

## COGNITIVE NEUROSCIENCE

# Does surprise enhancement or repetition suppression explain visual mismatch negativity?

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## Abstract

A long tradition of electrophysiological studies, using oddball sequences, showed that the neural responses to a given stimulus differ when their presentation occurs frequently (standards) as compared to rare, infrequent presentations (deviants). This difference, originally described in acoustic perception, can also be detected in the visual modality and is termed as visual mismatch negativity (vMMN). Also, a large number of studies detected the reduction of the neuronal response after the repetition of a given stimulus (repetition suppression – RS) and it was suggested that RS is the major mechanism of MMN, an explanation currently also supported by animal studies. However, human studies have proposed that a surprise-related response enhancement for the deviant stimuli might also underlie vMMN. Therefore, the aim of the current study was to disentangle which neural mechanism explains vMMN better: the surprise related response enhancement for the presentation of rare deviants or the RS related to the frequent presentation of the standards. Since the MMN depends strongly on the applied categories, we tested the neural mechanisms of vMMN for different stimulus categories (faces, chairs, real and false characters) using a visual oddball paradigm. We found significant vMMN for every stimulus category. Interestingly, the neural mechanisms behind vMMN were found to be category dependent (assuming no cross-adaptation effects): for faces and chairs it was largely driven by RS, whereas for real and false characters it was mainly due to surprise-related changes.

## Introduction

Neural responses to rare and frequently repeated stimuli deviate from each other, as revealed by the mismatch negativity in event-related brain potentials (ERP) for both acoustic and visual stimuli (Czigler *et al.*, 2004). Visual MMN (vMMN) is considered as an indicator of the discrepancy between the automatic representation of environmental regularities and their violations (Cammann, 1990; Stefanics *et al.*, 2014).

Repetition suppression (RS – Henson, 2003 for review see Grill-Spector *et al.*, 2006) has been suggested to explain vMMN. RS describes the phenomenon of neuronal response attenuation after repeated events. It is the traditional explanation of (v)MMN (Näätänen *et al.*, 1978) and is also termed as stimulus-specific adaptation (for review see Baldeweg, 2006; Nelken & Ulanovsky, 2007) or refractoriness (Schröger, 1997; Heslenfeld, 2003; Kimura, 2012). More recently, however, vMMN has been considered as a manifestation of active memory representations (Stefanics *et al.*, 2014). According to models of predictive coding (PC – see Friston, 2005), the brain actively generates predictions of its sensory inputs, using a generative model (Friston, 2012). Consequently, through hierarchical

memory representations, differences between predictions and the actual sensory input are computed and the (v)MMN would be a signal of these differences.

Typically, vMMN is identified in oddball paradigms, which consist of the presentation of a high probability (standard) stimulus intermixed with a low probability (deviant) stimulus. Recently, however, the so called “equiprobable” sequences (Jacobsen & Schröger, 2001; Jacobsen *et al.*, 2003) have been introduced to study vMMN (Kimura *et al.*, 2009). In these sequences, several stimuli are presented with the same probability as the deviants in common oddball sequences. It has been argued that the comparison of deviant responses embedded in the oddball and equiprobable conditions reveals a “genuine”, surprise related (v)MMN (Czigler *et al.*, 2002; Astikainen *et al.*, 2008). However, despite the existence of this “genuine” vMMN, other studies still suggest the contribution of RS to MMN as well (Kimura *et al.*, 2009; Li *et al.*, 2012; Astikainen *et al.*, 2013). Additionally, multi-unit and local field potential recording studies of non-human primates failed to show a surprise related response to the violations of regularities (Farley *et al.*, 2010; Fishman & Steinschneider, 2012; Kaliukhovich & Vogels, 2014).

Here we tested the neural mechanisms of vMMN elicited by different visual stimulus categories by comparing conventional oddball and equiprobable sequences (Kaliukhovich & Vogels, 2014). Our

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aim was to separate the potential vMMN effects that are due to RS from those related to surprise. We reasoned that the vMMN would be due to RS if the standards of the oddball sequences are significantly different from the responses within the equiprobable condition while it would be rather due to surprise enhancement if the deviant responses are significantly different from those in the equiprobable condition (Kaliukhovich & Vogels, 2014).

## Material and methods

### Participants

Twenty-one healthy subjects (eight male; two left-handed, mean age ( $\pm$ SD): 23.5 (0.68) years) participated in the experiment after giving written, informed consent in accordance to the Declaration of Helsinki. The protocols were approved by the Ethical Committee of the Friedrich Schiller University Jena. No participant had a history of neurological or psychiatric illness and all had normal or corrected to normal vision.

### Stimuli and procedure

Stimulus presentation was controlled via MATLAB R2014a (The Mathworks, Natick, MA, USA), using Psychtoolbox (Version 3.0.12). From a total 1842 grey-scale, digital photos of the 10 different stimulus categories, one image per category was randomly selected for each participant (396 full-frontal Caucasian adult faces (50% of female), similar to the face stimuli of Kovács *et al.* (2012, 2013) with mean luminance of 36.2 cd/m<sup>2</sup>; 32 non-frontal chairs with mean luminance of 35.13 cd/m<sup>2</sup> – Kovács *et al.* (2013); 241 false characters (mean luminance: 11.90 cd/m<sup>2</sup>); 281 real characters (mean luminance: 7.17 cd/m<sup>2</sup>); 183 birds (mean luminance: 13.83 cd/m<sup>2</sup>); 127 buildings (mean luminance: 23.84 cd/m<sup>2</sup>); 91 cars (mean luminance: 17.06 cd/m<sup>2</sup>); 32 fruits (mean luminance: 17.36 cd/m<sup>2</sup>); 229 objects (mean luminance: 16.61 cd/m<sup>2</sup>); 230 bodies (mean luminance: 26.27 cd/m<sup>2</sup>)). Please note that altogether only 10 images were used in the experiment, however the images were different for each participant, as they were randomly selected from the above described, larger stimulus pool. Faces and chairs were placed behind a circular mask. Bird, chair, fruit, car, body and object images were collected from the public domain of the World Wide Web. Real and false characters were identical to those of the study by Grotheer & Kovács (2014). False characters were scrambled versions of the real characters (1–4 components of a particular letter were moved randomly to a different position in a way similar to Grotheer & Kovács (2014). The stimuli were centered on a uniform grey background (17.11 cd/m<sup>2</sup>) and presented using a 19" CRT monitor (60 Hz refresh rate) from a 90 cm viewing distance. Stimulus size was 3° in radius. A chin rest was used to diminish head movements during data recording.

The experimental design was similar to what has previously been used to evaluate the presence of genuine surprise related responses to deviants in visual oddball sequences (Kaliukhovich & Vogels, 2014). Four stimulus categories were used (faces, chairs, real and false characters) based on prior neuroimaging results testing the effect of statistical probability on RS (faces: Grotheer *et al.*, 2014; Kovács *et al.*, 2012, 2013; Larsson & Smith, 2012; chairs: Kovács *et al.*, 2013; real and false characters: Grotheer & Kovács, 2014). The stimulus categories were arranged into two pairs (1. Faces vs. Chairs; 2. Real vs. False Characters) that were then used in the oddball sequences.

The stimuli were shown with specific stimulus presentation probabilities under five experimental conditions. Five blocks of 100 trials were administered per experimental condition, resulting in a total of 25 blocks and in approximately 45 min total recording time. The order of the blocks was counterbalanced across subjects. Two consecutive blocks were never taken from the same experimental condition. Two of the five experimental conditions are typical oddball sequences, where the two stimuli from a pair, for example *face1* and *chair1*, are randomly interleaved and displayed with probabilities of 0.9 and 0.1, respectively (Fig. 1). In the other two conditions the stimulus probability was reversed; following the given example that is, *face1* and *chair1* were shown with probabilities of 0.1 and 0.9, respectively. Therefore, both stimuli of a given category-pair were presented frequently (hereby designated to as a standard) as well as rarely (deviant). The number of consecutive standards was pseudo randomized between 2 and 5. In the fifth condition, the same stimuli that were presented in the oddball sequences (e.g. *face1*, *chair1*, *character1* and *falsecharacter1*) were interleaved randomly with six other stimuli from six different categories (birds, bodies, buildings, cars, fruits, and objects). In this condition the probability of each ten stimulus category was identical (i.e. 0.1). The face, chair, real and false character stimuli when presented in this "equiprobable" condition are further referred to as a control. In total, there were five possible experimental conditions: four oddball sequences (two reversed oddball sequences – one for each category pair) and one equiprobable sequence. Stimuli were presented for 350 ms each, separated by a random inter-trial interval (varied between 500 and 700 ms in 50 ms steps). The different sequences were separated by 1 s pause interval.

To ensure that subjects were attending the stimuli, a simple reaction time task was applied. The target was a red cross (16.4 cd/m<sup>2</sup>) with a shorter (0.13°) and a longer (0.3°) arm. The cross was continuously presented at the centre of the screen and its configuration was randomly changed in every 5–15 trials in a way that the position of the shorter and longer arms was exchanged. Participants were instructed to detect these changes and to reply as quickly (with a maximum response time-window of 1050 ms) and correctly as possible.

### ERP recording

The electroencephalographic (EEG) signal was recorded with silver Ag/AgCl electrodes using a 64-channel Biosemi Active II system (Biosemi, Amsterdam, The Netherlands). The electrodes were arranged according to the extended 10/20 system at the scalp positions Fp1, FT9, AF3, F1, F3, F5, F7, FT7, TP9, FC3, FC1, C1, C3, C5, T7, TP7, PO9, CP3, CP1, P1, P3, O9, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, FT10, AF4, Afz, Fz, F2, F4, F6, F8, FT8, TP10, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, PO10, CP4, CP2, P2, P4, O10, P8, P10, PO8, PO4 and O2. Note that the Biosemi system uses a combined ground/reference (CMS/DRL) circuit (cf. to <http://www.biosemi.com/faq/cms&drl.htm>). The data was digitally transformed to an average reference using EEGLAB (Delorme & Makeig, 2004), a signal processing toolbox for MATLAB. Horizontal electro-oculograms were recorded from the outer canthi of the eyes, while vertical electro-oculograms were monitored bipolarly from electrodes above and below the left eye. The signal was digitalized at a 512 Hz sampling rate (bandwidth: DC to 120 Hz) and filtered off-line with: 1. a 12 dB/octave Butterworth high pass-filter with a cut-off frequency of 0.1 Hz to remove DC drifts; 2. a digital 25 Hz 24 dB/octave low-pass filter, using ERPLAB (Lopez-Calderon & Luck, 2014). The EEG was

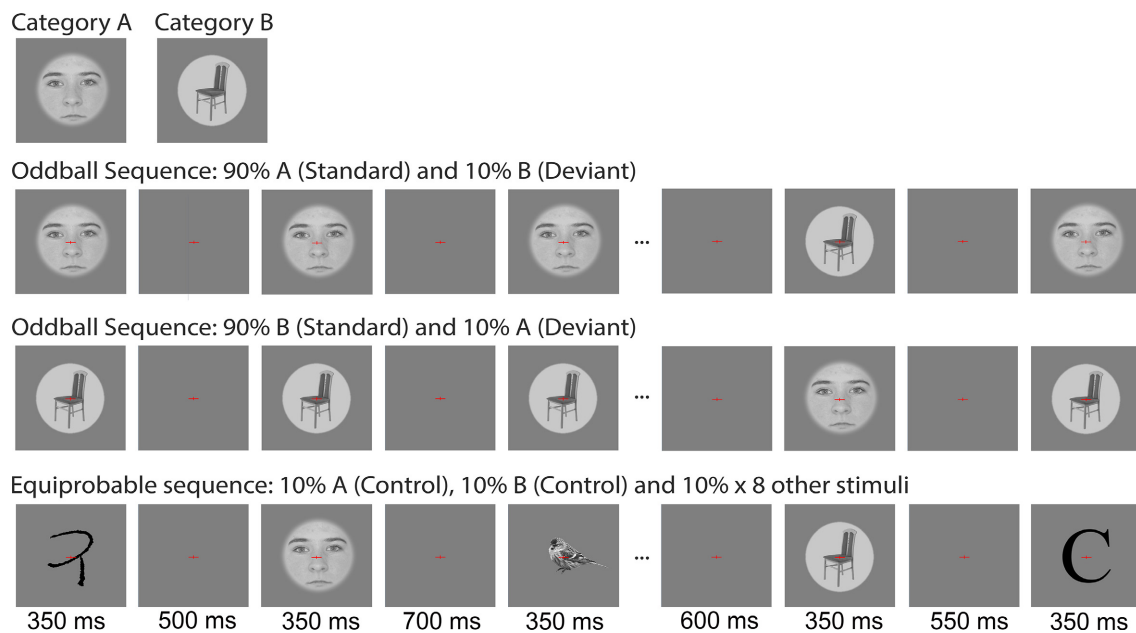


FIG. 1. Experimental design and conditions. Two images (A and B) were selected and displayed in oddball and reversed oddball sequences for each category pair (i.e. Faces vs Chairs and Characters vs False Characters), where each stimulus was presented either frequently (probability 0.9, standard) or rarely (probability 0.1, deviant). In addition, there was an equiprobable sequence with 10 different stimuli (including the 4 stimuli used in the oddball sequences and 6 other stimuli from various categories) presented with the same probability (0.1).

segmented off-line into 950 ms long epochs (100 ms pre-stimulus interval). Trials containing an amplitude change exceeding  $\pm 70 \mu V$  on any channel were rejected (this criterion was applied to all trial types and electrodes including the electro-oculogram recording ones). On average 21% of all the non-target trials were used for further analysis (the average trial amount for the different stimulus conditions was 322, 36 and 36 for all standards, deviant and control, respectively. Note that the number of trials was similar for the four probe-stimulus categories). The epochs were averaged for each stimulus condition (standard, deviant and control), stimulus category, recording channel and participant separately. Note that all standard stimuli were included in the final analysis. To identify change-related activities, the ERPs evoked by standard stimuli in the oddball sequences were subtracted from the ERPs elicited by the deviant stimuli in the reversed oddball sequences (Deviant-minus-Standard). The same procedure was used to evaluate differences between control and standard stimuli (Control-minus-Standard), testing for repetition related response reductions, as well as for the differences between deviants and controls (Deviant-minus-Control), testing for surprise related response enhancements. Note that only physically identical stimuli, i.e. from the same category were compared in the role of deviant, standard and control conditions, meaning that the described comparisons are performed separately for the four stimulus categories.

### Analysis and comparisons

To characterize the time-course of the vMMN objectively, we performed a point-by-point *t*-test (criterion: a cluster of at least two neighboring electrodes with a minimum of 20 consecutive data points, i.e. corresponding to a 40 ms time segment with a significant ( $P < 0.01$ ) difference) in a series of pair-wise comparisons between the different stimulus conditions (i.e. Deviant vs. Standard, Control vs. Standard and Deviant vs. Control) for each subjects separately

(Thorpe *et al.*, 1996). We carried out this analysis over the lateral and posterior recording channels (TP9, T7, TP7, PO9, CP3, CP1, P1, P3, O9, P7, P9, PO7, PO3, O1, Oz, POz, Pz, CPz, TP10, T8, TP8, PO10, CP4, CP2, P2, P4, O10, P8, P10, PO8, PO4 and O2), typically reflecting functions of the temporal and occipital visual cortexes (Sams *et al.*, 1997). While, prior MMN studies typically analyzed only certain, pre-defined time windows over a few electrodes, in the current study we included the entire ERP curve to test the category specificity of the vMMN in detail and in a hypothesis-free manner. Time by electrode statistical plots are used to present the results of this analysis, in which significant differences between the relevant conditions are color-coded as a function of the amplitude differences (Jacques *et al.*, 2007).

In this analysis a negative value at a certain time-point for the deviant-standard comparison indicates for example that the standard leads to a more negative voltage value than the deviant (Stand > Dev), while a positive value indicates that the deviant leads to a more positive value than the standard (Dev > Stand).

To determine the portion of the conventional vMMN that is due to repetition suppression or surprise enhancement, we calculated the percentage of significant difference present in the statistical plots of the conventional vMMN for the Control-Stand and Dev-Control conditions for each category separately. For this we considered the significant differences present in the statistical plots of the conventional vMMN as 100% and calculated the percentage of significant MMN time points which were overlapping with the Control-Stand (RS) and with the Dev-Control (surprise or “genuine” vMMN) conditions separately. Additionally, to quantify the dependence of the conventional vMMN on these effects, we correlated the wave differences of the different effects (Dev-Stand, Control-Stand and Dev-Control) with each other for each category separately. Note that the correlations of conventional MMN with Control-Stand and with Dev-Control were only performed for the time-windows in which the conventional vMMN could also be explained by RS or surprise

(genuine vMMN) or in other words, when the conventional vMMN was overlapping with RS (Control-Stand) or with surprise effects (Dev-Control).

An additional analysis was performed to evaluate how RS develops over time for the different categories. For this analysis, instead of including every standard stimuli in the calculation only the last standard of a row was included. As the number of standards varied from 2 to 9 in a row, only those with more than 3 standard trials were included in this analysis. This way, we could balance the number of standard (41) and deviant (36) stimuli better.

## Results

### Behavior

Participants needed on average 661 ms ( $\pm$ SD = 103 ms) to detect the configuration change of the central cross with an average accuracy of 77% ( $\pm$ SD = 24%) and there was no difference in accuracy between experimental conditions ( $F_{4,80} = 1.26$ ,  $P = 0.29$ ,  $\eta^2 = 0.06$ ). However, reaction times were significantly lower for the oddball and reversed oddball sequences of the real and false characters pair when compared to faces and chairs oddball and reversed oddball sequences as well as compared to the equiprobable sequence ( $F_{4,80} = 14.38$ ,  $P < 1e-6$ ,  $\eta^2 = 0.42$ ): equiprobable (Fisher LSD *post hoc* test:  $P < 1e-5$ ), oddball (Fisher LSD *post hoc* test:  $P < 0.001$ ); reversed oddball (Fisher LSD *post hoc* test:  $P < 0.01$ ). This difference might be explained by the fact that the characters were black, while the other stimulus types included different greyscale values as well. Furthermore, the reaction times of the equiprobable conditions were significantly longer when compared to the reversed oddball condition of the faces vs chairs stimulus pair (Fisher LSD *post hoc* test:  $P = 0.04$ ).

### ERP data

#### Event-related potentials

All stimuli elicited a large positive component in the 95–135 ms time window (P1) with a peak occurring at around 115 ms (Fig. 2). Other components such as the N1/N170 and the P2 could also be identified on the ERPs (Fig. 2). We observed that differences in amplitude between the standard, deviant and control were time and category dependent. Also, it was possible to detect strong differences between the deviant and standard conditions for all the four categories suggesting the existence of conventional vMMN in our paradigm for every stimulus category.

#### Conventional vMMN (Deviant-Standard)

We observed significant deviant-standard differences within the 139–650 ms and 377–623 ms time-windows for faces and chairs, respectively (Fig. 3). The analysis of these difference waves for faces revealed that ERPs are more negative for the deviants when compared to the standards. Note, however that a few channels showed a positive amplitude difference (CP3, CP1, CP2 and CPz) within the 139–300 ms time-window, which is due to a more positive signal for deviants when compared to standards. Yet within the 350–600 ms time-window 11 electrodes show an opposite direction, positive vMMN for faces. For chairs the deviants elicited elevated responses when compared to standards within the same time-windows.

False and real characters also showed a significant vMMN but within slightly different time-windows, between 156–787 ms and 147–630 ms, respectively (Fig. 4). Both real and false characters exhibited a combination of positive and negative amplitude differences. Specifically, negative vMMN amplitudes dominated the earlier while positive amplitude differences were more pronounced in

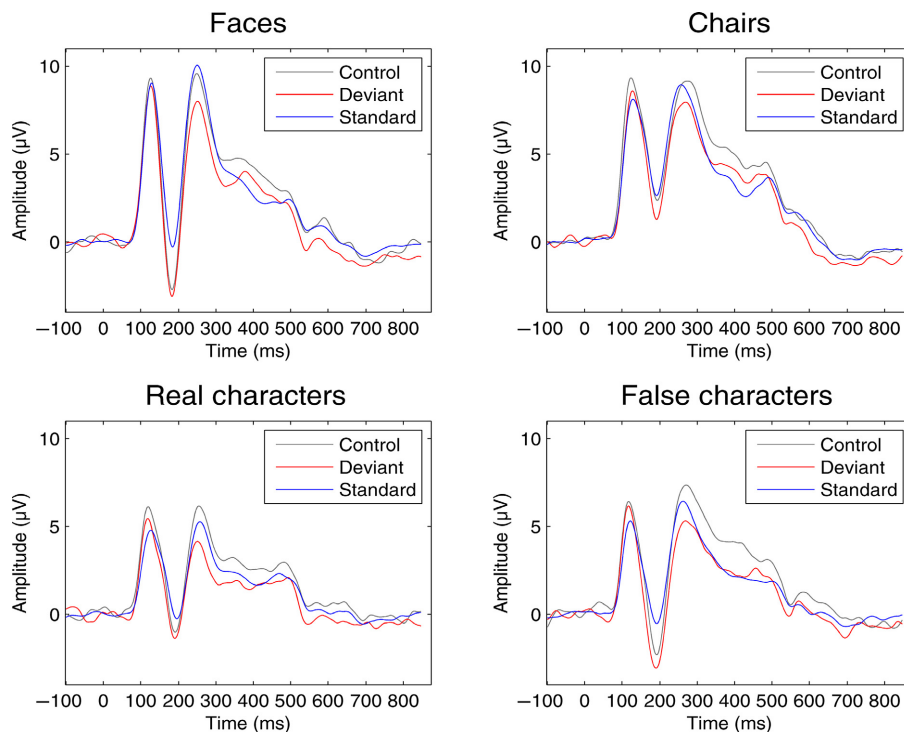


FIG. 2. Group average event-related potentials at PO8 electrode plotted from -100 to 850 ms for standard, deviant and control conditions of the 4 probe-stimuli categories.



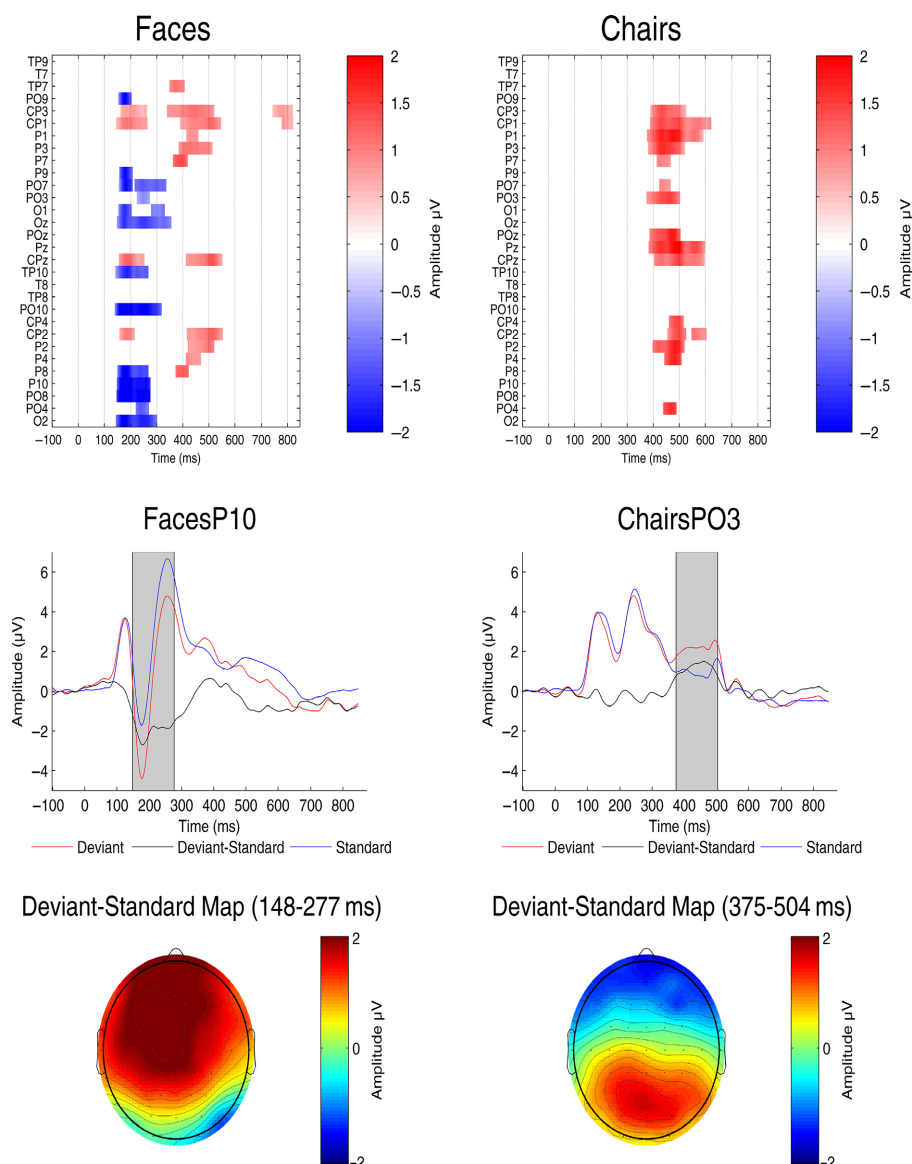


FIG. 3. Conventional vMMN – Differences between deviant and standard stimuli for faces (left) and chairs (right). Top: time by electrode statistical plots (color-coded as a function of the amplitude of ERP difference). Bottom: representative ERPs at channel P8 and PO3 electrodes with the highlighted (grey region) significant differences between stimulus conditions for faces and chairs respectively.

the later time-window (Fig. 4). Importantly, electrodes that showed a positive vMMN in the later phase did not show a negative vMMN in the early phase and vice-versa. Essentially, the same results were obtained when using only the last standards for the comparisons. Please note that in this case only the last of a continuous row of standard stimuli was chosen for the analysis, meaning that 41 standard stimuli were compared to the 36 deviant stimuli. The only difference between the results of this and the conventional analysis when every standard stimulus was included was that for false characters no significant conventional vMMN effect was observed for the former case.

#### Suppression (Control-Standard)

We observed significant differences associated with repetition related response suppression (RS) between the control and the standard conditions for every stimulus category (Figs 5 and 6). Significant RS was found for faces between 146 to 848 ms; for chairs between

111–556 ms; for real characters from 365 to 440 ms and for false characters between 92–555 ms.

Importantly, the earliest RS effect for faces had a similar time-window to the amplitude difference observed for the conventional vMMN effects, i.e. for the differences between deviants and standards. This suggests that the early vMMN effect, for faces is mainly driven by RS. It is essential to note that almost all the electrodes (P8, PO8, P10, O2, PO10, TP10, Oz, O1, PO7, P9, PO9, CP1 and CPz) that showed a significant RS effect, also showed a significant vMMN effect within the same time-window. Moreover, the scalp distribution presented of the Dev-Stand (Fig. 3) and the Control-Stand (Fig. 5) comparisons are very similar for faces at around 200 ms, suggesting further that the conventional vMMN for faces is due to RS effects.

Similarly, the RS obtained for chairs can also explain the observed vMMN effects of the PO3, P4, POz, PO4, P1, P3 and P7 electrodes. Regarding the character stimuli, we observed that the conventional vMMN effects can only be explained by RS at a few

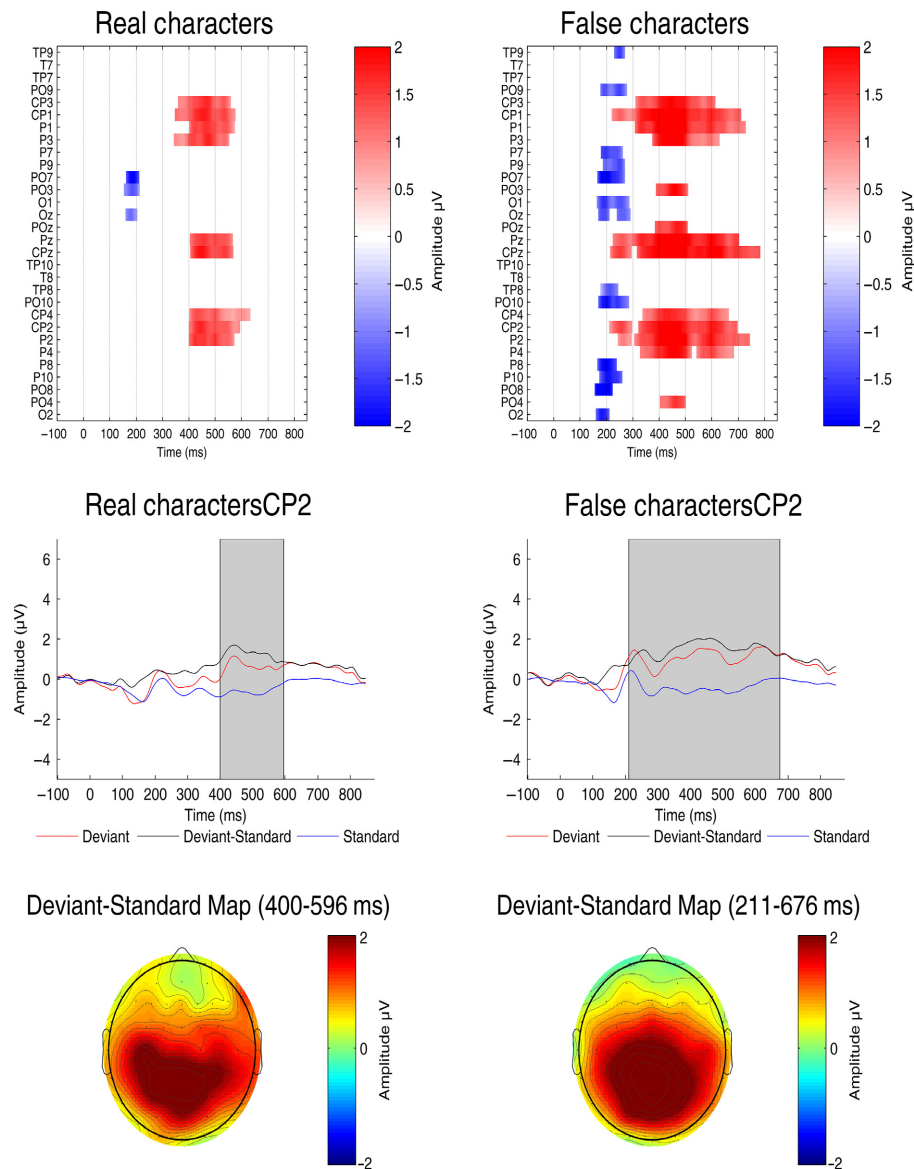


FIG. 4. Conventional vMMN – Differences between deviant and standard stimuli for real (left) and false (right) characters. Top: time by electrode statistical plots (color-coded as a function of the amplitude of ERP difference). Bottom: representative ERPs at channel P3 and P1 electrodes with the highlighted (grey region) significant differences between stimulus conditions for real and false characters respectively.

electrodes (Fig. 6) and therefore no example ERP is presented here on Fig. 6.

When the last standards (i.e. only the last standard of a row was chosen for analysis, resulting in the inclusion of 41 standards, where 41 is similar to the number of deviants – 36) were analysed the results were similar except for false characters that did not show any significant effect.

#### Surprise enhancement (Deviant-Control)

We only found significant deviant-control differences for chairs (see Fig. 7) and for characters in the form of positive and negative differences within the 362–717 ms and the 207–655 ms time-windows for real and false characters, respectively (Fig. 8).

Crucially, the majority of the significant electrodes sites and time-ranges with positive amplitude differences of the deviant vs control

comparison (Fig. 8) are comparable to the conventional vMMN effects (Fig. 4) for real and false characters. This suggests that most of the vMMN effects for characters can be explained by a surprise related response enhancement for the deviant stimuli, in other words a genuine vMMN.

#### Relations of vMMN with RS and surprise

The detailed comparison of the conventional vMMN with the RS and surprise related differences revealed that more than 40% of the vMMN effects can be explained by RS for faces and chairs (Table 1) and the correlation of these two effects is strong and significant. Note that the percentage refers to the amount of significant conventional MMN (i.e. the difference between Stand and Dev) time points which are overlapping with the Control-Stand (RS) or with the Dev-Control (surprise or “genuine” vMMN) conditions. On

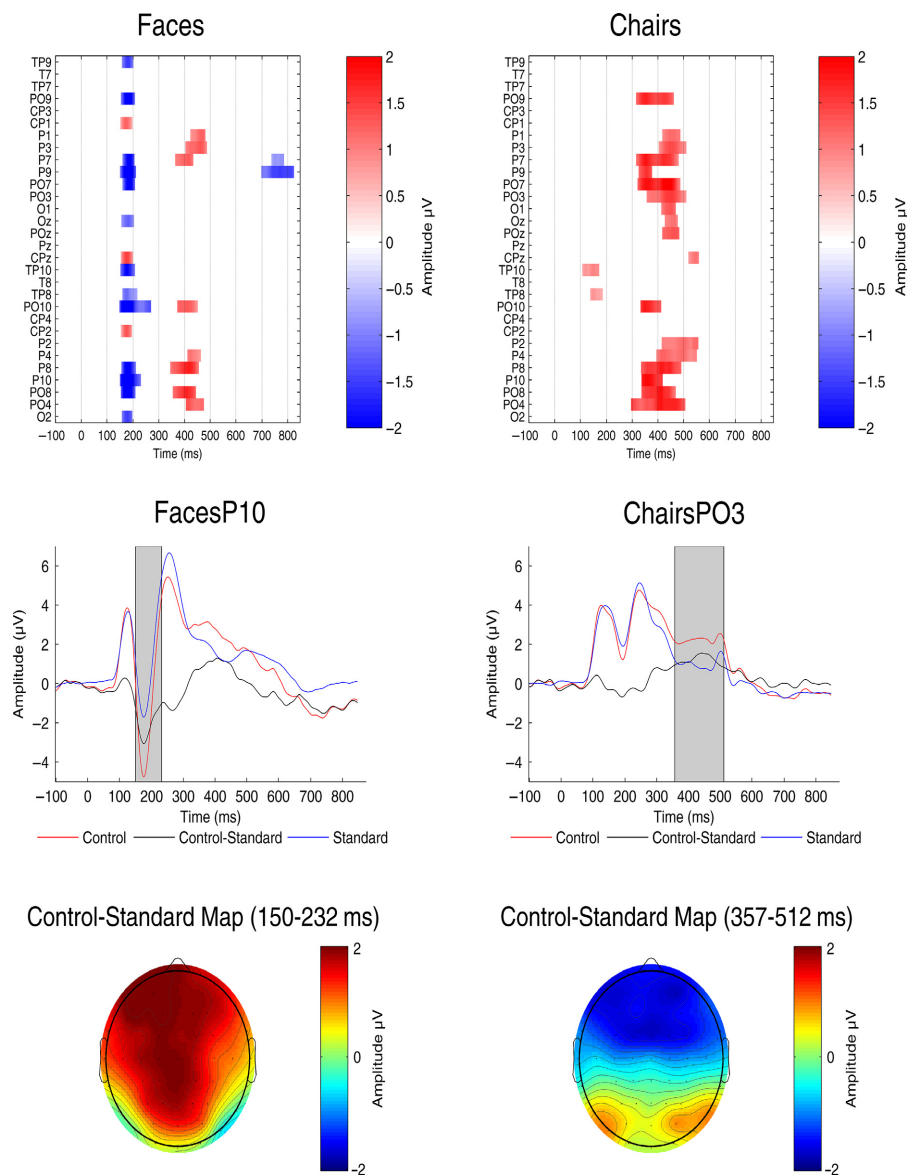


FIG. 5. Repetition Suppression – Differences between control and standard stimuli for faces (left) and chairs (right). Top: time by electrode statistical plots (color-coded as a function of the amplitude of ERP difference). Bottom: representative ERPs at channel P8 and PO3 electrodes with the highlighted (grey region) significant differences between stimulus conditions for faces and chairs respectively.

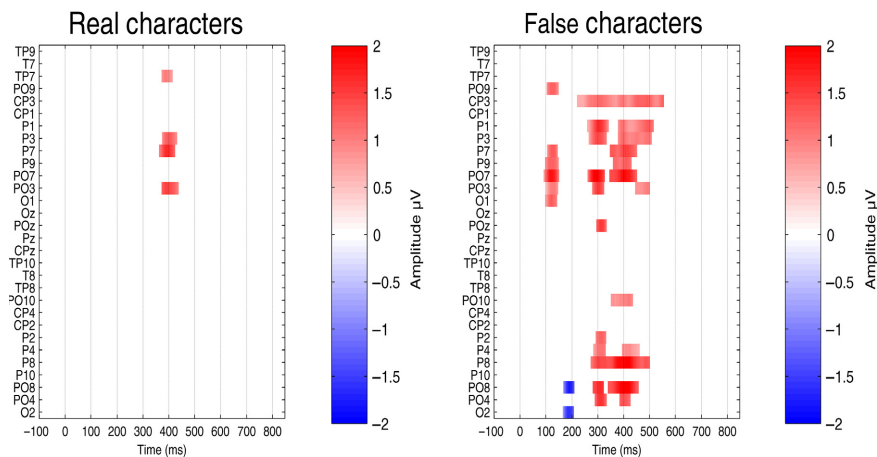


FIG. 6. Repetition Suppression – Differences between control and standard stimuli for real (left) and false (right) characters. Time by electrode statistical plots (color-coded as a function of the amplitude of ERP difference).

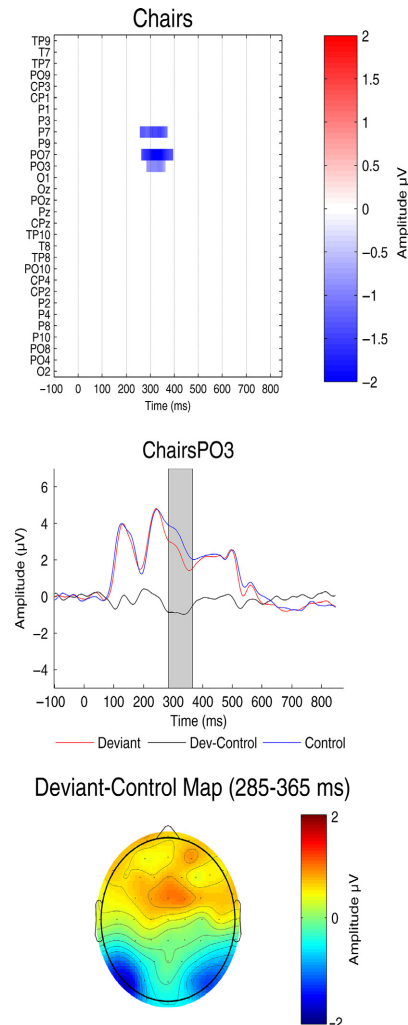


FIG. 7. Surprise Effect – Differences between deviant and control stimuli for chairs. Top: time by electrode statistical plots (color-coded as a function of the amplitude of ERP difference) for chairs. Bottom: representative ERPs at channel PO7 electrode with the highlighted (grey region) significant differences between stimulus conditions.

other hand, the vMMN that was observed for character stimuli overlapped more with surprise effects (Table 1). In addition, the vMMN of real characters also overlapped with some RS related effects. However, the correlation of the conventional vMMN with RS was not significant. Interestingly, false characters showed high correlation between RS and surprise effects as well.

Overall, the separate analysis of the last standard stimuli revealed the same results with exception of false characters (for which no vMMN was observed).

Altogether, these results support further the conclusion that while the conventional vMMN for faces and chairs is mostly due to RS, it is dominantly due to surprise for real and false characters, emphasizing the category specificity of the effect.

## Discussion

We found that the neural mechanisms that underlie the conventionally observed vMMN effects are stimulus category dependent. While vMMN is driven by repetition related RS for faces and chairs, it is mostly due to surprise-related response enhancement for real and false characters.

Previous (v)MMN studies using equiprobable control conditions, similar to the one of the present study have already suggested that the differences between deviant and standard stimuli are based on stimulus-specific adaptation processes (for review see Khouri & Nelken, 2015). Kaliukhovich & Vogels (2014) suggested that the inferior temporal cortex of the macaques boost activity to the deviants without a surprise related response for different stimulus categories, including faces. Similarly, our results show the complete lack of surprise related response in the conventional vMMN for faces and chairs. Furthermore, the neural contribution of repetition related RS to vMMN was present, although to a different degree, for every stimulus category. This is in agreement with previous studies which revealed that the vMMN effects elicited by facial expressions are based on stimulus-specific adaptation (Li *et al.*, 2012; Astikainen *et al.*, 2013). Unfortunately, Kaliukhovich & Vogels (2014) did not test for differences between the different stimulus categories, presenting only their results for the average of different categories. In the auditory domain, however, other animal studies showed no surprise related response to the violations of regularities in either rats (Farley *et al.*, 2010) or monkeys (Fishman & Steinschneider, 2012).

In humans, Kimura *et al.* (2009) presented bars with different visual angles to test for vMMN. They found that the vMMN, driven by surprise enhancements, appeared only within the 200–250 ms time-window while an earlier effect was driven by RS. This points to the involvement of two distinct neural mechanisms in vMMN: repetition and surprise related responses, acting within different time-windows. This conclusion is in agreement with our findings for real and false characters, where we found the contribution of the two mechanisms similarly. It is worth noting that, the character stimuli of the current study (simple, high-contrast shapes) are more similar to the 2D black bars used by Kimura *et al.* (2009) than to greyscale images of chairs and faces, which are more complex and are also commonly associated with a third dimension (Todd, 2004). Thus, the possibility that the dimensional representation nature or stimulus complexity influences vMMN should not be excluded.

Previously, Czigler *et al.* (2002) and Astikainen *et al.* (2008) could show genuine vMMN, i.e. surprise related response differences. The stimuli used in these two studies were simple geometric forms (colored vs. black vertical square-wave gratings – Czigler *et al.*, 2002; bars with changing orientation – Astikainen *et al.*, 2008). However, Kimura *et al.* (2009) also used bars with different orientations as stimuli and in addition to the genuine vMMN also found RS related differences. It is important to note, however, that the Czigler *et al.* (2002) and Astikainen *et al.* (2008) studies analyzed differences between the deviant and control conditions only. In other words no analysis was performed to exclude repetition related RS effects by calculating the difference between control and standard, which might therefore have also explained some vMMN effects in those studies.

Interestingly, our results indicate that the vMMN for real and false characters is mainly explained by surprise related differences. A recent study (Sulykos *et al.*, 2015) also tested vMMN effects in an oddball paradigm for a familiar (N) and an unfamiliar letter (H; the mirrored version of the familiar ones). The results from this study indicate that vMMN is sensitive to the familiarity in a way that the peak latency of vMMN is higher for the familiar letter, contrary to what we have found for real and false characters. Importantly, the compared latencies between the two stimulus types were only at 140 ms and 130 ms for familiar and unfamiliar stimuli in the same study, respectively. Furthermore it is visible on the Fig. 1 of the Sulykos *et al.* (2015) study that the amplitude differences between deviants and standards are higher for the unfamiliar as



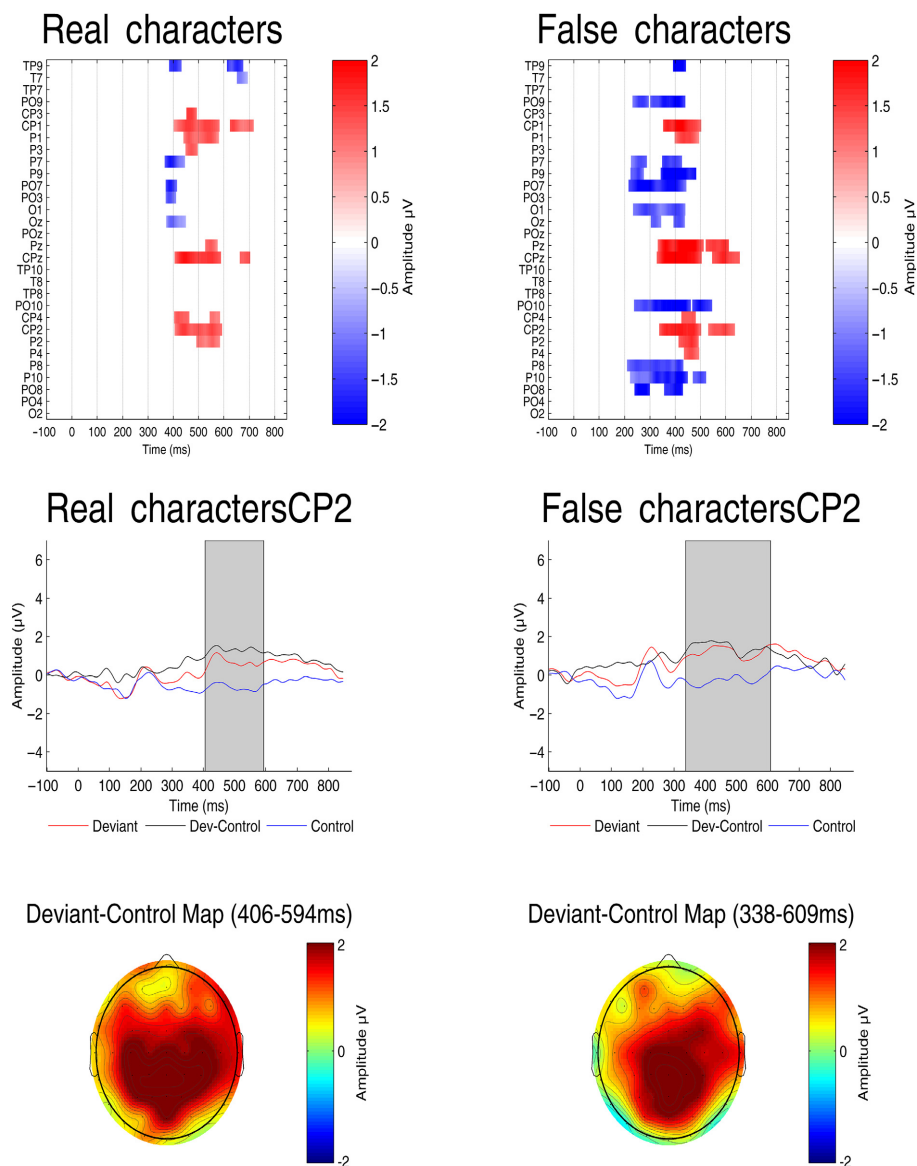


FIG. 8. Surprise Effect – Differences between deviant and control stimuli for real (left) and false (left) characters. Top: time by electrode statistical plots (color-coded as a function of the amplitude of ERP difference). Bottom: representative ERPs at channel P3 and P1 electrodes with the highlighted (grey region) significant differences between stimulus conditions for real and false characters respectively.

TABLE 1. Percentages and correlations of vMMN with RS and surprise

Comparison		Faces, %	Chairs, %	Real characters, %	False characters, %
All standards	MMN & RS	41.03 ( $R = 0.9$ ; $P = 0.01$ )	51.36 ( $R = 0.89$ ; $P = 0.02$ )	2.31 ( $R = 0.16$ ; $P = 0.39$ )	15.97 ( $R = 0.9$ ; $P = 1e-3$ )
	MMN & Surprise	0	0	42.44 ( $R = 0.87$ ; $P = 7e-7$ )	24.61 ( $R = 0.82$ ; $P = 3e-6$ )
Last standards	MMN & RS	31.08 ( $R = 0.93$ ; $P = 1e-5$ )	41.18 ( $R = 0.77$ ; $P = 0.15$ )	2.55 ( $R = 0.11$ ; $P = 0.6$ )	0
	MMN & Surprise	0	0	47.62 ( $R = 0.88$ ; $P = 6e-5$ )	0

compared to the familiar stimuli within the 200–300 ms and within 500–600 ms. Nevertheless, our results point to an overall larger vMMN effect for false as compared to real characters, even for earlier time-windows. The difference between this and prior studies might be explained however by the different tasks and paradigms. In the current study participant’s task was to detect changes in a centrally presented red cross and the stimuli were presented centrally behind the cross. Sulykos *et al.* (2015) divided the screen into two halves with an upper part (where the attention of the participants was

directed by a video game) and a lower part (where multiple stimuli were displayed). Therefore such differences in visual stimulation and attentional demands can explain the different results. It is well-known that stimulus luminance affects ERP waves. In addition, drastic luminance changes were also directly related to attentional modulations (Wijers *et al.*, 1997). Although the current experiment includes inherent differences of luminance, due to the different stimulus category sets, the performed analysis only compared ERP waves that were obtained for the same stimulus

categories. Therefore luminance differences are unlikely to affect our results. Yet, it is also possible that luminance differences between the character and other stimulus categories might have induced a surprise effect in the control, equiprobable blocks. However, if that was the case there would have been a similar response for the deviant and control conditions, leading to no differences between them. In other words, assuming that the same surprise based mechanisms are activated in the deviant and the control conditions there should be no or only a small difference between these two conditions. However, as our results show very strong differences between deviants and control for both character types, the role of different luminance of the stimuli for the control condition can be excluded.

There are a few experimental constraints related to our paradigm. One is related to the reduced number of trials for the deviant and control conditions, driven by the low probability (10%) of presentation of these conditions, the existence of four stimulus categories and of the target trials which are not used in the final analysis. Second, a cross-adaptation between different elements of the equiprobable sequence can theoretically also occur. This study assumes that there is no such cross-adaptation and therefore the performed comparisons are useful to identify the mechanisms behind vMMN. Yet, if there is some cross-adaptation the results might be explained by the sharpness of the neural tuning for the different stimulus categories (Li *et al.*, 1993; Wiggs & Martin, 1998).

Further, vMMN experiments ideally should include a control for attentional processing of the background stimuli to determine how much attention remains to process the stimuli and to verify that vMMN occurs pre-attentively or unintentionally (Sulykos *et al.*, 2015). Yet, the vast majority of the vMMN experiments adopt a target task, similarly to the one of the current study (e.g. Stefanics *et al.*, 2011).

Importantly, vMMN studies usually show late, parietal, positive effects (LPPs) which may reflect other processes, connected to attentional shifting or updating (for review see Morlet & Fischer, 2014).

It is possible that the overall early vMMN and RS effects for faces are related to the early face-sensitivity of the electrophysiological response (Linkenkaer-Hansen *et al.*, 1998; Itier & Taylor, 2002) and to a stronger N170 component for faces as compared to other stimulus categories (Bentin *et al.*, 1996; Carmel & Bentin, 2002). The relationship of the face sensitive N170, its category specific adaptation (Kovács *et al.*, 2006) and the face sensitivity of the currently observed RS in oddball paradigms will require further studies.

In conclusion, we observed that different stimulus categories lead to vMMN, but the underlying neural mechanisms are different: repetition related RS for faces and chairs, whereas surprise-related changes are more dominant for real and false characters.

## Conflicts of interest

The authors declare no competing financial interests.

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## Abbreviations

EEG, electroencephalography; ERP, event-related potential; fMRI, functional magnetic resonance imaging; PC, predictive coding; RS, repetition suppression; vMMN, visual mismatch negativity.

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