kojouharova. I am especially thankful for István Sulykos for giving me over the know-hows of experiment design and data analysis with his outstanding methodological accuracy. I'm also greatful for the members of our "sibling research group", lead by Zsófia Gaál. Our collaboration showed me interesting topics in neuroscience, which supported my overall understanding. Although I only had the chanche to work with the new members of the group for a short period, I would like to say thank for them too: Boglárka Nagy, Petra Csizmadia and Béla Petró.

I am greatful for Zsuzsanna D'Albini for providing the technical knowledge for recording our experiments, and for being there making the lab a much more cheerful place.

I also appreciate the conversations with the members of the room I worked in, with a special thanks for Márta Volosin for providing me the formal details to write the dissertation.

Finally, but not less importantly, I cannot thank enough for my family. Bálint File had a significant impact on my thinking, always helping my work with his great ideas and technical solutions. Also, I am greatful for my parents, sister and Lilla Pacsika for their patience and support.

## LIST OF PUBLICATIONS RELATED TO DISSERTATION

Kojouharova, P., **File, D**., Sulykos, I., Czigler, I. (2019). Visual mismatch negativity and stimulus-specific adaptation: the role of stimulus complexity. Experimental Brain Research, https://doi.org/10.1007/s00221-019-05494-2

**File, D**., Czigler, I. (2019). Automatic detection of violations of statistical regularities in the periphery is affected by the focus of spatial attention: A visual mismatch negativity study. European Journal of Neuroscience, doi: 10.1111/ejn.14306.

Gaál, Zs.A., Czigler, I., Sulykos, I., **File, D**., Kojouharova, P. (2019). Visual mismatch negativity to disappearing parts of objects and textures. PLOS ONE, doi: 10.1371/journal.pone.0209130

**File, D**., Sulykos, I., Czigler, I (2018). Automatic change detection and spatial attention: A visual mismatch negativity study. European Journal of Neuroscience, doi: 10.1111/ejn.13945

**File, D.** (2017). Unconscious perception during hypnosis. The International Society of Hypnosis, Newsletter, Volume 41, No. 4

**File, D**., File, B., Bodnar, F., Sulykos, I., Kecskes-Kovacs, K., Czigler, I.(2017). Visual mismatch negativity (vMMN) for low- and high-level deviances: A control study. Attention, Perception and Psychophysics 79, 2153-2170.

Bodnar, F., **File, D**., Sulykos, I., Kecskés-Kovács, K., Czigler, I. (2017). Automatic change detection in vision: Adaptation, memory mismatch, or both? II: Oddball and adaptation effects on event-related potentials. Attention, Perception and Psychophysics DOI 10.3758/s13414-017-1402-x

**File, D**., File, B., Bodnar, F., Sulykos, I., Kecskés-Kovács. K., Czigler, I. (2016). Intraindividual variation and the test-retest stability of visual mismatch negativity Poster presented at Neuronus 2016. Krakow, Poland

**File, D**., Bodnar, F., Kecskés-Kovács, K., Sulykos, I., Czigler, I. (2015). The role of stimulus complexity in various latency ranges of vMMN. Poster presented at Error Signals from the Brain – 7th Mismatch Negativity Conference (MMN 2015). Leipzig, Germany,

**File, D**., File, B., Bodnar, F., Sulykos, I., Kecskés-Kovács, K. Kardos, Zs., Tóth, B., Boha, R., Molnár, M., Tóth, Á., Fabó, D., Ulbert, I., Czigler, I. (2016). Resting state functional network determines properties of visual mismatch negativity. Poster presented at IBRO Workshop 2016. Budapest, Hungary,

**File, D.**, Bodnár, F., Kecskés-Kovács, K., Sulykos, I., Czigler, I. (2014). Investigation of the mechanisms behind the automatic change detection Poster presented at Unlimited Psychology, Marosvásárhely, Romania

# ABSTRACT

Humans have a poor ability to explicitly detect changes between two successive visual images that are separated by a blink or saccade. For cognitive psychology it has been a fundamental question that at what extent consciously not perceived changes are processed. Visual mismatch negativity (vMMN) is the electrophysiological correlate of automatic change detection, a tool to investigate the brains capability of detecting changes in the visual environment without voluntary control of the subject. The aim of my doctoral dissertation was to investigate key properties of vMMN, such as the underlying neural mechanisms and the effect of the focus of spatial attention on vMMN. We used the method of event-related potentials in all studies. The first two studies investigated the underlying mechanisms of vMMN. The results of Study I and II confirmed, that with the application of control paradigms, it is possible to separate the effect of adaptation from the signal of automatic change detection, i.e. genuine vMMN. Based on the results of Study I and Study II, we assumed that one uniform underlying mechanism that would generate vMMN probably does not exist, but there might be separate mechanisms, depending on the circumstances/stimulation. Study III and IV investigated the effect of the focus of attention on vMMN. In Study III low salience, offset stimulation was utilized and no modulatory effect of attention has been observed on vMMN. In Study IV higher salience, traditional onset stimulation was used, and vMMN was only elicited in the condition, where the focus of attention was spatially closer to the task-irrelevant stimulus sequence. We speculated, that for salient task-irrelevant stimuli a more efficient inhibitory activity was developed, which prevented the detection of changes.

# ABSZTRAKT

Sok esetben a vizuális környezet jelentős változásai is észrevétlenek maradnak. A kognitív pszichológiát régóta foglalkoztatja a kérdés, hogy a tudatosan nem észlelt változások milyen agyi feldolgozási folyamatokon mennek keresztül. A vizuális eltérési negativitás (vEN) az automatikus változás-detekció elektrofiziológiai korrelátuma, egy eszköz az agy nem tudatos változásokat detektáló képességének vizsgálatára. A doktori disszertációm célja a vEN neurális hátterének, valamint a téri figyelem fókuszának lehetséges hatásának a vizsgálata volt. Minden vizsgálatban a kiváltott potenciálok módszerét használtuk. Az első két tanulmány a neurális háttér vizsgálatával foglalkozott. Az első és második tanulmány eredményei alátámasztották, hogy a megfelelő kontroll paradigmák használatával szétválasztható az adaptációhoz és az automatikus változás-detekcióhoz köthető idegi aktivitás. Az első két tanulmány eredményeire alapozva valószínűnek tartjuk, hogy nem létezik egy egységes neurális mechanizmus a vEN hátterében, hanem valószínűbb, hogy a körülmények/ingerlés függvényében többféle mechanizmus is eredményezheti a változás detektálását. A harmadik és negyedik tanulmány a téri figyelem fókuszának távolságának a hatását vizsgálta a vEN-re. A harmadik tanulmányban alacsony szálienciájú, „offset" ingerlést alkalmaztunk és a figyelem fókuszának a távolsága nem volt hatással a vEN-re. A negyedik tanulmányban hagyományos, „onset" ingerlést alkalmaztunk és csak a figyelem közeli feltételben regisztráltunk vEN-t. A két kísérlet ellentmondó eredményeire egyértelmű válaszunk nincs. Feltételezzük, hogy a száliens feladat-független ingerekre erősebb gátló folyamatok érvényesülnek, ami a változás detekciójának hiányához vezet.

# INTRODUCTION

## Chapter 1: Theoretical and methodological background of vMMN

For cognitive science the understanding of our awareness of the visual world has been a fundamental question (Rosenholtz, 2017). The visual world is incredibly rich in details, so as our subjective experience what we perceive effortlessly (Levin, Momen, Drivdahl, & Simons, 2000). However, when perception is actually tested, subjects knows surprisingly little about their visual environment, and even significant changes of it remains unnoticed if they are not attended (Pazo-Alvarez, Cadaveira, & Amenedo, 2003). There are well known demonstrations of these effects, such as inattentional blindness, when clearly visible object(s) remains unattended (Mack, 2003). In the now-classic experiment by Neisser (1979) the participants were watching a video of people passing a ball to each other, while the task was to count the number of passes. Surprisingly only 21% of the participants noticed a women crossing the screen with a yellow umbrella in her hands. Another well-known phenomenon is change blindness, when changes of a visual scene between saccades (Grimes, 1996), blinks (Kevin O’Regan, Deubel, Clark, & Rensink, 2000) or cuts of motion picture (Simons, 1996) remain undetected. Importantly, change blindness persists if the observer expect or even search for the changes (Rensink et al., 1997). For the change blindness paradigm see Figure 1.1.

Change blindness demonstrates that not all stimuli appearing in the visual field are processed consciously. What is perceived consciously depends on attentional processes. If the subject of change before the cut is marked - in this way attended - change blindness does not occur (Scholl, 2000) and the probability of detecting changes which are thought to be important is higher (O’Regan, Rensink, & Clark, 1999). Also, humans are usually good at tracking changes of objects up to four, which is similar to the estimated capacity of attention (Rensink, 2000a) and working memory (Cowan, 2001).

**Figure 1.1. Change blindness is often investigated in the flicker paradigm by alternating an original and a modified version of an image, with a brief blank or mask between each presentation. Performance is measured by time required to see the change. (Rensink, 2007).**

There are various theories regarding the nature of the consciously not perceived stimuli. The classical explanation of Sperling (1960) states that the representation of the unattended visual world does not persist for longer than a few hundred milliseconds and focused attention is needed to allocate items to working memory for later use (Landman, Spekreijse & Lamme, 2003). By another explanation (Treisman & Gelade, 1980) attention is necessary to integrate features into objects, and to create the coherent representations of objects (Rensink, 2000a). There might be stored representation of the unintegrated features too, but are overwritten by new incoming stimuli (Rensink, 2000a).

The question, whether consciously not perceived stimuli have any behavioural modulatory effect is still open and popular in the field of perception research. Early researches focused on the consciously perceived and consciously not perceived measures, like the classical study of Sidis (1898), where cards with a number or letter on it were presented. The cards were presented from a distance from where the observers were not able to tell whether there was a letter or a number on the card. The idea was that subjective perception is probably a good indicator of conscious perception. Even though from a certain distance participants were not able to tell what they see on the cards, in a forced-choice situation they guessed better than chance level. This led to the conclusion that perception exists without consciousness (Merikle et al., 2001). The experiment of Sidis was followed by other studies strengthened his conclusion. Former studies proved perception without awareness for simple stimuli like bars with different angles (Baker, 1937), geometric shapes, like squares or triangles (Miller, 1942). Later studies demonstrated, that the meaning of words (Cheesman & Merikle, 1986) or facial emotions (Esteves & Öhman, 1994) are perceived in a similar way too. With the emergence of brain imaging techniques the effect of non-attended stimuli on brain activity became observable. For example Whalen et al. (1998) reported greater neural activity for fearful faces than for happy faces in a setting stimuli were impossible to consciously recognize.

Since the now-classic experiment of Sidis from the end of the 19th century, many other studies investigated the topic of unconscious perception. The methodology of these studies included introspective measures (e.g. Sidis, 1898), reaction time measurement (e.g. Marcel, 1983), event-related potential (ERP) recordings (e.g. Lamy et al., 2009), or fMRI recordings (e.g. Dehaene et al. 2001).

## 1.1 Automatic and attentional processes in information processing

The notion that human cognition can be divided into automatic and controlled processes has been a theme in psychology for over a century (Schneider & Chein, 2003). According to Schneider & Shiffrin (1977) automatic processes operates through a relatively permanent set of associative connections in long-term store, and the sequence is activated automatically without the necessity of active control or attention. Any new automatic process requires consistent training to develop fully and once learned, it is difficult to supress or to ignore (Schneider & Shiffrin, 1977). Controlled processes on the other hand are temporary sequences activated under control through attention. Because active attention is required, only one sequence at a time can be controlled without interference. Controlled processes are therefore capacity-limited. The cost of this limitation is balanced by the benefits that controlled processes can be applied in situation for which automatic sequences have never been learned (Schneider & Shiffrin, 1977).

The difference between automatic and controlled processing was elaborated using extended consistent mapping (CM) training. In the CM task the stimulus-response pattern is constant across a long period of time, so that an automatic process can develop slowly over time, typically after hundreds of trials. In varied mapping (VM) however no automatic processing can develop, since the stimulus-response patterns vary across trials, thus the prior and current associations are incompatible (Schneider & Chein, 2003).

The necessity of attention in controlled search is the limited perceptual resources available for a given process (Lee & Choo, 2011). Attentional mechanisms must select important aspects of the environment for additional processing while filtering out less salient information (Moran & Desimone, 1985). The resource limitation was originally conceptualized in Broadbent's work (Broadbent, 1958), known as the early selection theory. He proposed, that automatic processing occurs in parallel up to the level of a filter. Beyond the filter only those inputs are processed that selected by the filter (Schneider & Shiffrin, 1977). The filter is hypothesized to act like an all-or-none switch that could be focused on just one input at a time, and change the filter to a new channel requires time (Schneider & Shiffrin, 1977). This theory predicts, that an input on a nonattended channel will not be perceived. However, this is not the case, as certain kinds of inputs are perceived on a nonattended channel (Treisman, 1969). In the experiment of Treisman and Riley (1969) participants were listening to different word inputs presented to the two ears. Their task was to repeat back words arriving to the attended ear and detect a target word which could arrive to either ears. Participants performed significantly better at target detection, if the target was presented in a different tone than the tone of the attended ear, compared to the condition in which one tone was used for both ears. This result cannot be interpreted in terms of an all-or-none filter, leading Treisman (1964) to the attenuation model. The difference compared to Broadbent's model was that the hypothesized filter attenuates rather than eliminates the unattended input.

The question that at what stage of information processing the limited capacity bottleneck occurs first is unsettled. Theories ranging from early (e.g. Broadbent, 1958) to late selection (e.g. Deutsch and Deutsch, 1963) has been debated passionately. Pohl & Kiesel et al. (2010) draw attention to that "early vs. late selection" does not necessarily imply, that selection occurs in specific time ranges, but rather refers to the selection criteria, that is, early selection refers to physical selection criteria, while late refers to semantic selection criteria. Early selection theories assume, that no higher cognitive functions are involved in the processing of unattended stimuli, therefore it is considered Zombie-like (Tapia & Breitmeyer, 2006). On the other hand, late selection accounts assume, that there is no difference between the processing of visible and invisible stimuli (e.g. Cleeremans & Jiménez, 2002). Presumably the two selection positions do not exclude each other, but depends on whether selection takes place on the basis of elementary features or on the basis of the meaning of the stimuli (Pohl & Kiesel et al., 2010).

Since the 1960s, the event related potential (ERP) technique has played a significant role in our understanding of the mechanisms of attention (Luck, Woodman & Vogel, 2000). The simplest way to localize the locus of selection is to compare an ERP wave which was elicited by an attended event with an ERP wave which was elicited by a non-attended event. The first time point where the two waves differ signals the first effect of attention on sensory processing (Luck et al., 2000). This method is suitable to investigate a key question of cognitive psychology, namely that on what level of information processing attentional selection operates. For example when participants are asked to attend to a specific location, stimuli appearing on the attended location are processed faster.

### 1.2 EEG-ERP methodology

As introduced before, the ERP technology has been an important tool of cognitive science. Since all of the thesis studies used the EEG-ERP technique, a short introduction of the method is appropriate.

Electroencephalography (EEG) is a monitoring method allowing the graphical registration of electric voltage fluctuations of the brain (Atkinson & Hilgard, 2005). EEG is proved to be useful in both research and clinical use as it is typically non-invasive with electrodes placed along the scalp. Raw EEG is not suitable for investigating neural responses time locket to specific events, since the scalp electrodes are recording the activity of thousands of neurons, from which it is almost impossible to isolate specific neuro-cognitive processes (Luck, 2005). The ERP technique let someone to isolate specific motor, sensory or cognitive neural responses from the complex signal by averaging EEG sections time locked to a specific event. The theory behind the technique is that the neural response time locked to a specific event is more or less uniform, in this way by averaging the sections, the random fluctuations of neural activity independent from the event cancels out, while the signal of interest persists (Bernard & Nicole, 2010). This requires repeated presentation of stimuli. The required number of repetition largely depends on the size of the studied component, but usually ranges between 50 to 150. The ERP waveform is build up from successive positive and negative voltage differences which are called ERP components. ERP components are classified as exogen (sensory) and endogen components. Sensory components are modulated by the physical parameters of the stimuli and their latency is relatively short (>~150 ms in vision), while endogen components are related to higher order processes and no external stimuli is necessary to elicit them (Luck, 2005).

Luck et al. (2000) lists three main reasons, why the ERP technique can be regarded as the reaction time for the 21th century. First, they provide a link to the field of neuroscience. Second, ERPs provide much complex and detailed data compared to traditional reaction time measurements; ERPs are continuous waveforms with a time course, a scalp distribution and they are built up from components. With advanced techniques it is also possible to isolate components and estimate the source of the signal. A third aspect is that ERP responses require no active participation, which is particularly useful in attention research (Luck et al. 2000). For a detailed manual of the ERP technique see Luck et al. (2000) and for a comprehensive review see Woodman (2010).

# Chapter 2: Automatic change-detection

Although the topic of the current thesis is visual mismatch negativity (vMMN), a short introduction of its auditory counterpart – MMN - is necessary, since MMN research had a great influence on every aspect of vMMN research. MMN is an ERP component elicited by a rare, un-predicable deviant stimulus in the sequence of predicable stimuli, reported first by Näätänen, Gaillard & Mäntysalo (1978). The most frequently used paradigm is the so called oddball paradigm, a sequence of identical standard stimuli which is occasionally interrupted by the presentation of a physically different deviant stimulus (for example: sssssssdssssdssss…, where 's' indicates a standard and 'd' a deviant). MMN typically occurs 100-200 ms after the presentation of the deviant with negative polarity at the fronto-central electrode sites.

When Näätänen et al. (Näätänen, Gaillard & Mäntysalo, 1978) first reported MMN, they proposed an explanation for the underlying mechanisms, which largely defined the conceptual framework that MMN studies were interpreted in. They assumed, that the successive presentation of the standards build up a memory trace. Every stimuli are then compared to the memory trace; if the representation of the memory trace and the incoming stimuli does not match, an error signal, the MMN occurs. The application of more complex sequences than the oddball led for a better understanding of MMN, and the original theory was modified; the representation is storing the sequential regularities of the environment and also predictions are coded about the upcoming stimuli (see Winkler, 2007). Parallel to higher cognitive function explanations the adaptation hypothesis states that MMN is solely the consequence of the reduced response to the repeatedly presented standards (May and Tiitinen, 2010).

Since both the predictive coding and adaptation theories of MMN are fundamental theoretical bases of vMMN research, for a more detailed presentation see 2.1.3.

## 2.1 Visual mismatch negativity

The existence of a visual counterpart of MMN was the subject of long debate, partly because of the null results of early studies in the 90s, for example the study of Nyman et al., 1990. Czigler (2007) argues, that the absence of vMMN is also strengthened by the results of change blindness studies, which proved that the changes of the visual world remain unnoticed if (1) changes happen outside of the focus of attention, or (2) the intermediate states (transients) are unnoticed between the starting and final state of a change. Also, in auditory cognition a sensory memory or predictive system is obviously useful because of the temporal coding of auditory environment. For processing auditory streams, the function of a buffer-memory is significant, since the registration of the streams and their sequential regularities in a noisy environment is mandatory for segregation. However, the visual world is usually more stable and accessible for the observer, thus a short term memory system is less obvious (Czigler, 2007).

In 2003 Pazo-Alvarez et al. published a review, where they explicitly stated, that the visual homolog of MMN exists, and they contribute the early null results to methodological deficiencies. In the last two decades there are an increasing number of studies strengthen the notion, that there is a visual counterpart of MMN exists, the visual MMN (vMMN). VMMN has a posterior scalp distribution with negative polarity with a peak between 150 and 400 ms. The latency of vMMN depends on the complexity of the deviance; simple deviances – deviances that can be described with one feature change, i.e. orientation, colour – elicit vMMN with early peak, typically between 150 and 250 ms (e.g. Kumura et al., 2009; Czigler, Balázs, & Winkler, 2002). Complex changes however, e.g. gender or facial expressions elicit vMMN with peaks between 200 and 400 ms (e.g. Kecskés-Kovács et al., 2013a; Zhao & Li, 2006). The most frequently used paradigm is the oddball paradigm and in general vMMN has been investigated with similar paradigms as the auditory MMN, and the frameworks explaining it are essentially the same. Stefanics and Czigler (2014) draw attention to that although studying both visual and auditory mismatch processes rests on the same principle, there are also important methodological differences between visual and auditory mismatch paradigms. As such, the control for attention is ensured in significantly different ways. In auditory paradigms the primary task is usually visual, but in visual paradigms auditory primary task is not effective due the relative dominance of vision over hearing, so visual task is required (Stefanics & Czigler, 2014). This leads to a great heterogeneity among vMMN studies, which makes interpretation less obvious.

The sensory-cognitive system underlies vMMN is sensitive for a variety of visual deviant features, such as colour (e.g. Czigler et al., 2004; Kimura, Katayama & Murohashi, 2006a), shape (Maekawa et al., 2005), motion direction (Pazo-Alvarez, Amendo & Cadaveira, 2004), orientation (Antikainen et al, 2008; Czigler & Pató, 2009), spatial frequency (Maekawa, 2005), stimulus contrast (Stagg et al., 2004), stimulus omission (Czigler et al., 2006), stimulus offset (Sulykos, Gaál & Czigler, 2018?; File et al., 2018) and illusory brightness changes (Sulykos & Czigler, 2014). Object-based deviancies (Müller et al., 2013) and irregular lexical information (Shtyrov et al., 2013) are also automatically detected by the visual system. Complex stimuli, such as laterality of hands (Stefanics & Czigler, 2012) or socially more relevant stimuli such as facial expressions (Zhao & Li, 2006; Astikainen & Heitanen, 2009; Fujimura & Okanoya, 2013) and facial gender (Kecskés-Kovács et al., 2013a).

### 2.1.1. Paradigms

The most important two aspects of vMMN paradigms are stimulus sequence and the primary task, so I will present them in details.

#### 2.1.1.1 Sequences

The **oddball sequence** - repetitive stimuli, infrequently interrupted by a deviant stimulus - is the most frequently used sequence in vMMN research. Its main properties are the deviant features, deviant probability, inter-stimulus interval and stimulus duration. The deviant features are range from elementary deviances (such as colour, e.g. Czigler et al., 2004) to complex ones (such as facial expressions, e.g. Zhao & Li, 2006), as described above while presenting visual features the sensory-cognitive system underlies vMMN are sensitive for. The probability of the deviant ranges from p=0.05 (Tales et al., 2008) to p=0.2 (e.g. File & Czigler, 2018 or Kimura, Widmann & Schröger, 2010) across experiments. The ISI ranges from 80 ms (Kimura, Widmann & Schröger, 2010) to 2250 ms (Kecskés-Kovács, Sulykos & Czigler, 2013), while stimulus duration ranges from 80 ms (Kimura, Widmann & Schröger, 2010) to 300 ms (Kecskés-Kovács, Sulykos & Czigler, 2013) across experiments. As a rule of thumb, the amplitude of vMMN increases as a function of the increment of standard-deviant features difference and the decrement of deviant probability. For an illustration of the stimulus sequences see Figure 2.1.

The **roving standard** sequence is less frequently used (Czigler & Pató, 2009; Sulykos et al., 2013), where the first stimulus of a train can be considered deviant, which over several repetitions becomes the standard. The advantages of this paradigm are that the time course of response decrement over repetition is observable and running a roving standard paradigm requires less time compared to an oddball (Stefanics et al., 2014).

The aim of the use of an **equal probability** (EQ) control sequence is to separate the effect of adaptation and genuine vMMN and it is quite frequently applied (e.g. Kimura et al., 2009; Kojouharova et al., 2019; Astikainen et al., 2008). Within the EQ sequence, stimuli physically identical to the oddball's deviant are embedded in the sequence of other stimuli with equal probability. Within such sequence, the probability of each stimulus type is equal to the probability of the oddball deviant. Thereafter, the ERPs elicited by the oddball deviant and the equal probability control stimuli are compared. In the control sequence, there is no way of developing a strong memory representation (or a regularity-related memory representation) for any of the stimuli, and therefore, no additional activity is expected within the ERPs that are elicited by the control stimuli. A critical feature of the equal probability control paradigm is that the average physical separation between the control and other stimuli is equal or larger than between the standard and deviant stimuli. This excludes the possibility of a response decrement to the control stimuli relative to the deviant due to the additional activations of the afferent neurons responding to control stimuli by other stimuli with equal probability (Jacobsen & Schroger, 2001; Kimura et al., 2009). The difference between the activity elicited by the deviant and the control is called genuine MMN (gMMN)—that is, an additional activity without the involvement of adaptation effects.

**Cascade control** is a specific form of the equal probability control, addressing the problem, that the equal probability control procedure eliminates the sequential rule of the oddball stimuli (identical stimuli follow each other), not solely the effect of a particular physical feature (Ruhnau et al., 2012). Cascade control requires stimuli that regardless of the physical difference between them form some kind of sequential regularity. Up to date, there is one study (Study I) that used the cascade control in the visual modality with no significant difference in the elicited ERPs compared to the equal probability control.

The **rotating-oddball sequence** contains a sequential rule defined by stimulus change – similarly to the cascade control -, providing change-rule confirming (standard) and violating (deviant) stimuli. Kimura & Takeda (2015) used this sequence with rotating bar stimuli and reported prediction vMMN, that is stimuli did not match the preceding state of the rotation elicited a negative ERP component in the 260-300 ms latency range.

The **optimal paradigm** allows one to obtain vMMNs for several visual features in a short time. Quian et al. (2014) used this sequence, in which 5 kinds of deviants – colour, orientation, shape, size, duration- occurred within one sequence. Every second stimulus considered deviant, so every other stimulus was a standard. Stimuli follow each other in a manner that the other deviant stimuli can strengthen the memory trace of the standard with respect to those levels of stimulus features they had in common. They reported equal vMMNs elicited in the optimal paradigm compared to regular oddball sequences (Quian et al., 2014).

The aim of the use of **complex sequences** are to investigate the sensitivity of the neural structures generating vMMN to statistical regularities. The sequential rules of such sequences are more complicated than the sequential rule of an oddball, i.e. the repeating sequence of standard stimuli. A few examples; A/B/A/B/A/B/B (Kimura et al., 2011), A/A/B/B/A/A/B/B/B (Czigler et al., 2006a) or A/A-B/B-B/B-A/A-B/A where stimulus pairs have a probability of A/A 45%, B/B 45%, B/A 5%, and A/B 5% (Stefanics et al., 2011). VMMN was observed in response to the above complex sequences.

Up to date, **fixed sequence** was only used by Kimura et al. (2010). The aim of its use to determine the temporal characteristics of the memory system underlying vMMN. Kimura et al. (2010) used a SSSSDSSSSDSSSSD sequence and varied the ISI across sequences. They found, that during rapid presentation (ISI=80 ms) the sequential regularity was represented, i.e. no vMMN was elicited. However, in case of slower presentation (ISI>=400 ms) vMMN was elicited.

The **vanish paradigm** is a special form of the oddball sequence, in which the deviant event is the disappearing of certain parts of the standard. It was introduced by Sulykos, Gaál & Czigler (2017), and was used in a few other studies of our lab (Czigler et al., 2018; File et al., 2018; File & Czigler, 2018). An advantage of the vanish paradigm is that the ERP elicited by the vanishing part of an object is difficult to explain with adaptation, thus no control sequences are required. Another advantage is that the deviant related change is less salient compared to the traditional oddballs deviant, in this way chances are higher that the oddball sequence remains unattended.

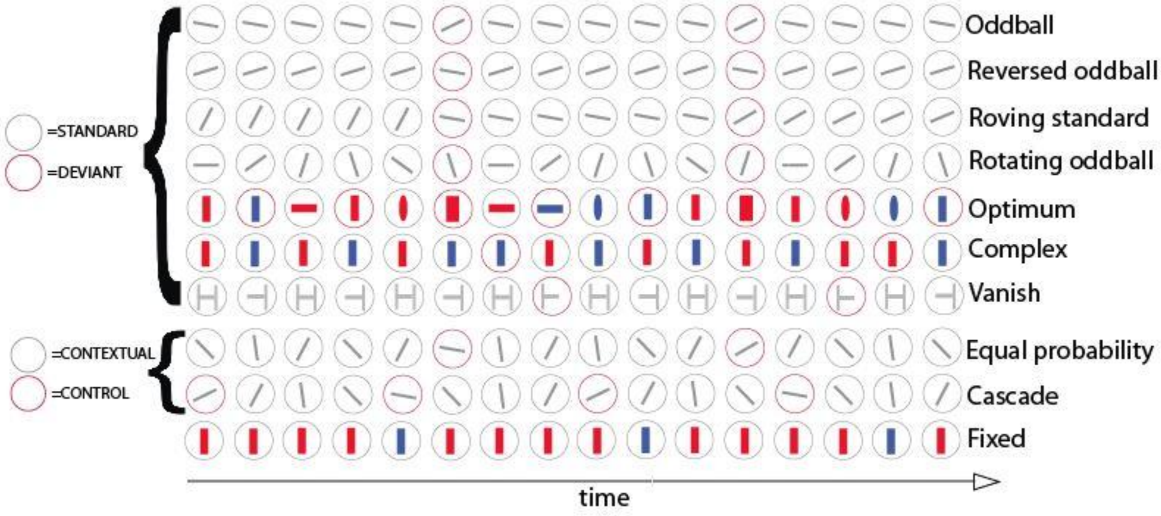

**Figure 2.1. Stimulus sequences used in vMMN studies**

#### 2.1.1.2 Primary task

vMMN can be elicited regardless of whether the subject pays attention to the oddball sequence or not (Czigler, 2007). This is a key property of vMMN, thus ensuring that the vMMN related stimuli remains outside the focus of attention has both theoretical and methodological significance in vMMN research (Stefanics & Czigler, 2014).

An important theoretical aspect is that attention strengthens the prediction error (Hohwy, 2012). Since vMMN is hypothesised to be the neural correlate of the error signal in the predictive mechanism (Stefanics et al., 2014), it is assumable that deviant stimuli in the focus of attention will elicit vMMN with enhanced amplitude.

The methodological aspect, as Stefanics and Czigler (2014) highlights, is that task-relevant, attended stimuli often elicit posterior negativities in comparable latencies (e.g. Czigler & Csibra 1990, Kenemans et al., 1993) and it is difficult to isolate those responses from the vMMN component. Therefore, control for attention is a crucial part of every vMMN study.

The control for attention is ensured with the so called primary task. The rationale behind is that while participants perform certain task, it is improbable that they will pay attention to the task irrelevant sequence of vMMN related stimuli. Therefore, in theory, the ideal task requires continuous attention to prevent shifts between the task and the vMMN related stimuli. In the following, primary tasks used in vMMN studies will be presented.

Some of the early studies investigating the existence of vMMN were using intermodal paradigms, where the attended stimulus was auditory, while the non-attended stimulus sequence was visual. The already mentioned study of Nyman et al. (1990) for example presented auditory, visual and auditory and visual oddball sequences together. Cammann (1990) also used auditory oddball sequence for controlling attention, subjects were instructed to detect the acoustic deviances while they were fixating to a task irrelevant visual oddball sequence. In another study (Iijima et al., 1996) subjects were listening to the radio, while visual stimulation was presented. This research practice is probably rooted in the MMN research protocol, where the primary task is usually visual. As Stefanics & Czigler (2014) later points out, in visual paradigms auditory primary task is not effective due the relative dominance of vision over hearing, so visual task is required.

Because of this consideration, intermodal paradigms are almost entirely vanished from the modern vMMN research practice and visual tasks took place. In some studies the task relevant object contains the task irrelevant change; for example when the task is to detect the changes of the corners of a bar (from squared to rounded), and its task irrelevant feature is that it is occasionally changes its orientation (Kimura, Katayama & Ohira, 2008). The problem with this procedure is that it is not continuous and it is hardly unlikely that attention can be "switched off" for certain feature changes happening in the focus of attention. In other studies the task is a central detection task, where the to be ignored vMMN related stimuli is presented to the background. The central task can be the detection of the occasional turning of a cross (e.g. Kecskés-Kovács et al., 2013; Maekawa et al., 2005), or the detection of the size change of an object (Kimura & Takeda, 2015). A similar, although more strict control is the so called ball-tracking task, where participants are asked to keep a moving ball at the center of the screen with a gamepad, while stimuli is presented in the background (Heslenfeld, 2003; Study I and II). It is considered a more strict control compared to the central detection task, because it requires continuous responses from participants. However, in such situations it is really difficult to not attend to the irrelevant stimuli, thus Czigler & Pató (2009) argue, that task irrelevant stimuli should be presented outside of the focal attentional field. Taking this into account, Sulykos et al. (2015) developed a paradigm which includes a discrimination and a tracking task, in which subjects are playing a videogame in the upper 1/3th of the screen, while the task irrelevant sequence is presented in the lower 2/3d of the screen.

### 2.1.2. The effect of primary task on MMN

Considering the great heterogeneity of the used control procedures for attention and their assumed effectiveness it is important to investigate their effect on MMN. By doing that, the attention dependence of MMN can be investigated in an indirect manner. Taking Lavie's (1995) perceptual-load theory into account, the difficulty of the primary task determines the allocation of attention to the task irrelevant information. So, if task difficulty does not effect vMMN, the neural mechanism that generates vMMN is considered attention-independent (Kimura & Takeda, 2013). In the following, studies investigated the effect of task difficulty on vMMN will be presented.

Pazo-Alvarez et al. (2004) investigated the effect of task difficulty in a motion-direction experiment. They used a central task with two levels of difficulty, while the task-irrelevant oddball sequence was presented to the left and right side of the screen. An unexpected result was that both the standard and deviant related ERP components had greater amplitude in the difficult condition, but vMMN did not differ between conditions. A limitation of the study is that the task did not require continuous attention, hence attention shifts to the oddball sequence cannot be ruled out (Pazo-Alvarez, Amenedo, & Cadaveira, 2004). In another experiment Kremláček et al. (2013) used three levels of task difficulty, while motion oddball sequences were presented in the periphery, and found no task load effect on vMMN. Similarly to the previous experiment, the task did not require continuous fixation. Heslenfeld (2003) used a tracking primary task in which continuous attention was needed for high performance and found no vMMN related effect as a function of task difficulty. Yucel et al. (2007) used event-related fMRI method to investigate the effect of task difficulty on the detection of task-irrelevant colour changes. They used visuomotor search task with two levels of difficulty, and found significantly reduced hemodynamic activity in the difficult condition in response to the deviant stimuli. Kimura & Takeda (2013) applied an equal probability sequence to investigate the effect of task load on adaptation free, genuine vMMN. They found that the latencies of the genuine vMMN was delayed in the difficult condition.

As another aspect of the influence of the primary task on vMMN, Czigler & Sulykos (2010) investigated the effect of visual feature similarity between the task-related and task independent (vMMN related) stimuli. They found, that in case of matching task-relevant and irrelevant visual features (e.g. orientation-orientation) vMMN had reduced amplitude accompanied by decreased performance, compared to the non-matched conditions (e.g. colour-orientation). This interaction suggested a competition between the processing of task-relevant and irrelevant stimuli when they were in the same category.

Another, more explicit approach was used in Czigler & Pató's experiment (2009), where vMMNs elicited by unnoticed deviants or by noticed changes were compared. They presented a sequence of grid-like stimuli in the background while participants performed a detection task in the center of the screen. The grid stimuli were presented in a roving-standard sequence, that is, series of identical stimuli (10-15) were followed by another sets of identical stimuli, and every first stimulus of the microsequences is considered as a deviant. In the first half of the experiment participants were not informed about the sequential regularities of the background sequence (by oral report, they did not notice it). In the second half of the experiment however, they were explicitly informed about the nature of the sequence in the background. In the first part of the experiment deviants elicited vMMN over the right posterior electrode locations in the 270-290 ms and in the 360-375 ms range, while in the second part of the experiment vMMN emerged in an earlier latency range with wider distribution. The results indicate, that the effect of attention not only enhances the activity, but results in a qualitatively different evoked response compared to automatic change detection.

### 2.1.3 Underlying processes

Following Kimura's (2012) thread, I will introduce theories explaining the possible underlying mechanisms of visual MMN with their limitations. The firs and the simplest account is the iconic memory account, which states that vMMN is elicited, if the incoming stimulus is incongruent with the iconic memory of the immediately presented standard. Iconic memory is described as a very brief (<1000 ms), pre-categorical, large capacity memory store (Sperling, 1960).

This theory, however, failed to explain the results of experiments using different number of stimulus repetitions preceding the occurrence of vMMN. Kimura et al. (2006c) used a random sequence consisting of two stimuli with equal probability (A and B, 50% each). Visual MMN was elicited, if four identical stimuli preceded a fifth, different one, e.g. AAAA**B**, but not in case of three, two or one stimulus trains (AAAB, AAB or AB).

This result indicates, that the number of repetitions of the standard might play an important role in the generation of vMMN.

This observation led to the extension of the iconic memory account, and the generation of vMMN was associated to a sensory memory system, in which the repetition of the standard stimuli builds up a memory trace. The incoming stimuli and the memory trace is compared, if they do not match, vMMN is elicited. Although this account was suitable to explain the majority of vMMN experiments, Kimura (2012) draw attention to a few important exceptions. Kimura et al. (2010b) observed vMMN elicited by the first standard preceding a deviant, which cannot be explained in the terms of sensory memory trace account, since the memory trace built up by the standards always matches with an incoming standard, so no vMMN should occur in response to any standard. In another experiment (Kimura et al. 2010c) oddball and fixed sequences were presented (SSDSSSSDSSSD vs. SSSSDSSSSDSSSSD…), with various inter stimulus intervals between blocks of 160, 480 and 800 ms. In case of the shortest ISI, vMMN had reduced amplitude in the fixed condition compared to the traditional oddball. The sensory memory trace account is not suitable to explain this observation, since it predicts, that every deviant will elicit vMMN that is preceded by sufficient number of standards. Also, Czigler et al. (2006) and Kimra et al. (2011a) both used regular stimulus patterns interrupted by infrequent repetitions; AABBAABBAABBB and ABABABABB respectively. In both experiments vMMN was elicited by the irregular stimulus repetitions, again, contradictory to the memory trace hypothesis.

Kimura (2012) argues, that the above findings indicate that, rather than the physical parameters of stimulus deviations, visual MMN is sensitive to violations of a regular sequential pattern that is repeatedly presented in a stimulus sequence. This leads to the assumption that the memory representation that underlies the generation of visual MMN must encode a regular sequential pattern (i.e., regularity representation; see Czigler, 2007, 2010) and visual MMN is elicited when a current visual stimulus violates the regular sequential pattern.

The regularity representation account gives plausible explanation for most vMMN studies, except one, as Kimura (2012) argues: Stefanics et al. (2011) used sequences of four stimulus pairs with different probabilities (AA 45%, BB 45%, AB 5%, BA 5%). Visual MMN was elicited by the second element of the improbable pairs, e.g. AA-BB-

BB-AA-A**B,** which is difficult to interpret in the sequential regularity account, since no concrete sequential pattern was present, but an abstract inter-stimulus relationship, therefore there was no stimulus representation that the incoming stimuli could be compared to. The assumption that the memory system underlies vMMN forms predictions based on the statistical regularities of the environment proposes a solution to the aforementioned problem with abstract sequences (Kimura, 2012).

Another, different theory is the so called adaptation account, which deduces the difference between the ERPs elicited by the standard and the deviant to a response decline in response to the repeating standard stimuli. At the time the dissertation was written, the latter two frameworks – predictive coding and adaptation – had the most significant impact on vMMN research, thus a more detailed presentation is adequate.

#### 2.1.3.1 Adaptation account

Adaptation is an intensively studied phenomena of neuroscience. It refers to the declined response to repeated stimuli relative to novel stimulus (Auksztulewicz & Friston, 2015). It is a well-known effect at each level of brain activity, from single cell recording (Sawamura, Orban, & Vogels, 2006) to conscious experience (Clifford, 2002; Gibson, 1937; Krekelberg, Boyton, & Wezel, 2006) and has been labelled as repetition suppression, adaptation, refractoriness, habituation, or stimulus specific adaptation (SSA). Traditionally it has been attributed to simple mechanisms such as neural fatigue (Grill-Spector, Henson & Martin, 2006), but its dependence on statistical regularities of the environment raised the possibility that it is the consequence of predictions (Summerfield et al., 2008).

Successive presentation of the standard stimuli is subject of adaptation, which – at least partly - contributes to the deviant-minus-standard difference. A few explanations have attempted to attribute the whole deviant-minus-standard difference as a repetition-related activity decrease of the standard response (e.g., May & Tiitinen, 2010, in the auditory modality; Kenemans, Jong, & Verbaten, 2003, in vision). However, based on the results of control experiments, it is more likely, that the neural correlate of adaptation only explains the MMN difference wave partly (e.g. Kimura et al., 2009; Study I.). Figure 2.2 shows a schematic illustration of the deviant-minus-standard difference wave, genuine vMMN, and adaptation.

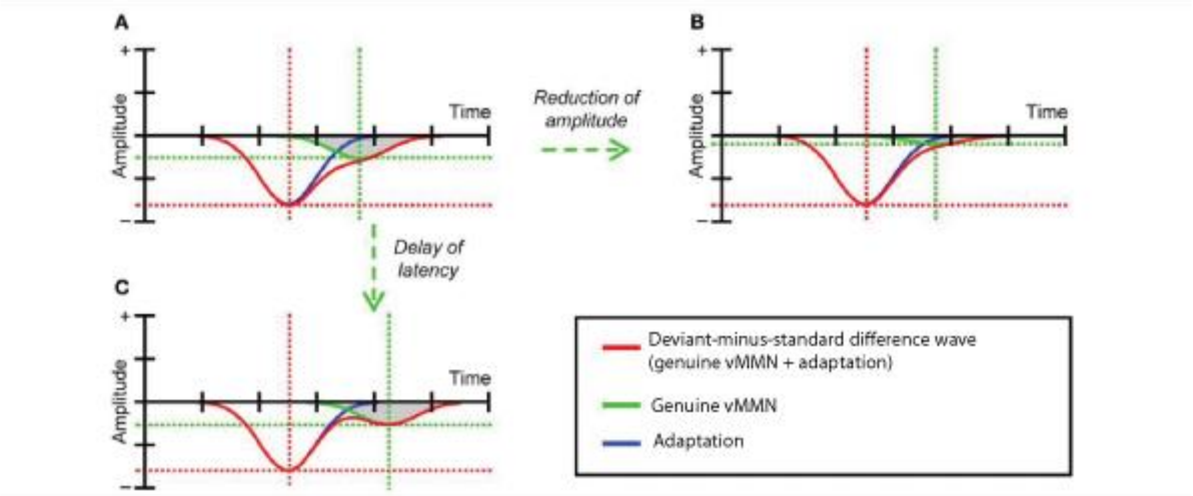

**Figure 2.2. (A) A schematic illustration of the deviant-minus-standard difference wave, genuine vMMN, and adaptation. (B) The modeled deviant-minus-standard difference wave as the sum of visual MMN with reduced amplitudes and adaptation. (C) The modeled deviant-minus-standard difference wave as the sum of visual MMN with delayed latencies and adaptation. (figure is modified from Kimura & Takeda, 2013; Figure 1, pp.2.)**

Kimura et al. (2009) applied an equal probability control consisted of bar stimuli of different orientations and found that adaptation explained the early, 100-150 ms range of the deviant-minus-standard difference wave, while the later, 200-250 ms range was contributed to deviant related effects, termed as genuine vMMN. Study I elaborated this topic, and used cascade control sequence of bar stimuli of different orientations in Experiment 1 and equal probability control sequence of windmill patterns in Experiment 2 and 3. We found that in case of bar stimuli the whole deviant-minus-standard difference wave was the consequence of adaptation, however the deviant-minus-standard wave elicited by the windmill patterns showed a similar origin to the one reported by Kimura et al., (2009). This result leads us to the assumption, that the mechanisms underlying vMMN might not be uniform, but depends on stimulus complexity. The results of Study II - where adaptor sequences were applied with identical stimuli to Study I – supported our assumption.

It is important to note, that adaptation and refractoriness are often used as synonyms in the vMMN literature. Here we followed O'Sheas (2015) reasoning and used the term “adaptation” instead of “refractoriness”. In this context adaptation is a rather passive process equivalent to the response decrease of the neurons due to continuous stimulation (but see Thesis I, Footnote 1.).

#### 2.1.3.2 Predictive coding framework

Predictive coding is the latest framework explaining MMN at the time the dissertation was written, so it is worth to be introduced in details.

The predictive coding framework has gained popularity in the last couple of decades, with Karl Friston worlds: “…predictive coding became dominant models in cognitive neuroscience, marking a watershed between 20th-century thinking about the brain as a glorious stimulus–response link and more constructivist 21st century perspectives that emphasized an active sampling of the sensory world.” (Friston, 2018). The motif of the framework is that the brain generates models of the environment which carries predictions of the following states, instead of representing it directly. This working mechanism is assumed to be more energy efficient than direct representation, which must have been an important factor for brain evolution (Kong et al., 2018), manifested in a trade-off between energy cost and performance (Betzel et al., 2016). Biological solutions for information processing are many orders of magnitude more effective than any digital system developed so far. This advantage can be attributed to that biological neural systems rarely represent input quantities directly, but in relative manners, which leads naturally to systems that learn about their environment (Mead 1990). Taking Aitchison & Lengyels’ (2017) examples, the human retina preprocesses the signal based on the neighbouring cells (Kuffler, 1953) and the recent past (Hartline,1938), and the visual cortex strongly modulated by the spatial and temporal context of stimuli (Cavanaugh, Bair, & Movshon, 2002). A great example from the visual cortex is that V1 cells are responding to illusory contours that are not physically present, but inferred from the context (Grosof, Shapley, & Hawken, 1993).

Overall, Aitchison & Lengyel (2017) argues, there are many evidences that neural responses in sensory cortical areas are as influenced by predictions and expectations as by the actual sensory input themselves (Kok, Jehee, & de Lange,2012). With Helmholtz’s words, who distinguished between perception and sensation: “It may often be rather hard to say how much from perceptions as derived from the sense of sight is due directly to sensation, and how much of them, on the other hand, is due to experience and training” (see Pollen 1999). The predictive coding framework provides a theoretical framework how contextual signals are computed and integrated with sensory ones. The framework itself is based on a simple idea; instead of representing the input directly, it is often preferable to represent the prediction error, the difference between sensory input and a prediction information (Aitchison & Lengyel, 2017). The reason for doing that is that if the prediction is correct no costly processing is required (Mead, 1990). A great example in vision is that spatio-temporal receptive fields of ganglion cells use the past and the surround to predict the current light intensity at the centre (Barlow, 1961).

Perception can be interpreted in a hierarchical predictive framework (Friston, 2005), which not only describes information flow between neighbouring processing stages but throughout the entire system. Figure 2.3 shows a simplified scheme of the hierarchical predictive coding framework (Friston 2005). In this framework there are top-down connections carrying predictions, which are regulating the operation of lower stages, and also bottom-up connections carrying prediction errors (MMN and vMMN), which are updating the higher level models forming the predictions.

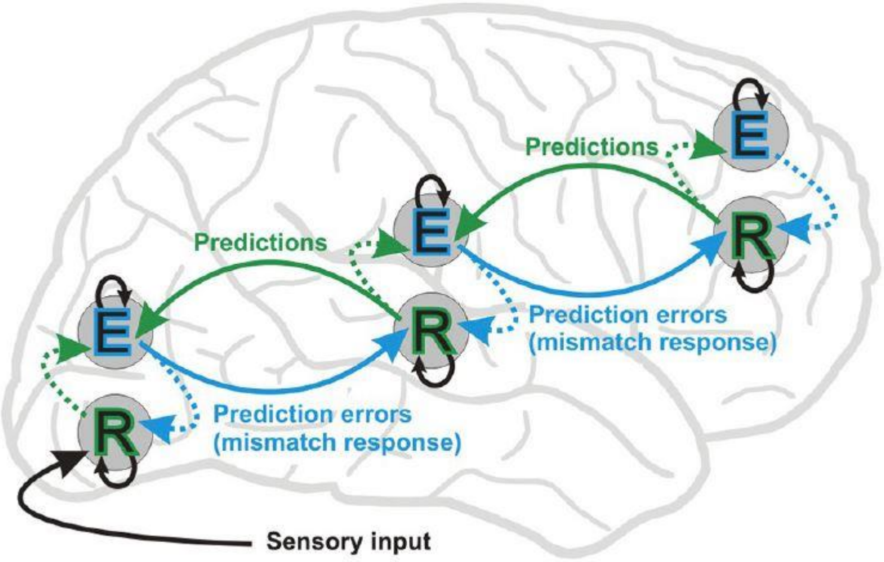

**Figure 2.3. Simplified scheme of the hierarchical predictive coding framework of Friston (2005, 2008, 2010). The figure shows message passing between two putative neuronal populations (E: error units; R: representation units). Bottom-up forward connections convey prediction errors (MMN and vMMN) and top-down backward connections carry predictions, which explain away prediction errors (adaptation). (in Stefanics et al., 2014; Figure 1, pp. 4).**

Regarding the predictive coding account, after a few presentations of the standard stimuli the brain builds up a model based on the statistical regularities of the sensory input, which carry predictions about the predicable future events. Appearance of a deviant stimuli does not match the predicted event, resulting in an error signal sent to the higher information processing stages responsible for updating the predictive model (Stefanics et al., 2014).

### 2.1.4 Cortical Sources

Czigler et al. (2004) assumed, that the cortical source of vMMN is probably localized in the occipital lobe, as the maximum amplitude of the deviant related activity is measured there. They based their experiment on the observation, that exogenous stimulus-specific ERP components have different polarity between upper and lower visual field presentation (Jeffreys & Axford, 1972). Thus, a polarity change in vMMN between the lower and upper visual filed presentation would have serve as an indirect evidence about its retinotopic prestriate visual sources . Accordingly, oddball sequences were presented either to the upper or lower half of the screen, while participants performed a detection task. Deviant stimuli elicited vMMN in the lower but not in the upper visual field, and the latency of vMMN was longer than the ERP components localized to the primary visual cortex, thus the assumed source was the prestriatal cortex (Czigler, Balász & Pató, 2004b).

More direct evidence emerged from the ERP studies using sLORETA source localization method. Kimura et al. (2010) localized the source of genuine vMMN in response to orientation deviancy to nonprimary visual areas, such as the right cuneus and to the frontal lobe. An important finding was that the early, adaptation related subcomponent of vMMN had different sources, localized to the primary and nonprimary visual areas. This result suggests that the sensory and cognitive change detection systems are fostered by distinct neural structures (Kiumra et al., 2010). The results of thesis study 1 confirmed the findings of Kimura and colleagues regarding the posterior sources; we also found the source of genuine vMMN to be located to the occipital lobe (right lateraloccipital cortex, left and right lingual gyrus, left and right pericalcarine cortex, left and right precuneus).

The study of Urakawa et al., (2010) allowed more accurate source localization with led stimulation and magnetoencephalography recordings, although no control procedures were applied for adaptation effects. The results of multi-dipole analysis showed that middle occipital gyrus is an important cortical area relating to the sensory memory-based visual change-detecting system (Urakawa et al., 2010).

The study of Susac et al. (2013) used magnetoencephalography (MEG) and spatio-temporal source localization to determine the generators of vMMN. They reported neuromagnetic sources of vMMN localized in the occipital cortex. The source of vMMN and adaptation related activity (evoked by equal probability gratings) had different sources (Susac et al., 2013).

The results of Yucel et al. fMRI experiment (2007) are consistent with the results of EEG and MEG studies, despite the methodological shortcomings (i.e. no oddball reverse control (which increase the possibility of detecting stimulus specific activations), or control for adaptation was used). Due to the methodological advantages however it allowed the researchers to define a more detailed network underlying the automatic change detection process. The deviant stimuli were followed by increased hemodynamic response in V1 and V2. Also, the geniculo-striatal pathway was activated (occipital lobe → fusiform gyrus → posterior parietal regions) and the tecto-pulvianr pathway (superior colliculus and thalamic regions). Also, significant activity was observable in the prefrontal regions, which showed reduced activity parallel to the increased difficulty of the primary task (Yucel et al., 2007).

# Chapter 3. Research questions

This thesis includes four ERP experiments, investigating basic properties of vMMN. The aim of Study I and II was to investigate the rate of adaptational effects in the deviant-minus-standard difference wave. The aim of Study III and IV was to investigate the effect of the focus of spatial attention on the generation of vMMN.

The main research questions and hypotheses were the following:

Study I: The aim of Experiment 1 was twofold: (1) separate the effects of violating a sequential rule (genuine vMMN) from the decreased activity in response to repeated stimuli (stimulus-specific adaptation; SSA) for simple stimuli (array of bars), and (2) test a new control paradigm (cascade) adapted from acoustic MMN research (Ruhnau et al., 2012). Kimura et al., (2009) presented oddball and equal probability control sequences, with a single bar of different orientations as stimuli. Based on their findings, we expected the emergence of a two component deviant-minus-standard difference wave.

Hypothesis: The first component will reflect adaptation related effects, while the later component will reflect genuine vMMN. We also hypothesized, that the deviant-minus-cascade control difference wave will have bigger amplitude than the deviant-minus-equal probability control difference wave.

The aim of Experiment 2 was also to separate the effects of genuine vMMN from SSA, but for complex stimuli (windmill patterns). Based on the study of Maekawa et al. (2005) using windmill patterns in passive oddball paradigm, we expected the emergence of a pronounced two component deviant-minus-standard difference wave.

Hypothesis: The first component will reflect adaptation related effects, while the later component will reflect genuine vMMN.

The aim of Experiment 3 was to investigate the observed asymmetry of the difference waves in Experiment 2 elicited by the different windmill patterns. Our intent was explanatory in nature, testing the validity of two possible explanations: (1) higher order account emphasized the cause of the differences in the complexity differences of the stimuli, while (2) the low level account attributed the differences for the overlapping edges of the stimuli, e.g. for adaptation related effects.

Hypothesis: Both higher and lower level explanation were plausible.

Study II: The aim of Study II was to investigate the relation between the effects of activity decrease following an adaptor (stimulus specific adaptation) and the effects of an infrequent stimulus within sequences of frequent ones. To this end, ERPs were compared recorded in two different paradigms; a passive visual oddball paradigm and an adaptation paradigm. Similarly to Study I, in Experiment 1 line textures and in Experiment 2 windmill patterns were presented. In Experiment 1 two adaptation sequence length was used (filled and squeezed).

Hypothesis:

> Experiment 1: Adaptation effect will be larger in case of longer adaptor stimuli (filled condition). The deviant-minus-control difference will not differ from 0 significantly.
>
> Experiment 2: We expected that the effect of adaptation will influence the earlier part of the difference wave, whereas in the later part the emergence of genuine vMMN was expected.

Study III: The aim of Study III was to investigate the effects of spatial attention on vMMN. VMMN has been described as “pre-attentive” or “attention-independent” (Kimura, 2012), based on the results of experiments that varied the difficulty of the primary task (Heslenfeld, 2003; Pazo-Alvarez et al., 2004a). Later studies however reported the modulation of vMMN as a function of task difficulty (Kimura et al., 2008d; Yucel et al., 2007) or direction of attention (Czigler & Sulykos, 2010; Kimura et al., 2010d). Based on the contradicting results, Kimura (2012) propose, that “unintentional” is a more appropriate description, with the need to describe which part of the process is attention-sensitive and insensitive. Study III investigated the sensitivity of the vMMN generating process to the focus of spatial attention. The aim of the study was to examine the effect of distance between the focus of attention and the task-irrelevant sequence on automatic change detection. To this end passive vanish stimulus sequences were presented either close or far from the primary task, in a modified Posner task-like paradigm, which ensured fixed retinal position. We assumed, that when the task-irrelevant oddball sequence is closer to the focus of attention, a larger effect of spatial attention is expected on the processing of vMMN-related stimuli.

Hypothesis: Both facilitative and inhibitory effects, or the lack of effect was a reasonable outcome of the experiment, thus no regarding hypothesis was formed.

Study IV: The aim of Study IV was to elaborate the research question of Study III. Since vanish stimulation is rare in ERP studies, we found it necessary to repeat Study III with regular, onset stimulation for better generalization. Also, it is possible that the lack of distance effect was the consequence of the offset stimulation itself, since vanishing parts of objects are less salient than abrupt stimulus onsets (Jonides & Yantis, 1988). To control for the effect of adaptation, additional equal probability sequences were applied.

Hypothesis: Based on the results of Thesis III, no modulatory effect of the attentional focus was expected.

# Chapter 4: Visual mismatch negativity (vMMN) for low- and high-level deviances: A control study[7]

## 4.1 Introduction

Change blindness studies have shed light on the poor ability of humans to explicitly detect changes between two successive visual images that are separated by a blink or saccade (Simons & Levin, 1997). Traditional interpretation of the phenomenon states that representations outside the focus of attention are volatile, thus focal attention is necessary to detect changes in the visual environment (Ronald A. Rensink, 2002). However, an increasing body of studies shows that the human brain is capable of detecting even small changes, especially if such changes violate automatic (non-conscious) expectations based on repeating experiences (Stefanics, Kremlacek & Czigler, 2014). Over the past 15 years, many studies have demonstrated that unattended visual stimuli that violate the rules of a stimulus sequence (deviants) elicit larger responses in event-related brain activity than regular (standard) stimuli. The difference between the standard and the deviant stimuli is called visual mismatch negativity (vMMN), which is considered to be the visual homolog of the auditory mismatch negativity (MMN) component of event-related potentials (ERPs; for reviews, see Czigler, 2007; Kimura, 2012; Stefanics, et al., 2014). The traditional paradigm in the field of vMMN research is the passive oddball paradigm, in which task-unrelated stimulus sequences of infrequent (deviant) and frequent (standard) stimuli are presented.

The ERP difference between the effects of the deviant and standard stimuli can be either the consequence of an activity decrease in response to the standards over the sequence or an additional activity elicited by the deviants. An activity decrease in response to repeated stimuli is a well-known effect at each level of brain activity, from single cell recording (Sawamura, Orban & Vogels, 2006) to conscious experience (Gibson 1937; Clifford, 2002, Krekelberg, Boyton & Wezel, 2006) and has been labelled as refractoriness, habituation or stimulus specific adaptation (SSA) (see *Footnote 1*). A few explanations have attempted to attribute the whole deviant-minus-standard difference as a repetition-related activity decrease of the standard response (e.g., May & Tiitinen

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[7] File, D., File, B., Bodnár, F., Sulykos, I., Kecskés-Kovács, K., Czigler, I. (2017) Visual mismatch negativity (vMMN) for low- and high-level deviances: a control study. Atten Percept Psychophys, 79(7):2153-2170. doi: 10.3758/s13414-017-1373-y.

(2010) in the auditory modality, Kenemans, Jong & Verbaten (2003) in vision). However, most theories explaining MMN, in addition to the repetition related response decrement are assuming a process attributed to the novel stimuli. Winkler, Karmos & Näätänen (1996) proposed a model-adjustment account, which states that the MMN reflects on-line modifications of a perceptual model (see also Czigler 2007 for vMMN). On a functional level, the model predicts the forthcoming stimulation, and updating such a predictive model is necessary when the incoming stimulus does not match the predicted stimulus (Friston, 2005; Garrido, Kilner, Stephan & Friston, 2009). This model was extended to the visual MMN; the successive visual stimulation is extracted into an abstract sequential rule, which is encoded as a prediction for the forthcoming visual events (Friston, 2003, 2005; Garrido et al., 2009; Kimura, 2012; Winkler & Czigler, 2012; Stefanics et al., 2014).

Although relationship of the adaptation and prediction theories has remained an unsettled issue, researchers on the field have attempted to develop methods for separating repetition-related effects from deviant-related additional activity. The most frequent method of separating the two sources of difference is equal probability control (Schröger & Wolff, 1996; Jacobsen & Schröger (2001) in the auditory modality, Czigler, Balázs and Winkler (2002), Astikainen, Lillstrang & Ruusuvirta (2008), Kimura, Katayama, Ohira & Schröger (2009), Astikainen, Cong, Ristaniemi & Hietanen (2013), Amando & Kovács, (2016) in vision). Within the equal probability sequence, stimuli physically identical to the oddball's deviant are embedded in the sequence of other equiprobable stimuli. Within such a sequence, the probability of each stimulus type is equal to the probability of the oddball deviant. Thereafter, the ERPs to the oddball deviant and the equal probability control stimuli are compared. In the control sequence, there is no way of developing a strong memory representation (or a regularity-related memory representation) for any of the stimuli, and therefore, no additional activity is expected within the ERPs that are elicited by the equivalent control. A critical feature of the equal probability control paradigm is that the average physical separation between the control and other equiprobable stimuli is equal or larger than between the standard and deviant stimuli. This excludes the possibility of a response decrement to the control stimuli relative to the deviant due to the additional activations of the afferent neurons responding to control stimuli by other equiprobable stimuli (Jacobson & Schröger, 2001; Kimura et al., 2009). The difference between the activity elicited by the deviant and the control is called “genuine MMN” (gMMN), i.e., an additional activity without the involvement of adaptation effects. In the auditory modality, the emergence of gMMN was frequently demonstrated (e.g., Schröger & Wolff, 1996; Jacobsen & Schröger (2001), Jacobsen, Schröger, Horenkamp & Winkler (2003), Ruhnau, Herrmann & Schröger (2012)).

In the following, a brief summary is given on vMMN studies applied control sequences. In the case of color deviancy, Czigler et al. (2002) obtained similar deviant-minus-standard and deviant-minus-control difference potentials in an early, 120-160 ms range. Pazo-Alvarez, Amenedo and Cadaveira (2004) obtained similar differences for motion-direction, again in an early (145-165 ms) range. In a recent MEG study with spatial frequency deviants, Susac, Heslenfeld, Huonker and Supek (2013) recorded differences in the 100-160 ms range and reported distinct localization for the gvMMN and the deviant-minus-standard difference. Facial emotion vMMN was investigated in two studies. Li, Lu, Sun, Gao and Zhao (2012) obtained early onset (~100 ms) of both deviant-minus-standard and deviant-minus-control differences, both in an early (100-200 ms) and later (200-350 ms) range. Importantly, in the early range, the amplitude of gvMMN was smaller than the deviant-minus-standard difference wave. However, Astikainen et al. (2013) obtained different scalp distributions between the oddball (bilateral) and the equal probability (right-dominant) conditions in the earlier range (peaking at 130 ms). In the later component of the difference potential, peaking at 170 ms, no such difference was observable between the conditions. Orientation deviancy was investigated by Astikainen et al. (2008) and Kimura et al. (2009). In both studies, the stimuli were single bars. Astikainen et al. (2008) obtained negativities in the oddball and control comparisons in similar ranges (185-205 ms), but the surface distribution of the gvMMN was narrower. In the study reported by Kimura et al. (2009), however, the application of equal probability control eliminated the difference in the range that corresponded to a posterior negativity (N1), but in a later latency range (200-250 ms), gvMMN emerged. Kimura et al. (2010) reported similar results. Kimura and Takeda (2013) investigated orientation-related vMMN in response to a pattern that consisted of eight lines around the center of the visual field (the location of a size-discrimination task). Again, the use of equal probability control eliminated the early part of the response but preserved a later difference as gvMMN. On the basis of these results, Kimura et al. (2009) argued that in vision, an early, standard-related process is followed by a memory-related mismatch process, and the later process is a correlate of a predictive mechanism.

As described above, vMMN does not have a uniform latency range. In many studies, complex or higher-order (*see Footnote 2)* deviances elicit a temporary wide (from approximately 100 to 350 ms) two-component vMMN (faces: Zhao & Li, 2006; Astikainen & Hietanen, 2009; Li et al., 2012; Stefanics et al., 2012; Csukly, Stefanics, Komlósi, Czigler & Czombor 2013, Kecskés-Kovács, Sulykos & Czigler, 2013a; Wang et al., 2014, categorical stimuli: Kecskés-Kovács et al., 2013b, Wang, Miao & Zhao 2013)). In contrast, simple deviances, such as orientation, colour or motion direction, often elicit a temporary restricted, one component negativity between 100 and 200 ms post stimulus (e.g., orientation: Czigler & Sulykos, 2010; Sulykos & Czigler, 2011; Takács, Sulykos, Czigler, Barkaszi & Balázs 2013, color: Czigler et al., 2002, motion direction: Pazo-Alvarez et al., 2004). It is important to note that this observation cannot hold true for all vMMN studies; for example, Kimura et al. (2009) recorded two-component vMMN in response to orientation change in the 100-250 ms latency range. A possible explanation for the discrepancy is that in studies that reported long-lasting negativities for orientation deviances, either single bars (Astikainen et al., 2004, 2008, Kimura et al., 2009, 2010) or a frame-like pattern of bars (Kimura & Takeda, 2013) were presented, whereas in studies that reported single negativities, line textures were presented (Czigler & Sulykos, 2010; Sulykos & Czigler, 2011; Takács et al. 2013). Also, among one dimension of deviance the characteristics of the deviant related response could vary as a function of stimulus properties. Heslenfeld (2003) found, that an early refractoriness (60-100 ms) effect was present only for high spatial frequencies, whereas a negative response in the 120-160 ms range was present for both low and high frequency deviants, followed by a later (160-200 ms) component of the difference.

The aim of the present study was to investigate the relationships between the gvMMN and the repetition-related decrease of the ERP activity to the standard stimuli for both low- and high-level stimuli (see Footnote 2). To accomplish this goal, different control procedures were applied, with the aim of finding the right control for vMMN studies. Two types of deviancies were used. In Experiment 1, orientation deviancy was investigated in a texture-like arrangement because orientation deviancy has been studied in a fairly large body of studies; some of them also applied equal probability control. We investigated whether equal probability control could eliminate the expected early difference within the 100-200 ms range. In this study, we introduced an additional control procedure. As Ruhnau, Herrmann and Schröger (2012) noted, the equal probability control procedure eliminates the sequential rule of the oddball stimuli (identical stimuli follow each other), not only the effect of a particular physical feature. Sulykos (2017) argues, that standard stimuli in the oddball sequence might be accompanied by specific neural response to stimulus match. In this way the equal probability control sequence “over controls” the oddball sequence, since no stimulus match is present for the control stimuli. Thus the standard and the control stimuli not only differs by their probability but also by their predictability. Addressing this problem, Ruhnau et al. (2012) developed a new procedure that used equal probabilities, but the various stimuli were presented in regular sequences. We applied this procedure – the cascade paradigm - in the visual modality.

The other type of stimulus was the windmill pattern (Experiment 2), which was introduced by Maekawa et al. (2005) into vMMN research. These authors obtained two distinct deviant-minus-standard difference components in two subsequent latency ranges. We assumed that the two subcomponents might reflect different processes, SSA and gvMMN, in this way allowing us to precisely separate them with the use of equal probability control. Similar to Experiment 1, we introduced a new control paradigm (modified control) that was adapted from auditory MMN experiments (Jacobsen, Schröger, Horenkamp & Winkler, 2003). The application of this paradigm was driven by practical and theoretical consideration. From methodological aspects, it is important to know whether is it possible to correctly estimate the amplitude of the gvMMN without presenting all contextual stimuli with equal probability in the control sequence. The theoretical motivation was to investigate the effects of putative response overlap for the incoming stimuli. Considering the tuning curves of sensitivity of the afferent neurons in the primary visual area, similar stimuli are expected to stimulate partly overlapping neuron populations, which leads to higher level of adaptation in the sensory neurons, comparing to when diverse stimuli are presented. Since the physical difference of contextual and control stimuli are smaller in the modified control than in the equal probability control (see Figure 4.4), the overlap is expected to be larger in the modified control compared to the equal probability control. Utilizing an additional condition in which the supposed level of adaptation is different, might serve for a better spatial and temporal localization of the effect of decreased responsiveness in the deviant-minus-standard difference wave.

The structure of Experiments 1 and 2 are the same, and three types of comparisons were made: (1) deviant-minus-standard, (2) deviant-minus-equal probability control and (3) deviant-minus-cascade in Experiment 1 and deviant-minus-modified control in Experiment 2. For identifying the cortical sources of different processes, the sLORETA inverse solution was applied on the average ERP time series.

An additional experiment was conducted to clarify the results of Experiment 2. In Experiment 3, windmill patterns were presented in oddball sequences, which is partly a replication of Experiment 2.

## 4.2. Experiment 1

### 4.2.1 Introduction

In Experiment 1, the deviancy effects of orientation change are investigated using textures that consist of tilted bars. The stimuli were presented to the lower half of the visual field, and the task required central fixation. The task was a simple video-game (Sulykos et al., 2015). Four conditions were used: two oddball sequences, an equal probability control and the cascade paradigm (Ruhnau et al., 2012). Our aim was to determine the extent of the adaptation effect on the ERPs that were elicited in an oddball sequence.

### 4.2.2 Methods

#### 4.2.2.1 Participants

Fifteen volunteers (eight women; mean age: 23.26; SD=0.48 year) participated in the study for monetary compensation. They had no ophthalmologic or neurological abnormalities. Written informed consent was obtained from all of the participants prior to the experimental procedure. The study was conducted in accordance with the Declaration of Helsinki and was approved by the Joint Committee of Ethics of the Psychology Institutes in Hungary.

#### 4.2.2.2 Stimuli and experimental design

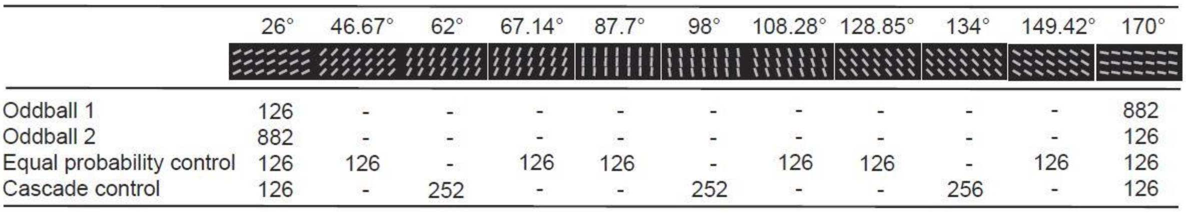
The four conditions consisted of bar patterns that had different orientations. Figure 4.1 illustrates the stimuli and their probabilities. During the experiment, a pool of 11 stimulus orientations was used (26°, 46.57°, 62°, 67.14°, 87.7°, 98°, 108.28°, 134°, 149.42°, 170°). The presented stimuli appeared against a black background (bar luminance of 36.67 cd/m$^2$). The visual angle of the individual bars was 1.26° (length) x 0.088° (width) from a viewing distance of 1.2 m. The bars were presented as a texture, which consisted of 3 rows and 7 columns, and thus, a total of 21 identical stimuli were presented to the lower two-thirds of the screen (17'', Samsung SyncMaster 740B, 60 Hz refreshing rate). The stimulus duration was 100 ms, and the average inter-stimulus-interval (ISI) was 500 ms (range: 450–550 ms, even distribution). The inter-stimulus interval was sufficiently long to prevent any type of motion percept.

During the oddball conditions, standards were presented with a probability of 87.5% and deviants with a probability of 12.5%. In one of the oddball conditions, 170° orientation stimuli served as the standard stimuli, and 26°orientation stimuli served as the deviant (Oddball 1). In the reverse oddball condition, the 26° orientation stimuli were the deviants (Oddball 2). Between two deviant stimuli, a minimum of 4 and a maximum of 10 standard stimuli were presented.

During the equal probability control condition, 8 different stimuli were presented, each with the probability of 12.5% (26°, 46.57°, 67.14°, 87.7°, 108.28°, 128.85°, 149.42°, 170°). Two identical stimuli never occurred successively. The difference between the standard and the deviant was 36°, while the minimum difference between the control and contextual stimuli was 20.5°. However, due to the random presentation, the average difference was greater than 36°.

During the cascade control paradigm, a regular sequence of 5 different stimuli was presented, which formed a chain of rising and falling micro-sequences (26°, 62°, 98°, 134°, 170°, 134°, 98°, etc.). The control stimuli (which were identical to the deviant stimulus of the oddball condition) were at the ends of the micro-sequences, and their probability of occurrence was the same as the deviants'.

All of the conditions totalled to 1008 stimuli, which were presented in 3 separated blocks in a random order.



| | 26° | 46.67° | 62° | 67.14° | 87.7° | 98° | 108.28° | 128.85° | 134° | 149.42° | 170° |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Oddball 1 | 126 | - | - | - | - | - | - | - | - | - | 882 |
| Oddball 2 | 882 | - | - | - | - | - | - | - | - | - | 126 |
| Equal probability control | 126 | 126 | - | 126 | 126 | - | 126 | 126 | - | 126 | 126 |
| Cascade control | 126 | - | 252 | - | - | 252 | - | - | 256 | - | 126 |

**Figure 4.1. Stimuli and their probabilities of Experiment 1 (times/experiment) in the oddball and control sequences**

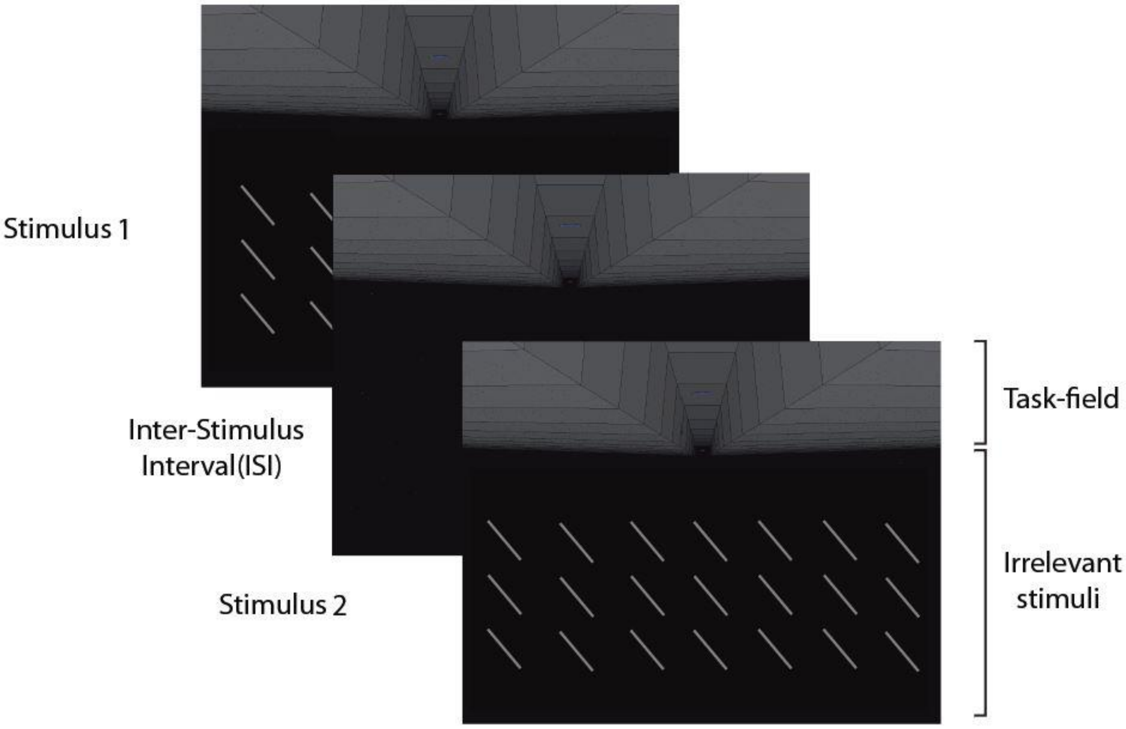


**Figure 4.2. An example of the stimulus display of Experiment 1.**

### 4.2.2.3 Task

To provide sufficient control of the participants' attention, the participants played a video game presented in the upper third of the screen while stimuli were presented in the lower two-thirds of the screen (see Figure 4.2). The participants had to control the movements of a spaceship to be able to avoid/catch certain approaching spaceships (one at a time). The task required focused attention on the location where the approaching spaceships appeared. For more details, see Sulykos et al. (2015).

### 4.2.2.4 Recording and measuring the electrical brain activity

The electroencephalographic activity was recorded (DC-70 Hz; sampling rate, 1000 Hz; Brain Vision recording system) with active electrodes placed at 64 locations according to the extended 10-20 system, using an elastic electrode cap (Acti-Cap). The online reference electrode was at FCz, and then, the activity was re-referenced offline to the electrode on the nose tip. Horizontal electrooculographic activity was recorded with a bipolar configuration between the electrodes that were positioned lateral to the outer canthi of the eyes. The vertical eye movement was monitored with a bipolar montage between the electrodes that were placed above and below the right eye. The impedance of the electrodes was kept below 10 kΩ.

EEG signals were filtered offline (0.1-30 Hz, 24 dB slope). Epochs of 500 ms, starting from 100 ms before the stimulus onset, were averaged separately for the standards, deviants and control stimuli. Trials with an amplitude change that exceeded +/- 100 μV on any channel were rejected from further analysis.

Only the responses from the standard preceding a deviant were included in the standard-related average ERPs, and orientations were not investigated separately. Three types of grand averaged differences were calculated: deviant-minus-standard (OddDiff), deviant-minus-equal probability Control (EQControlDiff) and deviant-minus-cascade control (CascDiff). The differences in these comparisons cannot be explained by stimulus-specific features because the standard, deviant and control stimuli had the same physical characteristics.

Based on previous vMMN studies (for review, see Czigler 2007), we expected the emergence of a deviant-minus-standard difference wave over the posterior electrode locations. To reinforce this expectation, we defined an electrode matrix, where the deviant-minus-standard difference wave differed from zero in the negative direction in at least 30 consecutive significant data points ($p<0.01$), based on the results of a point-by-point t-test applied on the whole scalp location. A 2x3 matrix of electrodes (PO3, POz, PO4, O1, Oz, O2) met this criterion, which consisted of two rows (anterior, posterior) and three columns (left, middle, right). However, because no laterality effects were present ($F(2, 28)=0.30$, $p=0.74$), to obtain easier traceability, two regions of interest were formed: parieto-occipital (PO4, POz, PO3) and occipital (O2, Oz, O1).

The amplitude values of the difference waves were calculated by averaging the amplitude values of all of the data points, which consisted of the sections defined by the point-by-point t-test on the difference waves.

### 4.2.3 Results

#### 4.2.3.1 Behavioural results

The average avoidance rate was 79%, while the average hit rate was 67%; thus, the average performance was 72.82% (standard error of the mean; S.E.N. =4.7%). There was no difference in the performance between the conditions.

#### 4.2.3.2 Event-related potential results

Figure 4.3 shows the ERPs and the difference potentials. The standard, deviant and control stimuli elicited a positive (P1) – negative (N1) – positive (P2) triphasic complex (Figure 4.3.A).

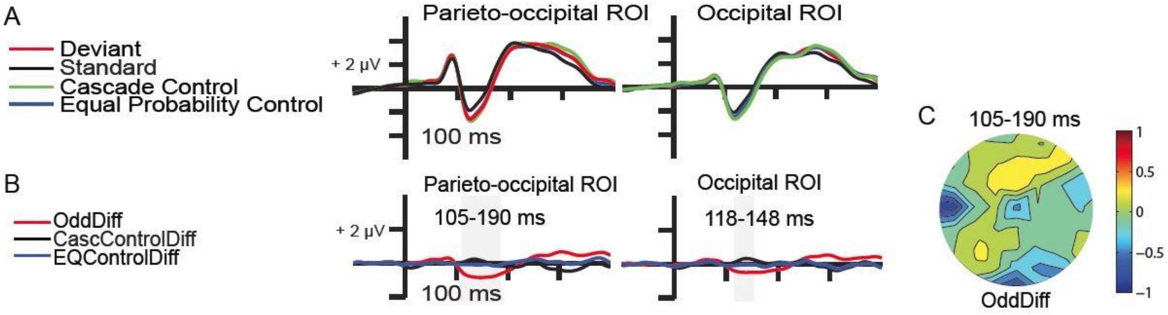


**Figure 4.3. Experiment 1: (A) Grand averaged ERPs elicited by deviant, standard, equal probability control and cascade control. (B) Grand averaged deviant- minus- standard, deviant- minus- equal probability control and deviant- minus- cascade control difference waves. (C) Topographical maps of the grand averaged difference waves within the 108–208 ms time-windows**.

The deviant–minus–standard difference differed from zero (t (14) =-4.3, p <0.01) at the parieto-occipital ROI in the 105-190 ms and in the 118-148 ms range at the occipital

ROI (t (14)=-2.98, p<0.01). Neither the deviant-minus-equal probability control, nor the deviant-minus-cascade control difference waves differed from zero, and the deviant-minus-control difference waves did not differ from each other in the given range. At the parieto-occipital region in the 105-190 ms range there was a significant difference between the amplitude values of the deviant-minus-standard (M=-0.69, SD=0.61) and deviant-minus-cascade control (M=0.04, SD=0,56); t (14)=-3.59, p<0.01, and for deviant-minus-standard and deviant-minus-equal probability control (M=-0.10, SD=0,34); t(14)=-4.60, p<0.01. Also at the occipital region, in the 118-148 ms range there was a significant difference in the amplitude values of the deviant-minus-standard (M=-0.43, SD=0.56) and deviant-minus-cascade control (M=0.25, SD=0,73); t(14)=-2.67, p<0.01, and for deviant-minus-standard and deviant-minus-equal probability control (M=-0.04, SD=0,39); t(14)=-2.75, p<0.01. An ANOVA with the factors Conditions (OddDiff, EQControlDiff, CascDiff) and ROI (parieto-occipital, occipital) revealed no latency differences between the difference waves. Table 4.1 shows the amplitude and latency values of the difference potentials.

| Region | Difference waves | 105–190 ms amplitude (µV) | 105 - 190 ms latency (ms) |
|---|---|---|---|
| Parieto-occipital | Deviant-minus-standard | -0.67 ± 0.15** | 144 ± 4.78 |
| | Devinat-minus-equal probability control | 0.03 ± 0.14 | 149 ± 10.50 |
| | Deviant-minus-cascade control | -0.09 ± 0.09 | 144 ± 6.20 |
| | | 118–148 ms amplitude (µV) | 118–148 ms latency (ms) |
| Occipital | Deviant-minus-standard | -0.43 ± 0.14 ** | 134 ± 5.03 |
| | Deviant-minus-equal probability Control | 0.24 ± 0.18 | 124 ± 6.14 |
| | Deviant-minus-cascade control | -0.04 ± 0.10 | 131 ± 6.21 |

**Table 4.1. Experiment 1: Grand averages of peak latencies and mean epochs of the difference waves measured at Parieto-occipital and Occipital ROIs . Values are listed in mean ± standard error.**

The results of Experiment 1 did not support the memory-comparison-based change detection accounts because the deviant-minus-standard and the deviant –minus-control differences were not significantly different, and also the deviant-minus-control differences did not differ from zero in the latency range defined by the difference of the deviant-minus-standard difference wave.

## 4.3. Experiment 2

### 4.3.1 Introduction

In Experiment 2, windmill patterns were used. In studies by Kimura et al. (2009) and Kimura and Takeda (2009), the equal probability control divided the long-lasting deviant-minus-standard difference potential into two parts. In the earlier temporal window, the control procedure eliminated the difference, whereas in the later latency window, gvMMN emerged. In studies with windmill patterns (e.g., Maekawa et al., 2005), two distinct difference potentials appeared, an earlier (150-200 ms) and a later (200-300 ms) component. We expect that the emergence of the first component of the difference wave is a consequence of adaptation (SSA) and the emergence of the latter component is a consequence of gvMMN.

To test this hypothesis, in addition to the oddball sequences, we applied three additional (control) sequences: an equal probability (E-control) sequence and two modified control (M-control) sequences. In the M-control sequences, the probabilities of the control stimuli were equal to that of the deviant ($p=0.1$), but in contrast to the E-control sequence, the probabilities of the individual contextual stimuli were higher than the probability of the deviant ($p=0.225$).

It is important to note that the deviant and standard windmill stimuli have different numbers of vanes, which leads to multidimensional deviances; the larger the number of vanes is, the larger the contribution of high spatial frequencies and also, the windmills that have a larger number of vanes can be considered to be more complex stimuli. However, we must emphasize that in this study, we did not intend to analyze the effect of a specific feature per se, but the effect of adaptation versus deviant-related additional activity on vMMN.

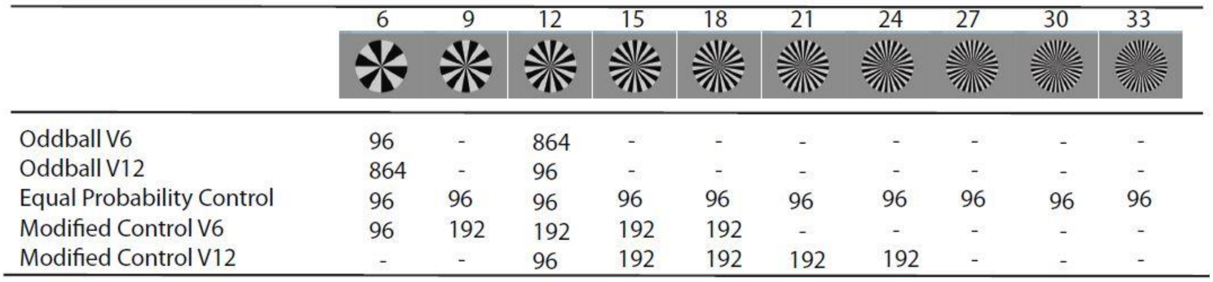
### 4.3.2.Methods

#### 4.3.2.1 Participants

Twenty-three volunteers participated in the study for monetary compensation or course credit. They had no ophthalmologic or neurological abnormalities. Written informed consent was obtained from all of the participants prior to the experimental procedure. The study was conducted in accordance with the Declaration of Helsinki and was approved by the Joint Committee of Ethics of the Psychology Institute in Hungary. One out of 23 participants was omitted from the data analyses due to the low signal-to-noise ratio, and thus, we report the data from 22 participants (fourteen women; mean age, 21.94; standard deviation, 1.61 year).

#### 4.3.2.2 Stimuli and experimental design

To apply similar stimulation to the studies by Maekawa et al. (2005), but to introduce a more stringent control of attention, the participants performed a tracking task similar to the one introduced by Heslenfeld (2003), but with one level of difficulty. In the tracking task, the participants were asked to keep a ball within a blue circle (1.79° diameter from the 120-cm viewing distance) located at the center of the screen, i.e., within the windmill pattern. The ball was moving on the horizontal axis, with a pseudo-random speed and direction. If the ball left the circle, the color of the circle changed from blue to red. The ball movement was controlled by a gamepad. At the end of each block performance, feedback was provided (duration within the circle / duration of the block * 100). This task required continuous central fixation, but in the case of proper fixation, a high performance was expected. The stimuli appeared on a 17-inch CRT monitor with a 60-Hz refresh rate. The stimulus duration was 200 ms, and the average inter-stimulus-interval (ISI) was 800 ms (range: 750–850 ms, even distribution). ERPs were recorded to windmill patterns. As Figure 4.4 shows, the patterns consisted of 6 to 33 vanes. The patterns had high contrast (37.21 cd/m$^2$ for the bright and 0.14 cd/m$^2$ for the dark segments). The diameter of the pattern was 13.82°, and the background was grey (15.96 cd/m$^2$).



| | 6 | 9 | 12 | 15 | 18 | 21 | 24 | 27 | 30 | 33 |
|---|---|---|---|---|---|---|---|---|---|---|
| Oddball V6 | 96 | - | 864 | - | - | - | - | - | - | - |
| Oddball V12 | 864 | - | 96 | - | - | - | - | - | - | - |
| Equal Probability Control | 96 | 96 | 96 | 96 | 96 | 96 | 96 | 96 | 96 | 96 |
| Modified Control V6 | 96 | 192 | 192 | 192 | 192 | - | - | - | - | - |
| Modified Control V12 | - | - | 96 | 192 | 192 | 192 | 192 | - | - | - |

**Figure 4.4. Stimuli and their probabilities of Experiment 2 (times/experiment) in the oddball and control sequences**

Five conditions were applied; Figure 4.4 illustrates the stimuli and their probabilities within the conditions. The conditions were as follows (S: standard; D: deviant, and the numbers are the vanes of the patterns): Oddball S6D12, Oddball S12D6 (reverse control paradigm), equal probability control (E-control) and two modified control (M-control). In the Oddball condition, the probability of the standard was 90 per cent (10 percent for the deviant). In each sequence, either the V6 or V12 stimuli were the standards/deviants. Between two deviant stimuli, a minimum of 7 and a maximum of 12 standard stimuli were presented.

In the E-control sequence, 10 different stimuli were presented with equal (10 percent) probability (V6, V9, V12, V15, V18, V21, V24, V27, V30 and V33). Two identical stimuli never occurred successively.

In the V6 M-control condition, 5 different stimuli were presented randomly. Four stimuli (V9, V12, V15, V18) had equal probabilities (22.5%), and one (V6) had the probability of 10%. In the V12 M-control, four stimuli (V15, V18, V21, V24) had equal probabilities of 22.5%, and one stimulus (V12) had a 10% probability.

Each condition consisted of 960 stimuli, which were presented in 6 blocks (30 blocks in total). The blocks were presented in a semi-random order; the 30 blocks were separated into 6 fragments that each contained one block from every condition, in a random order.

#### 4.3.2.3 Recording and measuring the brain electric activity

The EEG was recorded (DC-30 Hz, sampling rate 500 Hz; Synamps2 amplifier, NeuroScan recording system) with Ag/AgCl electrodes at 61 locations according to the extended 10-20 system using an elastic electrode cap (EasyCap). The tip of the nose was used as a reference, which was off-line re-referenced to average activity. The ground electrode was attached to the forehead. A horizontal EOG was recorded with a bipolar configuration between electrodes that were positioned lateral to the outer canthi of the two eyes. Vertical eye movements were monitored with a bipolar montage between electrodes that were placed above and below the right eye. The impedance of the electrodes was maintained below 10 kΩ.

EEG signals were filtered offline (0.1-30 Hz, 24 dB), and epochs of 500 ms, starting from 100 ms before the stimulus onset, were averaged separately for the standards and deviants and for the control stimuli. Trials with an amplitude change that exceeded +- 100 uV on any channel were rejected from further analysis.

Only the responses from the standard preceding a deviant were included in the standard-related ERPs. To identify the deviant-related effects, 3 types of grand averaged differences were calculated: deviant-minus-standard, deviant-minus-equal probability control and deviant-minus-modified control. The difference in these comparisons cannot be explained by stimulus specific features because the standard, deviant and control stimuli had the same physical attributes.

The difference potentials were formed as follows:

V6 OddDiff = V6 deviant-minus-V6 standard

V12 OddDiff = V12 deviant-minus-V12 standard

V6 EQControlDiff = V6 deviant-minus-V6 E-control

V12 EQControlDiff = V12 deviant-minus-V12 E-control

V6 MControlDiff = V6 deviant-minus-V6 M-control

V12 MControlDiff = V12 deviant-minus-V12 M-control

Similar to Experiment 1, we expected the emergence of vMMN at the posterior electrode sites. We defined an electrode matrix, where the OddV6Diff and OddV12Diff differed ($p<0.01$) from zero in at least 15 consecutive significant data points (30 ms), based on the results of a point-by-point t-test. A 2x3 matrix of channels (PO3, POz, PO4, O1, Oz, O2) met this criterion, and it consisted of two rows (anterior, posterior) and three columns (left, middle, right). No laterality-related effect that was associated with the conditions was present, and thus, for the sake of easier traceability, we formed two regions of interest similar to Experiment 1: parieto-occipital (PO4, POz, PO3) and occipital (O2, Oz, O1).

To assess the effects of the conditions, the mean amplitude and peak latencies of the previously defined sections were measured. ANOVAs on the mean amplitudes and peak latencies were conducted, with the factors Visual Features (V6, V12), Difference (OddDiff, EQControlDiff, MControlDiff), and ROI (parieto-occipital, occipital) on the difference potentials of the average amplitude values of the pre-defined ranges and on the peak latency values. The peak latencies were measured at the maxima of the differences.

The peak latencies and the scalp distributions of the exogenous components and the difference potentials were compared at the same ROIs. The effect size was characterized as partial eta-squared ($\eta^2$). Where appropriate, post-hoc analyses were calculated by the Tukey HSD test. Mauchly’s test of sphericity was conducted, when more than were more than 2 conditions in the F test. Surface distributions were compared under the method of the vector-scaled amplitude values (McCarthy and Wood, 1985).

Considering that nose reference was used in the original study (Maekawa et al, 2005), nose referenced data were also analysed. Since there was no relevant difference between the nose and the averaged referenced data, only results computed from the average referenced data are presented.

### 4.3.2.4 sLORETA analysis

For defining the cortical location of the vMMN identified at the scalp level, we applied a distributed source localization technique. The source signal of the average ERP time series was reconstructed on the cortical surface by applying the sLORETA inverse solution (Pascual-Marqui 2002). sLORETA gives a solution for the EEG inverse problem by applying a weighted minimum norm estimation with spatial smoothing and standardization of the current density map. The forward model was generated on a realistic BEM headmodel (Gramfort, Papadopoulo, Olivi & Clerc, 2011) by applying a template MRI (ICBM152; 1 $mm^3$ voxel resolution) with template electrode positions. The reconstructed dipoles (pA/m) were determined for every 15001 sources in 3 orthogonal directions (unconstrained solution). The difference potentials were calculated for every voxel on source level between the same conditions as described previously on scalp level. For every voxel, the different potentials were averaged to 10 equal, 35ms long interval from 0 to 350 ms. Similarly to the scalp level, a one-sample t-tests were applied on the difference potentials. Two conditions were reported as significantly different, if at least 5 voxels exceeded the Bonferroni corrected alpha level. Bonferroni correction was applied to control the type I error, resulted from multiple comparisons of the 15001 voxels and 10 time intervals of the condition pairs. Brain regions for the corresponding significant activations were identified based on the parcellation scheme introduced by Klein and Jason (2012).

### 4.3.3 Results

#### 4.3.3.1 Behavioural results

The participants kept the ball inside the circle 97.88 percent of the time (S.E.M: 1.96%). There was no performance difference among the conditions.

#### 4.3.3.2 Event-related potentials

As Figure 4.5 shows, standard, deviant and control stimuli elicited a positive (P1), a negative (N1) and a positive (P2) series of peaks. It is obvious from Figure 4.5 that there is a robust difference in both the amplitude and latency between the ERP elicited by stimuli comprised of 6 (V6) and 12 vanes (V12).

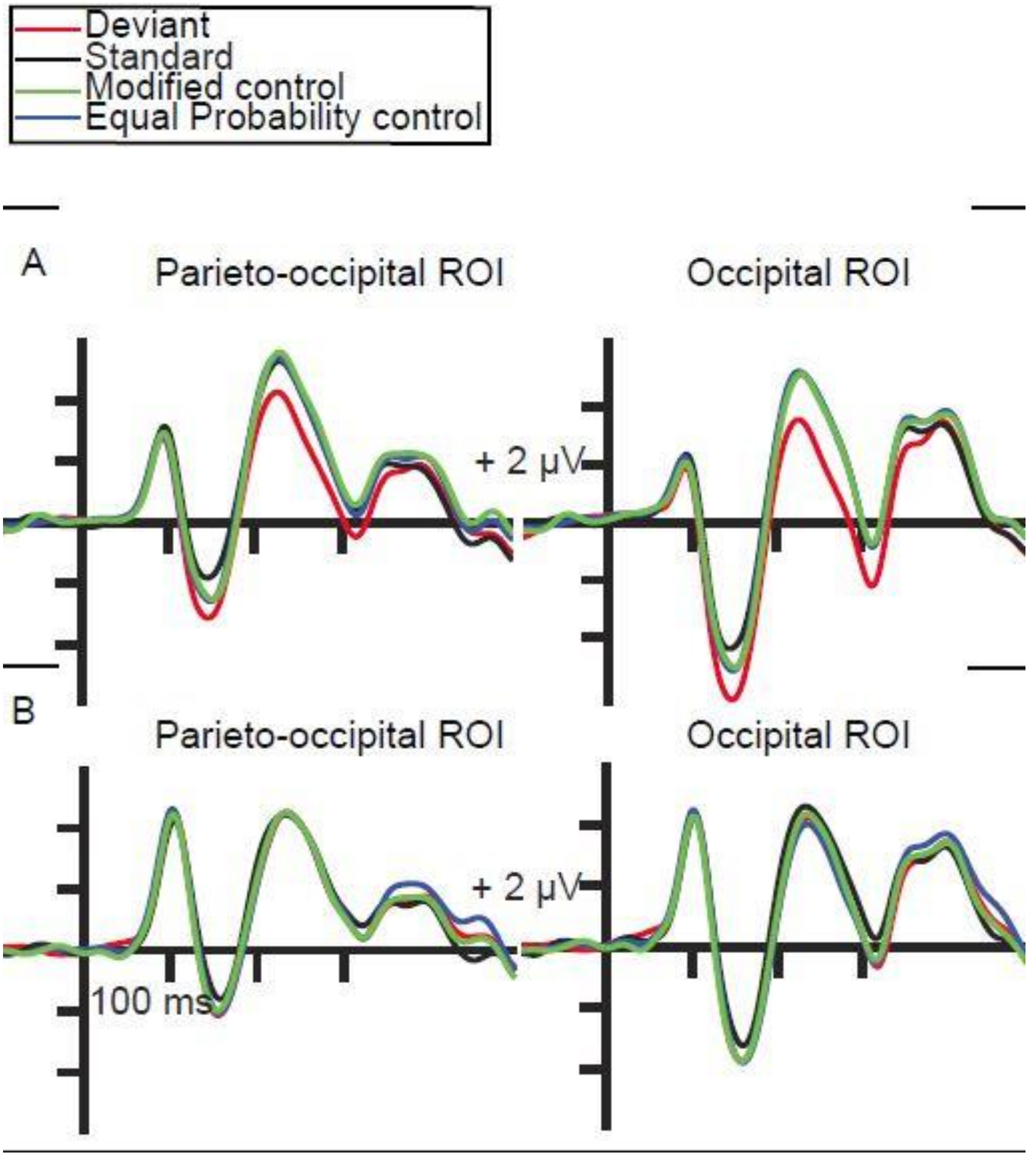


**Figure 4.5. Experiment 2: (A) Grand averaged ERPs elicited by the V12 deviant, V12 standard, V12 equal probability control and V12 modified control. (B) Grand averaged ERPs elicited by the V6 deviant, V6 standard, V6 equal probability control and V6 modified control.**

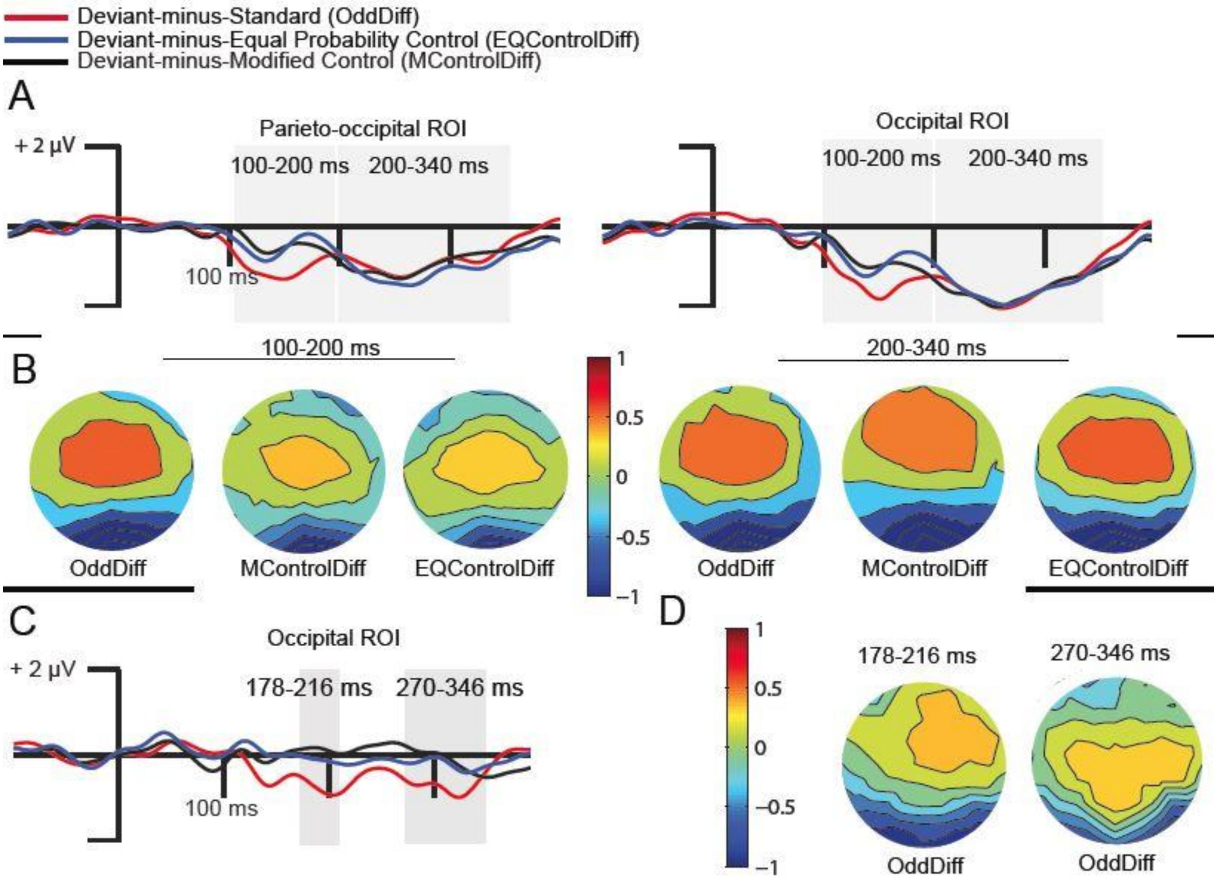
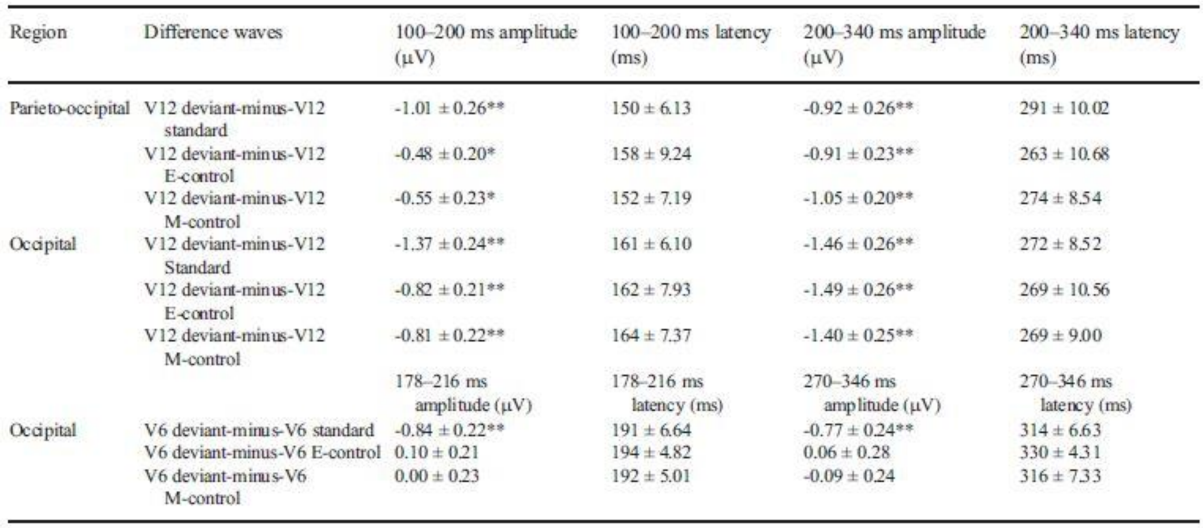


**Figure 4.6. Experiment 2: (A) Grand-averaged V12 deviant-minus- V12 standard, V12 deviant-minus- V12 modified control and V12 deviant-minus- V12 equal probability control difference waves. (B) Topographical maps of the V12 grand averaged difference waves within the 100–200 ms and 200-340 ms time-windows. (C) Grand-averaged V6 deviant-minus- V6 standard, V6 deviant-minus- V6 modified control and V6 deviant-minus- V6 equal probability control difference waves. (D) Topographical maps of the V6 grand averaged difference waves within the 178–216 ms and 270-346 ms time-windows.**



| Region | Difference waves | 100–200 ms amplitude (µV) | 100–200 ms latency (ms) | 200–340 ms amplitude (µV) | 200–340 ms latency (ms) |
|---|---|---|---|---|---|
| Parieto-occipital | V12 deviant-minus-V12 standard | -1.01 ± 0.26** | 150 ± 6.13 | -0.92 ± 0.26** | 291 ± 10.02 |
|  | V12 deviant-minus-V12 E-control | -0.48 ± 0.20* | 158 ± 9.24 | -0.91 ± 0.23** | 263 ± 10.68 |
|  | V12 deviant-minus-V12 M-control | -0.55 ± 0.23* | 152 ± 7.19 | -1.05 ± 0.20** | 274 ± 8.54 |
| Occipital | V12 deviant-minus-V12 Standard | -1.37 ± 0.24** | 161 ± 6.10 | -1.46 ± 0.26** | 272 ± 8.52 |
|  | V12 deviant-minus-V12 E-control | -0.82 ± 0.21** | 162 ± 7.93 | -1.49 ± 0.26** | 269 ± 10.56 |
|  | V12 deviant-minus-V12 M-control | -0.81 ± 0.22** | 164 ± 7.37 | -1.40 ± 0.25** | 269 ± 9.00 |
|  |  | 178–216 ms amplitude (µV) | 178–216 ms latency (ms) | 270–346 ms amplitude (µV) | 270–346 ms latency (ms) |
| Occipital | V6 deviant-minus-V6 standard | -0.84 ± 0.22** | 191 ± 6.64 | -0.77 ± 0.24** | 314 ± 6.63 |
|  | V6 deviant-minus-V6 E-control | 0.10 ± 0.21 | 194 ± 4.82 | 0.06 ± 0.28 | 330 ± 4.31 |
|  | V6 deviant-minus-V6 M-control | 0.00 ± 0.23 | 192 ± 5.01 | -0.09 ± 0.24 | 316 ± 7.33 |

**Table 4.2. : Experiment 2: Grand averages of peak latencies and mean epochs of the difference waves measured at Parieto-occipital and Occipital ROIs . Values are listed in mean ± standard error. Difference wave significantly differ from zero. * 0.01 > p < 0.05 ; **p < 0.01**

Figure 4.6 shows the grand average difference potentials, and Table 4.2 shows the mean amplitude and the latency values of the differences.

The point-by-point t-test conducted on the V12 OddDiff differed significantly from zero on the previously defined channel matrix in the 100-340 ms latency range. Based on the ERP wave characteristics, which is in agreement with Maekawa et al. (2005), we attempted to separate the difference into an early (100-200 ms) and a late (200-340 ms) latency range. However, the point-by-point t-test revealed restricted temporal and spatial extension for V6 OddDiff relative to V12 OddDiff; the deviant-minus-standard difference wave differed from zero in the 178-216 and in the 270-346 ms latency range at the occipital ROI. Investigating V6 and V12 separately was not planned a priori, but due to the large difference between them we have found it necessary to include a visual features factor into the design.

In the early time window (100-200 ms), the ANOVA on the amplitude values in the 100-200 ms revealed a significant main effect of Visual Features (F(1, 21)=5.75, $p<0.05$, $\eta^2_p$ =0.21); V12 differences were more negative. The main effect of Difference (F(2, 42)=12.02, $p<0.01$, $\eta^2_p$ =0.36) indicated that the OddDiff values were more negative than the control differences. Tukey HSD post-hoc analyses did not reveal a significant difference between EQControlDiff and MControlDiff. The Visual Features x ROI interaction (F(1, 21)=5.14, $p<0.05$, $\eta^2_p$ =0.19) revealed that V12 differences were more negative at the occipital site, while no such difference was specific for V6.

The ANOVA conducted on the latency values in the 100-200 ms range with the same factors revealed a significant interaction of Visual Features x Difference (F(2, 42)=4.86, $p<0.05$); V12 OddDiff had a later peak than the V12 control differences.

The ANOVA on the amplitude values in the 200-340 ms also revealed a significant main effect of Visual Features (F(1, 21)=11.92, $p<0.01$, $\eta^2_p$ =0.36); the V12 differences were greater. The differences were greater at the occipital ROI (F(1, 21)=22.42, $p<0.01$, $\eta^2_p$ =0.51). The Visual Features x Difference interaction (F(2,42)=3.78, $p<0.05$, $\eta^2_p$ = 0.15) revealed that V12 OddDiff was significantly bigger than the control differences, while there was no difference in the mean amplitude values in response to V6.

#### 4.3.3.3 sLORETA results

After the Bonferroni correction, significant difference of the difference potential from the baseline was identified in the V12 deviant-minus-V12 standard in the 105-245 ms range and in the V12 deviant-minus-V12 M-control and in V12 deviant-minus-V12 E-control both in the 140-280 ms range. The sources were localized at the occipital areas;

the lingual gyrus, cuneus and pericalcarine cortex showed the highest difference in the compared conditions (see Figure 4.7 and Table 4.3).

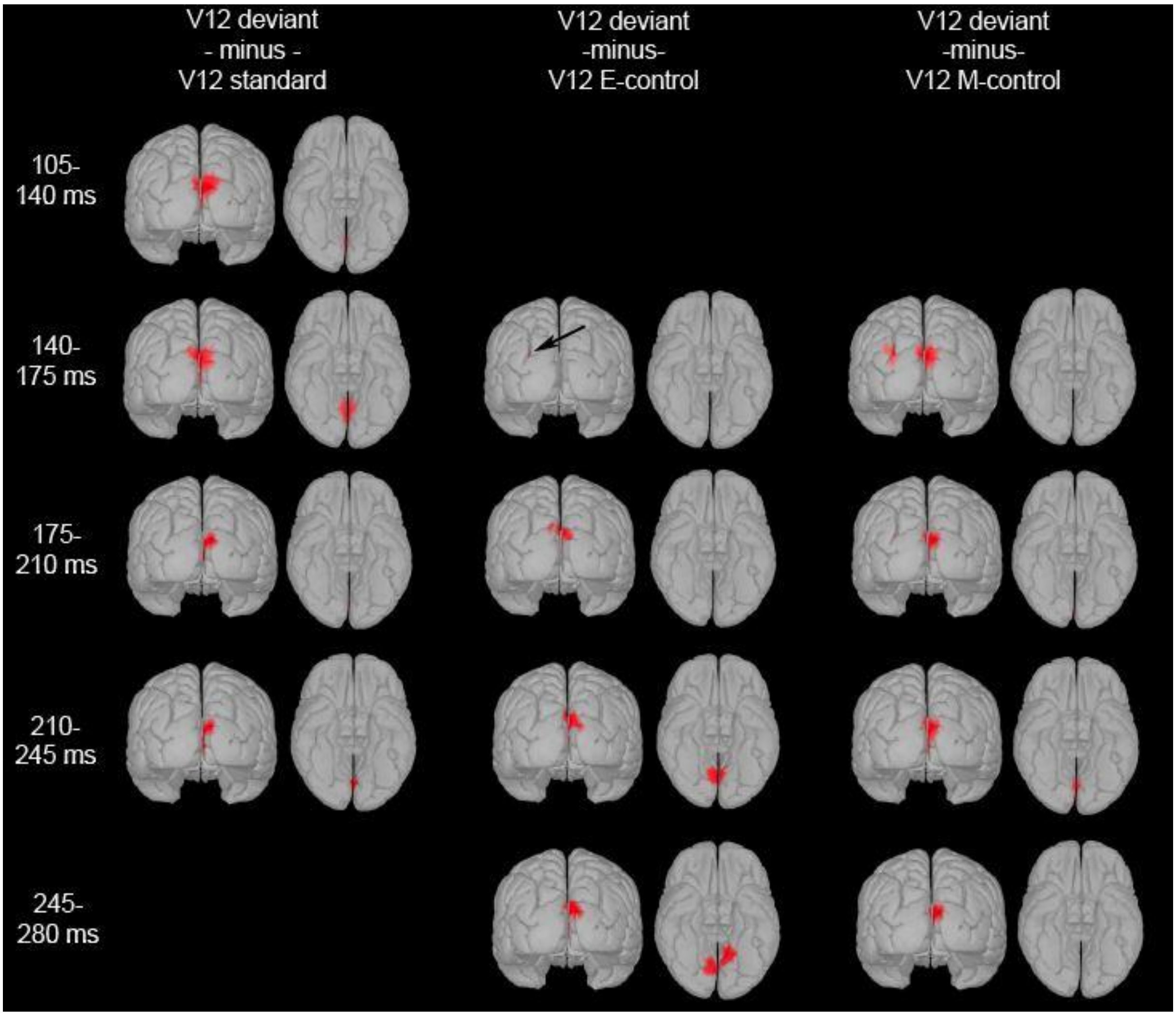
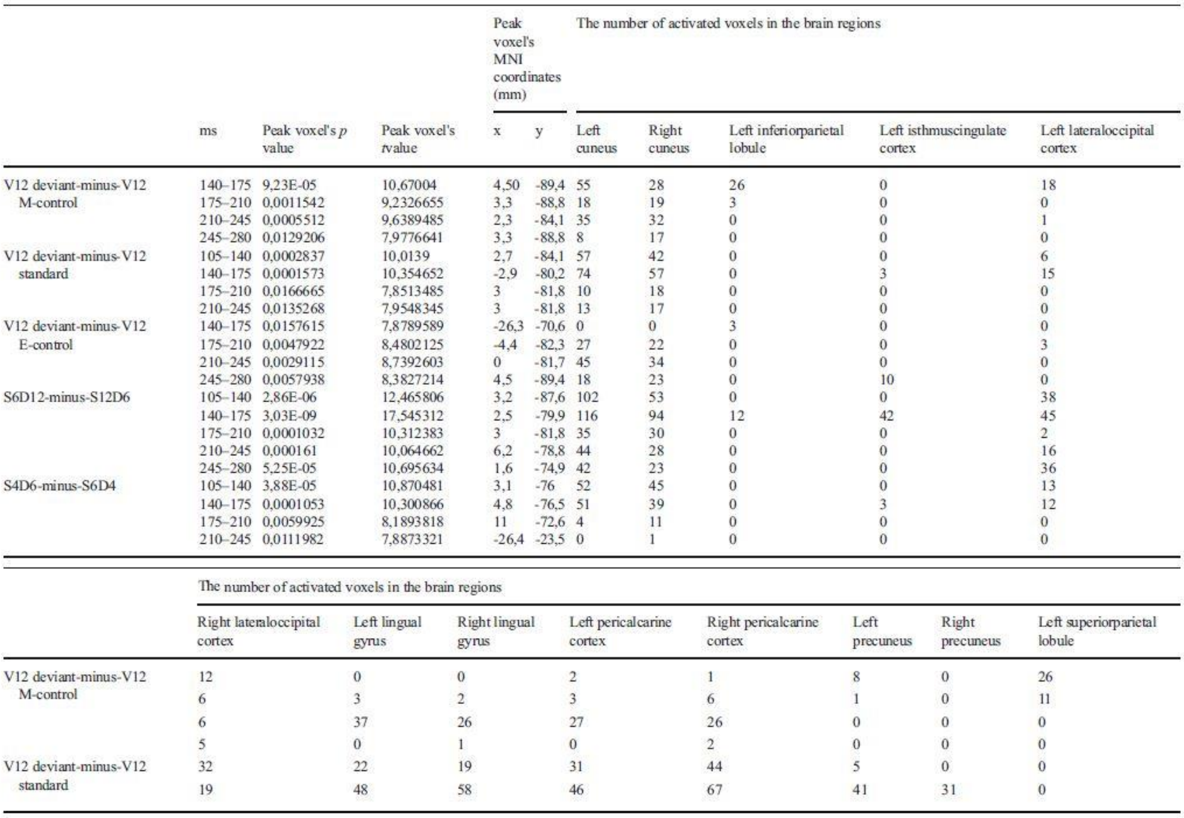
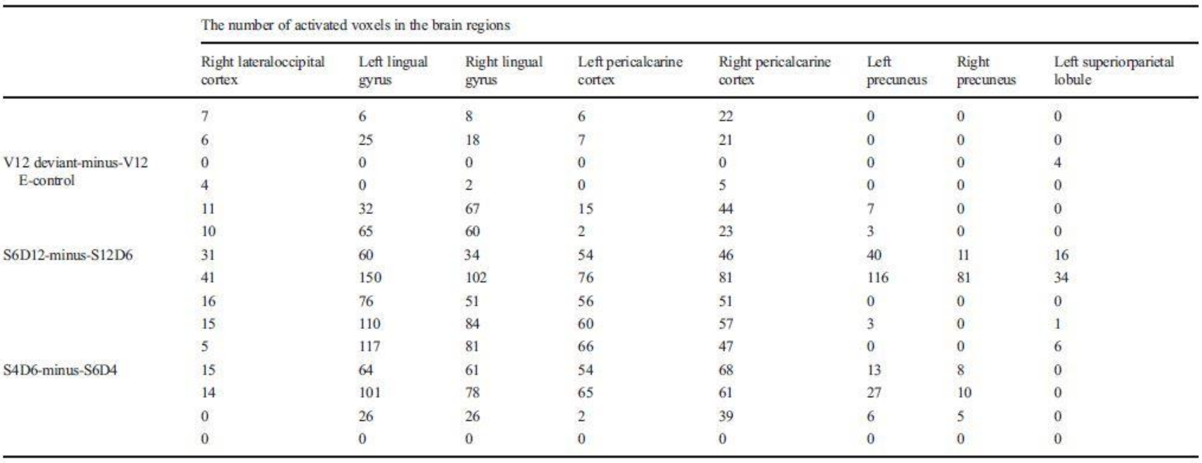


**Figure 4.7. Experiment 2: Source distribution of the significant differences between the difference potentials and baseline. Red colors indicating the significant voxels. For every voxel, the difference potentials were averaged to 10 equal, 35ms long interval from 0 to 350 ms. Difference potentials of two conditions on a given interval reported as significant, if at least 5 voxels exceeded the Bonferroni corrected alpha level.**



| | | | | Peak voxel's MNI coordinates (mm) | | The number of activated voxels in the brain regions | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | ms | Peak voxel's *p* value | Peak voxel's *t* value | x | y | Left cuneus | Right cuneus | Left inferiorparietal lobule | Left isthmuscingulate cortex | Left lateraloccipital cortex |
| V12 deviant-minus-V12 M-control | 140–175 | 9,23E-05 | 10,67004 | 4,50 | -89,4 | 55 | 28 | 26 | 0 | 18 |
| | 175–210 | 0,0011542 | 9,2326655 | 3,3 | -88,8 | 18 | 19 | 3 | 0 | 0 |
| | 210–245 | 0,0005512 | 9,6389485 | 2,3 | -84,1 | 35 | 32 | 0 | 0 | 1 |
| | 245–280 | 0,0129206 | 7,9776641 | 3,3 | -88,8 | 8 | 17 | 0 | 0 | 0 |
| V12 deviant-minus-V12 standard | 105–140 | 0,0002837 | 10,0139 | 2,7 | -84,1 | 57 | 42 | 0 | 0 | 6 |
| | 140–175 | 0,0001573 | 10,354652 | -2,9 | -80,2 | 74 | 57 | 0 | 3 | 15 |
| | 175–210 | 0,0166665 | 7,8513485 | 3 | -81,8 | 10 | 18 | 0 | 0 | 0 |
| | 210–245 | 0,0135268 | 7,9548345 | 3 | -81,8 | 13 | 17 | 0 | 0 | 0 |
| V12 deviant-minus-V12 E-control | 140–175 | 0,0157615 | 7,8789589 | -26,3 | -70,6 | 0 | 0 | 3 | 0 | 0 |
| | 175–210 | 0,0047922 | 8,4802125 | -4,4 | -82,3 | 27 | 22 | 0 | 0 | 3 |
| | 210–245 | 0,0029115 | 8,7392603 | 0 | -81,7 | 45 | 34 | 0 | 0 | 0 |
| | 245–280 | 0,0057938 | 8,3827214 | 4,5 | -89,4 | 18 | 23 | 0 | 10 | 0 |
| S6D12-minus-S12D6 | 105–140 | 2,86E-06 | 12,465806 | 3,2 | -87,6 | 102 | 53 | 0 | 0 | 38 |
| | 140–175 | 3,03E-09 | 17,545312 | 2,5 | -79,9 | 116 | 94 | 12 | 42 | 45 |
| | 175–210 | 0,0001032 | 10,312383 | 3 | -81,8 | 35 | 30 | 0 | 0 | 2 |
| | 210–245 | 0,000161 | 10,064662 | 6,2 | -78,8 | 44 | 28 | 0 | 0 | 16 |
| | 245–280 | 5,25E-05 | 10,695634 | 1,6 | -74,9 | 42 | 23 | 0 | 0 | 36 |
| S4D6-minus-S6D4 | 105–140 | 3,88E-05 | 10,870481 | 3,1 | -76 | 52 | 45 | 0 | 0 | 13 |
| | 140–175 | 0,0001053 | 10,300866 | 4,8 | -76,5 | 51 | 39 | 0 | 3 | 12 |
| | 175–210 | 0,0059925 | 8,1893818 | 11 | -72,6 | 4 | 11 | 0 | 0 | 0 |
| | 210–245 | 0,0111982 | 7,8873321 | -26,4 | -23,5 | 0 | 1 | 0 | 0 | 0 |

| | The number of activated voxels in the brain regions | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Right lateraloccipital cortex | Left lingual gyrus | Right lingual gyrus | Left pericalcarine cortex | Right pericalcarine cortex | Left precuneus | Right precuneus | Left superiorparietal lobule |
| V12 deviant-minus-V12 M-control | 12 | 0 | 0 | 2 | 1 | 8 | 0 | 26 |
| | 6 | 3 | 2 | 3 | 6 | 1 | 0 | 11 |
| | 6 | 37 | 26 | 27 | 26 | 0 | 0 | 0 |
| | 5 | 0 | 1 | 0 | 2 | 0 | 0 | 0 |
| V12 deviant-minus-V12 standard | 32 | 22 | 19 | 31 | 44 | 5 | 0 | 0 |
| | 19 | 48 | 58 | 46 | 67 | 41 | 31 | 0 |



| | The number of activated voxels in the brain regions | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Right lateraloccipital cortex | Left lingual gyrus | Right lingual gyrus | Left pericalcarine cortex | Right pericalcarine cortex | Left precuneus | Right precuneus | Left superiorparietal lobule |
| | 7 | 6 | 8 | 6 | 22 | 0 | 0 | 0 |
| | 6 | 25 | 18 | 7 | 21 | 0 | 0 | 0 |
| V12 deviant-minus-V12 E-control | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| | 4 | 0 | 2 | 0 | 5 | 0 | 0 | 0 |
| | 11 | 32 | 67 | 15 | 44 | 7 | 0 | 0 |
| | 10 | 65 | 60 | 2 | 23 | 3 | 0 | 0 |
| S6D12-minus-S12D6 | 31 | 60 | 34 | 54 | 46 | 40 | 11 | 16 |
| | 41 | 150 | 102 | 76 | 81 | 116 | 81 | 34 |
| | 16 | 76 | 51 | 56 | 51 | 0 | 0 | 0 |
| | 15 | 110 | 84 | 60 | 57 | 3 | 0 | 1 |
| | 5 | 117 | 81 | 66 | 47 | 0 | 0 | 6 |
| S4D6-minus-S6D4 | 15 | 64 | 61 | 54 | 68 | 13 | 8 | 0 |
| | 14 | 101 | 78 | 65 | 61 | 27 | 10 | 0 |
| | 0 | 26 | 26 | 2 | 39 | 6 | 5 | 0 |
| | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

**Table 4.3. Source results of Experiment 2. Significant differences between the difference potentials and baseline in 35 ms long time intervals. The MNI coordinates of the maximal T-value with the corresponding Bonferroni-corrected p-value were presented. The number of significant voxels in every brain regions are indicated.**

### 4.3.4 Discussion on Experiment 2

For V12, there was a robust ERP difference in both the 100-200 and 200–350 ms latency ranges. As the deviant-minus-control difference in the 100-200 ms range indicated, stimulus-specific adaptation explains a part of the observed difference but not all of it because both the deviant-minus-equal probability control difference and the deviant-minus-modified control difference were different from zero, which indicates an adaptation-free gvMMN. In the later latency range, the V12 deviant-minus-standard and the deviant-minus-control differences were identical, and thus, the deviant effects cannot be attributed to adaptation processes. In contrast to the results on the V12 stimuli, for V6, the control differences abolished vMMN in both of the latency ranges. According to the prevailing explanation, this finding means that the deviant-minus-standard difference was due to adaptation. For an adaptation explanation of the asymmetry between the effects of the V12 and V6 patterns, sequential presentation of V12 adapts the neuronal population sensitive to V6 (in other words, representation of the more complex stimulus included the representation of the less complex stimulus). However, the continuous presentation of V6 did not adapt the cell population that is responsible for V12. The V6 deviant does not elicit gvMMN because it did not carry new information within the sensory system. As a low-level variant of this account, all of the edges that form V6 are present in V12. This finding means that the contrast border orientations of V6 are present in V12, but not vice versa. When considering the S6D12 oddball sequence, the orientations that form the V6 stimuli are presented 180 times (100%), while the orientations that are specific to V12 are present only 18 times (10%). However, in the S12D6 sequence, the orientations that form the V6 stimuli are presented 180 times again, while the V12-specific orientations present 162 times (90%). This finding could lead to the observed asymmetry because a less pronounced stimulus-specific adaptation effect is expected for the V12 deviant compared with the V6. The difference between the explanations is conceptual. The former explanation emphasizes higher order (also less precisely defined) features, i.e., complexity, while the latter explanation is based on elementary visual features. Overall, the V12-V6 asymmetry requires further study, especially in light of other vMMN asymmetries (Kecskés-Kovács et al., 2013b, Sulykos et al., 2015).

## 4.4. Experiment 3

### 4.4.1 Introduction

In Experiment 3, we investigated a possible source of the different deviancy effects of the windmill patterns with 6 (V6) and 12 (V12) vanes. We presented two additional oddball sequences that had stimuli with 4 (V4) and 6 (V6) windmill patterns, i.e., the S4D6 and S6D4 sequences. In these sequences, the probabilities of having spatially matching edge orientations were balanced. In the S4D6 sequence, the probability of matching edge orientations within the standard was 0.95 and 0.4 for the deviant, while in the S6D4 sequence, it was 0.93 for the standard and 0.55 for the deviant. If the same asymmetry occurs between the V4 and V6 differences than in the case of the V6 and V12, the result favours the complexity explanation over the orientation specificity (low-level) account. In an attempt to replicate the results of Experiment 2, oddball sequences with V6 and V12 stimuli were also delivered.

### 4.4.2 Methods

#### 4.4.2.1 Participants

Twenty-five volunteers participated in the study for monetary compensation or for course credit. They had no ophthalmologic or neurological abnormalities. Written consent was obtained from all of the participants prior to the experimental procedure. The study was conducted in accordance with the Declaration of Helsinki and approved by the

Joint Committee of Ethics of the Psychology Institute in Hungary. Two out of 25 participants were omitted from the data analyses, due to the low signal to noise ratio, and thus, we report the data from 23 participants (eighteen women; mean age, 21.37; standard deviation, 1.83 year).

#### 4.4.2.2 Stimuli and experimental design

Four different conditions were used; S6D12, S12D6, S4D6, and S6D4.

#### 4.4.2.3 Stimuli and procedure

All of the aspects of the stimulations in Experiment 3 were identical to those of the stimuli that we applied in Experiment 2.

#### 4.4.2.4 Recording and measuring the electrical brain activity

The parameters of the EEG-recording, the processing of the EEG-signal and the statistical analyses of the behavioural data and the ERP data were identical to Experiment 2.

The differences were formed as follows:

S6D12Diff = S6**D12**-minus-**S12**D6

S12D6Diff **=** S12**D6**-minus-**S6**D12

S4D6Diff **=** S4**D6**-minus-**S6**D4

S6D4Diff = S6**D4**-minus-**S4**D6

The same 2x3 matrix of channels (PO3, POz, PO4, O1, Oz, O2) met the criteria that we set in Experiment 2. The occipital and parieto-occipital channels did not differ from each other, and thus, for easier traceability, 2 regions of interest were formed: Occipital, Parieto-occipital.

The point-by-point t-test (p=0.01) on the S6D12Diff differed significantly from zero in the 102-340 ms and in the 110–340 latency ranges on the S4D6Diff. Similar to in Experiment 2, we divided the difference potentials into an early (100-200 ms) and a late (200-340 ms) latency range, based on the characteristics of the sub-components of S6D12Diff (the difference wave components were not evident in the case of S4D6Diff). There were no sections in the S6D4Diff and S12D6Diff in which they differed from zero for at least 15 consecutive data points (30 ms).

To assess the effects of the conditions, two-way ANOVAs were conducted on the difference waves' amplitude values and latency values with the factors of Differences (S6D12**,** S4D6) and ROI (occipital, parieto-occipital).

#### 4.4.2.5 sLORETA analysis

The S4D6 vs. S6D4 conditions were statistically evaluated at the source level, using methodology that was identical to that used in Experiment 2.

### 4.4.3 Results

#### 4.4.3.1 Behavioral results

The participants kept the ball inside the circle 97.80% of the time (S.E.M.: 0.8%). There was no difference in their performances between the conditions.

#### 4.4.3.2 Event-related potentials

Similar to in Experiment 2, a positive (P1) – negative (N1) – positive (P2) deflection was elicited by both the standard and deviant stimuli (see Figure 4.8).

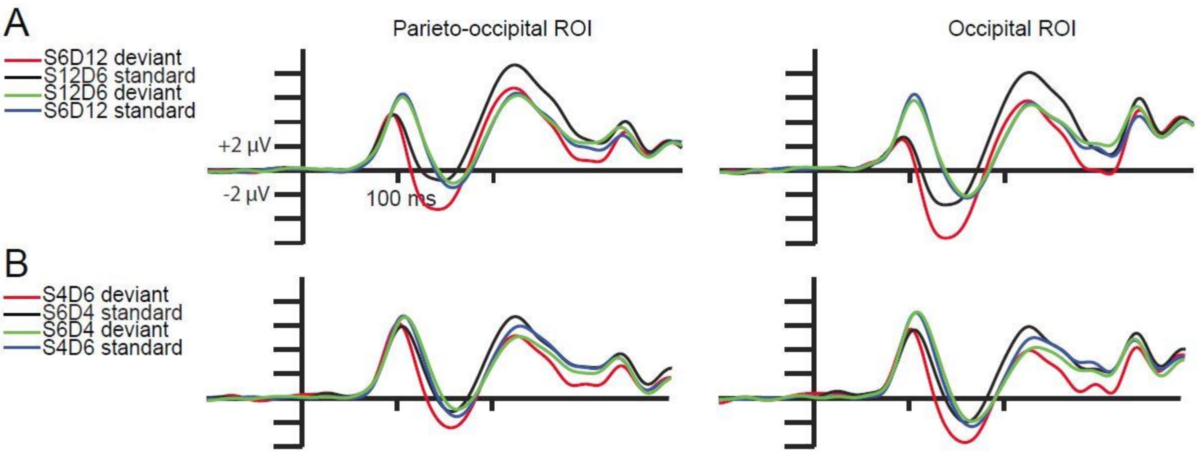


**Figure 4.8. Experiment 3: (A) Grand averaged ERPs elicited by the S6D12 deviant, S12D6 standard, S12D6 deviant and S6D12 standard (B) Grand averaged ERPs elicited by the S4D6 deviant, S6D4 standard, S6D4 deviant and S4D6 standard.**

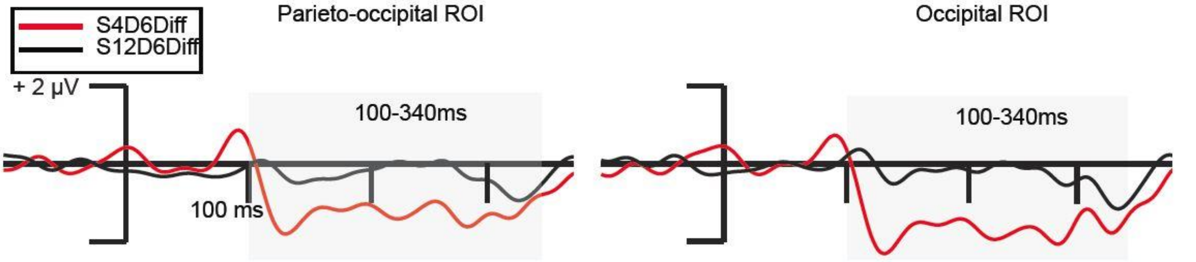
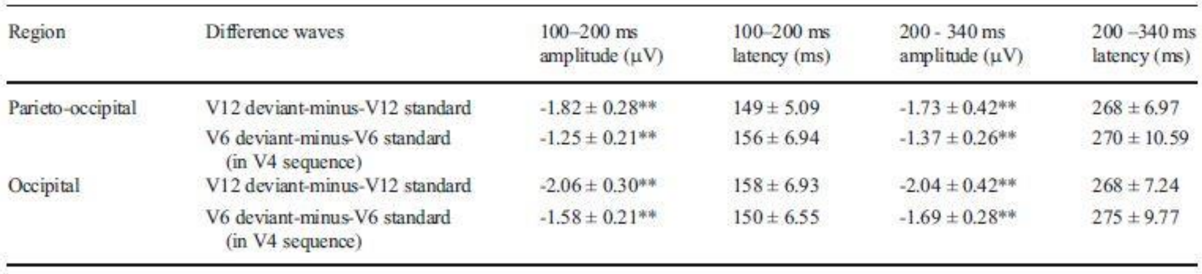


**Figure 4.9. Experiment 3: Grand averaged V6 deviant- minus- V4 standard and V6 deviant –minus- V12 standard difference waves.**



| Region | Difference waves | 100–200 ms amplitude (µV) | 100–200 ms latency (ms) | 200 - 340 ms amplitude (µV) | 200 –340 ms latency (ms) |
|---|---|---|---|---|---|
| Parieto-occipital | V12 deviant-minus-V12 standard | -1.82 ± 0.28** | 149 ± 5.09 | -1.73 ± 0.42** | 268 ± 6.97 |
| | V6 deviant-minus-V6 standard (in V4 sequence) | -1.25 ± 0.21** | 156 ± 6.94 | -1.37 ± 0.26** | 270 ± 10.59 |
| Occipital | V12 deviant-minus-V12 standard | -2.06 ± 0.30** | 158 ± 6.93 | -2.04 ± 0.42** | 268 ± 7.24 |
| | V6 deviant-minus-V6 standard (in V4 sequence) | -1.58 ± 0.21** | 150 ± 6.55 | -1.69 ± 0.28** | 275 ± 9.77 |

**Table 4.4. Experiment 3: Grand averages of peak latencies and mean epochs of the difference waves measured at Parieto-occipital and Occipital ROIs . Values are listed in mean ± standard error. Difference wave significantly differ from zero. * 0.01 > p < 0.05 ; **p < 0.01**

The ANOVA conducted in the 100-200 and 200-340 ms ranges on the amplitude values and peak latency values of the S6D12Diff and S4D6Diff revealed no difference. Figure 4.9 shows the difference waves of the V6 stimuli in the sequence in which V4 (S4D6Diff) and V12 (S12D6Diff) were the standard stimuli. Table 4.4 shows the amplitude and latency values of the differences.

#### 4.4.3.3 sLORETA results

After the Bonferroni correction significant difference of the difference potential from the baseline was identified in the S6D12 -minus- S12D6 in the 105-280 ms range and in the S4D6 -minus- S6D4 in the 105-245 ms range. Similarly to Experiment 2, the sources were localized to the occipital areas (see Figure 4.10 and Table 4.3 for a detailed description).

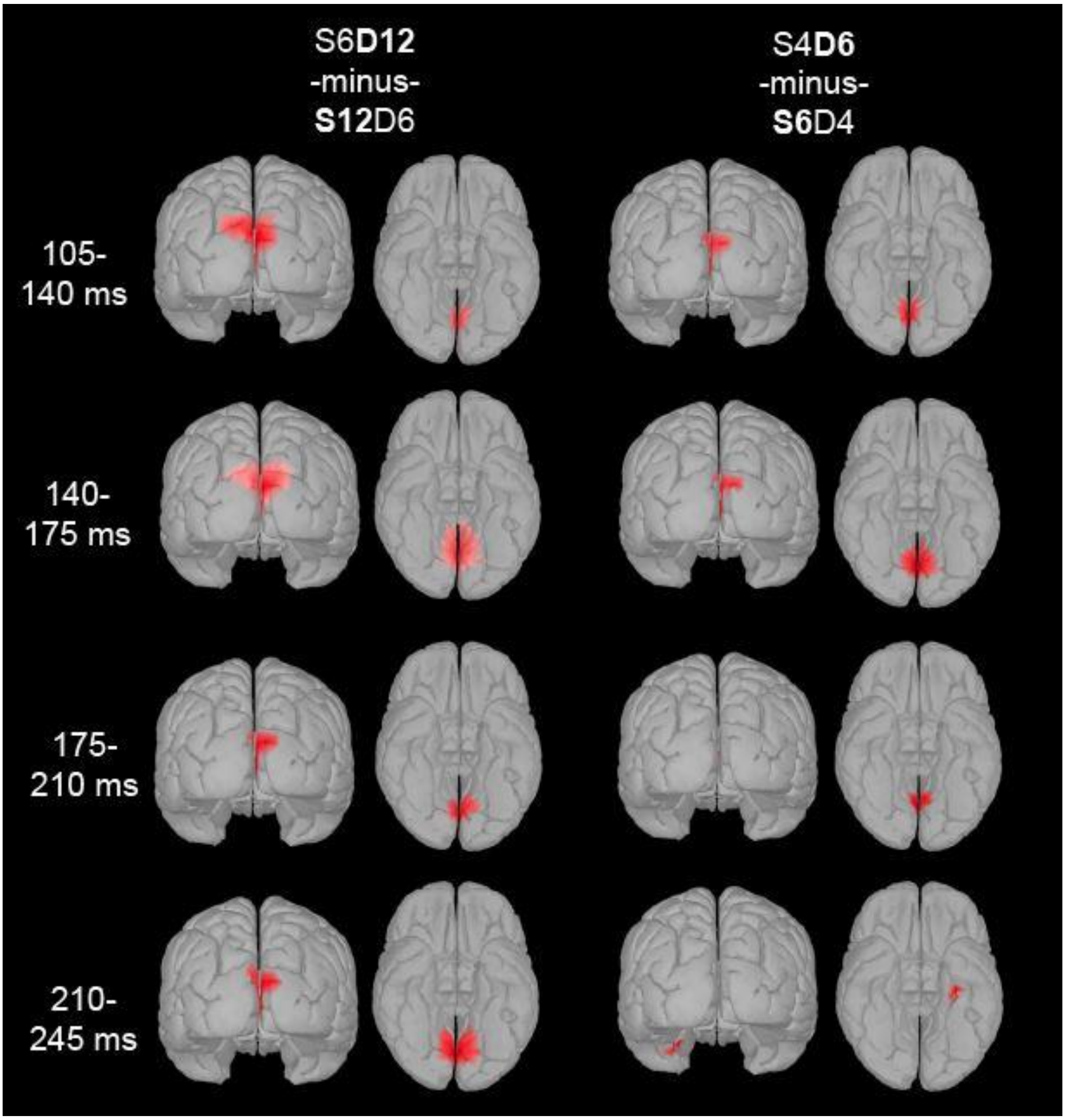


**Figure 4.10. Experiment 3: Source distribution of the significant differences between the difference potentials and baseline. Red colors indicating the significant voxels. For every voxel, the difference potentials were averaged to 10 equal, 35ms long interval from 0 to 350 ms. Difference potentials of two conditions on a given interval reported as significant, if at least 5 voxels exceeded the Bonferroni corrected alpha level.**

### 4.4.4 Discussion Experiment 3

A robust negative deflection was observable in the S6D12Diff and S4D6Diff waves in the 100-200 and 200-340 ms latency ranges. However, no negative deflection was observable in the S12D6Diff and S6D4Diff waves. These results support the notion that the observed asymmetry between the V6 and V12 difference waves is due to the complexity differences rather than the overlapping edges in the sequentially presented stimuli.

### 4.4.5 Reliability of Experiment 2 and 3

To test the reliability of Experiment 2 and 3, independent-samples t-tests were conducted on the amplitude values of the cognate difference waves measured in Experiment 2 and 3 (i.e.V6 OddDiff-S12D6Diff and V12 OddDiff-S6D12Diff).

There was no significant difference between the amplitude values of V12 OddDiff and S6D12Diff in the early (100-200 ms) and in the late (200-340 ms) range, neither at the occipital or the parieto-occipital ROIs.

There was significant difference between the amplitude values of V6 OddDiff (M=-0.86, SD=1.14) and S12D6Diff (M=-0.08, SD=1,21) in the early (178-216 ms) range at the occipital ROI; t(43)=2.19, p<0.05. No such difference was observable at the parieto-occipital ROI. There was no significant difference in the late (270-346 ms) differences between the two recording sessions.

## 4.5. General Discussion

In previous visual oddball studies, the deviant-minus-standard difference wave has been found to be negative at approximately 100-350 ms (e.g., Czigler et al., 2006; Takács et al. 2013, Kimura et al., 2009; however, see Sulykos & Czigler, 2010). This negativity is often labelled as vMMN regardless of its size, extension or occurrence in time. Despite the many studies that have been conducted in the field of vMMN research, it is still an open issue as to whether this negativity is a correlate of a memory comparison/prediction process (Czigler, 2007) or a consequence of a putatively more simple process, i.e., refractoriness/habituation/repetition suppression/stimulus specific adaptation. A possible explanation for the contradictory experimental results is that one uniform underlying mechanism that would generate vMMN does not exist and that instead there are separate mechanisms, depending on the circumstances/stimulation. Is it computationally effective to build a memory trace of certain orientations, when the same information is already present in the adaptational states of V1 neurons? However, higher level regularities probably cannot be coded on the level of sensory neuronal adaptation, and thus, the presence of a memory comparison process is justifiable.

In our study, we demonstrated that for simple features, such as orientation, SSA is a sufficient method for coding the regularities; the results of Experiment 1 can be fully explained by SSA. In the 105-190 ms range at parieto-occipital ROI and in the 118-148 ms range at the occipital ROI, the ERPs to the deviant and the control stimuli did not differ from each other, but they both elicited more negative responses than the standard, which supports the notion that the MMN is a modulation of the exogenous activity. Because the latency of the difference potential was similar to the latency of N1, the results fit the claim of May and Tiitinen (2010) and Kimura and his colleagues (2009). This result is in line with the findings in a study by Kenemans et al. (2003). This group presented a '*lonely deviant'* sequence, i.e., a sequence that consists of only rarely presented identical stimuli. The ERPs that are elicited by the "lonely deviant" and by the oddball deviant did not differ from each other in their latency and scalp distribution, which supports the notion that vMMN is better explained by stimulus rarity than by a mismatch process (Kenemans et al., 2003).

However, the results of Experiments 2 and 3 were markedly different and cannot be explained solely with SSA. They fit partly with the results of Maekawa et al. (2005) and partly support the findings of Kimura et al. (2009, 2015) and Czigler et al. (2002), i.e., in terms of the concept of memory-comparison-based change detection. In concordance with Kimura et al. (2009), in the early range of the deviant-minus-standard difference SSA was present, as the deviant-minus-control did not differ from zero in that range. However, contrary to Kimura's findings, in Experiment 2, gvMMN was obtainable too in the early, 100-200 ms range. The later range was absent of SSA because the Oddball and the Control differences were almost identical. It is important to note here, that the inter-stimulus interval (800 ms) used in our experiment is considerably larger, than in most vMMN studies, which might contribute to some of the differences observed in our results.

Traditionally in vMMN studies, the equal probability control is used to separate the memory-comparison and adaptation-based effects (i.e., Kimura et al., 2009, 2015). Here, we tested two additional paradigms, which were adapted from the auditory field. The difference waves that were formed from the various controls were almost identical. Considering this finding, we support the usage of equal probability control, which leads to better comparability among the vMMN studies.

The experimental protocol enabled us to investigate separately the neural generators of the deviant-related activity, which reflects partly SSA and gvMMN. The present results with respect to the visual areas are highly consistent with previous findings: Kimura et al. (2010) identified the source of MMN to the right cuneus and to the frontal lobe, Urakawa, Inui, Yamashiro and Kakigi (2010) indicated that the precuneus, while Susac et al. (2013) found that the middle occipital gyrus and cuneus is involved in the deviant-related activity. These results support the notion, that pre-attentive change detection is a relatively low level, modality-specific process in the visual cortex (Susac et al., 2013).

For the asymmetry of the V6 and V12 deviancy effects, the complexity-related explanation was supported by the results of Experiment 3 (an asymmetry between the V4 and V6 effects). According to this account, the V4 deviant within the sequence of V6 does not elicit vMMN because it did not carry new information within the sensory system.

This possibility is in line with the predictive coding account of mismatch responses (in both the auditory and visual modality), which leads to the claim that redundancy reduction is an essential feature of efficient coding. Direct representation of the raw images appears to be inefficient, and therefore, a possible role of a stimulus processing stage is to recode the sensory input into an efficient form. According to the predictive coding view, neuronal networks learn the statistical regularities of the world and reduce redundancy by transmitting only the unpredicted portions of an incoming sensory signal (Huang and Rao, 2011). The suggested mechanism relies on hierarchically organized neural systems in which top-down connections carry predictions from higher-level to lower-level areas, and bottom-up connections ensure the updating of the predictive models. As Garrido et al. (2009) highlight, the model adjustment hypothesis, which considers the MMN/vMMN to be an error signal that is elicited by a deviation from a learned regularity, is completely consistent with the predictive coding framework (Winkler et al, 1996, Näätätanen and Winkler, 1999; Kimura, 2011; Winkler and Czigler, 2012; Stefanics et al. 2014). In other words, MMN/vMMN is a correlate of a bottom-up signal that is responsible for the updating of the predictive model, and in this way, it minimizes the computational costs in higher areas (Garrido et al., 2009).

Based on our results, the conclusion of Kimura et al. (2009) - according to which the deviant-minus-standard difference wave consists of two subsequent posterior negativities reflecting adaptation effect and memory-comparison–based change detection effect - is supplemented with the observation, that the proportion of adaptation and memory effect in vMMN are not constant between experiments. The different level of adaptation among experimental settings might also contribute to the reported feature-related vMMN (Sulykos & Czigler, 2011; Susac et al., 2013) and is against the assumption, that vMMN is completely attributable to adaptation, and strengthen the notion that adaptation might have a functional role in the process of automatic change detection and not just a by-product of repetition.

### 4.6. Conclusions

In Experiments 1 and 2, we obtained highly different ERP effects, which suggests that as a function of the level of the deviance, different underlying mechanisms are responsible for the production of the observed negativity in the deviant-minus-standard difference wave. Additionally, the results of Experiments 2 and 3 highlight that the presented stimuli in the oddball sequence interact and that the complexity difference between the infrequent and frequent stimuli has considerable influence on the deviant-related response.

Footnote 1:

*There is no consensus with regard to the term that describes the response attenuation due to stimulus repetition. In MMN research, the most common term is refractoriness, as indicated by O'Shea (2015). However, as O'Shea highlights, the physiological meaning of "refractory" reflects the inactive state of a neuron due to previous electrical activity, which is on the order of milliseconds and is much too short to be the presumed process that underlies MMN. Furthermore, when considering that other terms are often in use as synonyms, O'Shea suggests the use of the term adaptation (O'Shea, 2015). We will use his suggestion, i.e., the term adaptation.*

Footnote 2:

*Higher/lower order/level, simple/complex stimuli are often mentioned in cognitive studies; however, as far as we know, a strict definition is lacking. In this study, high- and* *low-level deviances refer to the distinct dimensions of the deviance; low level is a unidimensional deviance, while high level is a multidimensional deviance. Complexity refers to the number of interconnected parts that build up the stimuli. In this sense, we use complexity as a relative term to describe the relationship between stimuli.*

## Acknowledgements

This study was supported by the Hungarian Research Fund (OTKA 104462). We thank Zsuzsa d'Albini and Zsuzsa Kovács for their technical help.

There are no conflicts of interest.

# Chapter 5: Automatic change detection in vision: Adaptation, memory mismatch, or both? Oddball and adaptation effects on event-related potentials[8]

## 5.1. Introduction

### 5.1.1. Visual mismatch negativity to various stimuli

Within sequences of homogeneous visual events, a violation of the sequence regularity (a deviant) elicits an electrical response in the brain that differs from those elicited by the frequent (standard) stimuli. This difference is present even when the deviants are unrelated to the task requirements (e.g., a task demanding focal attention). Differences in the event-related potentials (ERPs) in response to deviant and standard stimuli usually emerge as a posterior negativity and are usually termed the visual mismatch negativity (vMMN; for reviews see Czigler, 2007; Kimura et al., 2011, Stefanics et al., 2014). The vMMN occurs in response to deviant stimulus features (orientation, e.g., Astikainen et al., 2008; Bradley et al., 2015; Kimura et al., 2009; Kimura and Takeda, 2013; Sulykos and Czigler, 2011; Takacs et al., 2013; spatial frequency, e.g., Kenemans et al., 2010; Sulykos and Czigler, 2011; Susuac et al., 214; color, e.g., Czigler et al., 2002; Liu & Shi, 2008; Muller et al., 2012; Sysoeva et al., 2014 and motion direction, e.g., Kremlaček et al. 2006; Pazo_alvarez et al, 2004) or category (symmetry, Kecskés-Kovács et al., 2013; color as category, Athanasopoulos et al., 2010; Clifford et al., 2010; Mo et al., 2011; facial emotion, e.g., Astikainen et al., 2009; Huang et al., 2013; Kreegipuu et al., 2013; Stefanics et al., 2012; Zhao et al., 2009, face gender:

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[8] Bodnár, F., File, D., Sulykos, I., Kecskés-Kovács, K., Czigler, I. (2017). Automatic change detection in vision: Adaptation, memory mismatch, or both? II: Oddball and adaptation effects on event-related potentials. Atten Percept Psychophys, 79(8):2396-2411. doi: 10.3758/s13414-017-1402-x.
The first author of the article (Bodnár Flóra) agreed on to use this paper in the current thesis and to not use it in her own thesis.

Kecskés-Kovács et al., 2013; for reviews see Czigler, 2007; Kimura et al., 2011; Stefanics et al., 2014; Kremlaček et al., 2016).

### 5.1.2. Stimulus-specific adaptation and ‘genuine mismatch negativity’

ERP differences between deviant and standard stimuli can be attributed to two processes. First, repetition of events decreases the elicited activity to these stimuli (for a comprehensive discussion see May and Tiitinen, 2010). Accordingly, frequency difference between the presentation of deviant and standard stimuli are a putative source of these activity differences. Second, regular presentation of equivalent events forms memory representations of the sequential rule. Representations of incoming stimuli are compared to the representation of regular events. A mismatch between the stimuli violating the sequential rule and the regular stimuli elicits an additional ERP component. The equal probability control paradigm (Schröger and Wolff, 1996; Jacobsen and Schröger, 2001) is the most common method of separating the two sources of deviant-related activity. An equal probability sequence consists of stimuli with variable parameters. The probability of each parameter is equal to the probability of the oddball deviant. In this type of sequence the stimuli are presented in a random order (no sequential regularity). Differences between ERPs elicited by the oddball deviant and those elicited by physically identical stimuli from the control sequence are considered to be the consequence of sequential regularity violations (present in the oddball sequence, but absent in the control one, and called ‘genuine mismatch negativity’*;¸gvMMN*). As Kimura (2012) formulated, the gvMMN is a temporally-based ERP component (it should be noted that in the mismatch negativity literature the more frequently used term is ‘refractoriness’; for an attempt to clarify the terminology see O’Shea, 2015). In other fields of cognitive neuroscience changes in repetition-related activity are considered to be functionally significant phenomena (see e.g., O'Shea, 2015 for a short discussion). Stimulus-specific adaptation (SSA) is regarded as a consequence of memory acquisition or recalibration. SSA can be observed at almost all levels of the visual system (for reviews see Kohn, 2007; Webster, 2011), though the SSA characteristics differ across levels. The SSA effects (or repetition suppression)[1] measured with ERP and brain imaging (fMRI) are frequently used to investigate memory-related phenomena. In these studies adaptor and test stimuli were presented one after another. Presentation of the adaptor decreased responses to the test stimuli. Adaptation effects were present for both low-level stimulus features (e.g., tilt after-effect, Kanai, Tsuchiya and Verstraten, 2006; motion and orientation, Larsson and Harrison, 2015) and complex stimulus characteristics (e.g., gender of faces, Kovacs et al., 2008; memory for visual scenes Park et al., 2007).

### 5.1.3. Comparison of event-related potentials in an oddball and in an adaptation paradigm

The aim of the present study was to compare the effects of deviant stimuli in oddball paradigms to the effects of non-adapted (or less-adapted) stimuli (hereinafter deviant) in the adaptation paradigm. This comparison is essential in the field of mismatch negativity, because it provides a direct insight into the relationship between the results of visual adaptation and vMMN studies. Theories of mismatch negativity propose a comparison between representations of the input and existing memories, such as the memory trace theory (for a review see Näätäanen et al., 2009) and predictive coding processes (for a review see Garrido et al., 2008). According to these theories at least a part of the deviant-related activity is considered to be the consequence or the output of a comparison stage *(*'genuine mismatch negativity'). On the other hand, SSA does not require a separate comparison stage (May and Tiitinen, 2010*)*. With the direct comparison of the oddball and adaptation paradigms, the SSA and the genuine mismatch can be separated.

### 5.1.4. The two stimulus types of the present study: line textures and windmill patterns

In this study we selected two different stimulus types. The first type was a texture of oblique lines, and the deviance was the change of line orientation. Orientation deviance, the change of an elementary visual feature was frequently assessed in previous studies. Some studies employed the equal probability control method (Jacobsen and Schröger, 2001; Schröger and Wolff, 1998) using oblique lines in an attempt to separate adaptation from comparison-related effects (Astikainen et al., 2008; File et al., submitted; Kimura et al., 2009; Kimura and Takeda, 2013). However, the stimulus patterns in these studies differed. Astikainen et al. (2008) presented single lines; Kimura et al., (2009), Kimura and Takeda (2013) and Takács et al. (2013) presented lines surrounded by task-related stimuli, whereas Sulykos and Czigler (2011) presented a line texture in the hemifield opposite to the location of the task-related events. Though each study investigated ‘orientation deviancy’, the various stimulus arrangements produced different results. For example, the latency range of responses reported by Kimura et al., 2009 and Kimura and Takeda, 2013 were much longer than those reported by Sulykos and Czigler, 2011. In the present study we chose line texture stimuli. Differences between the deviant and standard orientation using these stimuli emerged as a single negativity with peak latency in the 130-140 ms range.

The second type of stimuli was the windmill pattern. These patterned stimuli were first used by Maekawa et al. (2005, 2009, 2013) to study the vMMN. Windmill patterns elicited deviant-related posterior negativities in two latency periods (~140-230 and ~230-320 ms). Our aim was to investigate whether early and late deviant-related negativities were similar in the Oddball and Adaptation conditions. In other words, as Kimura et al. (2009) suggested, only the later part of the negative difference potential is gvMMN.

### 5.1.5. General outline of the studies and expected results

In both experiments we introduced a traditional passive Oddball paradigm. In the Adaptation paradigm the adaptors preceded the test stimuli, and the adaptor and test stimuli had either identical or different visual characteristics. In Experiment 1 the adaptor duration corresponded either the sum of the average duration of the Oddball standards between two deviants (Squeezed adaptation sequences), or it was identical to the average duration of the whole periods between two oddball deviants (i.e. stimulus durations plus inter-stimulus interval; Filled adaptation sequences). Due to the longer adaptor duration we expected larger adaptation effect in the filled adaptation sequences. In Experiment 2 only the latter condition (larger expected adaptation effect) was introduced. As the main issue of the study, we compared the deviant-related ERP effects of the oddball condition to the ERP difference to stimuli preceded by different and identical adaptors. We expected that adaptation will influence the earlier part of the difference potential, whereas in the later part we expected genuine mismatch effects. It is important to emphasize that oddball deviants violated a sequential rule, in other words, these stimuli were non-predicted. In the adaptation tasks there were conditions where the test stimuli were identical to the adaptors (but they have shorter duration), and there were conditions where the test and adaptor stimuli were different. Accordingly, in both conditions of the adaptation tasks the test stimuli did not violated a sequential rule. Therefore the possible ERP difference between the two experiments can be regarded as a difference between non-predictability and the lack of non-predictability. It is important to note that regular stimulus presentation does not mean the automatic registration of the regularity at the level of automatic visual processing. This is because the sensitivity of the memory system underlying vMMN is limited in the time domain. Kimura et al. (2010a) compared ERPs to the last stimuli of regular AAAAB cycles to the ERPs to random deviants of oddball sequences. They obtained similar vMMNs in both sequences. Duration of a cycles was 3750 ms, i.e., at that duration the system did not register the regularity It is well established that elicitation of vMMN requires at least 4 preceding standards and the deviant following the standards (e.g. Maekawa et al., 2009). In our study even in the condition with shorter inter-stimulus interval the length of five cycles was in the range of 3000-4000 ms, and it was much longer in the adaptation condition with longer cycles. Therefore it is improbable that the automatic memory system was capable of predicting the characteristics of the following stimulus.

It is important to emphasize that in both experiments in both paradigm the ERP-related stimuli were task-irrelevant. Furthermore, we made attempts to introduce tasks requiring permanent attention and fixation, i.e., to ensure that the ERP-related stimuli were un-attended (Czigler, 2007). This way we avoided the involvement of attention-related negativities (e.g. Czigler and Csibra, 1992 , Hillyard and Münte, 1984; Wijers et al, 1989) into the ERPs.

## 5.2. Experiment 1.

### 5.2.1. Methods

#### 5.2.1.1. Participants

Seventeen paid students (10 female; mean age, 21.8 years; SD=2.03) with normal or corrected-to-normal vision participated in the study. Written consent was obtained from all participants prior to the experimental procedure. The study was conducted in accordance with the Declaration of Helsinki and approved by the Committee of Ethics of the Psychology Institutes in Hungary.

#### 5.2.1.2. Stimuli

The ERP-related stimuli were presented in the lower two-thirds of the screen (17-inch LCD monitor with a 60 Hz refresh rate). Stimuli consisted of a 6 x 4 matrix of grey oblique lines (Figure 5.1). The line orientations were either 45° or 135°. The luminance of the lines was 36.7 cd/m$^2$. The luminance of the dark background was 0.5 cd/m$^2$. The length of the lines was 1.3° and their width was 0.1° (from a 120 cm viewing distance). The distance between the line segments within a row was 2.62° and the distance between the rows was 2°.

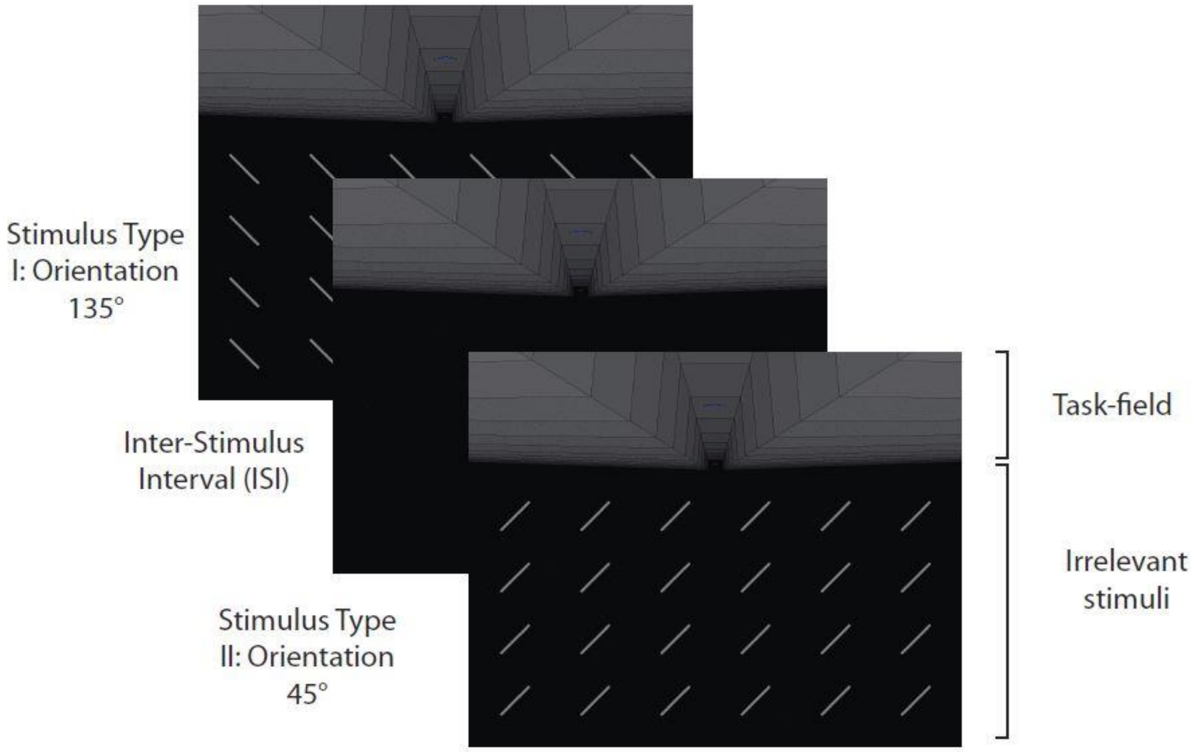


**Figure 5.1. Experiment 1: Experimental stimuli and a sample of the stimulus display**

The task-related events were displayed continuously. The task was a simple video game. The participants had to control a blue spaceship flying through a canyon using a gamepad. Every second, an "alien" spaceship appeared in the canyon and moved towards the participant's spaceship. The color of the "alien" spaceship was either green (p=0.4) or red (p=0.6). The aim of the task was to catch the green spaceships and avoid the red ones. The task demanded continuous fixation of the location from which the spaceships appeared. The "alien" spaceships never appeared simultaneously with the ERP-related stimuli. Figure 5.1 shows a sample of the stimulus display. For more details, see Sulykos and Czigler (2011). However, we modified the task described by Sulykos and Czigler (2011) to make it more demanding by increasing the speed of the spaceship. This modification increased the attentional demands of the task and required more stable fixation.[2] To assess performance, the average hit rate and the average rate of successful avoidance was measured.

#### 5.2.1.3. Procedure

The task consisted of three conditions: Oddball, Filled adaptation and Squeezed adaptation. In the Oddball condition the stimulus (line textures) duration was 100 ms and the stimulus onset asymmetry (SOA) was 500 ms. In the Oddball condition, 83 percent of the stimuli were standard and 17 percent were deviant. A reverse control procedure was introduced, i.e., both texture orientations (45 and 135 degrees) were presented as standard and as deviant. In both of the standard-deviant arrangements, 800 stimuli were presented (136 deviant). This procedure allowed us to compare stimuli with identical physical characteristics. To compare the Oddball and Adaptation conditions, we also presented homogeneous sequences, i.e., a series without deviant stimuli (‘standard only’). In the Filled Adaptation condition long and short stimuli were presented. Long stimuli served as the adaptors and short stimuli served as the test. The average length of the adaptors was equal to the sum of the duration of the oddball standards between the two deviants plus the inter-stimulus interval between the stimuli (1100-3100 ms; mean=2100 ms). During the Filled Adaptation condition, two types of sequences were presented. In the homogeneous sequences the orientations of the test and long stimuli were identical. The orientation of the test stimulus differed (deviant) in the heterogeneous sequences. The Filled condition consisted of 274 stimuli (137 test stimuli). During the Squeezed adaptation sequences the average duration of the long stimuli was identical to the sum of the duration of the oddball standards between the two deviants (400-700 ms; mean=550 ms). As in the Filled condition, the Squeezed condition consisted of both homogeneous and heterogeneous sequences. The Squeezed condition consisted of 289 stimuli (144 test stimuli). Similar to the Oddball condition, we applied the reverse control procedure in the two Adaptation conditions. In both adaptation conditions the interval between the adaptor offset and the test onset was 400 ms

There were 12 sequences within each session: two oddball sequences, two homogenous sequences with short standard stimuli only, four squeezed and four filled sequences. Due to the longer durations of the sequences, the Oddball and Filled conditions were divided into two blocks. Therefore, there were 20 blocks within a session: 4 oddball blocks, 4 blocks with ‘standard only’, 2 heterogeneous squeezed blocks, 2 homogeneous squeezed blocks, 4 heterogeneous filled blocks and 4 homogeneous filled blocks. The average block duration was 3.3 min. There was a ~30 sec break between the blocks. The block order was counterbalanced across participants.

The adaptation effect was defined as the difference between the ERPs in response to the test stimuli in the heterogeneous and homogeneous sequences. The vMMN was defined as the difference between the response to the deviant stimuli in the heterogeneous sequences and the standard in the homogeneous sequences. In summary, there were three conditions: Oddball, Filled adaptation and Squeezed adaptation. In each condition the reverse control procedure was introduced. Figure 5.2 shows the outline of the experimental design.

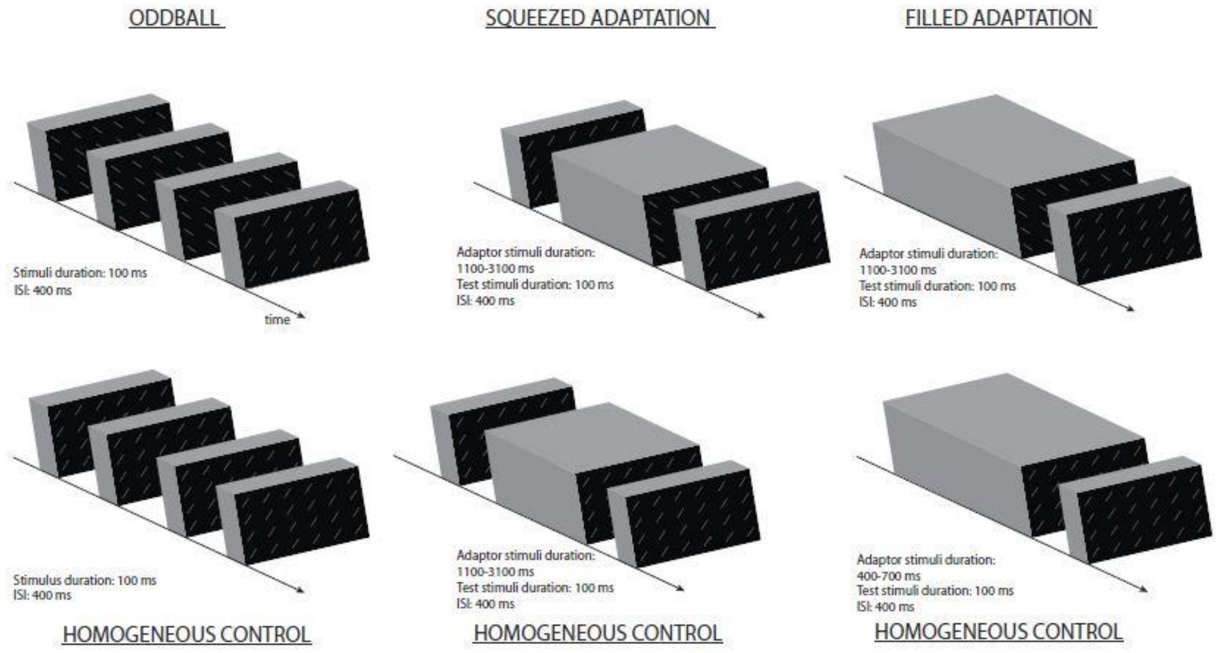


**Figure 5.2. Experiment 1: Outline of the stimulus sequences during the oddball, squeezed, and filled conditions**

#### 5.2.1.4. Measurement of electrical brain activity

Electrical brain activity was recorded from 61 locations (Ag/AgCl electrodes, EasyCap, Synamps2 amplifier, NeuroScan recording system) according to the extended 10-20 system (DC-70 Hz, 500 Hz sampling rate). The reference electrode was placed on the tip of the nose. The ground electrode was placed on the forehead. The horizontal EOG was recorded using a bipolar configuration between the electrodes positioned laterally to the outer canthi of the two eyes. Vertical eye movements were monitored using a bipolar montage between the electrodes placed above and below the right eye. The EEG and EOG signals were digitally low-pass filtered at 30 Hz with a finite impulse response (FIR) filter (filter order= 184, Kaiser Beta=5.6533), and high-pass filtered at 0.1 Hz with a finite impulse response (FIR) filter (filter order= 9056, Kaiser Beta=5.6533). Epochs ranging from -100 to 400 ms relative to the onset of the test stimulus were selected from the Adaptation trials. Equivalent epochs aligned on the deviant and standard stimuli were selected from the Oddball condition. We selected trials from the homogeneous blocks with short stimuli presented at the same position as the deviants in the oddball blocks. We calculated the averages of these ERPs. The mean voltage during the 100 ms pre-stimulus interval served as the baseline for the amplitude measurements. Epochs with an amplitude change exceeding ±100 μV on any channel were rejected from further analysis. To increase the number of averaged stimuli, we collapsed across ERPs in response to the corresponding events of the reversed sequences.

Deviance-related activity was determined in three steps. In the first step, we tested whether the difference between the deviant and standard potentials differed from zero in any of the channels for at least 10 sample *point* within a 20 ms bin centered on the peak of the difference potential (in t-tests). In the second step, only the differences that met this criterion were considered. We constructed two ROIs: one parieto-occipital ROI comprised of the PO3, POz and PO4 locations, and an occipital ROI comprised of the O1, Oz and O2 locations. The mean of the *differences* within a 20 ms time window centered on the largest negative value within each ROI was compared to zero using a t-test (separately for the Oddball, Filled and Squeezed conditions). In the third step, the negativities with significant differences were compared using a two-way ANOVA with condition and ROI as factors. Individual peak latency values were measured and compared within the same range.

To investigate the effects of different onset-to-onset durations of the stimuli in the three conditions, we compared the N1 of the deviant-related ERPs using a two-way ANOVA with condition and ROI as factors. To test the relationship between N1 and the difference potential, the latencies of these components were compared using a three-way ANOVA with component (difference potential or N1), condition and ROI as factors. Latency differences between the N1 and the difference potential would suggest that the sources of these two components were distinct from one another. When appropriate, the Greenhouse-Geisser correction procedure was applied. Post hoc analyses were carried out using Tukey's HSD test. Reported descriptions of the interactions were supported by the post hoc test. Only results that exhibited effects of stimulus and condition (main effects and interactions) will be reported. Behavioral performance was assessed in terms of hit and avoidance rates.

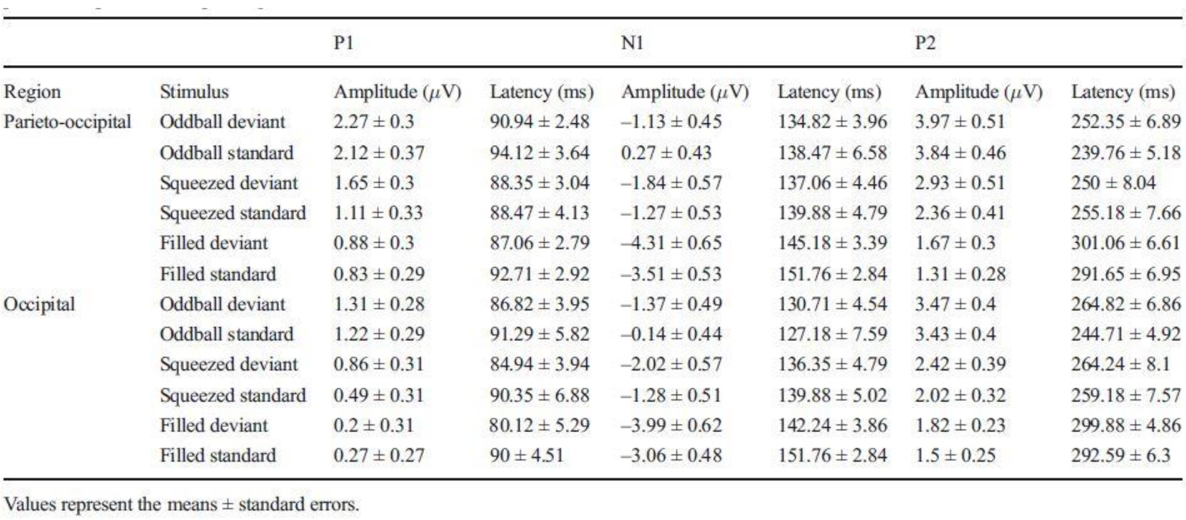
## 5.2.2. Results

### 5.2.2.1. Behavioral results

The hit rates during the Oddball, Squeezed and Filled conditions were 64.2, 62.5 64.2 percent, respectively. The correct avoidance rates were 75.1, 72.0 and 74.1 percent, respectively. The hit rates did not differ across conditions; however there was a significant effect of condition in the avoidance rate ($F(2,32)=5.34$, $p<0.05$, $\varepsilon=0.86$, $\acute{\eta}_p^2=0.25$). According to Tukey's HSD test, performance was lower on the Squeezed trials than on Filled trials.

### 5.2.2.2 Event-related potentials

As Figures 5.3 shows, the ERPs over the posterior locations consisted of three components: P1 (80-100 ms), N1 (100-200 ms) and P2 (200-400 ms). This component structure was similar in all conditions. The deviant *minus* standard difference (difference between the ERPs in response to the test stimuli in the heterogeneous and homogeneous sequences during the Adaptation conditions, and the difference between the ERPs in response to the deviant and corresponding stimuli in the homogeneous sequence during the Oddball condition) emerged in the 100-150 ms period. In all conditions the difference potentials had posterior maxima. Table 5.1 details the latencies and amplitudes of the exogenous components (P1, N1, P2) at the two ROIs.



| | | P1 | | N1 | | P2 | |
|---|---|---|---|---|---|---|---|
| Region | Stimulus | Amplitude (μV) | Latency (ms) | Amplitude (μV) | Latency (ms) | Amplitude (μV) | Latency (ms) |
| Parieto-occipital | Oddball deviant | 2.27 ± 0.3 | 90.94 ± 2.48 | −1.13 ± 0.45 | 134.82 ± 3.96 | 3.97 ± 0.51 | 252.35 ± 6.89 |
| | Oddball standard | 2.12 ± 0.37 | 94.12 ± 3.64 | 0.27 ± 0.43 | 138.47 ± 6.58 | 3.84 ± 0.46 | 239.76 ± 5.18 |
| | Squeezed deviant | 1.65 ± 0.3 | 88.35 ± 3.04 | −1.84 ± 0.57 | 137.06 ± 4.46 | 2.93 ± 0.51 | 250 ± 8.04 |
| | Squeezed standard | 1.11 ± 0.33 | 88.47 ± 4.13 | −1.27 ± 0.53 | 139.88 ± 4.79 | 2.36 ± 0.41 | 255.18 ± 7.66 |
| | Filled deviant | 0.88 ± 0.3 | 87.06 ± 2.79 | −4.31 ± 0.65 | 145.18 ± 3.39 | 1.67 ± 0.3 | 301.06 ± 6.61 |
| | Filled standard | 0.83 ± 0.29 | 92.71 ± 2.92 | −3.51 ± 0.53 | 151.76 ± 2.84 | 1.31 ± 0.28 | 291.65 ± 6.95 |
| Occipital | Oddball deviant | 1.31 ± 0.28 | 86.82 ± 3.95 | −1.37 ± 0.49 | 130.71 ± 4.54 | 3.47 ± 0.4 | 264.82 ± 6.86 |
| | Oddball standard | 1.22 ± 0.29 | 91.29 ± 5.82 | −0.14 ± 0.44 | 127.18 ± 7.59 | 3.43 ± 0.4 | 244.71 ± 4.92 |
| | Squeezed deviant | 0.86 ± 0.31 | 84.94 ± 3.94 | −2.02 ± 0.57 | 136.35 ± 4.79 | 2.42 ± 0.39 | 264.24 ± 8.1 |
| | Squeezed standard | 0.49 ± 0.31 | 90.35 ± 6.88 | −1.28 ± 0.51 | 139.88 ± 5.02 | 2.02 ± 0.32 | 259.18 ± 7.57 |
| | Filled deviant | 0.2 ± 0.31 | 80.12 ± 5.29 | −3.99 ± 0.62 | 142.24 ± 3.86 | 1.82 ± 0.23 | 299.88 ± 4.86 |
| | Filled standard | 0.27 ± 0.27 | 90 ± 4.51 | −3.06 ± 0.48 | 151.76 ± 2.84 | 1.5 ± 0.25 | 292.59 ± 6.3 |

Values represent the means ± standard errors.

**Table 5.1. Experiment 1: Grand averages of the epoch mean amplitudes and peak latencies of the exogenous components (P1, N1, P2) measured at the parieto-occipital and occipital regions**

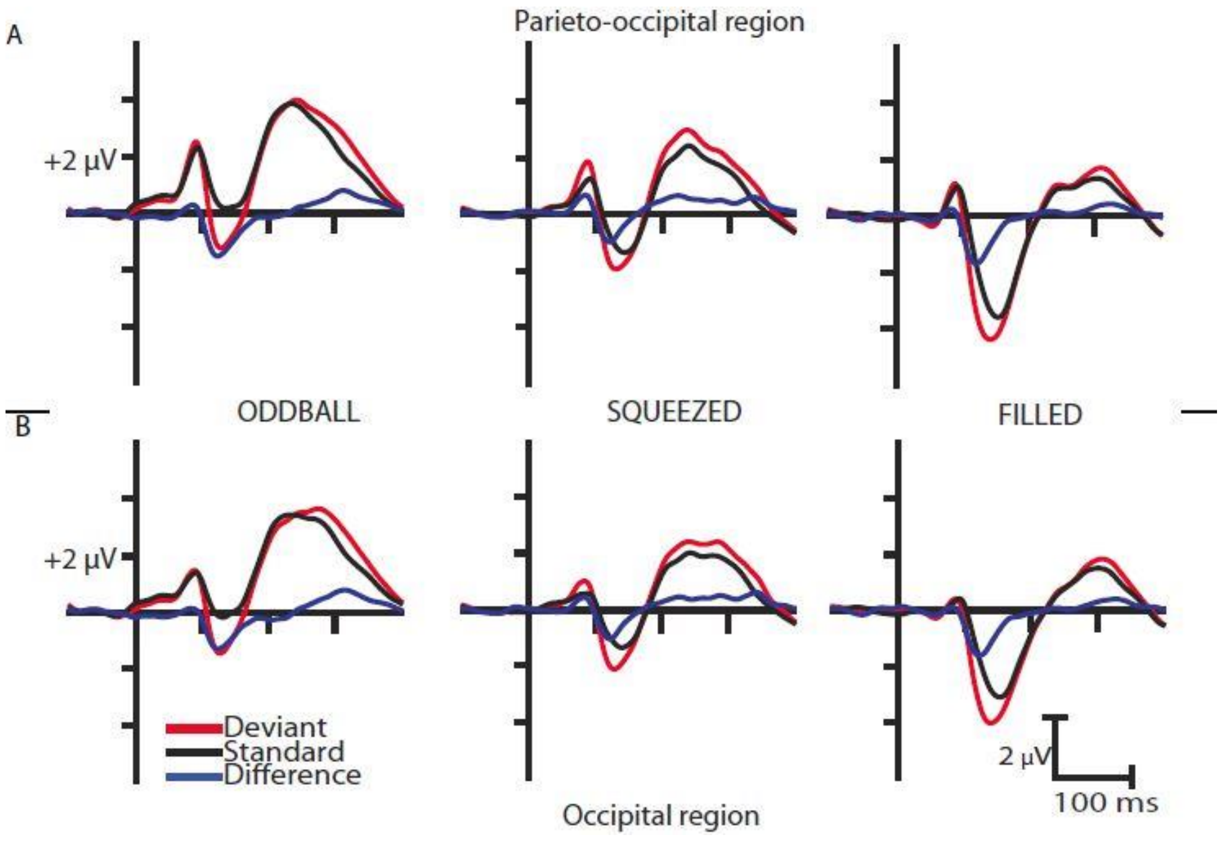
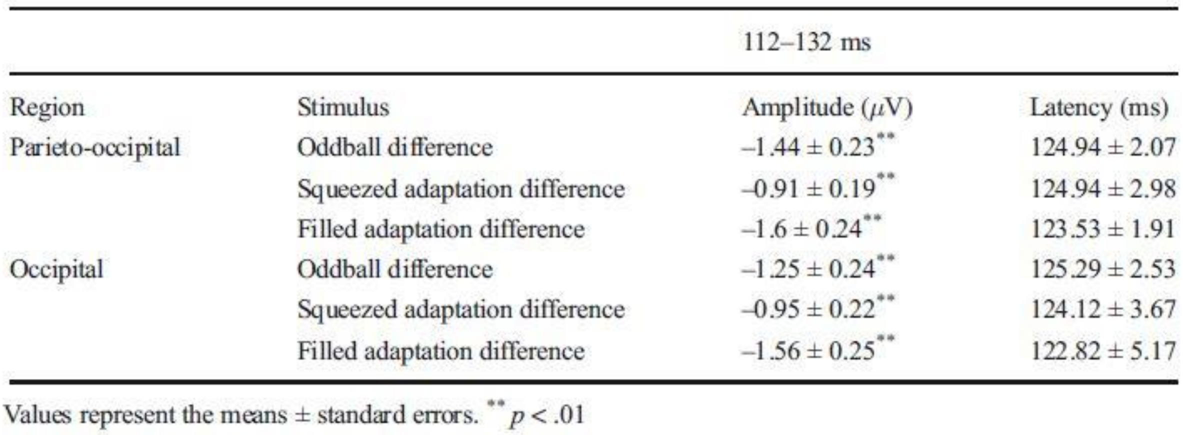


**Figure 5.3. Experiment 1: Event-related potentials and difference potentials in the three conditions (oddball, squeezed, and filled) from the parieto-occipital and occipital regions of interest**

### 5.2.2.3. Difference potentials

Difference potentials were measured during the 112-132 time window on adaptation trials and during the 114-134 ms time window on the oddball trials, i.e., the 20 ms window centered on the largest negativity within the range of significant t-tests (at least 10 consecutive values at any location).

Table 5.2 shows the peak amplitudes and latencies of the difference potentials in the two ROIs. The latencies did not differ across the three conditions. For the negativity amplitudes, the values differed significantly from zero in all conditions and in both ROIs ($t(16)=4.16\text{-}6.65$, Bonferroni corrected $p<0.001$). Because the negativity appeared in all conditions, we conducted a two-way ANOVA with condition and ROI as factors. The main effect of condition ($F(2,32)=3.86$, $p<0.05$, $\varepsilon=0.95$, $\acute{\eta}_p^2=0.19$) and the condition x ROI interaction ($F(2,32)=5.9$, $p<0.05$, $\varepsilon=0.93$, $\acute{\eta}_p^2=0.26$) were significant. The negativity was smaller in the Squeezed condition. Furthermore, on Oddball trials the negativity was larger in the parieto-occipital ROI than in the occipital. Figure 5.4 shows the difference potentials and their surface distributions.



| | | 112–132 ms | |
|---|---|---|---|
| Region | Stimulus | Amplitude ($\mu$V) | Latency (ms) |
| Parieto-occipital | Oddball difference | $-1.44 \pm 0.23^{**}$ | $124.94 \pm 2.07$ |
| | Squeezed adaptation difference | $-0.91 \pm 0.19^{**}$ | $124.94 \pm 2.98$ |
| | Filled adaptation difference | $-1.6 \pm 0.24^{**}$ | $123.53 \pm 1.91$ |
| Occipital | Oddball difference | $-1.25 \pm 0.24^{**}$ | $125.29 \pm 2.53$ |
| | Squeezed adaptation difference | $-0.95 \pm 0.22^{**}$ | $124.12 \pm 3.67$ |
| | Filled adaptation difference | $-1.56 \pm 0.25^{**}$ | $122.82 \pm 5.17$ |

Values represent the means ± standard errors. $^{**}p < .01$

**Table 5.2. Experiment 1: Grand averages of epoch mean amplitudes and peak latencies of the difference waves measured at parieto-occipital and occipital regions**

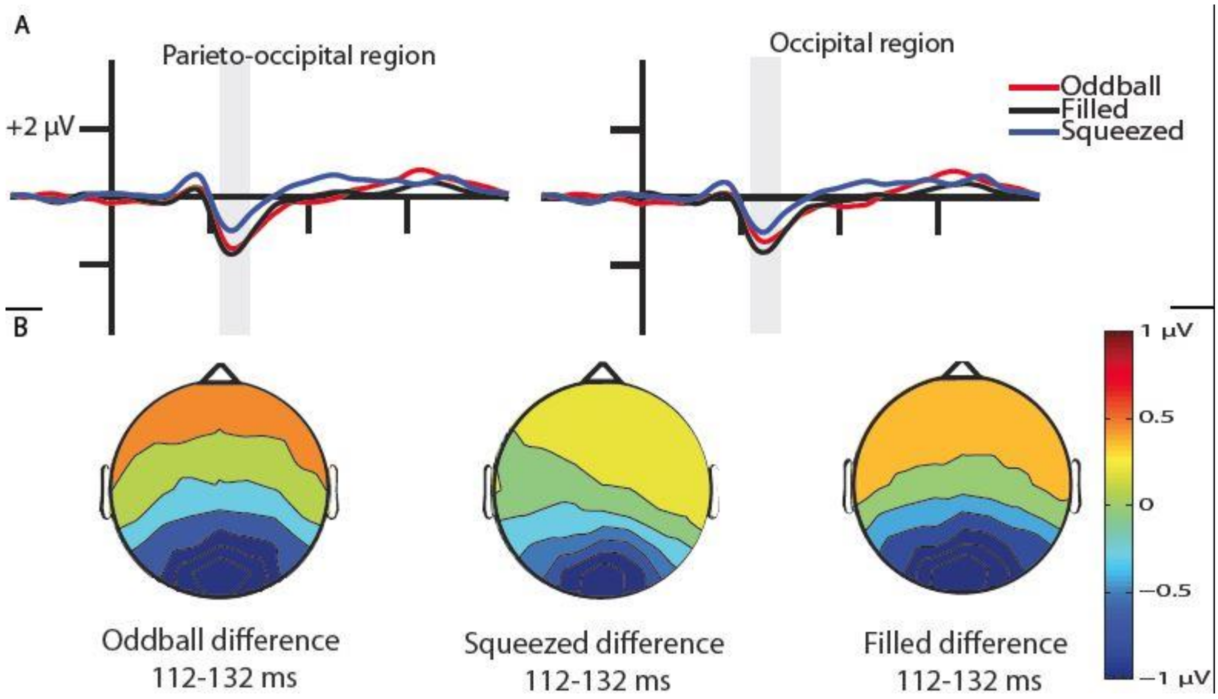


**Figure 5.4. Experiment 1: Difference potentials from the three (oddball, squeezed, and filled) conditions, as well as their surface distributions**

### 5.2.2.4. The effect of onset-to-onset time on N1 and the emergence of a long-lasting ERP effect

Irrespective of the deviancy effects, the ERPs in the three conditions were markedly different (see Figure 5.5). Due to the overlap in the negative difference potentials and to avoid effects contributed by the preceding stimuli with identical orientation (SSA), we compared the latencies and amplitudes of the N1 component from heterogeneous sequences. Table 5.1 shows the N1 latencies and amplitudes in the two ROIs. The N1 latency was longest on Filled trials and shortest on Oddball trials ($F(2,32)=5.5$, $p<0.01$, $\varepsilon=0.76$, $ή_p^2=0.26$). The N1 amplitude was largest on Filled trials and smallest on Oddball trials ($F(2,32)=61.77$, $p<0.0001$, $\varepsilon=0.87$, $ή_p^2=0.79$).

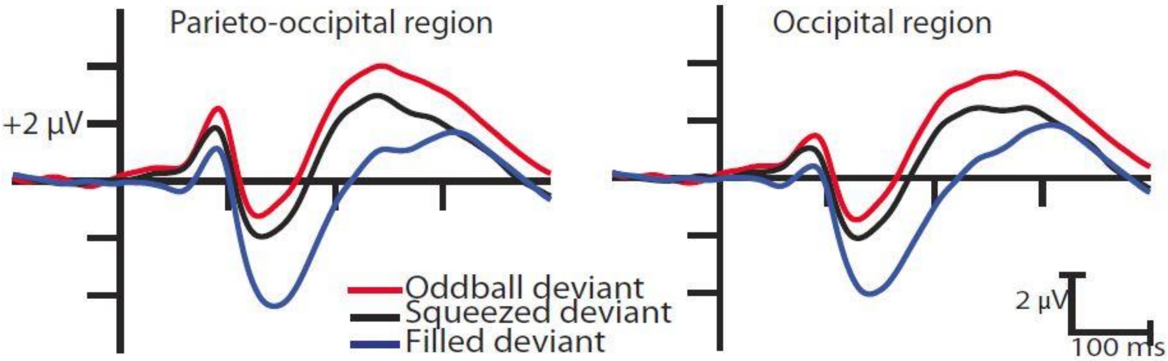


**Figure 5.5 Experiment 1: Event-related potentials from homogeneous sequences of the oddball, squeezed, and filled adaptation conditions**

### 5.2.2.5. N1 and deviancy

N1 latencies and the latencies of the difference potentials were compared using a two-way ANOVA with component (N1, difference potential) and ROI as factors. Only deviant-related N1 latencies were involved in the analysis. The main effect of component was significant ($F(1,16)=29.36$, $p<0.0001$, $\varepsilon=0.70$ $ή_p^2=0.64$). The deviant-related negativity had a shorter latency than the N1 component (124 vs. 138 ms).

### 5.2.3. Discussion

An important result of the present study was the significant difference between the ERPs in response to the test stimuli of the heterogeneous and homogeneous sequences in all conditions. In all conditions the deviant minus standard difference (i.e., textures with different orientations from the standard or adaptor) elicited posterior negativities within the 100-140 ms range. The magnitude of the negativity was slightly smaller in the Squeezed condition, and the behavioral performance during this condition was slightly lower. It is possible that the long duration of the filled stimuli relative to the squeezed stimuli, decreased their saliency. These saliency differences impacted both the behavioral performance (lower avoidance rate in the Squeezed condition) and the ERPs. Similar posterior negativities in the Oddball, Filled and Squeezed conditions are inconsistent with the traditional theoretical view on the deviance-related effect of the oddball paradigm. This is because mismatch components are considered to index violations of sequential regularities (e.g., Kimura, 2012; Stefanics et al.,2012; Winkler and Czigler, 2012). However, in the adaptation paradigm the deviants did not violate the sequential rules; test stimuli were preceded by a single event (adaptor). Unfortunately, we are not aware of any studies that evaluated this issue in the auditory modality. One reasonable explanation (at least in the visual modality) is that long-lasting stimuli form a representation in memory; therefore, ERPs in response to a stimulus with similar characteristics (orientation in the present study) are susceptible to SSA. It is important to note that this possibility does not exclude representations of sequential regularities or effects of sequential regularity violations for different types of stimuli in the ERP.

In addition to the memory mismatch interpretation of the deviant-related negativity (e.g., Näätänen et al., 2005) an alternative interpretation could be that ERP differences between the standard and deviant events result from decreased activity in response to the standard, i.e., ERP refractoriness or ERP adaptation (e.g., May and Tiitinen, 2010). Our results are consistent with this explanation. Studies investigating orientation deviancy using the equal probability control may help in clarifying the memory mismatch vs. adaptation issue. Astikainen et al. (2008) assessed deviant minus control differences in the 185-205 ms range, but only at short ISIs (400 ms). The scalp distribution of the genuine vMMN was smaller than the deviant minus standard difference. In this study single bars were presented. In an experiment by Kimura et al. (2009) the stimuli were also single bars. In this study the equal probability control abolished the early difference potential (in the 100-150 ms range), whereas in the 150-350 ms range these authors obtained genuine vMMN. It should be noted that attention was not well-controlled in these studies. One may suppose that the auditory task in the Astikainen and Hietanen (2009) study did not prevent attentional capture by the bars at the center of the visual field. Participants in the Kimura et al. (2009) study discriminated between the terminal shapes of the bars, whereas the bar orientation was irrelevant. However, as results in object-related attention studies show (e.g., Duncan, 1984), in the case of attended objects (presented on an otherwise empty field) attentional processing extends to the other features. Finally, in a study conducted by Kimura and Takeda (2013) the target stimuli were surrounded by bars, i.e., the bars made up a frame. In this study the genuine vMMN emerged in the 150-300 ms time period and the scalp distribution of this negativity (right side dominant) differed from the distribution of the deviant minus standard difference. To anticipate the finding of a companion study, we included the equal probability control in a paradigm similar to that of the present study (File at al., submitted). In this study the control procedure abolished the deviance effect completely. While neither of the above studies obtained a genuine vMMN in the early (100-140 ms) epoch, adaptation seems to be a plausible explanation of the present results.

The amplitude and the latency of the N1 in response to the deviants was larger in the Filled conditions than in the other conditions. The longer onset-to-onset duration of this condition may explain these differences. It should be noted that in contrast to findings in the auditory modality (e.g., Pereira et al., 2014), data on stimulus duration effects in the visual modality are rather sparse. Lehtonen (1973) obtained marked inter-stimulus interval (ISI) effects over the vertex. Comparing 400 and 600 ms ISIs, Neville et al. (1983) demonstrated that the N1 amplitude *decreased* at longer ISIs. In their oddball study, Astikainen et al. (2008) applied shorter (400 ms) and longer (1100 ms) ISIs. Unfortunately, the posterior N1 was not observed in this study; however, neither the posterior positivity nor the anterior negativity differed across the two ISI conditions. It seems that the effect of ISI on the N1 component requires further study. Wastell and Kleinmann (1980) reported less robust ISI effects at the occipital location than at a more anterior site. In a recent paper, Andrade et al. (2015) compared the ERPs in response to parafoveal checkerboards to those in response to stimulus pairs with varied intra-pair intervals using a paradigm where the ISI varied across blocks. Considerable inter-stimulus effects were reported in the blocked paradigm. The amplitude of the negativity increased during the 130-180 ms time period, Similar to our results, N1 increased and apparently decreased P2 at longer ISIs. It is important to note that long minus short ISI differences were present within a wide neural network, far beyond the locations of lower levels of visual structures.

In summary, in this study we observed enlarged negativities in response to deviant stimuli in the 100-140 ms range. This negativity was fairly similar in the Oddball and Adaptation conditions. As May and Tiitinen (2010) suggested, the emergence of this negativity can be explained by SSA (however, in the General discussion we put forth an alternative explanation). We also observed a long-lasting posterior negative shift that emerged as a function of the onset-to-onset duration.

In this study there was only a weak indication that the deviancy effect was not solely due to amplitude modulations of the N1 peak. The latency of the negative difference potential was shorter than the N1 latency. However, we have to note that the posterior negativity in the N1 range is an aggregate of various underlying processes (Di Russo et al.,2002). Such latency changes can be the consequence of different SSA effects on latent components (Luck, 2005).

## 5.3. Experiment 2.

In contrast to studies conducted by Maekawa and colleagues, we introduced a more stringent control of attention by requiring participants to perform a continuous tracking task. This task was not particularly demanding, but proper performance required sustained fixation and attention to the task field.

### 5.3.1. Methods

#### 5.3.1.1. Participants

Nineteen paid students (8 female; mean age, 23.6 years; SD=4.33) participated in the study. Written consent was obtained from all participants prior to the experimental procedure. The study was conducted in accordance with the Declaration of Helsinki, and approved by the Committee of Ethics of the Psychology Institutes in Hungary.

#### 5.3.1.2 Stimuli and procedure

Task-related stimuli appeared at the center of the screen. During the tracking task participants had to keep a ball within a blue circle (1.8° in diameter from a 120 cm viewing distance). The ball moved along the horizontal axis with a random speed and direction. If the ball left the circle, the circle's color changed from blue to red. Ball movement was controlled using a gamepad. Performance feedback was provided (duration within the circle/ duration of the block * 100) at the end of each block. Stimuli appeared on a 17-inch LCD monitor with 60 Hz refresh rate.

ERPs in response to the windmill patterns were recorded. As Figure 5.6 shows, the patterns consisted of either 6 or 12 vanes (V6 and V12). The patterns had a high contrast (37.2 cd/m$^2$ for the bright segments, and 0.1 cd/m$^2$ for the dark). The diameter of the pattern was 13.82°. The background was grey (16.0. cd/m$^2$).

There were two conditions, Oddball and Adaptation. In the Oddball condition the stimulus duration was 100 ms and the ISI was 400 ms. Both V6 and V12 stimuli served as deviants. As in Experiment 1, there were homogeneous (test stimulus identical to the standard/adaptor) and heterogeneous (test stimulus differed from the standard/adaptor) sequences. The Adaptation condition was identical to the Filled condition in Experiment 1. The duration of the test stimulus was 100 ms and 1100-3100 ms (mean=2100 ms) for the adaptor stimulus. The interval between the offset of the adaptor and the onset of the short stimulus was 400 ms. The experimental session consisted of 8 sequences: four Oddball sequences and four Adaptation sequences (homogeneous/heterogeneous sequences x reverse control sequences). The Oddball condition consisted of 800 stimuli (136 were deviant; p=0.13). The Filled condition consisted of 272 stimuli with 144 short stimuli. The average sequence duration was 4.9 min. The stimuli and an outline of the experimental design are shown in Figure 5.6.

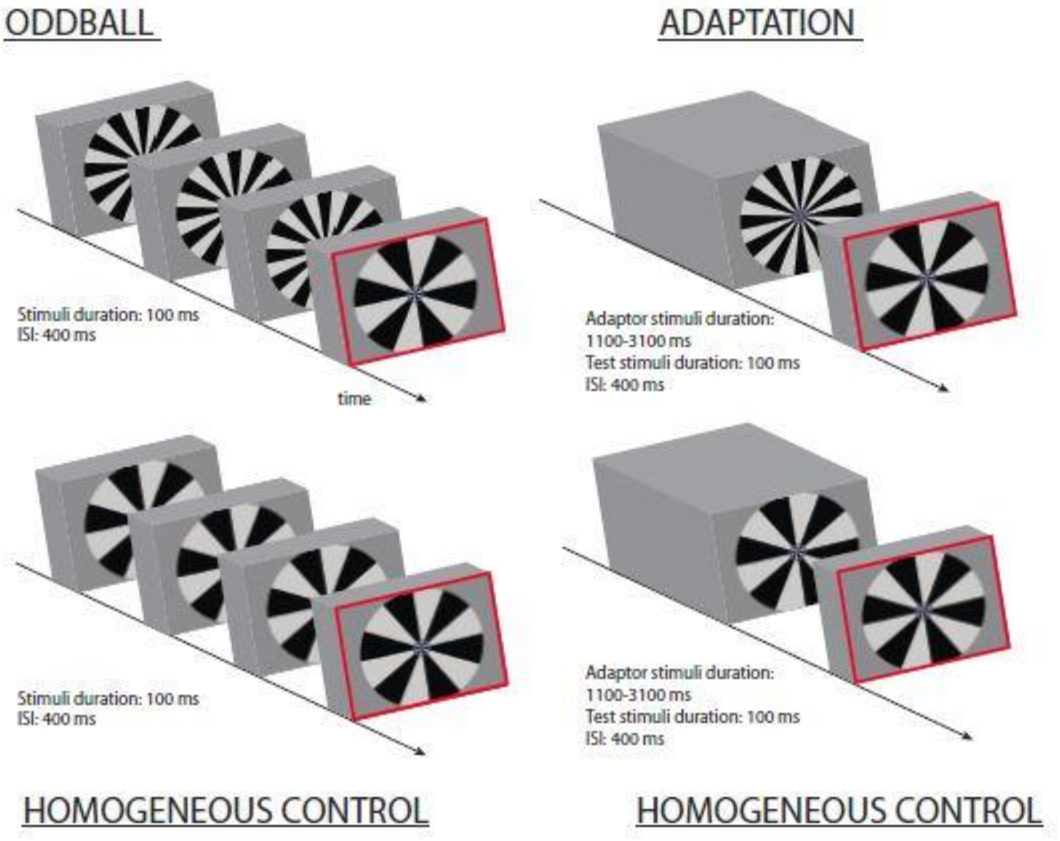


**Fig. 5.6 Experiment 2: Outline of the stimuli and stimulus sequences in the oddball and adaptation conditions. The color frames (not present in the real stimuli) indicate the stimuli that elicited the event-related potentials used for comparison**

### 5.3.1.3 Measurement of electrical brain activity

The procedures for EEG registration, ERP acquisition and measurement, and data processing were identical to Experiment 1. In Experiment 2 difference potentials were measured at two latencies. According to the series of t-tests on the deviant minus standard difference potentials, the t-values in the Oddball condition were significant within a long range (90-228 ms). Following Kimura et al., (2009) and Maekawa et al. (2009), we divided this range into two time windows. The difference was characterized within a 20 ms epoch centered on the peak negative value within each time window. Due to the large ERP differences between the V6 and V12 stimuli, we reported these differences in terms of a complexity factor.

### 5.3.2. Results

#### 5.3.2.1 Behavioral results

Performance accuracy was 98.8 and 98.0 percent during the oddball and adaptation task, respectively. According to a two-way ANOVA with factors of task and deviancy (V6 vs. v12) there were no performance differences.

#### 5.3.2.3. Event-related potentials

Figure 5.7 shows the event-related potentials and the deviant minus standard difference potentials in the two (Oddball and Adaptation) conditions. As in Experiment 1, only the condition-related effects are reported.

Exogenous components to the centrally presented windmill patterns were markedly different from those elicited be the texture of the oblique lines in Experiment 1. A positivity at a mean latency of 100-110 ms (P1) was followed by a wide negativity (N1) in the 140-200 ms range. This negativity did not reach the baseline on the majority of trials. Following the N1, a second positivity (P2) emerged within the 200-300 ms range. Table 5.3 shows the latencies and amplitudes of the exogenous components (P1, N1, P2) at the two ROIs.

| | | P1 | | N1 | | P2 | |
|---|---|---|---|---|---|---|---|
| Region | Stimulus | Amplitude ($\mu$V) | Latency (ms) | Amplitude ($\mu$V) | Latency (ms) | Amplitude ($\mu$V) | Latency (ms) |
| Parieto-occipital | V6 oddball deviant | 5.09 ± 0.61 | 114.56 ± 3.55 | 1.38 ± 0.42 | 157.67 ± 7.39 | 5.46 ± 0.93 | 249.44 ± 5.3 |
| | V6 oddball standard | 5.26 ± 0.6 | 119.56 ± 5 | 2.17 ± 0.44 | 164.44 ± 5.98 | 5.58 ± 0.73 | 235.33 ± 5.71 |
| | V6 adaptation deviant | 5.02 ± 0.54 | 113.22 ± 1.38 | –0.64 ± 0.6 | 190.67 ± 7.53 | 2.13 ± 0.65 | 238.22 ± 8.57 |
| | V6 adaptation standard | 5.19 ± 0.5 | 115.89 ± 1.51 | –0.42 ± 0.54 | 194.33 ± 3.95 | 2.64 ± 0.46 | 239.11 ± 6.19 |
| | V12 oddball deviant | 2.07 ± 0.59 | 96.56 ± 3.67 | –0.42 ± 0.64 | 145.89 ± 5.14 | 7.05 ± 0.9 | 242.78 ± 5.6 |
| | V12 oddball standard | 3.17 ± 0.62 | 112 ± 6.78 | 1.46 ± 0.6 | 140.44 ± 6.31 | 7.37 ± 0.76 | 237.22 ± 4.19 |
| | V12 adaptation deviant | 2.35 ± 0.51 | 107 ± 4.75 | –1.34 ± 0.64 | 168.44 ± 5.81 | 4.06 ± 0.67 | 241.22 ± 3.88 |
| | V12 adaptation standard | 3.7 ± 0.59 | 119.56 ± 5.31 | –0.73 ± 0.72 | 179 ± 5.27 | 3.32 ± 0.5 | 244.89 ± 4.53 |
| Occipital | V6 oddball deviant | 4.37 ± 0.76 | 115.22 ± 5.41 | 0.8 ± 0.73 | 162.44 ± 9.26 | 5.17 ± 1.06 | 248.11 ± 5.21 |
| | V6 oddball standard | 4.3 ± 0.7 | 122.78 ± 6.06 | 1.4 ± 0.71 | 173.33 ± 6.67 | 5.48 ± 0.84 | 241.67 ± 5.28 |
| | V6 adaptation deviant | 5.8 ± 0.63 | 112 ± 1.45 | –1.3 ± 0.67 | 205.33 ± 5.35 | 1.96 ± 0.68 | 243.67 ± 4.47 |
| | V6 adaptation standard | 6.08 ± 0.64 | 114.44 ± 2.04 | –0.97 ± 0.6 | 198.78 ± 3.62 | 2.83 ± 0.42 | 241.89 ± 4.4 |
| | V12 oddball deviant | 0.26 ± 0.69 | 91.78 ± 6.12 | –2.62 ± 0.94 | 145.22 ± 5.32 | 7.23 ± 1.11 | 243.44 ± 5.7 |
| | V12 oddball standard | 1.49 ± 0.82 | 110.67 ± 8.62 | 0.03 ± 0.73 | 132.44 ± 6.33 | 7.84 ± 1.03 | 237.11 ± 4.98 |
| | V12 adaptation deviant | 1.74 ± 0.64 | 104.11 ± 5.84 | –2.72 ± 0.83 | 172.22 ± 5.54 | 3.78 ± 0.88 | 248.33 ± 5.47 |
| | V12 adaptation standard | 4.04 ± 0.67 | 117.89 ± 4.49 | –1.51 ± 0.74 | 184.78 ± 7.03 | 3.83 ± 0.54 | 243.56 ± 4.57 |

Values represent the means ± standard errors

**Table 5.3 Experiment 2: Grand averages of the epoch mean amplitudes and peak latencies of the exogenous components (P1, N1, P2) measured at the parieto-occipital and occipital regions**

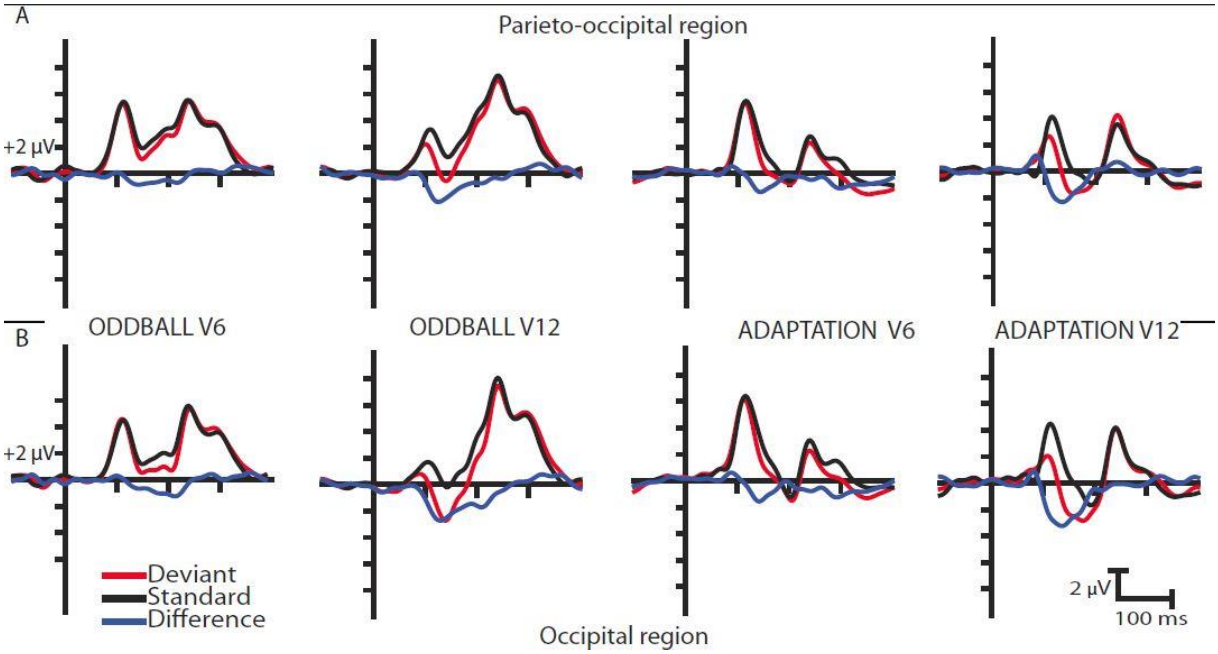


**Fig. 5.7 Experiment 2: Event-related potentials and difference potentials in the oddball and adaptation conditions at the parieto-occipital and occipital regions of interest**

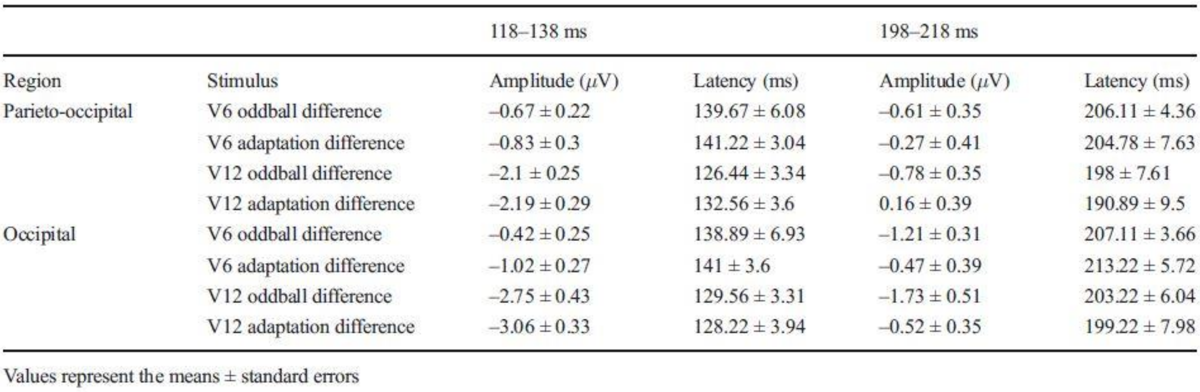
### 5.3.2.4. Difference potentials

With the exception of potentials at the occipital ROI in response to the V6 stimuli of the oddball task, the negative difference potentials significantly differed from zero (t(17)=1,76 - 9,77; for significant effects the alpha levels were at least 0.05, Bonferroni corrected) during the earlier latency period (118-138 ms).

The differences between the two conditions during the earlier latency period were analyzed using a three-way ANOVA with complexity (V6, V12), condition (Oddball, Adaptation) and ROI as factors.

Neither the latency nor the amplitude of the negativity differed between the Oddball and Adaptation conditions (no main effect of condition). For the amplitude values, the main effect of complexity F(1,18)=40.10, $p<0.001$, $ή_p^2=0.69$ and the condition x ROI interaction were significant (F(1,18)=4.78, $p<0.05$, $ή_p^2=0.21$).

During the later latency period (198-218 ms) the significant Bonferroni corrected t-tests only appeared at the occipital ROI in the Oddball condition (t(17)= 4.01 and 3.34 at V12 and V6, respectively, $p<0.05$) and at the parieto-occipital ROI with V12 stimuli of the Oddball condition (t(17)=2.12, $p<0.05$). Table 5.4 shows the latencies and amplitudes of the difference potentials. Figure 5.8 shows the difference potentials and their surface distributions within the ranges of the negativities.



| | | 118–138 ms | | 198–218 ms | |
|---|---|---|---|---|---|
| Region | Stimulus | Amplitude ($\mu$V) | Latency (ms) | Amplitude ($\mu$V) | Latency (ms) |
| Parieto-occipital | V6 oddball difference | –0.67 ± 0.22 | 139.67 ± 6.08 | –0.61 ± 0.35 | 206.11 ± 4.36 |
| | V6 adaptation difference | –0.83 ± 0.3 | 141.22 ± 3.04 | –0.27 ± 0.41 | 204.78 ± 7.63 |
| | V12 oddball difference | –2.1 ± 0.25 | 126.44 ± 3.34 | –0.78 ± 0.35 | 198 ± 7.61 |
| | V12 adaptation difference | –2.19 ± 0.29 | 132.56 ± 3.6 | 0.16 ± 0.39 | 190.89 ± 9.5 |
| Occipital | V6 oddball difference | –0.42 ± 0.25 | 138.89 ± 6.93 | –1.21 ± 0.31 | 207.11 ± 3.66 |
| | V6 adaptation difference | –1.02 ± 0.27 | 141 ± 3.6 | –0.47 ± 0.39 | 213.22 ± 5.72 |
| | V12 oddball difference | –2.75 ± 0.43 | 129.56 ± 3.31 | –1.73 ± 0.51 | 203.22 ± 6.04 |
| | V12 adaptation difference | –3.06 ± 0.33 | 128.22 ± 3.94 | –0.52 ± 0.35 | 199.22 ± 7.98 |

Values represent the means ± standard errors

**Table 5.4 Experiment 2: Grand averages of the epoch mean amplitudes and peak latencies of the difference waves measured at different regions(parieto-occipital and occipital)**

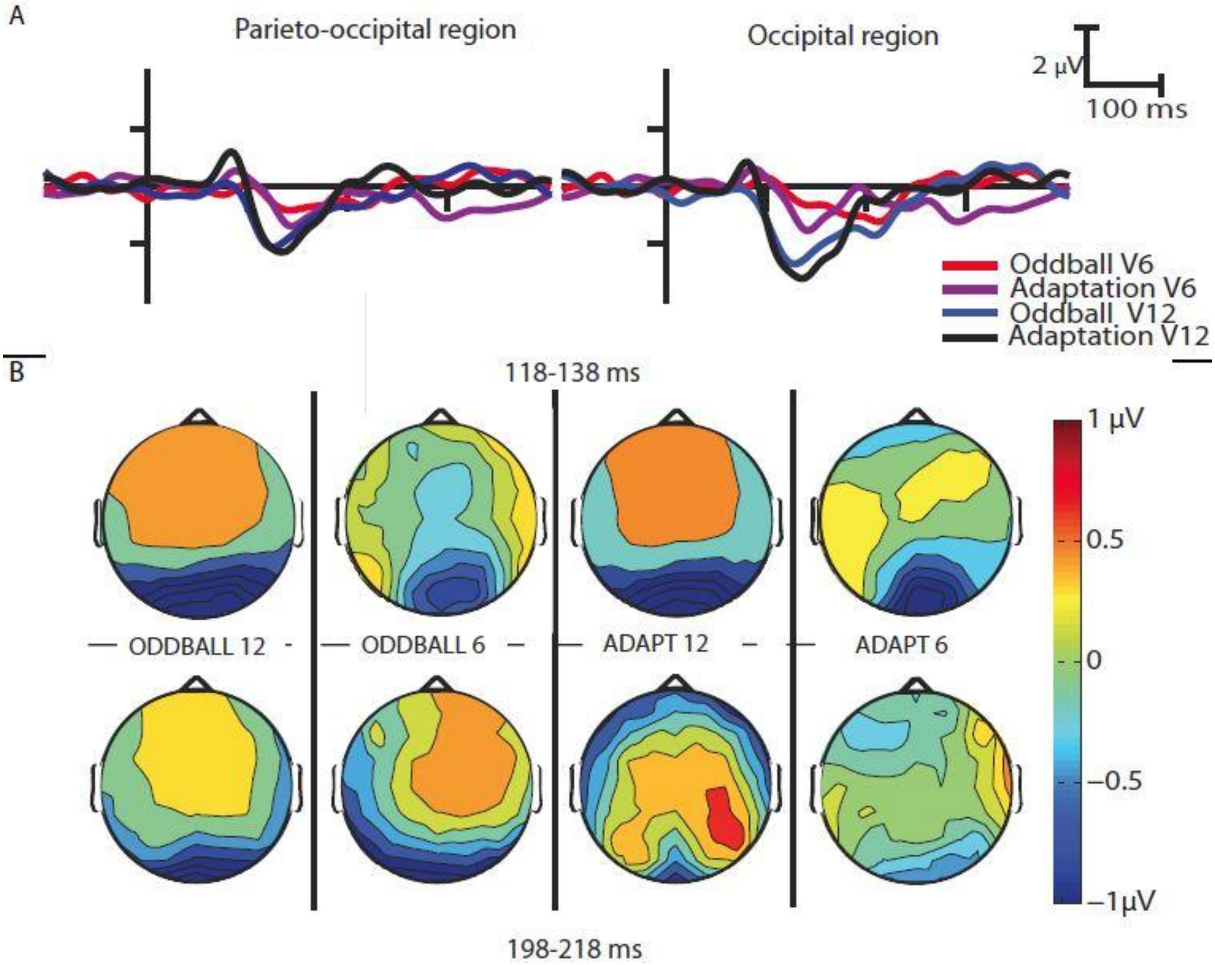


**Figure 5.8. Experiment 2: Difference potentials from the oddball and adaptation conditions, as well as the surface distributions of those difference potentials**

### 5.3.2.5. The effect of onset-to-onset time

Figure 5.9 shows ERPs in response to the deviant stimuli of the Oddball and Adaptation conditions, and the differences between them. As the figure shows, for both the V6 and V12 patterns the ERPs were more negative in the Adaptation condition. The difference remained significant over a long period of time (154-400 ms for V6 and 160-380 ms for the V12).

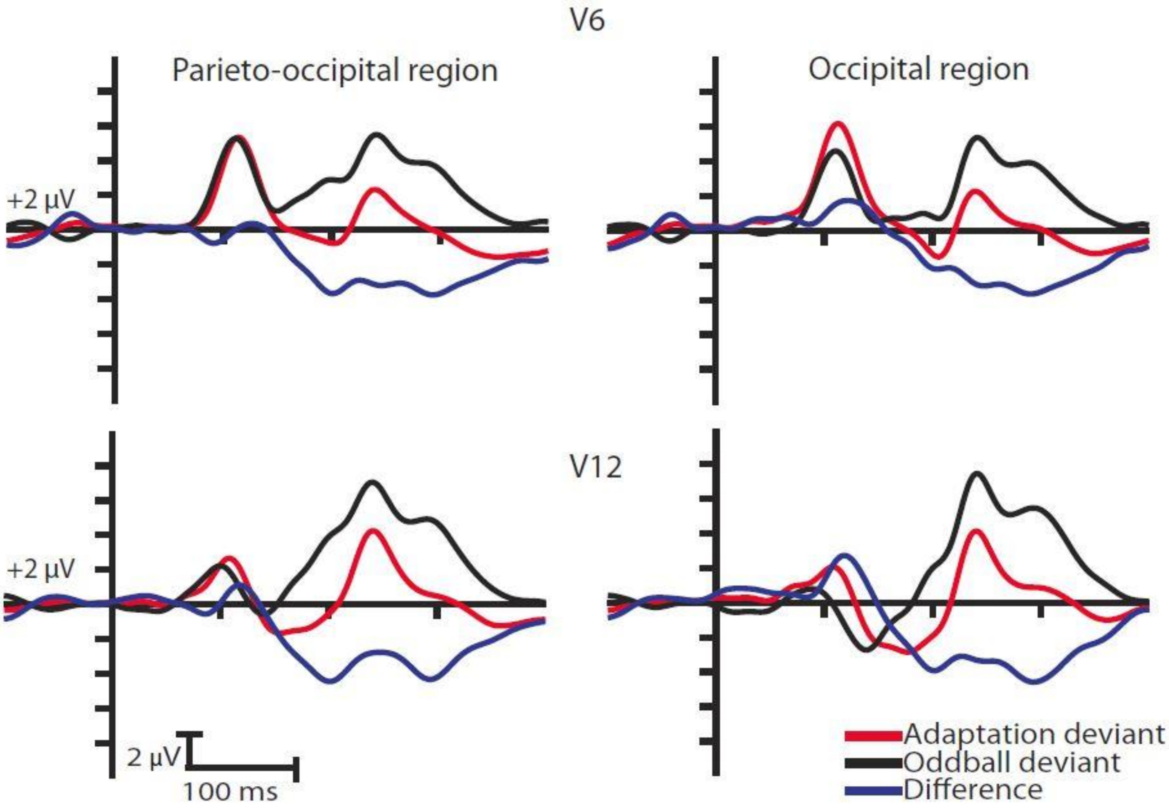


**Figure. 5.9 Experiment 2: Event-related potentials and difference potentials from the heterogenous sequences of the oddball and adaptation conditions**

### 5.3.2.6. N1 and deviancy

In Experiment 2 the stimuli elicited a small N1-like negativity at a much later latency than the difference potential. Therefore, in this experiment it was unnecessary to compare the exogenous negativities to the difference potentials.

### 5.3.3. Discussion

The Oddball condition of Experiment 2 replicated and extended the findings reported by Maekawa et al. (2005, 2009, 2013), in a design demanded continuous fixation to the task-related events. We obtained deviant minus standard differences during an early and late latency period. As for the comparison between the Oddball and Adaptation conditions, during the early latency period the latency and the amplitude of the negativities were similar. Therefore, within this latency period the negativity was unrelated to violations of a sequential rule, and can be considered as SSA effect. The negativity cannot be considered a modulation of the N1 component because the latency of the small N1 was outside of the latency period of the deviant-related negativity.

In the later latency period we did not find a significant negativity in the Adaptation condition; however, deviant-related negativity emerged in the Oddball condition. Negativities within this time period are considered to reflect violations of sequential regularity. The results of Experiment 2 correspond to the suggestion proposed by Kimura et al. (2009), i.e., while the early difference potential is a consequence of adaptation processes the appearance of genuine vMMN is restricted to a later time window.

Apart from the condition-related effects, deviant stimuli of the Oddball and Adaptation conditions elicited markedly different ERPs. This difference emerged as a long-lasting negativity in the Adaptation deviant-minus- Oddball deviant difference potentials. As these effects indicate, the event-related activities elicited by onset-to-onset durations differ from those elicited by stimulus changes.

### 5.4. General discussion

We compared deviance-related ERP effects during the Oddball and Adaptation conditions. Both paradigms were passive. The participants performed either a computer game or a tracking task, unrelated to the ERP-related stimuli. Task performance was different in the two experiments, but more importantly, both tasks demanded continuous fixation. Furthermore, as Kimura and Takeda (2013) pointed out, task difficulty does not affect vMMN amplitude, but in case of more difficult task vMMN latency becomes slightly longer. In both paradigms we investigated the effects of stimulus changes. During the Oddball conditions we examined the difference between ERPs in response to rare (deviant) and frequent (standard) stimuli. During the Adaptation condition we examined differences between ERPs elicited by stimuli that differed from the adaptor (deviant) and those that were identical to the adaptor (standard). Two types of stimuli were introduced: textures of oblique lines (Experiment 1) and windmill patterns (Experiment 2). As a general finding, the ERPs in response to deviant stimuli were more negative than the ERPs in response to the standard over the posterior region. In Experiment 1, when the orientation of the lines within the texture differed from the lines in the standard, the negativity emerged at a mean latency of 122 ms. In Experiment 2, where the vanes of the windmill patterns differed from the standard, the negativity in response to the deviant in the early period (with 128 ms mean latency) was larger. In the Oddball condition the negativity extended to a later window (208 ms mean latency). The similarities between the posterior negativities in Experiment 1 and those emerging in the early period in Experiment 2 on oddball and Adaptation trials can be adequately explained by stimulus-specific adaptation (SSA).

The difference between the deviancy effects of stimuli in Experiment 1 (line texture) and Experiment 2 (windmill pattern) are obvious, but these findings are not consistent with previous results (Sulykos and Czigler, 2011; Maekawa et al. (2005, 2009, 2013). To explain this difference, we can only speculate. Orientation deviancy was presented as a line texture, whereas the windmill pattern was presented as an object. In the visual world textures usually belong to the background and objects belong to the foreground. Assuming that objects are more important stimuli, it is possible that they are more efficient in establishing memory representations and signaling mismatch. The results from vMMN studies on orientation deviancy support this possibility. In a study by Kimura et al. (2009), the stimuli were objects (single bars). A deviant minus standard long-lasting negativity appeared; however, the early component was eliminated by the equal probability control (a ‘genuine’ vMMN within the 180-300 ms range). In another study using single bars, the peak latency of the vMMN was ~190 ms (Astikainen et al., 2009). Kimura and Takeda (2013) presented a pattern of lines around the task-field. These lines were arranged in a rectangular frame forming an object (a fairly good “Gestalt”). The time range of the ‘genuine’ vMMN was 150-300 ms. Finally, Takács et al. (2013) presented elongated Gábor-patches in two concentric circles (i.e., object-related stimuli) around the task-field and reported deviant-minus standard differences in two successive ranges within the 120-240 ms time windows in Experiment 1. In Experiment 2 the peak latencies occurred within the 136-162 ms window; however, the negativities terminated well beyond 200 ms. Undoubtedly, direct experimentation is required to address this possibility.

SSA is usually considered as a decrease in activity of particular ERP components. Specifically, in oddball studies the decrement of activity observed with the presentation of standard stimuli is generally connected to reduced N1 amplitude (e.g., May and Tiitinen, 2010 for the auditory, and Kimura et al., 2009 in the visual modality. Duration of the N1 was longer than the negative deflection within the difference potentials, *and* the peak latency of the N1 was longer. However, during vision tasks, the posterior N1 peaks consist of a set of sub-components (e.g., Di Russo et al., 2002, 2005); therefore it is possible that several subcomponents are prone to stimulus-specific adaptation and others are not. The adapted N1 explanation does not fit the results of Experiment 2. In this condition the N1 was rather small and the difference potentials were outside the N1 range. Maintaining the adaptation explanation, there is an obvious question: “What is adapting?”. The latency range of the deviant *minus* standard difference potential, and the source analysis of the exogenous activities within this range indicate that these activities originated from brain areas beyond the primary input structures of the visual cortex (e.g., Di Russo et al., 2002). Furthermore, in this range the event-related activity is influenced by factors other than the physical characteristics of the visual events and spatial attention effects. These factors involve the intention to discriminate (e.g., Hopf et al., 2002) and other task-related effects (Zani et al., 2015). These studies demonstrated the effects of different forms of attention, in other words *top-down* influences. Non-attentional factors, such as prior exposure and probability related effects may also influence the activity of various visual structures within this range in a proactive manner. In fact, anterior priming effects occurred at ~150 ms (Schendan and Kutas, 2003; Voss et al., 2010). Furthermore, in some vMMN studies anterior activity emerged in the range of the posterior negativity (e.g., Heslenfeld, 2003; Kimura et al. 2010b, 2012; Urakawa et al., 2010). We suggest that the SSA-related negativity is a consequence of the activity of a broader neural network, and the latency of this network's activity can differ from other exogenous ERP components.

In contrast to the traditional view (Stefanics et al., 2012; Kimura, 2012; Winkler and Czigler, 2012), we suggest that in vision, the memory-related deviant *minus* standard ERP difference does not always require sequential stimulation. To our knowledge, a similar possibility has not been explored in the auditory modality. In the Oddball condition of Experiment 2, a significant negativity during the later latency period emerged only in the Oddball condition. Therefore, this negativity can be considered as a genuine vMMN. Using the equal probability control (Jacobsen and Schröger, 2001; Schröger and Wolff, 1998) genuine vMMNs with similar latencies appeared in response to orientation deviancy (Kimura et al., 2009) and complex stimulus characteristics, such as facial emotions (Li et al., 2012). Accordingly, we suggest that the later negativity of Experiment 2 is connected to the violation of sequential rules.

In addition to the negativity in the deviant *minus* standard difference potentials, the effects of onset-to-onset duration also appeared in both experiments. In Experiment 1 a long-lasting negative potential difference emerged as a function of the duration between the two deviant stimuli (i.e., larger negativity in the Filled *minus* Oddball difference than in the Squeezed *minus* Oddball). This effect began within the range of the N1 component. In Experiment 2 we observed a negative shift in the Adaptation *minus* Oddball difference potentials. This shift was more pronounced in the later (P2) period. Stimulus onset asymmetry and/or inter-stimulus interval effects in ERP responses to auditory stimuli are well known, but are less investigated in vision. However, being a long-lasting negativity, this difference cannot be attributed to changes in a particular ERP component. It is an open question whether filled periods (as in the present study) are needed for the emergence of such a negativity, or if the effect is the same with empty inter-stimulus fields.

## 5.5. Conclusions

During the Oddball and Adaptation conditions in two experiments with two sets of stimuli (texture of oblique lines and windmill patterns), the posterior negativity ERP differences in response to the standard and deviant stimuli were similar in the 100-140 ms time window.  This results suggest that in vision, the acquisition of sequential regularities are unnecessary for eliciting posterior *negativities* in this early latency period. As results with the windmill patterns show, in a later latency period the negativity in the oddball sequence seems to be connected to the violation of sequential regularities.

## 5.6. Acknowledgements

This study was supported by the Hungarian Research Found (OTKA 104462). This study was supported by the Hungarian Research Found (OTKA 104462). We thank for the help by Szonya Durant in polishing our English style, and for Zsuzsa dAlbini and Zsuzsa Kovacs for their technical help.

## Footnotes

[1] It should be noted that the terms refractoriness, stimulus-specific adaptation, repetition suppression and habituation sometimes referring to the same phenomenon.

[2] Stimulation of identical locations is essential if neural structures with small receptive fields (V1) are investigated. However, the source of vMMN is beyond the straite cortex (e.g., Susac et al., 2014; Müller et al., 2012; Kimura et al., 2010, 2012).

# Chapter 6: Automatic change detection and spatial attention: A visual mismatch negativity study[9]

## 6.1. Introduction

A large number of studies have demonstrated that, in comparison to unattended, sequentially presented regular visual stimuli (standards), unattended stimuli that violate the regularities of a stimulus sequence (deviants) elicit a posterior negative ERP component approximately 100-350 ms after stimulus onset (for a review see Kimura et al. 2011; Stefanics et al., 2014). The difference between the standard and deviant stimuli is the sum of the effect of the decreased activity in response to the standard (stimulus-specific adaptation; O'Shea, (2015)) and the increased activity in response to the deviant, known as the visual mismatch negativity (vMMN; e.g., Kimura et al. 2009; File et al., 2017). VMMN is thought to be the electrophysiological correlate of a memory comparison-based change detection process Czigler, Balázs & Winkler, 2002). VMMN occurs in response to a variety of deviations from different stimulus features such as color (e.g., Czigler et al., 2002), orientation (e.g., Kimura, Katayama, Ohira & Schröger, 2009; File, File, Bodnár, Sulykos, Kecskés-Kovács & Czigler, 2017), shape (Stagg, Hindley, Tales, & Butler, 2004), motion direction (Pazo-Alvarez, Amenedo, & Cadaveira 2004), spatial frequency (Heslenfeld, 2003; Susac et al., 2014), stimulus size (e.g., Kimura, Katayama, & Murohashi, 2008), and gender (Kecskés-Kovács et al., 2013). Although there is a consensus that vMMN can be elicited regardless of whether the subject is paying attention to the sequence or not, relatively little is known about attentional modification of vMMN.

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[9] File, D., Sulykos, I. & Czigler, I. (2018). Automatic change detection and spatial attention: avisual mismatch negativity study. European Journal of Neuroscience, doi: 10.1111/ejn.13945

In the majority of studies, vMMN-related stimulus sequences are presented in passive paradigms. To ensure that participants “do not attend” to the sequence, primary tasks are introduced that are independent of the passive sequence. The primary task is usually visual (for exceptions see Astiakinen et al. 2008;  Maekawa et al., 2005 for an auditory task) and varies greatly among studies in regard to the effectiveness of distracting attention from the stimulus sequence. In some studies, the passive sequences are presented in the center of the visual field, and participants need to attend to a specific property of the stimuli, while vMMN-related deviancies occur in another dimension, as when responses are required for shape-related changes, but the target feature is the stimulus orientation (Kimura et al. 2008). This paradigm does not preclude the operation of object-related attention (Duncan, 1984). In a more efficient control, the task-related stimuli are completely independent of the passive sequence. An example of such a paradigm is the continuous ball-tracking task introduced by Heslenfeld (2003), in which a task-irrelevant sequence is presented on the background.

According to the perceptual load theory (Lavie, 1995), the difficulty of a primary task influences the attentional selectivity, including the size of attentional focus. A possible way to study the attentional influence on vMMN is to vary the difficulty of the task and to subsequently investigate the difficulty effects on vMMN. Pazo-Alvarez et al. (2004) investigated the effect of task difficulty on the detection of unattended motion. They did not find significant differences between the responses elicited by the standards and those by the deviants in either easy or difficult conditions. This result strengthened the view of the attention-independence of VMMN. However, the authors claimed that the results could be attributed to the discontinuous nature of the task, which allowed the participants to utilize a moment-to-moment attentional shift, and in this way, they processed the task-irrelevant information. The authors assumed that using a continuous task would result in a decline in deviant-related negativity during a difficult condition. However, Heslenfeld (2003) obtained no different posterior negativity as a function of the task difficulty of a continuous task, whereas the amplitude of the anterior positivity was smaller during the more difficult task. In contrast, in an fMRI study, Yucel et al. (2007) obtained smaller deviant-related BOLD activity during a more difficult version of a continuous primary task. Kimura & Takeda (2013) investigated the relationship between task load and the adaptation-free vMMN (genuine mismatch negativity, gvMMN). They found that the latencies of a gvMMN (deviant-minus-control difference) were delayed as a function of task difficulty, which supported the notion that vMMN is influenced by attention-demanding predictive processes.

As another aspect of the influence of task-related processing on vMMN, Czigler and Sulykos (2010) investigated whether the similarity between the task-related stimulus features and the deviant features of the passive oddball sequence influenced vMMN. They found that matching task-related and irrelevant changes (i.e., color-color, orientation-orientation) resulted in a smaller vMMN than the difference between task-related and irrelevant features (e.g., color-orientation). They also found decreased performance in the matching feature conditions. This interaction suggested a competition between the processing of task-relevant and irrelevant stimuli if they were in the same category.

Within the field of visual attention, spatial selection is a central issue. The size of the attended field is not fixed (e.g., Eriksen and Yeh, 1985, LaBerge, 1983). The size of the attentional field depends on the spatial extent of the task-related stimuli (LaBerge, 1983) and on the perceptual load of the task (Lavie, 1995). However, the attentional field has no sharp borders; instead the efficiency of attentional processes decreases gradually toward the borders of the attended field. (Downing and Pinker, 1985; Föcker et al., 2010.;

Magun and Hillyard, 1988). The aim of the present study was to examine the effect of distance on the focus of spatial attention on a task-irrelevant sequence. Passive stimulus sequences were presented either close or far from the primary task. It is reasonable to assume that the closer an event to the task-related part of the visual field, the larger the expected effect of spatial attention on the processing of the vMMN-related stimuli. Nevertheless, the direction of the effect is uncertain. As one possibility, closeness to the attentional field facilitates change detection, and accordingly, the ERP effects will be larger. As for the other (less plausible) possibility, irrelevant detection of stimulus change could be inhibited, and this inhibition would be stronger around the field of the visual task.

The stimuli of the present task were the disappearance (offset) of two sides of permanently presented objects (vanishing stimulation). The application of this kind of event was twofold. First, the appearance (onset) of new objects has a tendency to attract visual attention, but vanishing parts of permanently presented objects are less salient events (Yantis and Jonides, 1984; Kramer and Hahn, 1995). Second, stimulus-specific adaptation to the standard may contribute to the deviant minus the standard difference potential. The presence of the objects during the inter-stimulus interval diminishes the effect of low-level adaptation-related activity; in this way, the deviant-minus-the-standard difference potential can be considered as gvMMN. This procedure was introduced in a recent paper (Sulykos et al., 2017) and resulted in reliable vMMN.

Obviously, in the present design, the reappearance (onset) of the whole figure also sets up an oddball sequence. Importantly, the outcome of both the rare and frequent reappearance of the sides of the stimulus objects leads to identical consequence, i.e., to the presence of the objects as wholes. This onset is an expected event; in other words, it does not violate any regularities, as it is a rare but predicable event. On the basis of the prediction-related theories on visual mismatch components (Kimura et al., 2011; Stefanics et al., 2014) no vMMN is expected for a reappearance after deviant offset. In fact, this was what was the result of Sulykos et al.'s (2017) study. In the auditory modality, expected infrequent stimuli were found to elicit MMN if the stimuli were cued by visual stimuli (Ritter et al. 1999); Sussman et al., (2003). However, when the predictability of the infrequent stimuli was assured by the arrangement of the auditory sequence, no MMN emerged (Sussman et al., (2001); Horváth et al. (2011).

A changes in attentional focus elicits eye movements. Even if we emphasized the necessity of continuous fixation in the instruction, we could not exclude that covert (e.g., Posner, 1980) or even the overt, attention shifted to the vMMN-related deviant stimuli. Therefore, in the control condition, we recorded eye movements.

## 6.2. Methods

### 6.2.1 Participants

Thirteen volunteers (7 women; mean age: 22; SE=0.51 year) participated in the study for monetary compensation. They had normal or corrected to normal vision. Written informed consent was obtained from all participants prior to the experimental procedure. The study was conducted in accordance with the Declaration of Helsinki and was approved by the Joint Committee of Ethics of the Psychology Institutes in Hungary.

### 6.2.2 Stimuli and procedure

The experimental design followed a task location (attend close, attend far) x sequence (oddball, oddball reverse) arrangement. Regardless of the condition, participants continuously performed the same tracking and detection task. Stimuli were presented on a CRT monitor (60 Hz, 1280x1024) from a viewing distance of 100 cm. Stimuli were generated via MATLAB using the Cogent toolbox (http://www.vislab.ucl.ac.uk/cogent_2000.php).

### 6.2.2.1. Rotation task

A continuous central fixation to a rotating bar at the center of the screen (0.115 turn/sec, light gray (RGB 0.7, 0.7, 0.7, size: length 0.28°, width 0.0385°) was required during the experiment. Occasionally a second 'target bar' (light gray (RGB 0.7, 0.7, 0.7, size: length 1.12°, width 0.0385°) appeared, either 1.07° above (attend far condition) or below (attend close condition) the rotating bar for 200 ms. The position of the target was constant during each block. Participants were informed about this position at the beginning of each stimulus block (with an arrow pointing to the target location of the subsequent block). A response (button press) was only required when the central and the target bar were parallel, which occurred in 40% of all target appearances in a random order. Participants were instructed to respond as fast and as accurately as possible. In each stimulus block, 96 targets were presented. Reaction times and performance were measured. An illustration of the task and the conditions are presented on Figure 6.1 A.

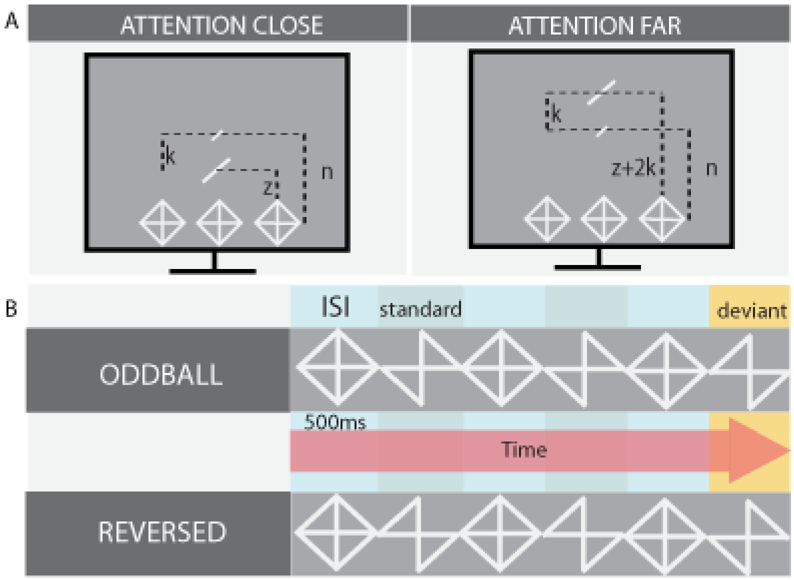

**Figure 6.1. A. Illustration of the display during Attend Far (left) and Attend Close (right) conditions. (dotted lines are for illustrating distances and were not present during the experiment) B. Illustration of the oddball and the reversed oddball sequence. (ISI= interstimulus interval)**

### 6.2.2.2. VMMN-related stimuli

The stimuli were three diamonds with their diameters presented side-by-side (separated by 0.77°). The length of the sides were 1.155°, the contours of the stimuli were light gray (RGB 0.7, 0.7, 0.7), and their widths were 0.0385°. From time to time, the parallel sides of the diamonds disappeared (vanish stimuli), resulting in 'hourglass shapes' and afterward reappeared. The stimuli were presented in a reverse oddball arrangement, i.e., both versions of the vanish – reappearance events were standard and deviant. The probability of a deviant event was 0.2. Within each block, 50 deviant stimuli were presented. As an important aspect, regardless of the condition, the task irrelevant (vMMN-related) sequences were presented on the lower part of the screen (2.15° from the fixation). The vanish (offset) stimulus appeared for 500 ms, and the inter-stimulus interval (whole objects) was also 500 ms. An illustration of the sequences is presented in Figure 6.1 B.

Both conditions [(two oddball versions) x (attend close and attend far)] were divided into 8 blocks, presented in a random order. Accordingly, there were 32 blocks. The blocks were 1.6 minutes long, so the total length of the ERP blocks was approximately 53 minutes.

### 6.2.3 Eye movement tracking

Eye movement tracking was recorded in two separate blocks for the attend close and attend far conditions after the ERP blocks. Eye movement was recorded with a Tobii x50 device and Clear View 2.5.1 software, using a normal validity filter and an average eye filter. The fixation radius was 30px, and the minimum fixation duration was 100 ms. During the eye movement tracking no EEG data were recorded. This was because of the technical limitations of the eye tracker, namely, during eye movement recording, the subjects sat closer to the screen than during the ERP recording session (55 cm vs. 100 cm). Although we emphasized that maintaining central fixation in the eye-movement blocks was more taxing than it was in the ERP blocks, the different viewing distance between recordings are limiting the validity of the eye movement recordings.

#### 6.2.3.1 Eye tracking data analysis

The screen was divided into 4 regions of interest: middle (x: (-9.1)°-9.1°, y: (-1.8°)-1.8°), top (x: (-9.1)°-9.1°, y: 1.8°- 5.9°), bottom (x: (-9.1)°-9.1°, y: (-1.8)°- (-5.9)°), and oddball (x: (-9.1)°-9.1°, y: (-5.9)- (-10.1°)), see Figure 6.2. The gaze lengths were calculated for the ROIs separately within the two blocks. Gaze times were then compared in a two-way ANOVA with the factors condition (attend close and attend far) x ROI (middle, top, bottom, oddball).

### 6.2.4 Recording and measuring the brain electric activity

The EEG data were recorded (DC-30 Hz, sampling rate 500 Hz; Neuroscan Synamps2 amplifier with Ag/AgCl electrodes at 61 locations, according to the extended 10-20 system, using an elastic electrode cap (EasyCap). The tip of the nose was used as a reference, but the off-line reference was the average activity. The ground electrode was attached to the forehead. A horizontal EOG was recorded with a bipolar configuration between the electrodes that were positioned lateral to the outer canthi of the two eyes. Vertical eye movements were monitored with a bipolar montage between the electrodes that were placed above and below the right eye. The impedance of the electrodes was maintained below 10 kΩ.

The data were processed using EEGlab (Delorme et al., 2011) and Matlab 2014a (Mathworks, USA). The EEG signal was bandpass filtered offline, with cutoff frequencies of 0.1 (60-dB slope) and 30 Hz (120-dB slope) and epochs of 600 ms, starting from 100 ms before the stimulus onset. The epochs were baseline corrected relative to 100ms pre-stimulus interval. Epochs were averaged separately for the standards preceding a deviant and deviants, in this way ensure that the standard and deviant related ERPs were formed from the same number of epochs. vMMN was calculated by subtracting the standard related ERP from the deviant related ERP. Trials with an amplitude change that exceeded ± 100 μV on any channel were rejected from further analysis.

Based on previous experiments vMMN was expected to occur over the posterior locations (e.g., File et al., 2017; Sulykos & Czigler, 2014; Kimura et al., 2009; Stefanics et al., 2014). The electrodes of interest were defined by running a point-by-point t-test ($p<0.05$) against zero on the deviant-minus-standard difference waves for all subjects. To reduce the chance of selecting sections reflecting solely noise, electrodes were only selected if the deviant-minus-standard difference wave differed from zero in at least 15 consecutive, significant data points (30 ms) at the posterior channels. A 2x3 matrix of channels (PO3, POz, PO4, O1, Oz, O2) met this criterion. As the vMMN component was largest at the PO4 location, and since vMMN frequently has right-side amplitude maxima (e.g., Clery et al., 2012 Kimura, 2012; Zhao and Li, 2006), for the sake of clarity, further statistical comparisons were made with that channel. Additionally, we conducted ANOVAs on the 2x3 matrix with the factors condition (attend far, attend close) x laterality (left, middle, right) x anteriority (anterior, posterior); the results are reported in the supplementary material. Additionally, tables containing the latency and amplitude values of the 2x3 matrix are reported in the supplementary materials.

The point-by-point t-test conducted on the attend far deviant-minus-standard difference wave at PO4 channel significantly differed from zero in the 130-200 ms range, which was followed by a positive deflection in the 270-330 ms range. In the attend close condition, the negative difference wave component differed from zero in the 152-202 ms range, while a positive deflection was present in the 224-434 ms range (see Figure 6.3. C). Since the attend far and close deviant-minus-standard difference waves differed from zero in different latency ranges, we only selected the ranges, where both difference waves differed from zero (i.e. the overlapping ranges). The amplitude values of vMMN were calculated as the average value of these sections. The latency values were derived as the latency value of the local maxima of the same ranges. The vMMN amplitude and latency values were compared using one-sample t-tests.

In addition to the deviant-minus-standard differences, we measured the latencies and amplitudes of the exogenous ERP components. ERP amplitude values were computed as the average of the 20 ms range around the components peak (peak +/-10 ms). As Figure 6.3. A shows, in both the attend far and close conditions, the offset deviant and standard stimuli elicited P1 – N1 – later positive series of exogenous components. Since the peak latency of the N1 and the later positive component varied as a function of probability and condition, different time windows were used. The amplitude values of the N1 component were calculated from the 146-166 (attend far standard), 150-170 (attend far deviant) and 160-180 ms (attend close standard and deviant) ranges. The amplitudes of the later positive component were calculated from the 204-224 (attend far standard), 230-250 (attend far deviant), 228-248 ms (attend close standard) and 250-270 ms (attend close deviant) ranges.

ERP latency values were derived from the same ranges as the latency value of the local maxima. The amplitude and latency values of the ERP components were investigated using two-way ANOVAs, with the factors probability (standard, deviant) and condition (attend far, attend close). Additionally, ANOVAs were conducted on the 2x3 electrode matrix with the factors probability (standard, deviant) x condition (attend far, attend close) x laterality (left, middle, right) x anteriority (anterior, posterior), as reported in the supplementary material.

Scalp distributions were compared with the permutation test described by Karniski et al. (1994).

In addition to the offset evoked responses, we constructed standard and deviant ERPs from the sections time-locked to the reappearance of the full diamond shape (indicated as ISI in Figure 6.1). The reappearance standard ERP was time-locked to the onset of the ISI following a standard preceding a deviant, while the reappearance deviant was time-locked to the onset of the ISI following a deviant. The same processing steps were applied to the reappearance ERPs as described previously to the offset ERPs.

The point-by-point t-tests conducted on the attend far reappearance difference waves showed a significant positive deflection in the 340-418 ms range. The attend close difference wave differed from zero in the 174-216 ms range (negative deflection) and in the 354-454 ms range (positive deflection, see Figure 6.3. D).

The reappearance of the stimuli also elicited a P1 – N1 – later positive series of exogenous components (Figure 6.3. B). The amplitude of the N1 component was calculated from the 158-178 ms range for the attend far deviant and standard and the attend close standard, and from the 168-188 ms range for the attend close deviant. There was no peak latency difference in the grand-averaged wave between the conditions and stimuli in the later positive component, which was calculated from the 254-274 ms range.

## 6.3 Results

### 6.3.1 Behavioral results

The average hit rate was 59.39% (SE=4.58), the average error rate (response to invalid target) was 27.96% (SE=2.34), and the average reaction time was 482 ms (SEM=15.01). Hit rate and reaction times did not differ between conditions, but there was a significant difference in the error rate between the attend close (M=30.79%, SE=2.37) and attend far (M=25.77%, SE=2.49) conditions; t(12)=-3.44, p=0.003518, r2=0.5219; that is error rate was higher in the attend close condition.

#### 6.3.1.1 Eye movement tracking

The focus of gaze was in the defined locations 98.04% of the time during the recordings. Subjects were focusing on the center 92.76% of the time. An ROI main effect revealed (F (F (3,36) = 38.168, p=0.0000, η2=0.76) that subjects were looking significantly longer at the center than at the other ROIs. Importantly, there was no difference between the attend far and close conditions. For a heat map of the relative gazing times, see Figure 6.2.

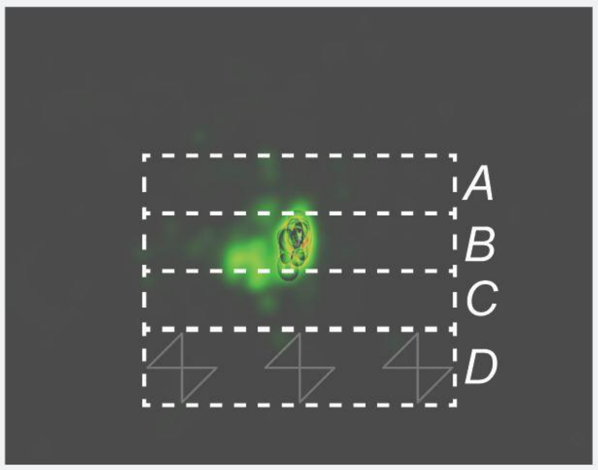

**Figure 6.2. Regions of interest during the eye tracking; A: top, B: middle, C: bottom, D: oddball. Heat map reveals the focus of attention during the eye tracking.**

### 6.3.2. Event-related potentials

#### 6.3.2.1. Offset-related exogenous components

The ANOVA conducted on the vanish N1 component amplitude revealed a main effect of condition (F(1, 12)=10.78, p=0.0065, η2=0.47); the amplitude of the N1 component was larger in the attend close condition. The main effect of probability (F

(1,12)=45.12, p=0.00002, η2=0.79) revealed that deviant stimuli elicited larger N1 amplitudes.

The ANOVA conducted on the vanish N1 latency values revealed a main effect of condition (F(1, 12)=18.96, p=0.00094, η2=0.61); N1 peaked earlier in the attend far condition.

In range of the later positivity the ANOVA revealed a main effect of condition (F(1,12)=8.68, p=0.1223, η2=0.42), that is attend far had larger amplitude. The probability main effect revealed that deviants elicited larger response (F(1,12)=12.16, p=0.00448, η2=0.50). There was also a condition x probability interaction (F(1,12)=27.14, p=0.00022, η2=0.69), post hoc Tukey test showed, that the attend close standard had a reduced amplitude compared to the attend close (p=0.00029) deviant and the attend far standard (p=0.00046) and deviant (p=0.00095).

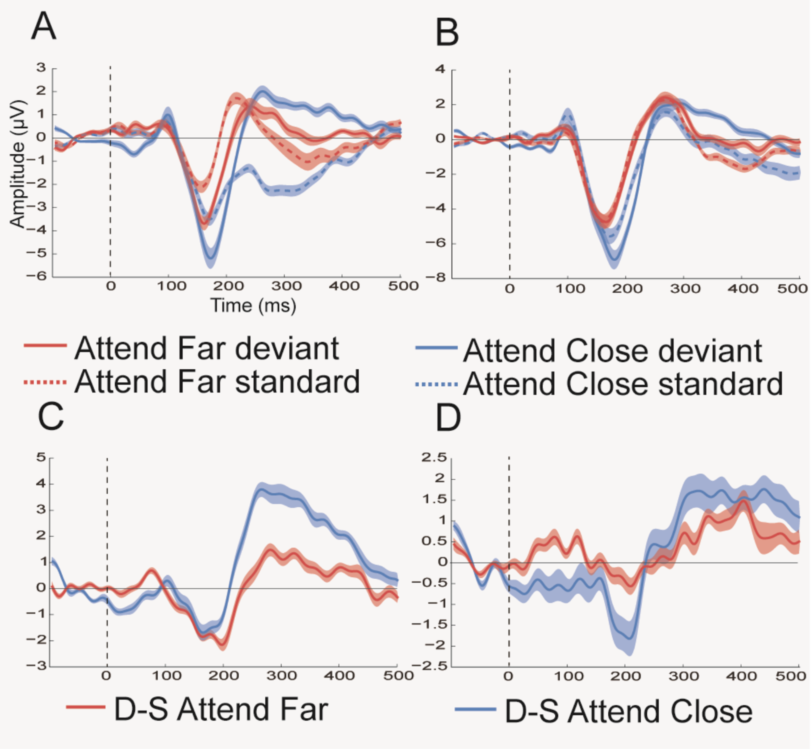

**Figure 6.3. Grand averaged ERPs elicited by the deviant, standard and their differences at PO4. A: offset ERPs (ERPs elicited by the disappearance of the edges). B: onset ERPs (ERPs elicited by the re-appearance of the edges). C: deviant-minus-**

**standard difference waves of the offset ERPs. D: deviant-minus-standard difference waves of the onset ERPs. Units on the x-axis represent 100 ms. The pale area around the curves indicates the standard deviation of the mean of the individual curves**.

### 6.3.2.2. Re-appearance-related exogenous components

The ANOVA conducted on the reappearing N1 amplitude revealed a main effect of condition (F (1,12)=8.50, p=0.01293, η2=0.41); attend close stimuli elicited larger N1. Also, the N1 peaked earlier in the attend far condition (F(1,12)=29.86, p=0.0001, η2=0.71), and the peak of N1 occurred earlier in response to the standard stimuli (F(1,12)=6.83, p=0.023, η2=0.36).

There was no difference between conditions and probabilities in the later positive components amplitude and latency.

### 6.3.2.3. Difference waves

#### 6.3.2.3.1. Offset-related differences

The dependent samples t-test conducted on the amplitude values of the early time window (154-202 ms) revealed no difference between the conditions. There was no significant difference between the conditions in terms of scalp distribution (Figure 6.4. A). In the late time window (positive difference, 270-330 ms), the amplitude of the attend close difference was significantly larger, t(12)=-2.27, p=0.0037, r2=0.52. (attend close: mean= 3.56, std=2.45; attend far: mean=1.29, std=1.64). In the later time window, there was a significant difference in the scalp distribution between the attend close and far conditions (p=0.046)( Figure 6.4. B).

There were no latency differences among the conditions.

#### 6.3.2.3.2. Re-appearance-related differences

In the 354-418 ms range, there was no significant difference between the conditions. For scalp distributions, see Figure 6.4. C and D.

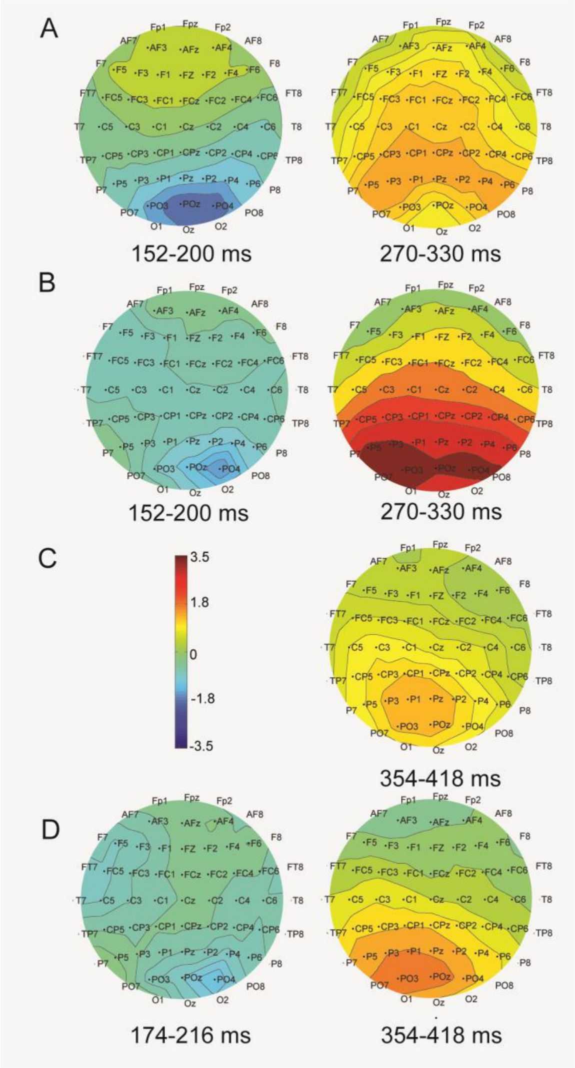

**Figure 6.4. Topographical maps of the deviant-minus-standard difference waves. A: Attend Far offset difference wave in the 152-200 ms range (left) and in the 270-330 ms range (right). B: Attend Close offset difference wave in the 152-200 ms range (left) and in the 270-330 ms range (right). C: Attend Far onset difference wave in the 354-418 ms range (right). Scalp distribution of the earlier range is not presented, since the difference wave did not yield significant difference from zero. D: Attend Close onset difference wave in the 174-216 ms range (left) and in the 354-418 ms range (right).**

## 6.4. Discussion

The results of the study can be summarized as follows: (1) re-appearance of the whole objects after the deviant offset, i.e. an expected irrelevant event, elicited vMMN but only in the attend close condition. (2) Deviant, vanishing events elicited a posterior positive component, and this component was much larger when the task-field was near to the vMMN-related stimuli. (3) Vanishing (offset) deviant parts of the stimulus objects elicited vMMN, and the distance between the task-field and the vMMN-related stimuli had no reliable effects. (4) The N1 amplitudes in response to the close stimuli were larger and their latencies were longer. (5) The error rate was slightly higher when the vMMN-related stimuli were closer to the task-field. (6) The amplitude of the (exogenous) N1 component was larger in the condition with shorter distance between the task-field and the task-irrelevant stimuli. (7) It should be noted, that direct conclusion from the control experiment cannot be drawn to the experimental conditions, since viewing distances were different (55 vs. 100 cm). However, we argue that the task was more difficult in the control condition, since the target stimuli were farther away from the center, thus attention was required to be covertly allocated farther from the center. We argue that if the task was feasible without eye movements in the more difficult control condition, it was probably feasible during the experimental conditions. If our argument stands, the ERP findings can be attributed to the allocation of covert attention, not to exogenous effects. (8) Finally, the average hit rate was 59.39%, which reflects that the task was difficult, thus required focused attention during the experiment.

The vMMN elicited by the vanishing part of the stimulus objects had right-side dominance (Clery et al., 2012, Kimura, 2012, Zhao and Li, 2006), and the vMMN on that side was similar in the attend close and attend far conditions. However, the reappearance of the whole objects (onset of the previously vanished sides) elicited vMMN only in the attend close condition. The results of the attend far condition corresponded to those reported by Sulykos et al. (2017), but the appearance of the vMMN in response to the reappearing parts of the objects is different from the findings of that study. However, there is a considerable difference between the two studies. Specifically, Sulykos et al. (2017) presented objects around the stimulus field, i.e., as objects in the background. In contrast, in the present study, the vMMN-related objects with vanishing and reappearing parts appeared in a particular part of the field, as an additional set of objects. Therefore, in the present study, the saliency of the vMMN-related stimuli was greater than in the study of Sulykos et al. (2017).

Another important aspect of the present results was that the processing of the vMMN-related stimuli was not independent of spatial attention. The deviant stimuli elicited a late positive component, which was much larger in the attend close condition for vanishing stimuli and slightly larger in response to the deviant reappearing stimuli. In the auditory modality, an MMN is frequently followed by a positive component, and this anterior positivity is categorized as P3a. However, the positivity in the present study had a clear posterior distribution. The latency of the posterior positivity was earlier than the usual latency range of the P3b component. Therefore, we considered that the positive component of the present study was a modality-specific attention-related component. Similar components were described previously in scalp-recorded (Czigler et al., 2006) and intracranial (Halgren et al., 1995) studies, and also in the auditory modality (Escera et al. 2001). The positive component following MMN was categorized as a P3a or novelty-P3 by Escera and Corral (2001). This component has been considered a sign of the orienting response (Friedman, Cycowicz & Gaeta, 2001). It is important to note that the amplitude of the deviants in the P3 range is different from that of the standards. This observation is in line with the results of Noyce & Sekuler (2014), who showed the tendency of active inhibition of predicable irrelevant events. Emergence of this component seems to be independent from vMMN, as a large positivity appeared only in the attend close condition and not in the attend far condition, i.e., in a condition with a vMMN of equal amplitude. Furthermore, positivity had no difference whether the vMMN was present or absent for the reappearance of the objects as a whole. The lack of an inter-dependence of MMN and subsequent positivity has also been demonstrated in the auditory modality (Horváth et al., 2008). Furthermore, it should be noted that Silverstein et al. (2015) reported late positive components in response to the infrequent stimuli of an oddball paradigm, where all stimuli were below the threshold of visibility, i.e., in response to non-conscious events. At any rate, it is likely that the positivity that was observed in the present study was related to the orientation and/or further processing of a deviant event.

The difference between the vMMN in response to the attend close and attend far conditions at the reappearance stimuli can be related to another attention-related effect. Kimura et al. (2010) investigated the representation of large scale regularities (SSSSDSSSSD…) in the visual modality and found that such sequences were represented only at SOAs no longer than 160 ms, i.e., at (5 x 160) -80 = 720 ms cycle duration. This duration was measured as the lack of a vMMN in response to regular stimulation in comparison to the random sequence with stimulus SOAs. (For similar studies in the auditory modality, see Sussman and Gumenyuk, 2005). In the present study, whole objects reappeared regularly every ~500 ms. It is possible that in the attend far condition only this regularity was represented, whereas the attend close condition was also sensitive to the oddball-type appearance of the sides. According to this interpretation, the system underlying the visual mismatch negativity separately represents a lower-level deviancy (line onset) and a higher-level regularity (disappearance and reappearance of the parts of stimulus objects). The operation of the memory system is similar in the auditory modality (e.g., Horváth et al. 2001).

The sensitivity of the N1 component to spatial attention is a classical finding in ERP research (e.g., Harter and Aine, 1984; Van Voorhis and Hillyard, 1977; Mangun and Hillyard, 1988). In this respect, the results of the present study align with this literature, i.e., the N1 amplitude was larger in the attend close condition. However, the shorter peak latency in the attend far condition deserves a comment. As Di Russo et al. (2001) noted, the visual N1 consists of a set of subcomponents with somewhat different latencies and sources. The apparent latency change can be a consequence of the different effects of spatial attention on these subcomponents.

### 6.5 Conclusions

Infrequently vanishing parts of objects are detected automatically. However, these deviant events initiate orientation only if the objects are close to the field of task-relevant events. Similarly, automatic registration of the rare but expected events occurs only in the visual field close to the focus of attention.

Acknowledgments

This study was supported by the Hungarian Research Fund (NKFIH 119587). We thank Zsuzsa d'Albini for her technical help.

There are no conflicts of interest.

Dataset are available from the corresponding author at file.domonkos@ttk.mta.hu

### 6.6 Supplementary

#### 6.6.1. Offset related event-related results

The ANOVA conducted on the N1 amplitude values revealed a main effect of condition (F(1 ,12)=8.58, p=0.01259, η2=0.42), that is the responses to the attend close stimuli were larger. Also, a main effect of probability (F (1, 12)=13.87, p=0.00291, η2=0.54) indicated, that deviant stimuli elicited larger response. The main effect of laterality (F(2,24)=4.56, p=0.02098, η2=0.29) and anteriority (F(F, 12)=4.9430, p=0.04617, η2=0.28) indicated, that the responses were smaller on the left and on the occipital electrode sites.

The ANOVA conducted on the latency values of the N1 revealed a main effect of condition (F(1,12)=36.90, p=0.00006, η2=0.75) that is the first negative component peaked earlier in the attend far condition.

The ANOVA conducted on the amplitude values of the later positivity revealed a main effect of probability (F(1, 12)=11.58, p=0.0052, η2=0.49); that is the responses elicited by the standards were reduced. The condition x probability interaction (F (1, 12)=49.73, p=0.00001, η2=0.80) revealed, that the responses elicited by the attend close standard were significantly reduced compared to the other responses, while the other responses did not differ from each other.

The ANOVA conducted on the latency values of later positivity revealed a main effect of probability (F(1, 12)=19.65, p=0.00082, η2=0.62), that is the responses elicited by the deviants peaked later. The condition main effect (F (1, 12)= 6.30, p=0.02739, η2=0.34) revealed, that latencies were shorter in the attend far condition.

### 6.6.2. Onset related event-related results

The ANOVA conducted on the N1 amplitude values revealed a main effect of condition (F(1 ,12)=7.85, p=0.016, η2=0.39), that is the responses to the attend close stimuli were larger.

The ANOVA conducted on the latency values of the N1 revealed a main effect of condition (F(1,12)=3690, p=0.00037, η2=0.66) that is the first negative component peaked earlier in the attend far condition. The probability main effect (F(1,12)=5.77, p=0.03337, η2=0.32) indicated, that the peak of the N1 was later for deviant stimuli. The laterality main effect (F(2,24)=9.29, p=0.00103, η2=0.43) indicated, that N1 peaked later at the left electrodes.

There was no difference between the amplitude and latency of the late positive component.

### 6.6.3. Offset difference wave

The ANOVA conducted in the early time window (152-200 ms) with factors condition (attend far and close), laterality (left, middle, right) and anteriority (parieto-occipital and occipital) revealed a main effect of laterality (F(2, 24)=5.97, p=0.00785, η2=0.30). Tukey HSD post hoc analysis revealed significant differences across channels between the left and right electrodes (p<0.01). The condition x laterality x anteriority interaction (F (2, 24)=6.33, p=0.00618, η2=0.35) revealed that the amplitude of the difference waves did not differ significantly at PO4 and while the amplitude in the attend close condition gradually decreased from the right to the left (right<middle<left (p<0.01)), in the attend far condition the middle and the right electrodes did not differ.

The ANOVA conducted in the late time window (270-330 ms) with the same factors revealed a main effect of condition (F(1, 12)=15.49, p=0.00198); attend close had significantly larger amplitude. The main effect of laterality indicated (F (2, 24)=5.60, p<0.05, η2=0.56) that the amplitudes of the differences were significantly smaller at the middle compared to the left electrodes. The main effect of anteriority indicated (F(1, 12)=6.19, p<0.05, η2=0.34), that the difference potentials had a smaller amplitude over the occipital electrodes. The main effect of laterality (F (2, 24)=5.60, p=0.01, η2=0.32). No latency differences were among the conditions and locations.

### 6.6.4. Onset difference wave

A main effect of anterioirity in the 330-420 ms range indicated (F (1, 12)=20.85, p=0.00065, η2=0.42), that differences were bigger over the parieto-occipital sites.

No latency differences were among the conditions and locations.

# Chapter 7: Automatic detection of violations of statistical regularities in the periphery is affected by the focus of spatial attention: A visual mismatch negativity study[10]

## 7.1 Introduction

Processing of visual events close to the locus of attended (task-related) parts of the visual field is different from those far from the locus of attention. In behavioral studies, this difference can be investigated by varying the distance between the attended locus and the distractor (e.g., Eriksen & St James, 1986; Miller, 1991), as well as an effect of task difficulty and magnitude of distraction (e.g., Handy et al., 2001; Lavie, 2005). Brain activity elicited by irrelevant stimuli within and outside the focus of attention provides insight into the processing of non-attended events. Event-related potentials (ERPs) recorded in response to a task-irrelevant probe nearer or farther away from the loci of task-related stimuli show that stimuli in close proximity to the task-related stimuli elicit a larger response (Heinze et al., 1994; Kornrumpf & Sommer, 2015; Nigbur et al., 2015). Recently, we (File et al., 2018) investigated the detection irrelevant violation of sequential regulation nearer or farther away for task-related parts of the visual field. To assess the effect of distance on violated regularities, we analyzed the visual mismatch negativity (vMMN) component of the ERPs. The vMMN is elicited by deviant visual stimuli within the sequence of physically or categorically equivalent stimuli, and by stimuli-violated complex sequential regularities (for reviews, see Czigler, 2014; Kimura et al., 2011; Kremlaček et al., 2016; Stefanics et al., 2014).

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[10] File, D. & Czigler, I. (2019). Automatic detection of violations of statistical regularities int he periphery is affected by the focus of spatial attention: A visual mismatch negatiivty study. European Journal of Neuroscience, 49(10):1348-1356. doi: 10.1111/ejn

In a previous study (File et al., 2018), we applied the offset-stimulation method developed by Sulykos et al. (2017). Instead of presenting the stimuli on a blank inter-stimulus field, stimulus sequences were constructed from vanishing elements of continuously present objects. Contrary to the regularly vanishing parts of the objects, infrequently vanishing parts elicited a posterior negative ERP component, the vMMN. File et al. (2018) applied the same method, but in one of the conditions, the task (continuous tracking) was presented in close proximity to the vMMN-related stimuli, whereas in the other condition, it was farther away from the stimuli. Both the offset stimuli and the reappearance of the previously vanishing parts elicited larger endogenous activity (N1), which corresponds with the results of previous studies using task-irrelevant probes. Unexpectedly, vMMN to stimulus offset was identical in the attend close and far conditions. The processing difference of infrequent events is reflected by a later ERP difference between the two conditions and the emergence of a vMMN-like activity after the reappearance of the stimulus objects after the infrequent frequency stimulus offset. It is possible that the lack of distance effect was due to offset stimulation. Vanishing pairs of objects are much less salient events than abrupt stimulus onset (Jonides & Yantis, 1988). As an example, Kramer & Hahn (1995) demonstrated that offset stimuli between the task-relevant ones did not impair matching performance, whereas the effect of stimuli with sudden onsets was considerable. Accordingly, we suggest that in our previous study, the processing of the vanishing stimulus parts did not interfere with the ongoing task, but vMMN to sudden onset stimulation (i.e., the usual method in vMMN research and ERP research in general) is dependent on spatial attention. Therefore, in the present study we used a similar task in which the vMMN-related stimuli were presented either closer to or farther away from the task field. However, the oddball sequence consisted of onset stimuli.

A source of ERP differences between deviant and standard stimuli is the different stimulus-specific adaptations to the infrequent and frequent stimuli. To control the adaptation effect, the equiprobable control sequence was introduced (e.g., Jacobsen & Schröger, 2011; Kimura et al., 2009). In this procedure, the ERPs to the oddball deviant are compared to physically identical stimuli from a sequence of variable stimuli. In this control sequence, each stimulus has the same probability as the oddball deviant. In this study, we applied this procedure.

## 7.2 Methods

### 7.2.1 Participants

Fifteen students (9 women; mean age: 22.6; SE=0.4 year) participated in the study for monetary compensation. They had normal or corrected to normal vision. Written informed consent was obtained from all participants prior to the experimental procedure. The study was conducted in accordance with the Declaration of Helsinki and was approved by the Joint Committee of Ethics of the Psychology Institutes in Hungary.

### 7.2.2 Stimuli and procedure

The experimental design followed a task location (attend close, attend far) x sequence (oddball, oddball reverse, control) arrangement. Regardless of the condition, participants continuously performed the same task parallel to the presentation of the oddball sequence. Stimuli were presented on a CRT monitor (60 Hz, 1280x1024) from a viewing distance of 100 cm. Stimuli were generated via MATLAB using the Cogent toolbox (http://www.vislab.ucl.ac.uk/cogent_2000.php).

### 7.2.3 Task-related events

We used the same task as in File et al. (2018); participants had to perform a continuous rotation task during the experiment to draw their attention away from the task irrelevant sequences. The task required a continuous central fixation to a rotating bar at the center of the screen (*0.115* turn/sec, light gray (RGB 0.95, 0.95, 0.95, size: length 0.56°, width 0.077°, against light gray background (RGB 0.6, 0.6, 0.6)). Additionally, participants were instructed to keep their eyes at the center of the screen. Occasionally a second target bar (light gray (RGB 0.95, 0.95, 0.95, size: length 2.24°, width 0.077°, against light gray background (RGB 0.6, 0.6, 0.6)) appeared, either 2.14° above (attend far condition) or below (attend close condition) the rotating bar for 200 ms. A response (button press) was only required when the central and the second target bar were parallel, which occurred in 40% of all target appearances in a random order. Participants were instructed to respond as fast and as accurately as possible. The position of the second bar (target) was constant during each block. Participants were informed about this position at the beginning of each stimulus block (with an arrow pointing to the target location of the subsequent block). In each stimulus block, 96 targets were presented. Reaction times and performance were measured. An illustration of the task and the conditions are presented in Figure 7.1.

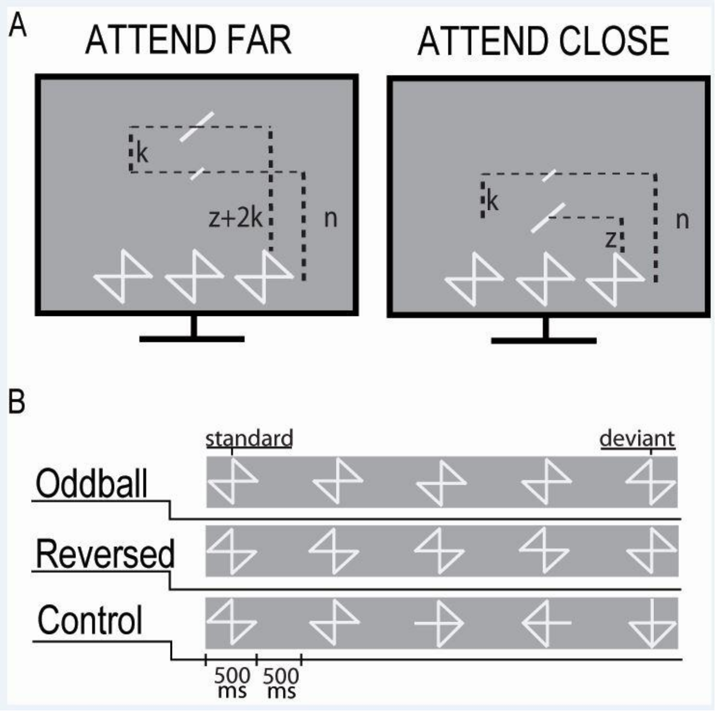


**Figure 7.1 Illustration of the (a) attend far and attend close conditions and (b) the stimulus sequences**

### 7.2.4 Task irrelevant sequences

The stimuli of the oddball sequences were three tilted hourglass shapes with their diameters presented side-by-side (separated by 3.86°). The diameter of an hourglass shape was 2.31°, the contours of the stimuli were white (RGB 0.95, 0.95, 0.95), and their widths were 0.077°. The background was light gray (RGB 0.6, 0.6, 0.6). The hourglass shapes were either tilted by 45° or 135°, 3 hourglass shapes presented at the same time always had the same angle. The stimuli were presented in a reverse oddball arrangement, i.e., in half of the oddball sequences the standard stimuli (p=0.8) had an angle of 45°, while the deviants (p=0.2) had an angle of 135°; the probabilities were reversed in the other half of the sequences. Within each condition, 114 deviant stimuli were presented. The control sequence comprised 3 additional shape triplets besides the 2 hourglass shapes presented in the oddball sequences. The 3 additional shape triplets were arrow-like shapes that shared the basic characteristics of the hourglass shapes, i.e., they were separated by 3.86°, their diameters were 2.31°, the contours of the stimuli were white (RGB 0.95, 0.95, 0.95), and their widths were 0.077°. The five stimuli of the control sequence had the same probability (0.2) and were presented in a random order

As an important aspect, regardless of the condition, the task irrelevant sequences were presented on the lower part of the screen (4.30° from the fixation). The onset of the stimuli was 500 ms, followed by a blank interstimulus interval of 500 ms. An illustration of the sequences is presented in Figure 7.1.B.

All conditions [(two oddball versions, control) x (attend close and attend far)] were divided into 6 blocks that were presented in a random order. Accordingly, there were 36 blocks. The blocks were 1.6 minutes long, so the total length of the ERP blocks was approximately 57 minutes.

### 7.2.5 Eye movement tracking

Eye movement tracking was recorded in the same way as in File et al. (2018) and the same limitations are true for this study. Eye movement tracking was recorded in two separate blocks for the attend close and attend far oddball conditions after the ERP blocks. During the eye movement tracking, no EEG data were recorded due to the technical limitations of the eye tracker (during eye movement recording, the subjects sat closer to the screen than during the ERP recording session (55 cm vs. 100 cm)). Because of this limitation, the eye movement results should be interpreted carefully. However, it should be emphasized that maintaining central fixation in the eye-movement blocks was more taxing than it was in the ERP blocks. Eye movement was recorded with a Tobii x50 device and Clear View 2.5.1 software, using a normal validity filter and an average eye filter. The fixation radius was 30 px, and the minimum fixation duration was 100 ms. The diameters of the stimuli were 4.21° (width: 0.144°); they were separated by 6.98° and presented 7.8° from the fixation. The length of the central rotating bar was 1.01° (width: 0.144°), and its rotating speed was 0.418°/sec. The length of the target bar was 4.07° (width: 0.144°), presented either 3.89° below or above the center.

### 7.2.6 Eye tracking data analysis

The same eye tracking data analysis was conducted as in File et al. (2018); the screen was divided into 4 regions of interest: middle (x: (-9.1)°-9.1°, y: (-1.8°)-1.8°), top (x: (-9.1)°-9.1°, y: 1.8°- 5.9°), bottom (x: (-9.1)°-9.1°, y: (-1.8)°- (-5.9)°), and oddball (x: (-9.1)°-9.1°, y: (-5.9)- (-10.1°)), see Figure 7.2. The gaze lengths were calculated for the ROIs separately within the two blocks. Gaze times were compared in a two-way ANOVA with the factors condition (attend close and attend far) x ROI (middle, top, bottom, oddball).

### 7.2.7 Recording and processing brain electric activity

The recording of brain electrical activity was identical to File et al. (2018). The EEG data were recorded (DC-30 Hz, sampling rate 500 Hz; Neuroscan Synamps2 amplifier with Ag/AgCl electrodes at 61 locations, according to the extended 10-20 system, using an elastic electrode cap (EasyCap). The tip of the nose was used as a reference, but the off-line reference was the average activity. The ground electrode was attached to the forehead. A horizontal EOG was recorded with a bipolar configuration between the electrodes that were positioned lateral to the outer canthi of the two eyes. Vertical eye movements were monitored with a bipolar montage between the electrodes that were placed above and below the right eye. The impedance of the electrodes was maintained below 10 kΩ.

The data were processed using EEGlab (Delorme et al., 2011) and Matlab 2014a (Mathworks, USA). The EEG signal was bandpass filtered offline, with cutoff frequencies of 0.1 (60-dB slope) and 30 Hz (120-dB slope) and epochs of 600 ms, starting from 100 ms before the stimulus onset. The epochs were baseline corrected relative to 100 ms pre-stimulus interval. Epochs were averaged separately for the standards preceding a deviant, deviants, and controls. Thus, it was ensured that the standard, deviant and control related ERPs were formed from the same number of epochs. The vMMN was calculated by subtracting the standard-related ERP from the deviant-related ERP. Trials with an amplitude change that exceeded ± 100 uV on any channel were rejected from further analysis (this principle was applied to all trial types and electrodes including the electro-oculogram recording ones). On average 91.67% (mean = 209.133, min = 176, max = 218, SE = 1.3799) of the epochs were used for further analysis.

Based on our previous experiment (File et al., 2018), we conducted statistical comparisons on channel PO4, as vMMN was found at this channel location to be the largest. To test whether vMMN was present, a point-by- point t-test ($p < 0.05$) was run against zero on the deviant-minus- standard and deviant-minus- control difference waves for all subjects. To reduce the chance of selecting latency ranges reflecting solely noise, the same procedure were repeated 1,000 times on simulated data (reflecting the characteristics of the original data) for every difference wave. If the latency range of the difference wave was longer than the 95% of the maximum length of the significant latency ranges of the simulated difference waves, it was selected for further statistical analysis, otherwise it was rejected. vMMN is expected to emerge in the 150–300 ms range, so the simulated data were compared in this range, while the later positive difference were investigated in the 300–500 ms range.

There was no latency range that met the criteria in the deviant-minus- control attend far difference wave. The deviant-minus- control attend close difference wave significantly differed from zero in the 170–210 ms (negative polarity) and in the 340–498 ms (positive) ranges. The control-minus- standard attend far difference wave differed from zero in the 170–208 ms (negative polarity) and in the 294–352 ms (positive) ranges. The control-minus- standard attend close difference wave differed from zero in the 260–374 (positive) ms range. The control-minus- standard differences were compared in a one-sample t test in the 294–352 ms range.

Besides investigating the vMMN difference wave, exogenous ERP components elicited by the deviants and the control stimuli were also investigated. The sole aim of this measurement was to investigate whether in this study the exogenous components were similar to the usual activity of ERP studies. ERP component amplitudes were measured as the largest values in the group mean (peak ±10 ms) at PO4. ERP component latencies were calculated as the time point reflecting the local maxima in the peak ±10 ms range at PO4. Amplitude and latency values were compared in ANOVAs with factors of stimulus type (deviant, standard, control) and condition (close and far). To control for multiple comparisons the Holm–Bonferroni method was applied.

## 7.3 Results

### 7.3.1 Behavioral results

The average hit rate was 62.37% (SE=3.52), the average error rate (response to invalid target) was 26.76% (SE=3.88), and the average reaction time was 478 ms (SE=18.89). Hit rate and error rate did not differ between conditions, but there was a significant difference in the reaction times between the attend close (M=491 ms, SE=19.41) and attend far (M=459 ms, SE=19.99) conditions (t(14)=-4.08, p=0.01). That is, reaction times were shorter in the attend far condition.

### 7.3.2. Eye movement tracking

Subjects were focusing on the center 82.06% of the time. An ROI main effect revealed (F(3,42)=37.93, p=0.0001, ηp2=0.73) that subjects were looking significantly longer at the center than at the other ROIs. There was no difference between the attend far and close conditions. Figure 7.2 illustrates a heat map of the relative gazing times.

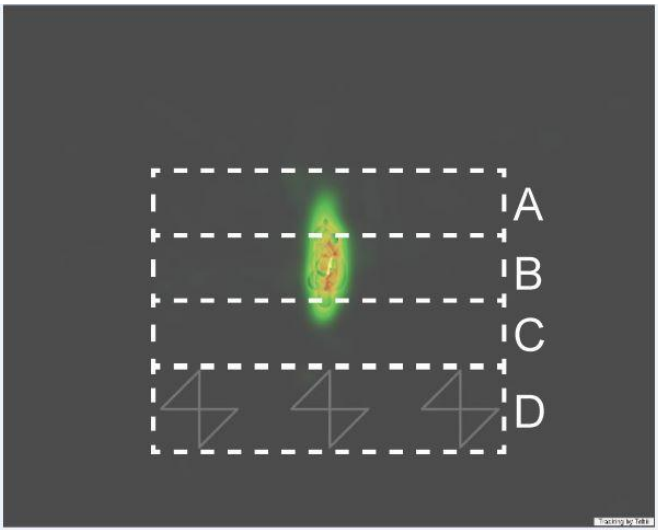


**Figure 7.2. Regions of interest during the eye tracking; (a): top, (b) middle, (c): bottom, (d) oddball. Heat map reveals the focus of attention during the eye tracking**

### 7.3.3. Event-related potentials

#### 7.3.3.1. Early visual evoked components

Figure 7.3 shows the ERPs for the deviant, standard and control stimuli in the far and close conditions. Stimuli in all conditions elicited P1, N1 and P2 components. In the attend far condition ERP component time ranges were as follows; P1 (88–108 ms), N1 (146–166 ms) and P2 (244–264 ms), while in the attend close condition P1 (82–102 ms), N1 (150– 170 ms) and P2 (254–274 ms). In the attend far and close conditions, the appearance of the N1 component was different. As Figure 7.3 illustrates, in the attend far condition in the N1 range the component has a single peak, whereas in the attend close component, we recorded double peaks.

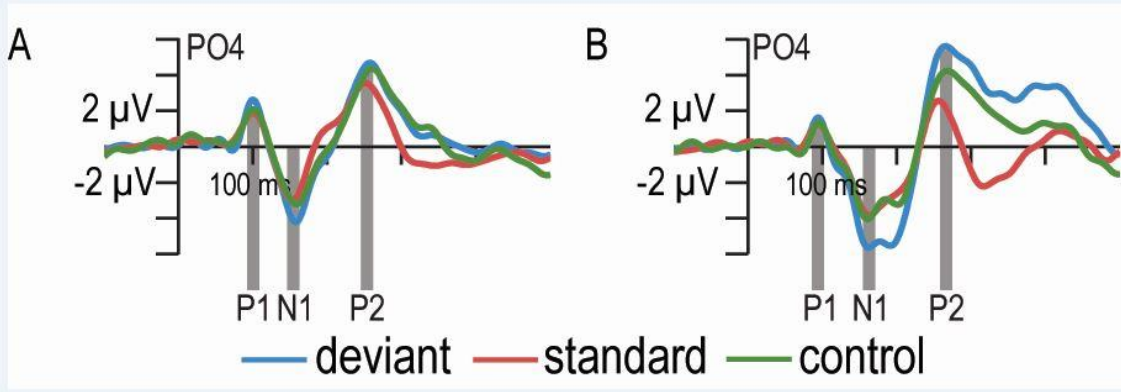


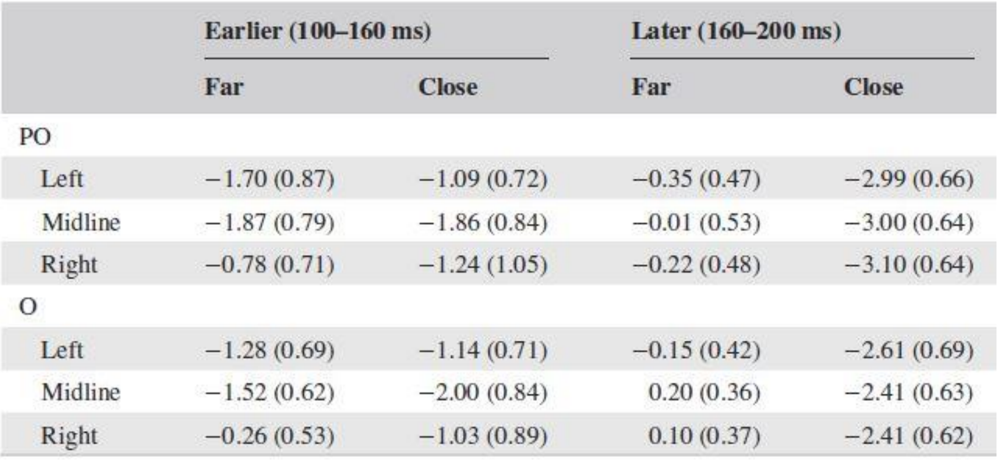
**Figure 7.3 Grand averaged ERPs elicited by the (a) attend far and (b) attend close stimuli**

Inspecting the individual records, double peaks appeared in the majority of participants. For the attend close condition we selected the first, since it was closer in time to the peak we observed in the attend far condition.

The ANOVA on the P1 amplitude values revealed a significant difference of the amplitude values between conditions, F(1, 14) = 5.0460, p = 0.041338, η2p = 0.264939, that is P1 has bigger amplitude in the attend far condition. There was no significant difference between stimulus type, F(2,28) = 0.71109, p = 1.000, η2 p = 0.048337. There was no significant difference between latencies between conditions, F(1, 14) = 2.0849, p = 0.512, η2p = 0.129617, and stimulus type, F(2, 28) = 0.48549, p = 1.000, η2p = 0.033516.

The ANOVA on the N1 amplitude values revealed no significant difference of the amplitude values between conditions, F(1, 14) = 7.1797, p = 0.054, η2p = 0.338991. There was a significant difference between stimulus type, F(2, 28) = 7.9593, p = 0.007, η2p = 0.362457; N1 in the attend close condition has bigger amplitude and deviant stimuli elicited N1 with greater amplitude than the standard and the control stimuli. There was no significant difference between latencies between conditions, F(1, 14) = 2.2370, p = 0.276, η2p = 0.137773, and stimulus type, F(2, 28) = 1.2460, p = 0.30311, η2p = 0.081727. For the N1 amplitude values see Table 7.1.

The ANOVA on the P2 amplitude values revealed no significant difference of the amplitude values between conditions, F(1, 14) = 0.2939, p = 0.86634, η2p = 0.002095. The significant main effect of stimulus type, F(2, 28) = 5.9038, p = 0.029, η2p = 0.296617, revealed that standard stimuli elicited P2 with reduced amplitude compared to the deviant. The significant condition x stimulus type interaction, F(2,28) = 5.6141, p = 0.029, η2p = 0.286226, indicated, that while in the attend close condition standard, deviant and control stimuli significantly differed from each other, in the attend far condition only the standard and deviant differed significantly. The ANOVA on the P2 latency values revealed a significant difference of the amplitude values between conditions, F(1,14) = 8.8280, p = 0.029, η2p = 0.386719, that is P2 peaked later in the attend close condition. The stimulus-type main effect, F(2, 28) = 12.680, p = 0.00012, η2p = 0.475266, revealed, that P2 peaked earlier in response to standard stimuli.

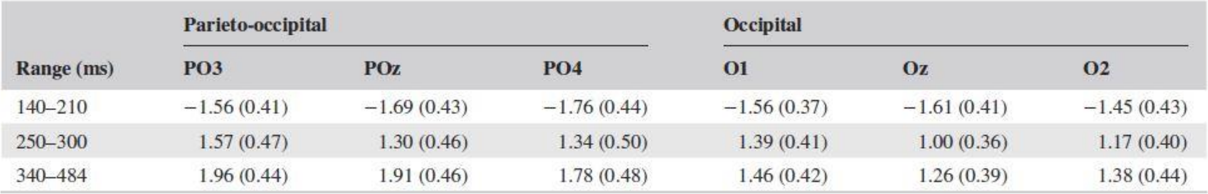


| | Earlier (100–160 ms) | | Later (160–200 ms) | |
|---|---|---|---|---|
| | Far | Close | Far | Close |
| PO | | | | |
| Left | −1.70 (0.87) | −1.09 (0.72) | −0.35 (0.47) | −2.99 (0.66) |
| Midline | −1.87 (0.79) | −1.86 (0.84) | −0.01 (0.53) | −3.00 (0.64) |
| Right | −0.78 (0.71) | −1.24 (1.05) | −0.22 (0.48) | −3.10 (0.64) |
| O | | | | |
| Left | −1.28 (0.69) | −1.14 (0.71) | −0.15 (0.42) | −2.61 (0.69) |
| Midline | −1.52 (0.62) | −2.00 (0.84) | 0.20 (0.36) | −2.41 (0.63) |
| Right | −0.26 (0.53) | −1.03 (0.89) | 0.10 (0.37) | −2.41 (0.62) |

**Table 7.1. N1 amplitudes (μV) in the earlier and later latency ranges (SE in parenthesis)**

### 7.3.3.2. Visual mismatch negativity and posterior positivity

The main purpose of the present study was the investigation of vMMN as a function of distance from the task-related events. We considered vMMN as the difference between the ERPs to the deviant and control. Figure 7.4a shows the deviant-minus-control difference potentials and Figure 7.4b the topographical distribution. In the far condition there was no significant difference from zero according to t tests. However, in the close condition the difference was significant in three epochs: from 170 to 210 ms (negativity) and 340–498 ms (positivity). A 2 × 2 condition (far, close) by stimulus type (control, deviant) ANOVA was conducted on the averaged amplitude values of the 170– 210 ms section to test for interactions. The ANOVA revealed a significant interaction, $F(1, 14) = 8.8608$, $p = 0.010$, $\eta 2p = 0.387597$, that is deviant stimuli in the close condition elicited more negative response relative to the control than in the far condition. For the difference potential amplitude values see Table 7.2.



| | Parieto-occipital | | | Occipital | | |
|---|---|---|---|---|---|---|
| Range (ms) | PO3 | POz | PO4 | O1 | Oz | O2 |
| 140–210 | −1.56 (0.41) | −1.69 (0.43) | −1.76 (0.44) | −1.56 (0.37) | −1.61 (0.41) | −1.45 (0.43) |
| 250–300 | 1.57 (0.47) | 1.30 (0.46) | 1.34 (0.50) | 1.39 (0.41) | 1.00 (0.36) | 1.17 (0.40) |
| 340–484 | 1.96 (0.44) | 1.91 (0.46) | 1.78 (0.48) | 1.46 (0.42) | 1.26 (0.39) | 1.38 (0.44) |

**Table 7.2 Difference potential amplitudes (µV; SE in parenthesis)**

### 7.3.3.3. Adaptation of event-related potentials

Figure 7.4c shows the control-minus-standard difference potentials in the far and close conditions. As the figure shows, in the far condition, a negative difference is followed by a positivity, whereas in the close condition, only positivity appeared. To the results from t tests show that the negative difference was significant in the 170–210 ms range in the far condition and that the positive differences were significant in the 294–352 ms and 260–374 ms ranges in the far and close conditions respectively. The t test conducted on the amplitude values of the overlapping time window (294–352 ms) revealed a significant difference between the attend far ($M = 2.083$, $SE = 0.60$) and the attend close ($M = 3.977$, $SE = 0.76$) conditions, $t(14) = 2.53$, $p = 0.0239$, that is the attend close difference had bigger amplitude. Figure 7.4d,e shows the topographical distributions of the control-minus-standard difference waves.

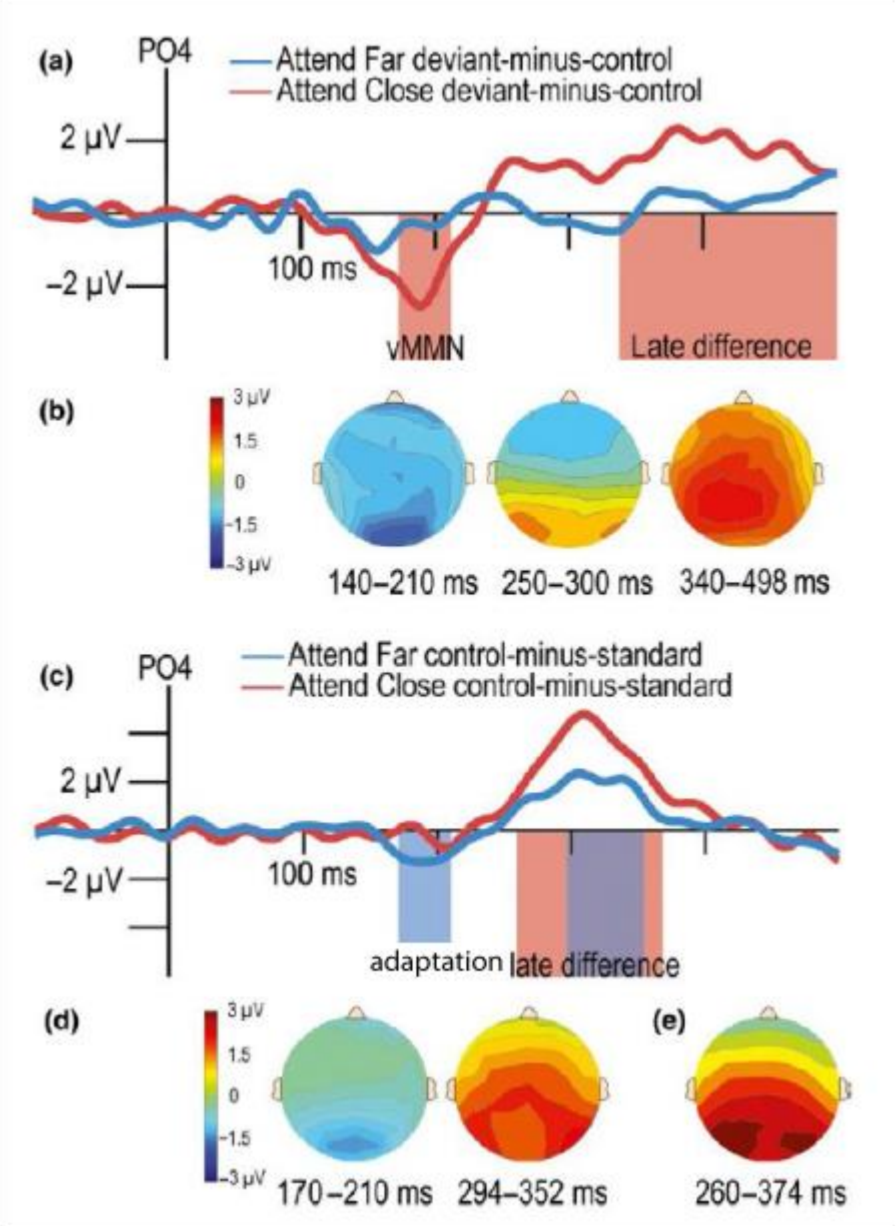


**Figure 7.4. (a) Grand averaged deviant-minus-control difference wave (b) Topographical maps of the deviant-minus- standard difference waves of the attend close condition. (c) Grand averaged control-minus- standard difference waves. (d) Topographical maps of the control-minus- standard difference waves in the attend far condition. (e) Topographical map of the control-minus- standard difference waves in the attend close condition**

## 7.4. Discussion

According to the results of the present study, infrequent (deviant) visual stimuli in close proximity to a continuously attended field elicit larger vMMN than similar stimuli farther away from the stimulus field. The distance-related effect appeared as the ERP difference between the deviant of the oddball sequence and the stimuli of the equiprobable control sequence. Thus, in the close condition, a posterior positivity followed the vMMN. ERPs to the standard stimuli of the oddball sequence were more negative/less positive than the ERPs to both the oddball deviant and control stimuli. Concerning the exogenous ERP components, stimuli near to the attended field elicited posterior negativity (N1) in a wider range with double peaks compared with stimuli far from the attended field.

In contrast to File et al. (2018), in the present study, similarly to the majority of vMMN, the stimuli were presented as rapid onset. These stimuli capture attention more effectively than the offset stimuli in the File et al. (2018) study (e.g., Jonides & Yantis, 1988; Kramer & Hahn, 1995; Mounts, 2000). To obtain high performance in the present study, participants had to attend to the task field. Spatially selective attention involves facilitation of processing within the field of attention as well as inhibition of adjacent regions (e.g., Facoetti & Molteni, 2000; Luck et al., 1997; Mangun & Hillyard, 1988; Woldorff et al., 2002; Mounts, 2000; Shiori et al., 2016; Slotnick et al., 2003). Models of selective attention emphasize that the size of the attentional field depends on the extent of task-related stimuli (LaBerge & Brown, 1989; Eriksen & St. James, 1986), and task demand (Handy et al., 2001; Lavie, 2005). This research concentrated on the characteristics of the field of an attended event, but less is known about the extent of the field of inhibition.

In ERP studies of spatial attention, the larger P1 in response to stimuli at attended locations is considered as an index of inhibition of ERPs to non-attended stimuli, and the increased N1 as a correlation to the facilitation of processing within the attentional field (Luck et al., 1997). Unfortunately, in the File et al. (2018) and in the present study we obtained only small P1, but the larger N1 in the File et al. (2018) and the broader N1 in the present study shows that facilitative activity was larger near to the attended area. More specifically, in the close condition, we recorded two peaks in the N1 range, the second of which was sensitive to distance from the attended field. The posterior N1 has more than one source (Di Russo et al., 2002). As our results indicate, sensitivity of the two subcomponents is different from spatial attention. To prevent the distracting effects of salient (abrupt onset) infrequent but irrelevant deviant events in fields farther from the distracting stimulus, a more efficient inhibitory activity was developed. As a consequence, the deviants in the far condition of the present study did not elicit vMMN. We are aware of the speculative nature of the present account. However, two findings of the File et al. (2018) study supports these results. First, even if there was a vMMN amplitude difference between the close and far conditions in that study, a later effect of deviant processing (posterior positivity) emerged only in the close condition. Second, the reappearance of the objects after the infrequent (deviant) stimulus offset elicited posterior negativity only in the close condition, showing that abrupt onset of infrequently appearing stimulus elements was a more efficient stimulus, even if the stimulation was not unexpected.

To diminish the effects of stimulus-specific adaptation, we measured vMMN as the difference between the ERPs to the deviants and the stimuli physically identical to the deviant from the equiprobable control sequences (Jacobsen & Schröger, 2001; Kimura et al., 2009). The effects of stimulus-specific adaptation were illustrated by taking the deviant-minus-standard difference potentials. In the far condition, the control stimulus was more negative that the standard in the 170-210 ms range. The N1 peak latency in this condition was 150 ms; therefore, it is improbable that it is an adaptation of the particular exogenous component. Another range of the control minus standard difference is centered at ~320 ms – that is, later than the P2 component. Again, the difference is unlikely to be due to the diminished exogenous activity to the standard.

According to our results early adaptation effect appeared in the far condition, but in the later period the adaptation of the standard was larger in the close condition. In the auditory modality adaptation seems to be an active inhibitory process (Escera & Malmierca, 2014). In vision we have no direct evidence for such mechanism. Nevertheless, considering a similar mechanism in vision, the later phase of the adaptation effect, being under attentional influence can be tentatively considered as a signature of active inhibitory processes.

### 7.5 Conclusions

In conclusion, infrequent (deviant) stimuli of non-attended oddball sequences of abrupt onset stimuli elicited the signature of automatic change detection (vMMN) only if the stimuli appeared near to the field of the ongoing task. A posterior positivity followed VMMN, which indicates further processing of the deviant events, but the emergence of this activity is confined to the deviant stimuli near to the attended field.

### Acknowledgments

This study was supported by the Hungarian Research Fund (NKFIH 119587). We thank Zsuzsa d’Albini for her technical help.

### Competing interests

There are no conflicts of interest.

# Chapter 8: GENERAL DISCUSSION

The aim of the present dissertation was to introduce visual mismatch negativity, with special emphasis on the adaptation issue and on the attention relatedness of vMMN. Study I and Study II focused on adaptation, including theoretical aspects and the methodological possibilities to separate the effect of adaptation and genuine vMMN. Study III and Study IV focused on the effect of spatial attention on vMMN.

We demonstrated in Study I and Study II, that adaptation related response decrement is a plausible explanation to the observed difference in the deviant-minus-standard-difference wave in case of simple, one visual feature deviances. However, in case of complex deviances, adaptational processes are not sufficient to explain the whole deviant-minus-standard difference wave, and an additional activity is present, the genuine vMMN. We proposed an explanation, that one uniform underlying mechanism that would generate vMMN does not exist and that instead there are separate mechanisms, depending on the circumstances/stimulation. These results have a significant contribution to the long held adaptation vs. genuine vMMN debate and redefine the question. The first question of the debate was that weather MMN/vMMN is different from adaptation (e.g., May & Tiitinen, 2010, in the auditory modality; Kenemans, Jong, & Verbaten, 2003, in vision), i.e. the existence of “genuine” MMN/vMMN. The second question was that which part of the deviant-minus-standard difference wave is attributable to adaptation, and to MMN (Kimura et al., 2009). The third question, raised by the results of Study I and Study II, is something like: what are the features that can be represented throughout adaptational mechanisms and what are those which requires the activation of the MMN generating mechanisms? Also, based on the result of Study I and II and other experiments used the equal probability control (e.g. Kimura et al., 2009; Kojouharova et al., 2019), vMMN is always accompanied by adaptation, raising the fourth question regarding their functional interaction. Kojouharova et al. (2019) investigated the role of stimulus complexity on vMMN and reported similar vMMN in response to simple and complex stimuli. However, it is important to note, that in the complex equal probability control it is difficult to interpret the methodological rule of keeping larger distances on average between the control, than between the oddball stimuli. The aim of this rule is to prevent the possibility of having larger adaptational effect on the control stimuli than on the oddball deviant.

However, in this case it is possible, that in the complex equal probability control condition the adaptational state is significantly lower, than in the simple control condition, i.e. over controls the adaptation effect, leading to the reduced deviant-minus-control difference wave for the complex stimuli.

In Study I Experiment 1 arrays of oblique bars were presented either in oddball, equal probability or cascade control sequences, while participants played a video game. The deviant-minus-standard difference wave showed a negative deflection in the 105-190 ms and in the 118-148 ms ranges at the parieto-occipatal and at the occipital electrode sites, respectively. In line with our hypothesis, the difference waves formed from the deviant and the control stimuli however did not differ from zero in the latency range defined by the difference of the deviant-minus-standard difference wave. This result did not support the memory-comparison based change detection account. Oblique bar stimuli in equal probability control condition was used in former (Astikainen et al., 2008; Kimura et al., 2009; Kimura et al., 2010; Kimura & Takeda, 2013) and later studies (Kojouharova et al., 2019), with markedly different results. The studies of Kimura and his colleges found that the earlier part of the deviant-minus-standard difference wave is accountable to adaptation, while the later, around 200-250 ms post-stimulus range is the reflection of genuine vMMN. Astikainen et al., (2008) obtained a deviant-minus-control difference in the 185-205 ms range, while Kojouharova et al. (2019) obtained a wider, from 120-210 ms (POz channel) difference. The reported differences draw attention to the complex interactions between primary task and stimulus arrangement. Since the effect of attention results in qualitatively different evoked responses (Czigler & Pató, 2009), it is not possible to interpret those observations in a comprehensive manner.

The cascade control sequence investigated in Study I Experiment 1 did not result in different wave forms compared to the widely used equal probability control. The use of cascade control is restricted to special cases anyway, where a successive sorting of the stimuli is possible. Based on those, we concluded, that the use of equal probability control is a better research practice, for its more universal usability and better comparability.

In Study I Experiment 2 windmill patterns were presented in oddball, equal probability and modified sequences, while subjects participated in a tracking task. Since there was no difference between the ERPs recorded in the equal probability and modified control, for the sake of easier traceability, I will refer them as control. An unexpected result was that the deviant-minus-standard difference waves showed a robust difference between the 6 and 12 vane conditions. In line with our hypothesis the deviant-minus-standard difference in the 12 vanes condition comprised two wide negative components in the 100-200 and 200-340 ms ranges and the deviant-minus-control difference preserved the two negative components. The same difference wave in the 6 vane condition also comprised two, narrower component in the 178-216 and in the 270-346 ms ranges, but contradictory to our hypothesis the control condition completely abolished the 6 vane difference. To test the validity of a low level adaptation and a higher level complexity related account, we conducted Experiment 3.

In Experiment 3 windmill patterns were presented in four conditions. Two conditions were the replication of the oddball sequences of Experiment 2, in which 12 or 6 vanes stimuli served as standard or deviant, and vice versa. In the two new conditions 4 and 6 vanes stimuli formed the oddball sequence, since the complexity difference is present between the 4 and 6 vanes stimuli, without the overlapping edges, which could result in unbalanced adaptation effects between conditions. In the sequence of 4 vanes standards the 6 vanes deviant elicited vMMN in the 100-340 ms latency range, supporting the notion of the complexity related notion. The results of Study I Experiment 2 and 3 partly support the findings of Kimura et al. (2009, 2010) and Kimura & Takeda (2013) that is adaptation was present in the early component of the deviant-minus-standard difference wave and genuine vMMN in the late. However, in our experiment genuine vMMN was present in the early range too. The source localization of vMMN conducted in Experiment 2 and 3 are highly consistent with previous findings, identified the cortical sources of vMMN to the right cuneus, precuneus, middle occipital gyrus and the frontal lobe. These results support the notion of Susac et al. (2013) that preattentive change detection is a relatively low level, modality-specific process in the visual cortex.

Since Experiment 3 was partly the replication of the 6 and 12 vanes conditions of Experiment 2, we could test the reliability of the ERPs we recorded. We found no significant difference between the 12 vanes deviant-minus-standard differences in the latency range (100-200 and 200-340 ms) or region of interests (occipital and parieto-occipital). There was significant difference between the amplitude values of the 6 vanes difference wave in the early (178–216 ms) range at the occipital ROI. No such difference was observable at the parieto-occipital ROI. There was no significant difference in the late (270–346 ms) differences between the two recording sessions.

For the best of our knowledge, Study II used an adaptation paradigm at the first time in vMMN research, wheres there was no such investigation in the auditory modality. Experiment 1 utilized two kind of presentation: the traditional stimulus-ISI-stimulus, and the adaptor-ISI-stimulus sequences. There were two adaptor sequences, the length of the squeezed adaptor was the sum of the length of the standards, while the length of the filled adaptor was the sum of the length of the standards with ISI. Study 2 Experiment 1 used the same stimuli as Study 1 Experiment 1, i.e. arrays of oblique bars. In all conditions the deviant-minus-standard differences showed a negative deflection in the 100-140 ms post-stimulus interval at the posterior electrode sites. In line with our hypothesis, the difference waves of different conditions did not differ from each other, supporting the adaptation account of MMN (May & Tiitinen, 2010). Contradictory to our hypothesis the filled adaptor condition did not resulted in higher level of adaptation compared to the squeezed condition. Experiment 2 used the same stimulus presentation as Experiment 1 without the squeezed condition. The stimuli were windmill patterns. In the early, 118-138 ms range difference waves were highly similar between conditions, indicating adaptation related processes in the background. However in the later, 198-218 ms range only the oddball deviant-minus-standard difference differed significantly from zero, indicating genuine vMMN, supporting our hypothesis. These results showed a really similar pattern to the results of Study I, that is the deviant-minus-standard difference wave was the consequence of adaptation when stimuli was an array of oblique bars. However, windmill patterns elicited genuine vMMN in comparable – although much narrower - latencies to Study 1. Here we proposed another possible explanation for the differences between the results of the windmill and the bar stimuli experiments. In both Study I and II Experiment I an array of stimuli was presented whereas in Experiment II a single object served as stimuli. In the visual world, textures belong to the background, while objects to the foreground. Assuming that objects are ecologically more important, it is possible that they are more efficient in establishing memory representations and signaling mismatch (Bodnár et al., 2017). A third possibility is that the difference is the consequence of the primary task. In the light of the results of Study I Experiment 1 however, we argue that the complexity account is the most plausible.

In general, Study I and II pointed out, that vMMN and adaptation are different processes, in line with previous studies (e.g. Kimura et al., 2009, 2010; Astikainen et al., 2008; Kojouharova et al., 2019). We proposed, that adaptational processes might be sufficient in representing one dimensional visual feature related regularities, while automatic detection of the violation of the sequential regularity of complex stimuli operates through the vMMN generating process. Adaptation in the MMN and vMMN literature has been considered as a passive physiological process, with no functional significance (e.g. Kimura et al., 2009). However, researchers from the field of stimulus specific adaptation assume, that the mechanism of adaptation can enhance the saliency of unexpected, deviant stimuli against a background of repetitive signals (e.g. Ulanovsky, Las, & Nelken, 2003). We proposed, that investigating adaptation and vMMN as a functional unit might be a fruitful research direction.

The attention relatedness of vMMN is usually investigated throughout the manipulation of the primary task's difficulty, as described in the Introduction. To the best of our knowledge, Study III was the first study to investigate the effect of the focus of spatial attention on vMMN. This question has both theoretical and methodological consequences on the field of vMMN research. As a theoretical aspect, any kind of knowledge on the attention-vMMN relationship is significant, since a distinctive property of vMMN is it's automatic, task irrelevant nature. The methodological aspect has it's relevance during the design and the evaluation of a primary tasks. As presented in the Introduction, primary tasks show a great heterogeneity between experiments, with varying spatial distances from the location of the vMMN related stimulus sequence. Evaluation of it's effect might contribute to a better understanding of the variance of the outcomes of vMMN studies.

In Study III passive oddball sequences were presented in two conditions, either relatively close or far from the focus of attention. We used vanish stimulation (Sulykos et al., 2017), where the deviant offset was the disappearance of certain parts of a diamond shape. Subjects were participated in a simultaneous tracking and discrimination task, which required the allocation of covert attention. The paradigm worked well, as it was feasible with minimal or no eye movements and required focused attention during the experiment. vMMN was elicited in both condition in the 152-200 ms post-stimulus range, with no significant difference between them. This result suggests, that the distance of the focus of attention had no effect on vMMN. This result is in line with the results of previous experiments (Pazo-Alvarez et al., 2004; Heslenfeld, 2003), regarding the attention independence of vMMN. Another important finding was that vMMN was followed with a posterior positive component, but only when the task irrelevant sequence was close to the focus of covert attention. Based on its characteristics we identified it as a novelty P3, an indicator of the orienting response (Friedman et al., 2001). Importantly vMMN and P3a was independent. Seemingly, this result does not support the attention-triggering hypothesis (see Naatanen, 1990; Schröger, 1990), that is the functional significance of vMMN might be a call for attention for the extensive processing of predictive-incongruent events (Kimura 2012). However, it is important to note, that the P3b modulation of the deviant-minus-standard difference was largely the consequence of a P3b amplitude decrement in response to the standards. This response decrement is probably attributable to an active inhibition of predicable irrelevant events, as reported by Noyce & Sekuler (2014). This possibility implies, that the memory-system responsible for the generation of predictions is formed in the case of active inhibition, strengthening the attention-independent notion of vMMN. Another important finding was that the re-appearance of the whole objects after the deviant offset, i.e. an expected irrelevant event, elicited vMMN but only in the attend close condition. We proposed a *post hoc*, by which the system underlying vMMN separately represents a lower-level deviancy (line onset) and a higher-level regularity (disappearance and reappearance of the parts of stimulus objects). It is possible, that in the condition where the focus of attention was far from the task irrelevant sequence, both the higher and lower, while when it was close, only the lower level regularity was represented. This assumption supposes, that the generation of vMMN is not independent of attention in case of ‘higher level’ regularities. As another assumption, we propounded, that the processing of the vanishing stimulus parts did not interfere with the ongoing task, but the sudden onset stimulation did, leading to the presence of vMMN. Those speculations points towards the conclusion drawn up in Study I, that there might be no uniform mechanism underlies vMMN.

Study IV was highly similar to Study III, with the exception of stimulus presentation. In Study IV traditional, onset stimulation was used, that is the inter-stimulus intervals were blank spaces. This kind of stimulation made the use of equal probability control necessary. Contrary to our hypothesis, when stimuli was far from the focus of attention there was no significant difference from zero in the deviant-minus-control difference wave. However, in the close condition the difference was significant in two epochs: from 170 to 210 ms (negativity) and 340–498 ms (positivity). In contrast to the results of Study III, vMMN was only present in the close condition. According to this, spatial attention not only facilitates automatic change detection, but it is prerequisite of it. Importantly, vMMN was followed by novelty P3, but it was absent in the far condition. This result is in line with previous experiments reporting vMMN followed by attention-related ERP components, such as the N2b or P3 (Kimura et al., 2008a, 2008c, 2008d; Liu & Shi, 2008). Also, contrary to Study III, this result supports the attention-triggering hypothesis.

To sum up, Study I and II investigated the relation of vMMN and adaptation, while Study III and IV the spatial attention relatedness of vMMN. We agree with Stefanics et al. (2014), that future vMMN studies should take the adaptation issue into account. We tested two control sequences – cascade and modified - adopted from the field of auditory MMN research and the adaptation paradigm. We recommend the use of the equal probability control, as comparability is a major issue in vMMN research, and there is a solid number of studies applied the equal probability control (e.g. Kimura et al., 2009, 2010; Astikainen et al., 2008; Kojouharova et al., 2019; File et al., 2017; File et al., 2019).

## 8.1 Methodological necessities and thoughts derived from the studies

The use of strict attention control is recommended. We tested three continuous primary tasks: a video game, a tracking task and a modified Posner task. The video game included a tracking and a discrimination task, and was moderately difficult with an average performance of 72.82% in Study 1 and 68.68% in Study II. An advantage of the video game is that the primary task and the task irrelevant stimulus sequence was spatially separated. The ball tracking task was fairly easy with a performance of 97.88% in Study I and an average performance of 98.4% in Study II. Although it is a continuous task, the high performance raises doubts about its effectiveness to draw attention away from the oddball sequence. Also, the task irrelevant sequence is presented in the background of the tracking task, which makes difficult to ignore it (Czigler & Pató, 2009). The modified Posner task was fairly difficult with an average hit rate of 59.39% and 62.37% and an average error rate of 27.96% and 26.76% in Study III and Study IV, respectively. An advantage of this task is that it is feasible with continuous central fixation, as we verified in the control conditions using eye tracker. Another advantage is that it allows the manipulation of the distance of the focus of spatial attention from the task irrelevant sequence. More detailed relationship of attention-vMMN could be obtained by varying the difficulty of the task. This could be done by either varying the speed of the central rotating bar or by varying the difference of the non-target stimuli from the reference (central rotating bar).

We recommend the use of the video game or the modified Posner task to control attention. Since automaticity is a key characteristic of the MMN response (Stefanics et al., 2014), the use of experiment based primary tasks would be beneficial in the future. A possible way to test the effectiveness of the primary tasks is that participants are required to respond to the appearance of the deviant stimuli of the oddball, while they perform the primary task. In case of effective primary task, a drop of performance in the primary task or a low performance in the deviant detection would be expected, compared to a passive condition. Quantifiable effectiveness of the primary task would increase the comparability and the interpretability of vMMN studies.

Also, more basic research on vMMN would be beneficial. At the moment difference components formed from ERPs elicited in task irrelevant oddball sequences in the ~100-350 ms range are considered vMMN, regardless of the stimuli, the presentation parameters or the primary task. Despite the experimental differences and the differences between the outcomes, vMMN is treated as a uniform process, with its unique cortical source, stimulus sensitivity and temporal characteristics. Considering the presented experiments, such uniform interpretation requires caution, as vMMN like responses might have fundamentally different properties as a function of stimulus features or attentional context.

Generalized interpretation might contribute to significant misconceptions. For example Kimura et al. (2010c) investigated the representation of large scale regularities in the visual modality. They found, that those regularities were only represented in case of relatively fast stimulus presentation, but not with stimulus presentation parameters most vMMN studies are conducted. In another study, Czigler et al. (2006) presented AABBAABBB sequences, where deviant repetition of a stimulus elicited vMMN. However, the stimulus duration was extremely short (17 ms), with relatively short SOAs (350 ms), which is not common in vMMN studies. Despite the unusual experimental variables, the results of both studies serves as important evidence regarding the sequential rule sensitivity of the vMMN generating mechanism (Kimura, 2012), the experimental base of the predictive coding explanation of vMMN. As the thesis studies showed however, genuine vMMN is sensitive to the changes of the experimental conditions.

We argue, that more experiments investigating the sequential rule violation sensitivity of vMMN would be recommended. For example, in the experiment of Kimura at al. (2010c), vMMN was elicited in the fixed sequence of the 480 and 800 ms SOA conditions, indicating that the sequential regularity was not represented. Considering this result, it is not grounded to state, that vMMN elicited in an oddball sequence is the correlate of the violation of a sequential rule derived from the statistical probabilities of the environment, since based on the experiment of Kimura et al. (2010c), vMMN would been elicited in a fixed sequence too, where no sequential rule violation was present. Also, we argue, that investigating the positions of the deviant and standard stimuli of the oddball sequence might be beneficial for a better understanding of the capability of representing statistical regularities of the system generating vMMN. Oddball sequences are pseudorandom sequences, with the rule that there is a minimal and maximal number of standards between deviants. For example, in case of an oddball sequence, where the probability of the deviant is 0.2, the rule would be that a minimum of 3 and a maximum of 8 standards must be between the deviants, resulting in 6 possible positions for every deviant. This implicates, that the local probability of a first deviant is around 0.166, while the probability of a 6th deviant is 1, that is, predicable.

Altogether, the results of the studies presented above contributed to both the methodological and theoretical literature of vMMN. Our studies strengthened the notion, that vMMN and adaptation are separable processes. We tested three control paradigms with two relatively frequently used stimulus in vMMN research (tilted bars and windmill patterns). The most significant finding of Study I and Study II was that the deviant-minus-standard difference wave is not necessarily the consequence of vMMN. Based on our results, we assume that adaptation related neural mechanisms are sufficient to automatically detect changes in case of one dimensional changes. We hypothesize a hierarchical process in which vMMN is only elicited if adaptation related mechanisms cannot represent the changes. The results of Study III and Study IV demonstrated, that vMMN is sensitive to the allocation of spatial attention. The complex interaction of experimental variables manifested in our results draw attention to the importance of mapping those factors to enable the use of well designed, evidence based experimental protocols.

# Chapter 9: CONCLUSIONS

The aim of the present dissertation was to investigate basic properties of the visual mismatch negativity. The present results support and extend previous results in the literature. Our results supported the notion that the human brain is able to automatically detect changes in the visual environment. Based on the results of Study I and Study II, we assume that one uniform underlying mechanism that would generate vMMN does not exist and that instead there are separate mechanisms, depending on the circumstances/stimulation. We assume, that it is not computationally effective to build memory trace of a certain stimulus feature, when the same information is already present in the adaptational states of the efferent neurons. However, higher level regularities probably cannot be coded on the level of sensory neuronal adaptation, and thus, the presence of a memory comparison process is justifiable. This would explain the contrary results on the field of vMMN research.

The third and fourth studies of the thesis investigated the sensitivity of vMMN to the focus of spatial attention. In Study III low salience, offset stimulation was utilized and no modulatory effect of attention has been observed on vMMN. Although when the focus of attention was closer to the task-irrelevant sequence, vMMN was followed by the P3b component, reflecting a possible orientation of attention. In Study IV higher salience, traditional onset stimulation was used, and vMMN was only elicited in the attention close condition, followed by a P3b. We had no clear explanation for the contradictory results, but speculated, that for salient task-irrelevant stimuli a more efficient inhibitory activity was developed.

In summary, our studies contribute to the current knowledge on vMMN research, with important methodological and theoretical findings for future experiments.

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