

Brain activity from stimuli that are not perceived: Visual mismatch negativity during binocular rivalry suppression

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Abstract

Predictive coding explains visual perception as the result of an interaction between bottom-up sensory input and top-down generative models at each level of the visual hierarchy. Evidence for this comes from the visual mismatch negativity (vMMN): a more negative ERP for rare, unpredictable visual stimuli—deviants, than for frequent, predictable visual stimuli—standards. Here, we show that the vMMN does not require conscious experience. We measured the vMMN from monocular luminance-decrement deviants that were either perceived or not during binocular rivalry dominance or suppression, respectively. We found that both sorts of deviants elicited the vMMN at about 250 ms after stimulus onset, with perceived deviants eliciting a bigger vMMN than not-perceived deviants. These results show that vMMN occurs in the absence of consciousness, and that consciousness enhances the processing underlying vMMN. We conclude that generative models of visual perception are tested, even when sensory input for those models is not perceived.

Descriptors: Visual mismatch negativity (vMMN), Binocular rivalry, Prediction, Prediction error, Visual consciousness, ERPs

How do we see? A recent, popular theory, predictive coding, states that we make predictions about upcoming sensory input based on past experience and context, constructing a generative model of the sensory environment that we then perceive and become conscious of (Arnal & Giraud, 2012; Clark, 2013; Friston, 2010). Specifically, top-down neural signals transmit the prediction from a higher to a lower brain area in the visual hierarchy, and if the prediction matches the sensory input, then the sensory input is explained away; if the prediction does not match the sensory input, bottom-up neural signals transmit the mismatch or discrepancy between the prediction and sensory input—the prediction error, from a lower to a higher brain area in the visual hierarchy (Barlow, 1961; Mumford, 1992; Rao & Ballard, 1999). When the prediction error is sufficiently minimized, that is, when the sensory input is explained away by the model, the perceptual problem is solved and we perceive the generative model (Friston & Kiebel, 2009; Schröger et al., 2014).

One electrophysiological brain signature of predictive coding is the visual mismatch negativity (vMMN; Kimura, 2012; Stefanics, Kremláček, & Czigler, 2014; Winkler & Czigler, 2012). vMMN is a negative-going component of ERPs, it has a posterior scalp distribution, it occurs between 150 and 400 ms after stimulus onset, and it is typically revealed by the oddball paradigm: a rare visual stimulus (i.e., a deviant) is randomly and unpredictably presented in a sequence of frequent, predictable visual stimuli (i.e., the standards; Jack, Roeber, & O'Shea, 2015; Kimura, Katayama, Ohira, & Schröger, 2009; Müller, Widmann, & Schröger, 2013). vMMN is considered a brain signature of predictive coding because the regularity of the standard establishes a prediction that is tested and violated by the deviant (Kimura, 2012; Stefanics et al., 2014; Winkler & Czigler, 2012; for auditory MMN, see Garrido, Kilner, Stephan, & Friston, 2009; Wacongne, Changeux, & Dehaene, 2012). An everyday example of a visual oddball situation is as follows: if we are stopped in a car at a traffic light and the indicator light of the car in front of us is blinking regularly, rather than process every new blink as a new object of our environment, we form the prediction that it will continue to exist and to blink in the same way. However, when a prediction related to the blinking light is violated, say, when one of the blinks is dimmer than all the others, the generative model for the blinking light no longer accounts for sensory input and therefore needs to be updated.

An important feature of the vMMN is that it is an automatic brain response (Kimura, 2012; Stefanics et al., 2014; Winkler &

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Czigler, 2012), because the standards and deviants do not need to be attended or consciously experienced (i.e., perceived) in order for it to be elicited. This suggests that generative models are established, tested, and updated, even when sensory input for those models is not attended or consciously experienced (Friston & Kiebel, 2009; Schröger et al., 2014). That is, when we attend to or are conscious of something other than the blinking indicator light, such as a pedestrian crossing the road or a song on the car stereo, generative models for the blinking light continue to be established, tested, and updated. Although there is plenty of evidence showing that vMMN occurs in the absence of attention to the standards and deviants (Berti, 2011; Heslenfeld, 2002; Kimura & Takeda, 2013; Kremláček et al., 2013; Kuldkepp, Kreegipuu, Raidvee, Näätänen, & Allik, 2013; Pazo-Alvarez, Amenedo, & Cadaveira, 2004; for reviews, see Czigler, 2007; Stefanics et al., 2014), to the best of our knowledge, there is no evidence showing that vMMN occurs in the absence of consciousness of those stimuli: previous attempts have failed either to elicit a vMMN from stimuli that are not perceived (Czigler, Weisz, & Winkler, 2007; Flynn, Liasis, Gardner, & Towell, 2016; Meng et al., 2015) or to hide their stimuli from consciousness (Jack et al., 2015; Kogai, Aoyama, Amano, & Takeda, 2011; van Rhijn, Roeber, & O'Shea, 2013). In the experiment we report here, we sought to provide that evidence.

To manipulate visual consciousness, we used binocular rivalry—a powerful form of bistable perception in which consciousness alternates unpredictably between two dissimilar images presented one to each eye (Alais, Cass, O'Shea, & Blake, 2010; Breese, 1899; Wheatstone, 1838; for reviews, see Alais & Blake, 2004; Blake & O'Shea, 2009; Miller, 2013). That is, at any given moment, one of the images is dominant (i.e., perceived) and reaches consciousness, whereas the other is suppressed (i.e., not-perceived) and does not reach consciousness. For example, when one eye views a horizontal grating and the other eye views a vertical grating, an observer usually perceives the horizontal grating for a few seconds, then the vertical grating for a few seconds, then the horizontal grating again, and so on, for as long as he or she cares to look. Sometimes the transition from one image to the other can be abrupt in which there is a sudden change in consciousness (Levelt, 1965), sometimes the transition can be gradual in which a dynamic, patchy, mosaic-like combination of both images is briefly perceived at the same time (Yang, Rose, & Blake, 1992), and sometimes the transition can return to the previously dominant percept (Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006). Therefore, one's experience of binocular rivalry is that of continual, unpredictable changes in consciousness.

To elicit vMMN during binocular rivalry, we compared the electrical activity of the brain to standards comprising a horizontal grating to one eye and an otherwise identical vertical grating to the other eye with deviants that showed the same gratings, except that the contrast and luminance of one (we call these monocular deviants) or both (we call these binocular deviants) were reduced. We refer to the deviants as luminance decrements because the luminance of the deviants was 33% less than that of the standards, whereas the contrast was only 1% less. We chose to use luminance-decrement deviants for three reasons:

1. Random and unpredictable reductions in the luminance of a stimulus reliably elicits the vMMN at right posterior electrodes between 200 and 300 ms after stimulus onset (Kimura, Katayama, & Murohashi, 2008a, 2008b; Kimura, Widmann, & Schröger, 2010a, 2010b; Stagg, Hindley, Tales, & Butler, 2004).
2. Luminance decrements stimulate the same neurons as full-luminance stimuli (Roeber, 2012; Spekreijse, van der Twell, &

Zuidema, 1973); thus, adaptation (or “refractoriness”; e.g., Stefanics et al., 2014, p. 1; see also O'Shea, 2015; Stefanics, Kremláček, & Czigler, 2016) is assumed to make little contribution to the ERP differences between the standards and deviants (Kimura, 2012).

3. During pilot testing, we found that monocular deviants presented to the dominant eye were perceived (we call these perceived monocular deviants), whereas monocular deviants presented to the suppressed eye were not (we call these not-perceived monocular deviants). This is consistent with the binocular rivalry literature using forced-choice techniques to measure detection thresholds to changes made to a suppressed stimulus (Alais et al., 2010; Blake, 1977; Blake & Camisa, 1979; Blake & Fox, 1974; Fox & Check, 1966, 1972; Ling, Hubert-Wallander, & Blake, 2010; Nguyen, Freeman, & Wenderoth, 2001; Wales & Fox, 1970). Binocular deviants were always perceived, because either the left or right eye was dominant or because a combination of inputs from both eyes was perceived (we call these perceived binocular deviants); we included this deviant as a control.

We sought to answer two empirical questions. First, do deviants that are not perceived elicit the vMMN? Second, does consciousness modulate the vMMN?

Method

Ethics Statement

The study was performed in accordance with the ethical standards laid down in the Declaration of Helsinki (World Medical Association, 2004) and with the ethics guidelines of the German Psychological Association. We obtained written informed consent from each participant prior to the experiment.

Participants

Fifteen volunteers participated in our study for course credit or payment (6 €/h). All participants had normal or corrected-to-normal visual acuity in both eyes and showed normal binocular rivalry in a 12-min pretest session. Data of five participants were excluded from further analyses: one because she misunderstood the experimental task, the others because too many monocular deviants were presented during a mixed phase of binocular rivalry, meaning that we could not classify them as perceived or not. Mean (*SD*) age of the remaining 10 participants, all of whom were right-handed and three of whom were male, was 26 (11) years.

Apparatus

The experiment was conducted in the BioCog Research Laboratory at the University of Leipzig, Leipzig, Germany, in a sound-attenuated and electrically shielded cabin with the display of the stimuli providing the only light. During the experiment, each participant sat in a chair at a desk with his or her head stabilized by a chin and forehead rest. Stimuli were presented on a linearized, 19-inch, color, cathode-ray-tube monitor (SonicView G90fB; showing $1,024 \times 768$ pixels at 100 Hz) and viewed through a mirror stereoscope (Screenscope-SA-200-Monitor-Type) at a viewing distance of 57 cm. The experiment was controlled by a Windows XP PC running specially written MATLAB scripts using the Psychophysics Toolbox (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997). Participants responded using two keys on a response pad connected via an ActiveWire USB I/O board.

The EEG was recorded from 59 Ag/AgCl active electrodes (ActiCap, Brain Products, Germany) placed according to the extended 10–20 system (FP1, FP2, AF7, AF3, AFz, AF4, AF8, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FC5, FC3, FC1, FCz, FC2, FC4, FC6, T7, C5, C3, C1, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO9, PO7, PO3, POz, PO4, PO8, PO10, O1, Oz, O2) and referenced to Cz, with the ground at FPz. A vertical electrooculogram (EOG) was recorded by placing an electrode above (we used FP2) and below the right eye; a horizontal EOG was recorded by placing an electrode on the outer canthi of each eye. We also placed an electrode on each earlobe. The signals were amplified using BrainAmp amplifiers (Brain Products) and recorded using BrainVision Recorder (Brain Products). The sampling rate of the EEG was 500 Hz, and the online filtering was 0.01 to 250 Hz.

Stimuli

We used three types of stimuli in our experiment: standard stimuli, deviant stimuli, and blank stimuli. Standards were annulus-shaped patches of black (0.40 cd/m^2) and white (86.67 cd/m^2) sine-wave gratings on a black background. The grating presented to one eye was vertical (0°) and the grating presented to the other eye was horizontal (90°). The gratings had a spatial frequency of 1.6 cycles per degree, a mean luminance of 43.54 cd/m^2 , and a Michelson contrast of .99. The outer diameter of the gratings was 3.2° of visual angle; the inner diameter was 0.67° . The central area contained a central red fixation cross of 0.3° with a line width of 0.1° . The gratings were surrounded by three white fusion rings; these served to lock vergence. The outer diameter of the largest ring was 6.4° . Each ring had a line width of 0.05° and was 0.3° from its neighbor.

Deviants were identical to standards, except that they had a lower contrast and luminance. For binocular deviants, both gratings had a mean luminance of 29.03 cd/m^2 and a Michelson contrast of .98. For monocular deviants, one eye viewed a grating with a mean luminance of 43.54 cd/m^2 and a Michelson contrast of .99, and the other eye viewed a grating with a mean luminance of 29.03 cd/m^2 and a Michelson contrast of .98. For left-eye deviants, the left eye viewed the luminance decrement; for right-eye deviants, the right eye viewed the luminance decrement. Because of binocular rivalry, monocular deviants presented to the dominant eye reached consciousness (i.e., perceived monocular deviants), whereas monocular deviants presented to the suppressed eye did not reach consciousness (i.e., not-perceived monocular deviants).

Blank stimuli consisted only of the fixation rings and the fixation cross on a black background without any grating.

Design and Procedure

We used two types of blocks: oddball-decrement blocks and oddball-increment blocks. In oddball-decrement blocks, participants were presented with binocular deviants (randomly on 2% of trials), left-eye deviants (randomly on 2% of trials), right-eye deviants (randomly on 2% of trials), and standards (on the remaining 94% of trials). There were 12 of these blocks in our experiment, each of which contained 900 trials; thus, there were 216 trials for each type of deviant and 10,152 trials for the standard. An individual trial comprised a display of binocular rivalry gratings—a vertical grating to one eye and a horizontal grating to the other eye, for 100 ms, followed by a display of blank stimuli for 100 ms. The gratings, therefore, were showing on-off flicker at 5 Hz with each onset marking the beginning of a new trial (see Figure 1).

According to Wolfe (1983), this time is sufficient for binocular rivalry to survive from one display to the next (if anything, binocular rivalry dominance durations are slightly enhanced by this; O'Shea & Crassini, 1984). The order of trials within a block was random and different for each participant with the constraint that any two deviants had to be separated by at least 10 standards.

We also included four oddball-increment blocks in our experiment so that we could collect ERPs from standards that were physically identical to deviants in the oddball-decrement blocks (i.e., deviants in the oddball-increment blocks were luminance increments). However, when we calculated difference waves between physically identical standards (from the oddball-increment blocks) and deviants (from the oddball-decrement blocks), we found a pronounced 10 Hz periodicity, even in the prestimulus onset period. This made the difference waves, calculated from separate blocks of trials, impossible to interpret. We do not report any data from the oddball-increment blocks.

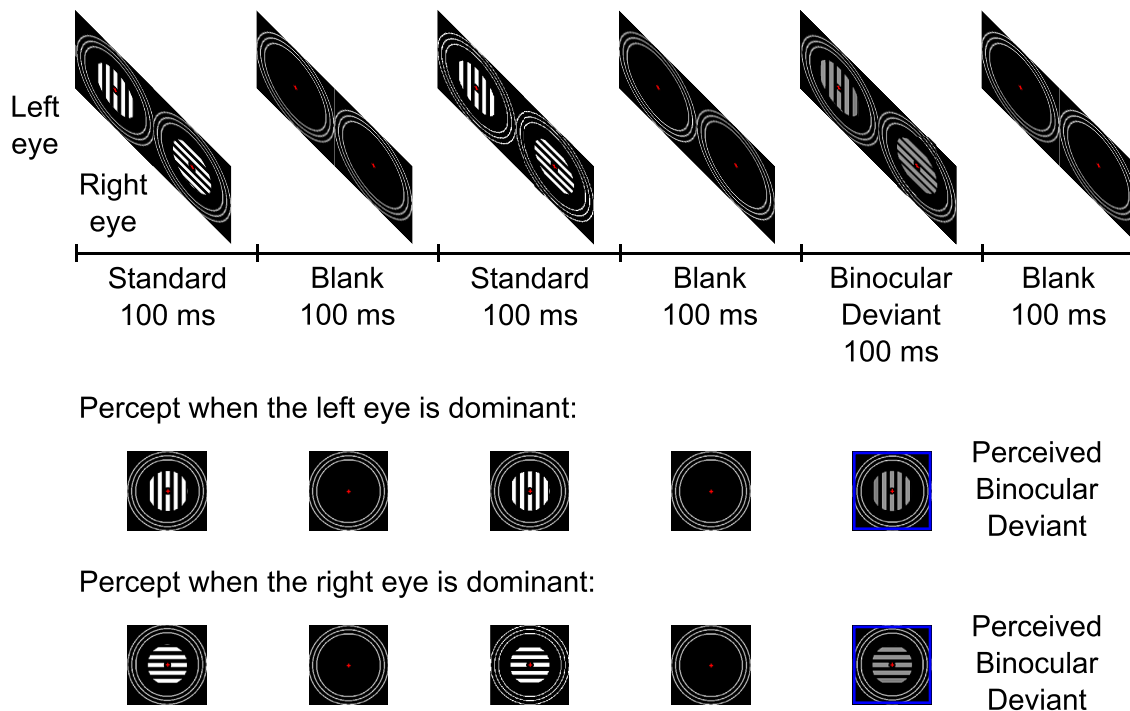
The participant's task was to look at the fixation cross in the center of the grating stimuli, to report binocular rivalry dominance of one or the other grating by pressing down (with his or her thumbs) one or another key on the response pad, and to refrain from pressing either key if any combination of the two gratings was perceived. This yielded two events: key presses (i.e., when a key was pressed) and key releases (i.e., when a key stopped being pressed). The assignment of thumbs to keys was counterbalanced over participants. We used key presses and releases to determine participants' mean binocular rivalry dominance duration, to classify monocular deviants as perceived or not, and to assess the intrusiveness of deviants on consciousness.

ERP Analysis

For data analyses, we re-referenced the EEG data offline to the average of all scalp electrodes, and we filtered the data using a 0.1 to 40 Hz zero-phase Butterworth filter (48 dB/oct slope). We extracted the epochs from -100 to 400 ms relative to stimulus onset, and we baseline-corrected all epochs to their mean voltage from -100 to 0 ms. We excluded all epochs with signals exceeding peak-to-peak amplitudes of $200 \mu\text{V}$ at any EEG channel, or of $60 \mu\text{V}$ at any EOG channel, as well as any standards that immediately followed a deviant. We also excluded all epochs when there was a key press or a key release between -300 ms and 150 ms (see below for a rationale). We computed ERPs separately for each stimulus (standard, perceived binocular deviant, perceived monocular deviant, not-perceived monocular deviant) for each participant, and excluded any data sets containing fewer than 100 epochs for any ERP. On average (*SD*), ERPs were computed from 7,504 (646) standard, 173 (19) perceived binocular deviant, 158 (20) perceived monocular deviant, and 147 (24) not-perceived monocular deviant epochs per participant.

To classify monocular deviants as perceived or not-perceived, we used key presses and releases. Specifically, if a left- or right-eye deviant was presented, and if the left or right eye was dominant, respectively, we classified it as a perceived monocular deviant; if a left- or right-eye deviant was presented, and if the right or left eye was dominant, respectively, we classified it as a not-perceived monocular deviant. However, because binocular rivalry alternations are about 450 ms ahead of a key press or release (Alais et al., 2010), we classified monocular deviants as perceived or not-perceived only if a key was pressed 300 ms before the onset of the deviant and only if the key continued to be pressed until at least 150 ms after the onset of the deviant. We chose these times to be

(a) Sequence of Standards and A Binocular Deviant



(b) Sequence of Standards and A Left-Eye Monocular Deviant

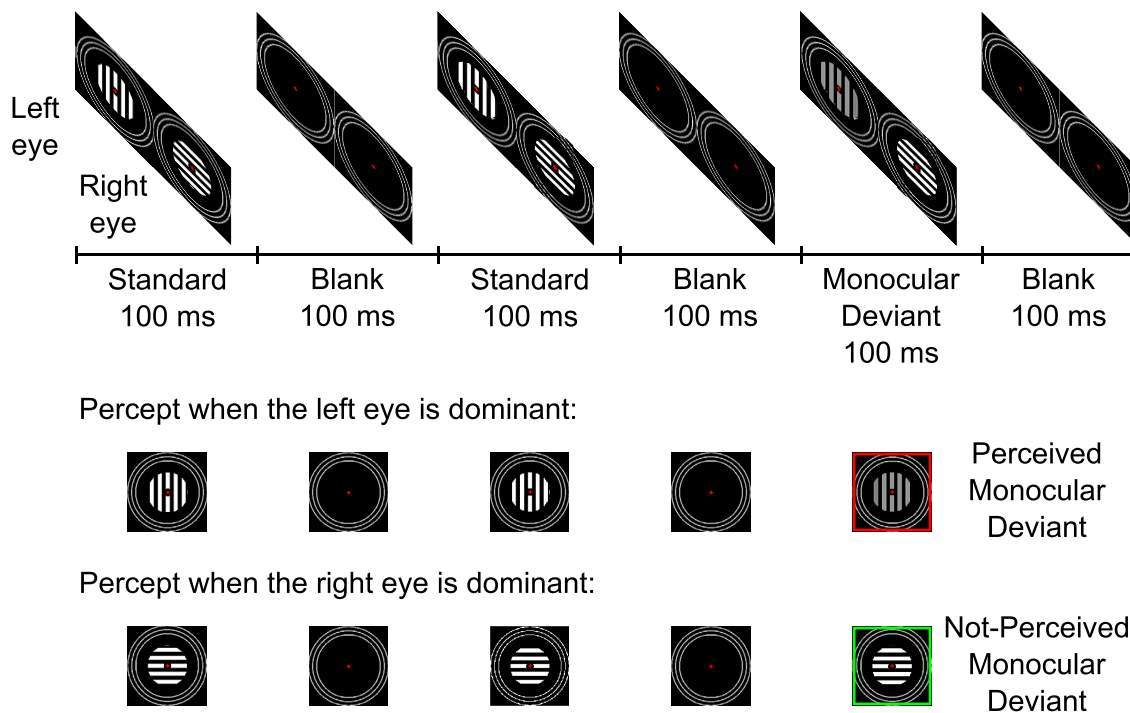


Figure 1. Experimental paradigm. a: Top—Schematic illustration of a sequence of standards (in this case, a vertical grating to the left eye and a horizontal grating to the right eye) and a binocular deviant (a decrease in the contrast and luminance of both eyes' gratings). Middle—Illustration of what would be perceived if the left eye were dominant and the right eye suppressed. Bottom—Illustration of what would be perceived if the right eye were dominant and the left eye suppressed. b: Top—Schematic illustration of a sequence of standards and a monocular deviant (in this case, a decrease in the contrast and luminance of the left eye's grating). Middle—Illustration of what would be perceived if the left eye were dominant and the right eye suppressed. In this case, the deviant was perceived. Bottom—Illustration of what would be perceived if the right eye were dominant and the left eye suppressed. In this case, the deviant was not perceived.

Table 1. Means and Standard Deviations

	Binocular rivalry dominance durations (s)		Key release after a deviant (s)		ERP amplitudes for the temporal ROI (μ V)	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Standard	1.66	0.27	N/A	N/A	0.00	1.44
Perceived binocular deviant	2.35	0.74	0.86	0.24	−1.25	2.02
Perceived monocular deviant	2.25	0.72	0.89	0.24	−1.72	2.02
Not-perceived monocular deviant	2.27	0.63	0.87	0.26	−0.97	1.93

consistent with others using binocular rivalry and ERPs to study consciousness (Kaernbach, Schröger, Jacobsen, & Roeber, 1999; Roeber & Schröger, 2004; Roeber, Vesper, Schröger, & O'Shea, 2011; Roeber et al., 2008; Vesper, O'Shea, Schröger, Trujillo-Barreto, & Roeber, 2008). We did not analyze monocular deviants presented during a mixed-phase of binocular rivalry.

We defined a spatiotemporal region of interest (ROI) according to the literature: Kimura et al. (2008a, 2008b, 2010a, 2010b), and Stagg et al. (2004) reported the vMMN from luminance-decrement deviants at right posterior electrodes between 200 and 300 ms. Next, we subtracted the ERP for the standard from the ERP for the perceived binocular deviant (we call this the perceived binocular difference wave). This allowed us to identify the vMMN at right posterior (P8, PO4, PO8, PO10, O2) electrodes between 230 and 274 ms. This time window is similar to that used in previous research (e.g., Kimura et al., 2008a, analyzed a time window between 240 and 260 ms; the subtle differences between our time window and theirs could be due to the 5 Hz on-off flicker). We then computed two more difference waves: we subtracted the ERP for the standard from the ERP for the perceived monocular deviant (we call this the perceived monocular difference wave) and from the ERP for the not-perceived monocular deviant (we call this the not-perceived monocular difference wave). Finally, we analyzed the mean amplitudes of the ERPs at right posterior electrodes between 230 and 274 ms using repeated measures analysis of variance (ANOVA).

Results

Behavioral Data

The time between a key press and its subsequent release yielded the time of one episode of binocular rivalry dominance. As expected, the distribution of these times had the typical gamma-like shape (Levelt, 1967; Walker, 1975; Zhou, Gao, White, Merk, & Yao, 2004). Mean (*SD*) binocular rivalry dominance duration was 1.96 (0.49) s; this time is almost 10 displays of the gratings, and is consistent with what we know about binocular rivalry during 5 Hz on-off flicker (O'Shea & Crassini, 1984; Wolfe, 1983). These results show that consciousness of one or the other grating survived the 5 Hz on-off flicker.

Next, we assessed the intrusiveness of deviants on consciousness by comparing dominance durations containing only standards with those containing standards and one of the three types of deviants (see Table 1). Repeated measures ANOVA on log-transformed data found that these times were significantly different, $F(3,27) = 34.71$, $p < .001$, $\eta_p^2 = .79$. An analysis of simple effects revealed that dominance durations containing only standards were shorter than those containing a perceived binocular deviant, $t(9) = 6.15$, $p < .001$, than those containing a perceived monocular deviant, $t(9) = 5.44$, $p < .001$, and than those containing a not-perceived monocular deviant, $t(9) = 6.85$, $p < .001$.

Consistent with Levelt (1965), these results show that luminance decrements increase binocular rivalry dominance durations.

We also analyzed the time between the onset of a deviant and a key release (see Table 1). Repeated measures ANOVA on log-transformed data found that these times were not significantly different, $F(2,18) = 1.65$, $p = .220$, $\eta_p^2 = .16$. Because reaction times during binocular rivalry are about 450 ms (Alais et al., 2010) with a standard deviation of about 10% (Jaskowski, 1983), and because our means and standard deviations are at least twice this, we think that it is rather unlikely that the deviants prompted a change in consciousness. This is consistent, albeit indirectly, with what we know about forced-choice techniques to measure detection thresholds to contrast changes made to a suppressed stimulus (Alais et al., 2010; Blake, 1977; Blake & Camisa, 1979; Blake & Fox, 1974; Fox & Check, 1966, 1972; Ling et al., 2010; Nguyen et al., 2001; Wales & Fox, 1970).

ERP Data

Figure 2 shows the grand-averaged ERPs and their difference waves at the spatial ROI (to see ERPs and difference waves outside the spatial ROI, see online supporting information Figure S1 and S2, respectively), as well as the distribution of voltages over the scalp for the temporal ROI. The ERPs show a pronounced 10 Hz periodicity with amplitude deflections of more than 4 μ V, even in the prestimulus onset period. This periodicity likely arises from the 5 Hz on-off flicker of the stimuli that was necessary so as not to perturb binocular rivalry (O'Shea & Crassini, 1984; Wolfe, 1983). The difference waves show a negativity at about 130 ms—the change-related negativity (CRN; Kimura et al., 2008a, 2008b), a positivity at about 180 ms—the change-related positivity (CRP; Kimura et al., 2008a, 2008b), and another negativity at about 250 ms—the vMMN (Kimura et al., 2008a, 2008b, 2010a, 2010b; Stagg et al., 2004). The voltage maps show that the three vMMNs were similar in that there were positive voltages at frontocentral electrodes and negative voltages at parieto-occipital electrodes.

Finally, we analyzed the mean amplitudes of the ERPs (see Table 1) using repeated measures ANOVA (to see analyses outside the spatial ROI, see online supporting information Table S1). The ANOVA revealed a significant main effect of the four-level factor stimulus, $F(3,27) = 7.08$, $p = .001$, $\eta_p^2 = .44$. An analysis of simple effects revealed that the ERP amplitudes elicited by perceived binocular deviants were more negative than those elicited by standards, $t(9) = 2.36$, $p = .043$, that the ERP amplitudes elicited by perceived monocular deviants were more negative than those elicited by standards, $t(9) = 4.05$, $p = .003$, and that the ERP amplitudes elicited by not-perceived monocular deviants were more negative than those elicited by standards, $t(9) = 2.34$, $p = .044$. These results show that not-perceived deviants elicit the vMMN. Furthermore, we found that ERP amplitudes elicited by perceived

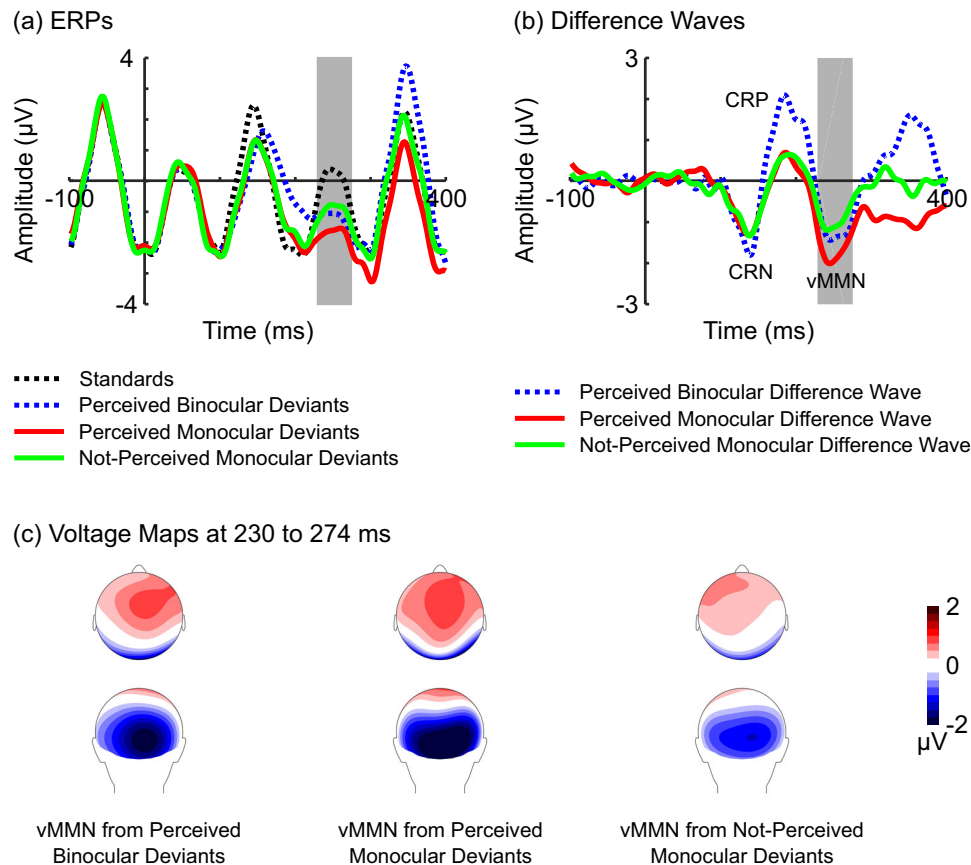


Figure 2. ERPs, difference waves, and voltage maps. a: ERPs averaged over right posterior (P8, PO4, PO8, PO10, O2) electrodes, showing time (ms) on the *x*-axis, with 0 indicating the onset of the stimulus, and voltage (μV) on the *y*-axis, with positive voltages plotted upward. The gray bar shows the temporal ROI (230–274 ms). b: Difference waves averaged over right posterior electrodes. c: Voltage maps of the difference waves for the temporal ROI.

monocular deviants were more negative than those elicited by not-perceived monocular deviants, $t(9) = 2.46$, $p = .036$. This result shows that consciousness enhances the processing underlying vMMN. There were no other significant differences.

Discussion

We sought to answer two empirical questions. First, do deviants that are not perceived elicit the vMMN? Second, does consciousness modulate the vMMN? To answer these questions, we measured the vMMN from monocular luminance-decrement deviants that were either perceived or not during binocular rivalry dominance or suppression, respectively. We found that the answer to both questions is yes. Specifically, we found that both sorts of deviants elicited the vMMN, with perceived deviants eliciting a bigger vMMN than not-perceived deviants. These results show that vMMN occurs in the absence of consciousness, and that consciousness enhances the processing underlying vMMN. We conclude that generative models of visual perception are tested, even when sensory input for those models is not perceived.

However, there is at least one limitation for our conclusion: we did not use physically identical standards and deviants, meaning that our results could be explained by physical differences in the stimuli (Kujala, Tervaniemi, & Schröger, 2007). Specifically, because luminance decrements stimulate the same neurons as full-luminance stimuli and because luminance decrements elicit smaller

exogenous components than full-luminance stimuli (Roeber, 2012; Spekreijse et al., 1973), it is possible that any smaller absolute voltages for deviants than for standards are from the luminance differences. In our experiment, the greatest amount of light was delivered to the eyes by the standards, next by the monocular deviants, and least by the binocular deviants, so if physical differences were to explain our results, then that is the order of voltage differences one would expect to see in the ERPs.

We see this order of voltage differences at the CRN and CRP. Furthermore, because the timing of the CRN overlaps with that of the exogenous P1 (typically between 80 and 120 ms; Luck, 2014; O'Shea, Roeber, & Bach, 2009; Pratt, 2012), because the timing of the CRP overlaps with that of the exogenous N1 (typically between 150 and 200 ms; Luck, 2014; O'Shea et al., 2009; Pratt, 2012), and because the P1 and N1 are sensitive to physical differences (Kimura et al., 2009; Roeber, 2012), we concede that these components could possibly be explained as a reduced P1 and N1, respectively, due to physical differences. However, because the observed pattern of amplitudes for the vMMN is inconsistent with the expected order of voltage differences, and because the timing of the vMMN is beyond the exogenous potentials expected to be modulated by luminance, we can exclude any simple explanation that light intensity is responsible for the voltage differences we found at the vMMN.

As mentioned above, the main contribution of our study is that we provided, for the first time, empirical evidence for the testing of

generative models in the absence of consciousness, as is assumed by the predictive coding framework of brain function (Friston & Kiebel, 2009; Schröger et al., 2014). Specifically, we found that not-perceived monocular deviants elicited the vMMN. However, it is important to acknowledge that we did not provide any evidence for the establishing of generative models in the absence of consciousness, because our prediction-establishing stimuli (i.e., the standards) were presented to both eyes, meaning that they were always perceived, because either the left or right eye was dominant or because a combination of inputs from both eyes was perceived (similar to our perceived binocular deviants). Furthermore, we did not provide any evidence for the updating of generative models in the absence of consciousness, because it is an open issue as to whether or not the vMMN reflects the prediction-updating process (for evidence in the auditory modality, see Winkler & Czigler, 1998). We are designing new approaches to address these limitations.

Another contribution of our study is that we found that consciousness enhances the processing underlying vMMN. Specifically, we found that perceived monocular deviants elicited a bigger vMMN than not-perceived monocular deviants. It is important to emphasize that the extra processing of perceived monocular deviants over not-perceived monocular deviants arises from physically

identical stimuli that differ only in consciousness. We propose that the enhancement of the vMMN by consciousness arises because consciousness increases the precision of the prediction error by modulation of synaptic gain (Bastos et al., 2012), and because the violation of a precise prediction elicits more prediction error than a less-precise prediction (Friston, 2010; Schröger, Marzecová, & SanMiguel, 2015). It is also possible that the enhancement reflects the prediction-updating process, because deviants presented to the dominant eye must be explained by the generative model before they can be perceived (Friston & Kiebel, 2009; Schröger et al., 2014), whereas the same process may not be necessary or have occurred for deviants presented to the suppressed eye; however, we concede that this is speculation.

In conclusion, we measured the vMMN from monocular luminance-decrement deviants that were either perceived or not during binocular rivalry dominance or suppression, respectively. We found that both sorts of deviants elicited the vMMN at about 250 ms after stimulus onset, with perceived deviants eliciting a bigger vMMN than not-perceived deviants. These results show that vMMN occurs in the absence of consciousness, and that consciousness enhances the processing underlying vMMN. We conclude that generative models of visual perception are tested, even when sensory input for those models is not perceived.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1: Results of the statistical analysis of the ERP amplitudes for the temporal ROI (230 to 274 ms).

Figure S1: ERPs outside the spatial ROI.

Figure S2: Difference waves outside the spatial ROI.