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Domonkos File

Investigating the underlying mechanisms of visual mismatch negativity

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INVESTIGATING THE UNDERLYING MECHANISMS OF VISUAL MISMATCH NEGATIVITY

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1. Introduction

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).

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).

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. Kimura 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.

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, 2017; 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).

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). 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, 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).

The relationship of the adaptation and prediction theories has remained an unsettled issue, thus Thesis study I and II investigated it with the utilization of different control paradigms.

Since an important property of vMMN is its task-independence, 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 spatial distance between the primary task and the passive stimulus sequence varies greatly among studies, thus the effect of spatial attention on vMMN is an important research question.

The aim of Thesis study III and IV was to examine the effect of distance on the focus of spatial attention on a task-irrelevant sequence, either in case of relatively less (Study III) and more salient (Study IV) deviances.

2. Visual mismatch negativity (vMMN) for low- and high-level deviances: A control study (Thesis study I)[1]

The aim of our studies was to separate the effects of violating a sequential rule (genuine visual mismatch negativity; gvMMN) from the decreased activity in response to repeated stimuli (stimulus-specific adaptation; SSA) for simple and more complex stimuli. To accomplish this goal, different control procedures were applied with the aim of finding the correct control for vMMN studies. Event-related brain electric activity (ERPs) was measured in response to nonattended visual stimuli that were presented either in an oddball manner or in various control sequences. To identify the cortical sources of the different processes, the sLORETA inverse solution was applied to the average ERP time series. In Experiment 1, the stimuli were line textures, and the deviancy was different line orientations. SSA fully explained the deviant-related ERP effects (increased posterior negativity in the 105-190 ms range). In Experiments 2 and 3, windmill patterns were used. Infrequent windmill patterns with 12 vanes elicited gvMMN (posterior negativities in the 100-200 and 200-340 ms ranges), whereas in the case of the less complex (six vanes) stimuli, SSA explained the negative deflection in both latency ranges (178-216 and 270-346 ms). In Experiment 3, infrequent stimuli with six vanes elicited deviant-related posterior negativity within the sequence of less complex (four vanes) frequent patterns. We reconcile the discrepant results by proposing that the underlying processes of vMMN are not uniform but depend strongly on the eliciting stimulus and that the complexity difference between the infrequent and frequent stimuli has considerable influence on the deviant-related response.

[1] 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.

3. Automatic change detection in vision: Adaptation, memory mismatch, or both? Oddball and adaptation effects on event-related potentials (Thesis study II)[2]

In this study we compared the event-related potentials (ERPs) obtained in two different paradigms: a passive visual oddball paradigm and an adaptation paradigm. The aim of the study 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. In Experiment 1, participants were presented with different line textures. The frequent (standard) and rare (deviant) texture elements differed in their orientation. In Experiment 2, windmill pattern stimuli were presented in which the number of vanes differentiated the deviant and standard stimuli. In Experiment 1 the ERP differences elicited between the oddball deviant and the standard were similar to the differences between the ERPs to the nonadapted and adapted stimuli in the adaptation paradigm. In both paradigms the differences appeared as a posterior negativity with the latency of 120-140 ms. This finding demonstrates that the representation of a sequential rule (successive presentation of the standard) and the violation of this rule are not necessary for deviancy effects to emerge. In Experiment 2 (windmill pattern), in the oddball paradigm the difference potentials appeared as a long-lasting negativity. In the adaptation condition, the later part of this negativity (after 200 ms) was absent. We identified the later part of the oddball difference potential as the genuine visual mismatch negativity-that is, an ERP correlate of sequence violations. The latencies of the difference potentials (deviant minus standard) and the endogenous components (P1 and N1) diverged; therefore, the adaptation of these particular ERP components cannot explain the deviancy effect. Accordingly, the sources contributing to the standard-versus-deviant modulations differed from those related to visual adaptation; that is, they generated distinct ERP components.

[2] 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.

4. Automatic change detection and spatial attention: A visual mismatch negativity study (Thesis Study III)[3]

Visual mismatch negativity (vMMN) is the electrophysiological correlate of automatic detection of unattended changes in the visual environment. However, vMMNs' relatedness to spatial attention has not been explicitly tested. Thus, the aim of the study was to investigate the effects of spatial attention on the vMMN event-related potential component. To this end, participants were instructed to fixate and attend to task-related stimuli. In an oddball sequence, offset stimuli were applied, i.e., from time-to time, the two sides of permanently presented objects disappeared. Distance between the task-related and unrelated events resulted in the typical finding of spatial attention; the amplitude of the N1 component was larger at the shorter distance between the two kinds of events. VMMN was elicited by the deviant vanishing parts, with no reliable effect of distance between the task-field and vMMN-related stimuli. In terms of the difference potentials, vMMN was followed by a positive posterior component in the 270-330 ms range. This positivity was much larger when the task-field was close to vMMN-related stimuli. The reappearance of the vanishing parts was also investigated. The reappearance of the whole objects after a deviant offset elicited vMMN but only when the task-field was close to the oddball sequence. We concluded that 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 are registered only in the visual field close to the focus of attention.

[3] 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

5. Automatic detection of violations of statistical regularities in the periphery is affected by the focus of spatial attention: A visual mismatch negativity study (Thesis study IV)[4]

We investigated the effect of spatial attention on an event-related potential signature of automatic detection of violations of statistical regularities, namely, the visual mismatch negativity (vMMN). To vary the task-field and the location of vMMN-related stimulation, in the attentional field the stimuli of a tracking task with a steady and a moving (target) bar were presented. The target stimuli of the task appeared either relatively close or far from a passive (task-irrelevant) oddball or equiprobable sequence at the lower part of the screen. Stimuli of the oddball sequence were shapes tilted either 45° (standard, $p = 0.8$) or 135° (deviant, $p = 0.2$), while the equiprobable sequence consisted of additional three shapes with identical number of lines to the oddball stimuli. Deviant stimuli in close proximity to a continuously attended field elicited larger vMMN than similar stimuli farther away from the stimulus field. In the condition with a smaller distance between the field of the tracking task and the vMMN-related field, the deviant stimuli and the vMMN was followed by a posterior positivity. According to these results, spatial attention modulates vMMN and is capable of initiating further processing of the deviant stimuli.

[4] 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

6. 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. 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.

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. The result of Study

III 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).

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. Contrary to our hypothesis derived from the results of Study III, 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). We speculated that the more salient task irrelevant stimulation had a greater disturbing effect, resulted in more significant inhibitory processes applied on the stimulus sequence, which prevented the representation of the sequential regularities.

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).

7. References

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