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Conscious and not-conscious processing of visual mismatch negativity

Bradley N. Jack
Southern Cross University

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Conscious and not-conscious processing of
visual mismatch negativity

A Thesis Presented for the
Degree of Doctor of Philosophy
Southern Cross University, Australia

Bradley N. Jack
October 27, 2014
I certify that the work presented in this thesis is, to the best of my knowledge and belief, original, except as acknowledged in the text, and that the material has not been submitted, either in whole or in part, for a degree at this or any other university.

I acknowledge that I have read and understood the University’s rules, requirements, procedures, and policy relating to my higher degree research award and to my thesis. I certify that I have complied with the rules, requirements, procedures, and policy of the University.

Print name: Bradley N. Jack
Signature: [Signature]
Date: October 27, 2014
Abstract

The general aim of my thesis is to investigate conscious and not-conscious processing of sequences of stimuli that yield visual mismatch negativity (vMMN), a well-established brain signature of prediction and prediction-error. vMMN is typically observed in the oddball paradigm: an infrequent visual stimulus—a deviant, is randomly and unpredictably presented in a sequence of more frequent visual stimuli—the standards. vMMN is a negative component of event-related potentials (ERPs), and is seen most clearly in the difference wave: the ERP for the deviant minus the ERP for the standard, between 150 and 400 ms after stimulus onset.

To investigate conscious and not-conscious processing of vMMN, I conducted four electroencephalography (EEG)/ERP experiments. In Experiment 1, I showed that it is easier to find neural correlates of visual consciousness—differences in brain activity between conscious and not-conscious visual stimuli, with cardinal gratings than with oblique gratings. In Experiment 2, I showed that a source of information about which we are not-conscious, eye-of-origin (utrocular) information, yields a reliable vMMN. In Experiment 3, I hid my deviants from visual consciousness using binocular rivalry suppression, and found that the size of vMMN is smaller to that elicited by the same stimulus when it is conscious during binocular rivalry dominance. In Experiment 4, I hid my standards and deviants from
visual consciousness using continuous flash suppression (CFS), and found that the size of vMMN is bigger than that elicited by the same stimuli when they are conscious.

My results are consistent with the notions that our brains establish predictive models of visual perception about regular visual input, that our brains are constantly testing the reliability of these models, and that our brains update these models when something unexpected occurs. My results also show that these processes are independent of visual consciousness. I conclude that visual consciousness is not necessary to elicit vMMN, confirming that vMMN is an automatic brain response.
Acknowledgements

I would first like to thank my principal supervisor, Professor Robert O’Shea, for absolutely everything. I would also like to thank my co-supervisors, Dr Steve Provost, for his friendship and support, and Dr Urte Roeber, for her expert advice and encouragement.

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I would like to thank my PhD friends for sharing this journey with me. I am also grateful to Ruth Minkov, Martin Reiche, and Erin Corkett, for their assistance with data collection, and to Duncan Blair, for technical support.

I also acknowledge my family and friends for their support. I am eternally grateful to my dearest Madison, for her love and patience. You are still the centre of my personal universe.

Finally, I would like to dedicate this thesis to my supervisors, for their unfailing belief in me, for excusing my naivety, for trusting my ability, and for the opportunities and responsibilities they gave me.
List of Publications

The following is a list of publications arising from my thesis:

**Peer-reviewed journal publications:**


**Conference proceedings:**


are never perceived. *Paper presented at the 12th International Conference on Cognitive Neuroscience, Brisbane, Australia.*


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<tr>
<td>ANOVA</td>
<td>Analysis of Variance</td>
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<tr>
<td>BA</td>
<td>Brodmann Area</td>
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<td>BOLD</td>
<td>Blood Oxygen Level-Dependent</td>
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<td>CFS</td>
<td>Continuous Flash Suppression</td>
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<td>EEG</td>
<td>Electroencephalography</td>
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<td>ERP</td>
<td>Event-Related Potential</td>
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<td>fMRI</td>
<td>Functional Magnetic Resonance Imaging</td>
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<tr>
<td>LGN</td>
<td>Lateral Geniculate Nucleus</td>
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<tr>
<td>LORETA</td>
<td>Low Resolution Brain Electromagnetic Tomography</td>
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<td>MEG</td>
<td>Magnetoencephalography</td>
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<tr>
<td>MMN</td>
<td>Mismatch Negativity</td>
<td></td>
</tr>
<tr>
<td>MNI</td>
<td>Montreal Neurological Institute</td>
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<td>PET</td>
<td>Positron Emission Tomography</td>
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<tr>
<td>sLORETA</td>
<td>Standardised Low Resolution Brain Electromagnetic Tomography</td>
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<tr>
<td>SnPM</td>
<td>Statistical Non-Parametric Mapping</td>
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<td>V1</td>
<td>Primary Visual Cortex</td>
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<td>vMMF</td>
<td>Visual Mismatch Field</td>
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Chapter 1
Overview of the Thesis

1.1 Introduction

Imagine you are sitting in a car at a busy intersection waiting for the traffic light to turn green. You notice that the left indicator light of the car in front is blinking regularly, signalling that the driver wishes to turn left. You realise that you might have to wait a little after the traffic light turns green to allow the car in front time to turn, and then think no more about it. Instead, you will probably pay attention to the traffic light, or to the song playing on the radio, or to pedestrians crossing from one side of the street to the other. Now, imagine that one of the blinks from the indicator light changes from yellow to blue. Regardless of whether you notice this change, there will be a sudden change in the electrical activity of your brain, because something unexpected happened. This change in electrical activity is our brain’s way of processing unexpected changes.

Although the story I have told above is not particularly likely, it is an example of the sorts of processes I deal with in this thesis. The questions I consider include the following:

- What happens in our brains when we see something that repeats regularly, such as a blinking indicator light?
What happens in our brains when that regular something changes unexpectedly, such as when one of the blinks from the indicator light changes from yellow to blue?

What happens in our brains if we do not notice something that repeats regularly, or if that regular something changes unexpectedly without our noticing?

To answer these questions, I have recreated the story I told above in the laboratory in various ways while measuring the electrical activity of people’s brains from electrodes on the scalp: electroencephalography (EEG). My thesis is that our brains process regular and unexpected visual events, that there are systematic differences in the way that our brains process these events, and that these differences in processing occur even when an observer never consciously sees these events.

There is a rich literature on how EEG signals alter when sensory input changes unexpectedly: there is a pattern of negative voltages over sensory regions of the brain (i.e., auditory cortex for auditory changes, visual cortex for visual changes, and so on) beginning at about 100 ms after the change and lasting up to about 400 ms, called the mismatch negativity (MMN; for reviews, see Näätänen, 1990, 1992; Näätänen, Paavilainen, Rinne, & Alho, 2007; Schröger, 2007; Winkler, 2007; Winkler & Czigler, 2012). In the case of visual input, unexpected changes yield what is referred to as the visual MMN (vMMN; for reviews, see Czigler, 2007; Kimura, 2012; Kimura,
vMMN and visual consciousness


MMN and vMMN are often interpreted in terms of predictive coding (e.g., Garrido, Kilner, Stephan, & Friston, 2009; Schröger et al., 2013; Stefanics, Kremláček, & Czigler, 2014; Wacongne, Changeux, & Dehaene, 2012; Winkler & Czigler, 2012): somehow, the brain encodes the statistical regularities of visual input, it establishes top-down predictive models of visual perception based on past experience and learning, it tests the accuracy of these predictive models by comparing them to upcoming visual input, and it updates these predictive models when they are found to be mismatched with visual input—prediction-error (e.g., Friston, 2005; Rao & Ballard, 1999). Therefore, vMMN is a brain signature of the processing of prediction and prediction-error of visual input.

The general aim of my thesis is to investigate conscious and not-conscious processing of sequences of stimuli that yield vMMN. The reasons for this are:

1. vMMN is thought to be an automatic brain response—it is elicited in the absence of top-down attention (Czigler, 2007; Stefanics et al., 2014). However, attention is not the only tool for assessing automatic processing of vMMN; one can also manipulate visual consciousness. Although attention and visual consciousness are often treated as essentially the same
psychological construct (e.g., Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006), there is a growing body of research that shows that they perform separate functions in the brain (e.g., Crick & Koch, 2003; Lamme, 2003) and that they can be doubly dissociated (e.g., Koch & Tsuchiya, 2007; but see Cohen, Cavanagh, Chun, & Nakayama, 2012; Suzuki, Grabowecky, & Paller, 2014). Therefore, one reason for conducting this research is to study the automatic processing of vMMN.

2. An important component of theories of predictive coding, the current consensus explanation for vMMN (e.g., Garrido et al., 2009; Schröger et al., 2013; Stefanics et al., 2014; Wacongne et al., 2012; Winkler & Czigler, 2012), is that the brain establishes, tests, and updates predictive models of visual perception, even when visual input for those predictions does not reach conscious visual perception (e.g., Hohwy, Roepstorff, & Friston, 2008; Mill, Böhm, Bendixen, Winkler, & Denham, 2011, 2013; Spratling, 2008). However, to the best of my knowledge, this has never been tested experimentally. Therefore, another reason for conducting this research is to provide evidence confirming this assumption of theories of predictive coding.

To investigate conscious and not-conscious processing of vMMN, I compared brain activity from regular stimuli—standards, and unexpected
stimuli—deviants, that were conscious with brain activity from standards and deviants that were not-conscious. To manipulate conscious visual perception, in Experiments 1–3, I used binocular rivalry, a powerful form of bistable perception in which visual consciousness alternates unpredictably between two dissimilar images presented one to each eye (Wheatstone, 1838; for reviews, see Alais & Blake, 2004; Blake & O’Shea, 2009; Miller, 2013).

Similarly, in Experiment 4, I used continuous flash suppression (CFS), a powerful form of interocular suppression in which an image presented to one eye is suppressed from visual consciousness indefinitely by a rapidly changing sequence of Mondrian patterns presented to the other eye (Tsuchiya & Koch, 2004, 2005; Yang & Blake, 2012; for review, see Yang, Brascamp, Kang, & Blake, 2014).

1.2 Structure of the thesis

My thesis has the following structure:

In Chapter 2, I review relevant literature in three sections:

1. I briefly review EEG and event-related potentials (ERPs), the tools I used to measure vMMN.
2. I review vMMN and I discuss the general aim of my thesis. The goal of this section is to provide the theoretical reasons for conducting my research.

3. I review binocular rivalry and CFS, and I discuss how they can be combined with vMMN to investigate conscious and not-conscious processing of vMMN. The goal of this section is to outline how I will accomplish the general aim of my thesis.

In Chapters 3–6, I describe Experiments 1–4, respectively. A general summary of each experiment is as follows:

- In Experiment 1, I set out to determine the better stimulus for studying conscious and not-conscious processing of visual stimuli: cardinal (horizontal and vertical) gratings or oblique (diagonal) gratings. I presented one grating to one eye and an identical, orthogonally oriented grating to the other eye, yielding binocular rivalry, and I asked participants to press keys on a response keypad indicating which of the two gratings was visible, dominant. After doing so for at least 6 seconds, I changed one of the gratings to match the grating shown to the other eye, yielding binocular fusion. Because of binocular rivalry, changes made to the dominant grating were conscious and changes made to the other, suppressed grating, were not-conscious. I compared ERPs from conscious changes with ERPs
from not-conscious changes, and ERPs from cardinal gratings with ERPs from oblique gratings. I found that the amplitudes of ERPs were bigger for conscious changes than for not-conscious changes—these are neural correlates of visual consciousness. I also found that changes to cardinal gratings yielded more reliable neural correlates of visual consciousness than changes to oblique gratings. These results suggest that it is easier to find neural correlates of visual consciousness with cardinal gratings than with oblique gratings (see Chapter 3).

- In Experiment 2, I set out to demonstrate that a source of information about which we are not-conscious, eye-of-origin (utrocular) information (Blake & Cormack, 1979; Logothetis, Leopold, & Sheinberg, 1996), can be used to elicit vMMN. To vary eye-of-origin, I presented standards comprising a grating to one eye and an identical, orthogonally oriented grating to the other eye, yielding binocular rivalry, and deviants in which gratings were swapped between the eyes—an eye-swap deviant. The participant’s task was to press keys indicating which of the two gratings was dominant. I found that eye-of-origin information can be used to elicit vMMN (I call this an eye-swap vMMN). However, the behavioural data suggested that participants were aware of when an eye-swap deviant was
presented. Although this does not necessarily limit my conclusion that swapping binocular rivalry stimuli between the eyes yields a vMMN from information of which observers are unaware (i.e., observers are unaware of which eye is viewing which stimulus; Blake & Cormack, 1979), I went on to use different techniques for hiding the deviants (see Experiment 3) and the standards and deviants (see Experiment 4) from visual consciousness (see Chapter 4).

- In Experiment 3, I set out to compare vMMN from conscious deviants with vMMN from not-conscious deviants. I presented standards comprising a horizontal grating to one eye and an otherwise identical vertical grating to the other eye, and deviants in which the contrast and luminance of either the grating presented to the left eye or the grating presented to the right eye were reduced. The participant’s task was to press keys indicating which of the two gratings was dominant. Because of binocular rivalry, deviants were either conscious or not-conscious. I found that conscious deviants yielded a bigger vMMN than not-conscious deviants. These results show that vMMN occurs in the absence of visual consciousness, and that predictive models of visual perception are tested and updated,
vMMN and visual consciousness

even when visual input for those predictions does not reach conscious visual perception (see Chapter 5).

- In Experiment 4, I set out to show vMMN from not-conscious standards and deviants during CFS. To prevent my standards and deviants (identical, orthogonally oriented gratings) from being perceived, I presented them to one eye and a rapidly changing sequence of Mondrian patterns to the other eye, yielding CFS. To allow participants to perceive the gratings, in other blocks, I presented a blank stimulus to the eye viewing the Mondrian patterns whenever I presented a grating to the other eye. In other sorts of blocks, some of which were conscious and some of which were not-conscious, I presented the same gratings along with others of different orientations so that all were equiprobable. The participant’s task was to perform a demanding target-detection task at fixation by pressing keys on a response keypad. I found a vMMN from standards and deviants that were not-conscious; surprisingly, I did not find a vMMN from standards and deviants that were conscious. Despite these curious results, they show that vMMN occurs in the absence of attention and visual consciousness. When I compared deviants with equiprobable gratings, I found that prediction-error-based mechanisms of deviance detection
were processed earlier and longer when the gratings were not-conscious than when the gratings were conscious. These results show that vMMN occurs in the absence of visual consciousness, that predictive models of visual perception are established, tested, and updated, even when visual input for those predictions does not attract attention or reach conscious visual perception, and that visual consciousness slows the processing of predictability of visual input (see Chapter 6).

In Chapter 7, I provide a general discussion on the outcomes of the studies reported in Chapters 3–6, I detail their contribution to the field, and I provide a direction for future research. A summary of some of the conclusions drawn from the results of the thesis include:

- Visual consciousness is not necessary to elicit vMMN, showing that vMMN is an automatic brain response.

- Our brains establish predictive models of visual perception about regular visual input and update these models when something unexpected occurs, even when we do not notice the regular and unexpected visual inputs.

- Not-conscious processing of predictability of visual inputs is not simply a weaker version of conscious processing of predictability of visual inputs.
Chapter 2

Literature Review

The basic aspects of human vision are well understood: light from objects passes through the cornea, the pupil, and the lens, and falls on the light sensitive surface of the retina as a focussed image. The retina is made up of two types of photoreceptor cells, rods and cones, whose purpose it is to detect light and convert this energy into a signal that is communicable to the rest of the brain. The signal is then passed to horizontal cells, bipolar cells, amacrine cells, and ganglion cells (whose axons exit the eye at the optic disk to form the optic nerve), and toward the optic chiasm. Here, the signals from the inside half of the retina, the nasal half, cross over and project to the opposite half of the brain; the signals from the outside half of the retina, the temporal half, do not cross over and project to the same half of the brain. This ensures that signals from both eyes go to both hemispheres of the brain. After passing through the optic chiasm, the signal travels to primary visual cortex (V1), the part of the brain responsible for the early processing of visual information, via the lateral geniculate nucleus (LGN) in the thalamus (for a review of the visual system, see Frisby & Stone, 2010).

Although the basic aspects of vision are well understood, we do not yet know how it is that we come to have visual consciousness of the world.
According to Freeman (2003), one model assumes that visual consciousness arises from interactive processes between bottom-up visual input and top-down predictions about visual input. That is, the visual system is a sophisticated hypothesis tester that evaluates predictions and generates error-correction processes. In this thesis, I show that the visual system makes predictions about visual input, but that these processes seem to be independent of visual consciousness.

In this chapter, I review the tools I used to measure the neural operations of the brain: EEG and ERPs, the neural processes I focussed on: the vMMN, and the techniques I used to manipulate conscious and not-conscious processing of vMMN: binocular rivalry and CFS.

2.1 Electroencephalography and event-related potentials

In this section, I briefly review EEG and ERPs, the tools I used to measure the electrical activity of the brain and vMMN.

2.1.1 What is electroencephalography?

EEG is a non-invasive technique for measuring the electrical activity of the brain via electrodes placed along the scalp of a human participant or animal subject (Kirschstein & Köhling, 2009; Olejniczak, 2006). Electrodes are usually placed in standardised positions, such as according to the
International 10-20 system (Jasper, 1958) or to one of its extensions, and are thought to measure large-scale extracellular current flow from the dendrites of pyramidal neurons, especially from those orientated perpendicular to the scalp (Luck, 2005). Pyramidal neurons comprise approximately 70% of neurons in the brain and consist of a triangularly-shaped cell body, a single axon, a single apical dendrite, and multiple basal dendrites (for reviews, see Nieuwenhuys, 1994; Spruston, 2009).

EEG recordings depict fluctuations of voltage over time, and can be classified into waveforms depending on the frequency of positive peaks and negative troughs within a one-second period and by the location on the scalp at which they were recorded. Table 2.1 (based on Sanei & Chambers, 2007) summarises some of the features of the most common EEG waveforms.

Table 2.1
Summary of Some of the Features of the Most Common EEG Waveforms Giving the Name of the EEG Waveform (Greek Symbol), Frequency (Hz), Location on the Scalp, and Functional Significance

<table>
<thead>
<tr>
<th>Waveform</th>
<th>Frequency (Hz)</th>
<th>Location</th>
<th>Functional Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delta (δ)</td>
<td>0.5-4</td>
<td>Anterior, Central</td>
<td>Deep sleep, may be present when awake</td>
</tr>
<tr>
<td>Theta (θ)</td>
<td>4-8</td>
<td>Central</td>
<td>Drowsiness</td>
</tr>
<tr>
<td>Alpha (α)</td>
<td>8-13</td>
<td>Posterior</td>
<td>Tiredness</td>
</tr>
<tr>
<td>Beta (β)</td>
<td>13-30</td>
<td>Anterior, Central</td>
<td>Thinking, attention</td>
</tr>
</tbody>
</table>
There are at least three advantages to using EEG to study the brain compared with other neuroimaging methods (for reviews, see Luck, 2005; O’Shea, Roeber, & Bach, 2009):

1. EEG is inexpensive; it is much cheaper to purchase, use, and maintain/repair than functional magnetic resonance imaging (fMRI) or magnetoencephalography (MEG).

2. EEG is non-invasive. That is, the electrical activity of the brain is recorded by placing electrodes on the scalp of a participant. For comparison, positron emission tomography (PET) exposes participants to radiation.

3. EEG has temporal resolution in the millisecond range. This allows researchers to assess when a process occurs in the brain, and is at least 1,000 times better than fMRI and PET.

However, there are at least two disadvantages to using EEG to study the brain compared with other neuroimaging methods (for reviews, see Luck, 2005; O’Shea et al., 2009):

1. EEG has poor/undefined spatial resolution. Because there are an infinite number of distributions of sources consistent with any set of EEG recordings, it is impossible to localise EEG activity in the brain unambiguously. This is called the inverse problem of EEG sources. Despite this, techniques such as low resolution brain electromagnetic tomography (LORETA;
Pascual-Marqui, Michel, & Lehmann, 1994), standardized LORETA (sLORETA; Pascual-Marqui, 2002), and variable resolution electromagnetic tomography (VARETA; Bosch-Bayard et al., 2001) are mathematical models of current flow in the brain that attempt to solve the inverse problem. These techniques are said to offer spatial resolution of EEG sources that are about three times less accurate than that provided by fMRI (Grech et al., 2008).

2. Because EEG activity reflects thousands of ongoing processes, EEG waveforms tell us very little about neural processing specific to a particular stimulus. Fortunately, there is a simple solution to this problem: the ERP technique.

2.1.2 What are event-related potentials?

ERPs are an average of EEG activity time-locked to a specific event, such as the onset of a stimulus (Luck, 2005; O’Shea et al., 2009; Woodman, 2010). A specific stimulus is likely to yield a similar pattern of neural responses over numerous presentations, so averaging leaves it unchanged, whereas all the processes that are not time-locked to that stimulus will average to zero. Such an average waveform is called an ERP waveform. ERPs have fluctuations in voltage over time, usually slower and of lower
amplitude than the peaks and troughs visible in any individual EEG trace. These peaks and troughs are labelled by letters indicating the component’s polarity (P, positive; N, negative), followed by a number indicating either the component’s ordinal position in the waveform or the component’s latency in milliseconds after stimulus onset. For instance, the first positive deflection at about 100 ms after the onset of a visual stimulus is often called the P1 or the P100, the first negative deflection at about 170 ms is often called the N1 or the N170, and so on. Table 2.2 (based on Luck, 2005 and on Woodman, 2010) summarises some of the features of the major visual ERP components.

Table 2.2

<table>
<thead>
<tr>
<th>Component</th>
<th>Polarity/Latency (ms)</th>
<th>Hypothesized Processes</th>
</tr>
</thead>
<tbody>
<tr>
<td>C1</td>
<td>P/N50–75</td>
<td>Sensory processing</td>
</tr>
<tr>
<td>P1</td>
<td>P100</td>
<td>Sensory/perceptual processing</td>
</tr>
<tr>
<td>N1</td>
<td>N150–250</td>
<td>Perceptual/attentional processing</td>
</tr>
<tr>
<td>vMMN</td>
<td>N150–400</td>
<td>Prediction/prediction-error</td>
</tr>
<tr>
<td>P2</td>
<td>P200–300</td>
<td>Not well understood</td>
</tr>
<tr>
<td>N2</td>
<td>N200–350</td>
<td>Object recognition</td>
</tr>
<tr>
<td>P3a/P3b</td>
<td>P300 onwards</td>
<td>Cognitive load, categorization</td>
</tr>
</tbody>
</table>

The ERP technique is popular among neuroscientists, because it tells us about the neural processing of a particular stimulus and because it tells us when that process occurs in the brain (Luck, 2005; O’Shea et al., 2009; Woodman, 2010). This makes ERPs a valuable tool for testing theories of visual perception, top-down attention, and visual consciousness. However,
similar to EEG recordings, because there are an infinite number of distributions of sources consistent with any set of ERP recordings, it is impossible to localise ERP sources in the brain unambiguously.

To date, ERPs have been used in thousands of studies (a Web of Science database search yielded more than 35,000 items) as a tool to assess brain processing for a wide range of processes, including perception, learning, and memory (e.g., Luck, 2005; Woodman, 2010). My particular interest is in the way in which EEG and ERP signals alter when visual input changes unexpectedly, which I review in the next section.

2.2 Visual mismatch negativity and the thesis

In this section, I review vMMN and I discuss the general aim of my thesis. The goal of this section is to provide the theoretical reasons for conducting my research.

2.2.1 Visual mismatch negativity: An introduction

When an unexpected visual event occurs in our field of view, there is a sudden change in the electrical activity of our brains as measured from electrodes on the scalp (EEG), called the vMMN (for reviews, see Czigler, 2007; Kimura, 2012; Kimura et al., 2011; Pazo-Alvarez et al., 2003; Winkler
vMMN and visual consciousness

& Czigler, 2012). vMMN is typically observed in the oddball paradigm (Kimura, Katayama, Ohira, & Schröger, 2009; see Figure 2.1).

Figure 2.1. Visual Mismatch Negativity and the Oddball Paradigm. (a) vMMN is typically observed in the oddball paradigm: an infrequent visual stimulus—a deviant (in this case, a grey bar orientated 18° from vertical), is randomly and unpredictably presented in a sequence of more frequent visual stimuli—the standards (in this case, a grey bar orientated –18° from vertical). (b) There is a more negative ERP for the deviant than for the standard from 100 to 250 ms after stimulus onset. (c) vMMN is seen most clearly in the difference wave: the ERP for the deviant minus the ERP for the standard, between 100 and 400 ms (in this case, vMMN is maximal at about 180 ms). Figure from Kimura (2012; his Figure 1).
Several explanations have been proposed to explain the generation of vMMN. The current consensus explanation is predictive coding (e.g., Garrido et al., 2009; Schröger et al., 2013; Stefanics et al., 2014; Wacongne et al., 2012; Winkler & Czigler, 2012): somehow, the brain encodes the statistical regularities of visual input (i.e., it detects the regular presentation of a standard), it establishes top-down predictive models of visual perception based on past experience and learning (i.e., it predicts that the next stimulus will also be a standard), it tests the accuracy of these predictive models by comparing them to upcoming visual input (i.e., it compares bottom-up visual input with a top-down predictions, in this case, a prediction of the standard), and it updates these predictive models when they are found to be mismatched with visual input (i.e., when visual input is not the standard)—prediction-error (e.g., Friston, 2005; Rao & Ballard, 1999). Therefore, vMMN is a brain signature of the processing of prediction and prediction-error of visual input. In Section 2.2.1.3, I review two other explanations for vMMN: the memory-trace hypothesis and the adaptation (or “refractoriness”) hypothesis.

The study of the MMN brain response is not limited to the visual modality, to EEG, or to healthy adults. For example, MMN has been studied in the auditory (e.g., Näätänen, Gaillard, & Mäntysalo, 1978; for reviews, see Näätänen, 1990, 1992; Näätänen et al., 2007; Schröger, 2007; Winkler, 2007), olfactory (e.g., Krauel, Schott, Sojka, Pause, & Ferstl, 1999; Pause &
Krauel, 2000), and somatosensory modalities (e.g., Akatsuka et al., 2005; Kekoni et al., 1997; Shinozaki, Yabe, Sutoh, Hiruma, & Kaneko, 1998; Spackman, Boyd, & Towell, 2007); vMMN can be obtained with MEG (e.g., Kogai et al., 2011; Urakawa, Inui, Yamashiro, & Kakigi, 2010), with fMRI (e.g., Gomot, Giard, Fonlupt, & Bruneau, 2011), and with intracranial recordings (e.g., Astikainen, Ruusuvirta, & Korhonen, 2000, 2005); and vMMN can be studied for diagnostic purposes (for review, see Maekawa, Hirano, & Onitsuka, 2012), such as in the case of Alzheimer’s disease and mild cognitive functioning (e.g., Stothart, Tales, & Kazanina, 2012; Tanaka, Okubo, Fuchigami, & Harada, 2001; Tales, Haworth, Wilcock, Newton, & Butler, 2008; Tales, Muir, Bayer, Jones, & Snowden, 2002; Tales & Butler, 2006), schizophrenia (e.g., Maekawa et al., 2008; Urban, Kremláček, Masopust, & Libiger, 2008), bipolar disorder (e.g., Maekawa et al., 2013), panic disorder (e.g., Tang et al., 2013), and alcohol intoxication (e.g., Kenemans, Hebly, van der Heuvel, & Grent-T-Jong, 2010), as well as in animals (e.g., Astikainen et al., 2000, 2005). Even though these studies offer fascinating insights into the generation of vMMN brain response and its functional significance, because these topics are beyond the scope of this thesis, I will not discuss them further.

I will now summarise the general characteristics of vMMN.
2.2.1.1 Stimulus features and paradigms

vMMN is elicited by an unexpected change in visual input (Czigler, 2014; Kimura, 2012). Stimulus features that yield a vMMN include:

- Colour (e.g., Cammann, 1990; Grimm, Bendixen, Deouell, & Schröger, 2009; Müller et al., 2010; for a corresponding MEG study, see Urakawa et al., 2010).
- Direction of motion (e.g., Amenedo, Pazo-Alvarez, & Cadaveira, 2007; Kremláček, Kuba, Kubová, & Langrová, 2006; Pazo-Alvarez, Amenedo, & Cadaveira, 2004).
- Orientation (e.g., Astikainen, Lillstrang, & Ruusuvirta, 2008; Astikainen, Ruusuvirta, Wikgren, & Korhonen, 2004; Czigler & Pató, 2009; Kimura et al., 2009; Sulykos, Kecskés-Kovács, & Czigler, 2013).
- Spatial frequency (e.g., Heslenfeld, 2002; Maekawa et al., 2005; Sulykos & Czigler, 2011; for a corresponding MEG study, see Kogai et al., 2011).
- Shape (e.g., Alho, Woods, Algazi, & Näätänen, 1992; Grimm et al., 2009; Maekawa et al., 2005; Tales, Newton, Troscianko, & Butler, 1999).
• Size (e.g., Alho et al., 1992; Kimura, Katayama, & Murohashi, 2008a; Woods, Alho, & Algazi, 1992).
• Contrast/luminance (e.g., Kimura, Katayama, & Murohashi, 2008b, 2008c; Kimura, Widmann, & Schröger, 2010a, 2010b; Stagg, Hindley, Tales, & Butler, 2004).
• Conjunction of colour and orientation (e.g., Winkler, Czigler, Sussman, Horváth, & Balázs, 2005).
• Human facial expression (e.g., Astikainen & Hietanen, 2009; Kreegipuu et al., 2013; Stefanics, Csukly, Komlósi, Czobor, & Czigler, 2012; Zhao & Li, 2006).
• Gender of human faces (e.g., Kecskés-Kovács, Sulykos, & Czigler, 2013a).
• Lateralization of human hands (Stefanics & Czigler, 2012).
• Eye-of-origin (e.g., Jack, Roeber, & O’Shea, 2012; van Rhijn, Roeber, & O’Shea, 2013).
• Symmetrical-to-asymmetrical patterns (but not asymmetrical-to-symmetrical patterns; e.g., Kecskés-Kovács, Sulykos, & Czigler, 2013b).
• Stimulus duration (e.g., Khodanovich, Esipenko, Svetlik, & Krutenkova, 2010; Qiu et al., 2011).
• Stimulus omission (e.g., Czigler et al., 2006).
• Sequential regularity (e.g., Czigler, Weisz, & Winkler, 2006).
In most of the studies mentioned above, vMMN was generated using the oddball paradigm: an infrequent visual stimulus—a deviant, was randomly and unpredictably presented in a sequence of more frequent stimuli—the standards. However, in a typical oddball sequence, standards and deviants can differ in at least three ways:

1. Standards and deviants cannot be physically identical, and it is possible that physical differences in stimulation contribute a source of variability between standard and deviant ERPs. A simple solution to this problem is to use the so-called flip-flop technique whereby the standards and deviants in one sequence are deviants and standards, respectively, in another. This allows one to compare physically identical standards and deviants (e.g., Kujala, Tervaniemi, & Schröger, 2007).

2. Because the standards are more frequent than the deviants, they are presumably processed by neurons that are more adapted than neurons processing the deviant (Jääskeläinen et al., 2004; May & Tiitinen, 2010). By adapted, I mean that neurons alter their responsiveness to a stimulus if it is repeated, usually by decreasing responsiveness to all stimuli, including those other than their preferred stimulus (O’Shea, In preparation). A pragmatic solution to this issue is to use the combined oddball-equiprobable paradigm in which deviants
are compared with physically identical controls that are equally infrequent set in a context from which no predictions can be made (see below; e.g., Schröger & Wolff, 1996).

3. According to the predictive coding interpretation of vMMN, standards and deviants differ in terms of prediction—the standards are predicted and the deviants are not (e.g., Garrido et al., 2009; Schröger et al., 2013; Stefanics et al., 2014; Wacongne et al., 2012; Winkler & Czigler, 2012). Indeed, this difference can also be explored using the combined oddball-equiprobable paradigm (see next; e.g., Schröger & Wolff, 1996).

To dissociate the underlying mechanisms that give rise to vMMN, adaptation and prediction-error, Schröger and Wolff (1996) proposed the combined oddball-equiprobable paradigm. In the oddball sequence, deviants are randomly and unpredictably presented in a sequence of standards; in the equiprobable sequence, a stimulus that is physically identical to the deviant from the oddball sequence—a control, is embedded in a sequence with many other sorts of stimuli, all of which are as frequent as the deviant from the oddball sequence. Because there are no standards or deviants in the equiprobable sequence, and because controls are as frequent as the deviant, control minus standard comparisons yield differences in adaptation—an adaptation-based mechanism of deviance detection, and deviant minus control comparisons yield differences in
prediction and prediction-error—a prediction-error-based mechanism of deviance detection (e.g., Astikainen et al., 2008; Czigler, Balázs, & Winkler, 2002; Kimura et al., 2009; Pazo-Alvarez, Amenedo, & Cadaveira, 2004).

For example, Kimura et al. (2009) set out to study the underlying mechanisms that give rise to vMMN. They used an oddball sequence that consisted of standards—a grey bar orientated −18° from vertical, and deviants—a grey bar orientated 18° from vertical, and found a vMMN from 100 to 250 ms. To dissociate adaptation and prediction-error, they also used an equiprobable sequence that consisted of control stimuli—grey bars that were aligned to one of five orientations (−90°, −54°, −18°, 18°, 54° from vertical). Kimura et al. (2009) found an adaptation-based mechanism of deviance detection (controls minus standards) from 100 to 150 ms, and a prediction-error-based mechanism of deviance detection (deviants minus controls) from 200 to 250 ms (see Figure 2.2).
Figure 2.2. Visual Mismatch Negativity and the Combined Oddball-Equiprobable Paradigm. (a) vMMN and the oddball paradigm (for review, see Figure 2.1). (b) In the combined oddball-equiprobable paradigm: standards and deviants from the oddball sequence are compared with controls from the equiprobable sequence. (c) The ERPs for standards, deviants, and controls. (d) vMMN and its underlying mechanisms are seen most clearly in the difference waves: deviant minus standard comparisons yield the vMMN, control minus standard comparisons yield an adaptation-based mechanism of deviance detection, and deviant minus control comparisons yield a prediction-error-based mechanism of deviance detection. Figure from Kimura (2012; his Figure 1).
2.2.1.2 Scalp topography and neural generators

Deviant minus standard comparisons show that vMMN is a negative component of ERPs, that it has a peak latency between 150 and 400 ms after stimulus onset, and that it has a peak amplitude of about 2 to 5 µV. Deviant minus standard voltage maps of the scalp show that vMMN has a posterior scalp distribution (most typically, a right parieto-occipital and occipito-temporal maximum; Czigler, 2007; Kimura, 2012). In addition, some studies have shown positive voltages over frontal and prefrontal regions of the brain (e.g., Astikainen et al., 2008; Wei, Chan, & Luo, 2002). This is often interpreted as indirect evidence for the involvement of top-down processes in the generation of vMMN, such as those described by theories of predictive coding (e.g., Garrido et al., 2009; Schröger et al., 2013; Stefanics et al., 2014; Wacongne et al., 2012; Winkler & Czigler, 2012).

What regions of the brain are involved in the generation of vMMN? Kimura (2012) summarised three studies showing that the neural generators of vMMN can be found in visual extrastriate areas (both hemispheres) and prefrontal areas of the brain (with a hint of a right hemisphere bias). I review them here:

- Pazo-Alvarez, Amenedo, Lorenzo-López, and Cadaveira (2004) used LORETA (Pascual-Marqui et al., 1994) to locate the neural generators of vMMN elicited by changes in direction of motion
information. They found that the neural generators of vMMN were in visual extrastriate areas (both hemispheres), especially V5 (also known as the middle temporal visual area), an area of the brain responsible for the processing of motion (e.g., Frisby & Stone, 2010).

- Urakawa et al. (2010) used MEG to locate the neural generators of vMMN elicited by changes in colour information. MEG has some important advantages over ERPs in localising neural activity, because the brain and skull are transparent to magnetic fields (Luck, 2005). They found that the neural generators of visual mismatch field (vMMF; the MEG equivalent of vMMN) were in visual extrastriate areas (both hemispheres) and in ventrolateral prefrontal areas (right hemisphere only).

- Finally, Yucel, McCarthy, and Belger (2007) used fMRI to localise the neural generators of vMMN elicited by changes in colour information. One reason for using fMRI is that it has spatial resolution (in the order of millimetres) which is much better than that provided by ERPs and MEG (Luck, 2005). They found that the neural generators of vMMN were in visual striate and extrastriate areas (both hemispheres), parietal areas (both hemispheres), and dorsolateral prefrontal areas (both hemispheres with a right hemisphere bias).
However, because these studies used the oddball paradigm to elicit vMMN, they could not control for the different states of adaptation that exist between standards and deviants. Therefore, these studies could not dissociate adaptation-based mechanisms from prediction and prediction-error-based mechanisms. To dissociate these mechanisms successfully, one would need to use the combined oddball-equiprobable paradigm. That is exactly what Kimura, Ohira, and Schröger (2010) did.

Kimura, Ohira, and Schröger (2010) reanalysed the data of Kimura et al. (2009; for review, see Figures 2.1 and 2.2) using sLORETA (Pascual-Marquï, 2002). They found that the neural generators of adaptation-based mechanisms of deviance detection were in visual striate and extrastriate areas (both hemispheres). This is consistent with Pazo-Alvarez, Amenedo, Lorenzo-López, and Cadaveira (2004), Urakawa et al. (2010), and Yucel et al. (2007). They also found that the neural generators of prediction-error-based mechanisms of deviance detection were in visual extrastriate areas (both hemispheres) and medial prefrontal areas (right hemisphere only), including the orbital gyrus. This is consistent with Urakawa et al. (2010) and Yucel et al. (2007), but not with Pazo-Alvarez, Amenedo, Lorenzo-López, and Cadaveira (2004), because Pazo-Alvarez, Amenedo, Lorenzo-López, and Cadaveira (2004) did not find any differences between standards and deviants in prefrontal regions of the brain. I conclude that the overall results suggest that the neural generators of vMMN are located in visual
extrastriate areas (both hemispheres) and prefrontal areas of the brain (right hemisphere bias).

2.2.1.3 *Explanations for visual mismatch negativity*

So far, I have characterised vMMN as a brain signature of prediction and prediction-error (e.g., Garrido et al., 2009; Schröger et al., 2013; Stefanics et al., 2014; Wacongne et al., 2012; Winkler & Czigler, 2012): somehow, the brain encodes the statistical regularities of visual input (i.e., it detects the regular presentation of a standard), it establishes top-down predictive models of visual perception based on past experience and learning (i.e., it predicts that the next stimulus will also be a standard), it tests the accuracy of these predictive models by comparing them to upcoming visual input (i.e., it compares visual input with the prediction of a standard), and it updates these predictive models when they are found to be mismatched with visual input (i.e., the prediction is incompatible with the unexpected presentation of a deviant)—prediction-error (e.g., Friston, 2005; Rao & Ballard, 1999). Therefore, vMMN is a brain signature of the processing of prediction and prediction-error of visual input.

Although predictive coding is the current consensus explanation for the generation of vMMN (e.g., Garrido et al., 2009; Schröger et al., 2013; Stefanics et al., 2014; Wacongne et al., 2012; Winkler & Czigler, 2012), I will
now provide two other explanations: the memory-trace hypothesis and the adaptation hypothesis.

The memory-trace hypothesis proposes that vMMN is elicited when the current visual stimulus—the deviant, is dissimilar to the memory representation that is generated by the previous stimulus—the standard (e.g., Näätänen, 1992). Indeed, this explanation is similar to predictive coding, because a previous event is compared to the current event. However, unlike predictive coding, which states that vMMN is the result of top-down and bottom-up processes in the brain, the memory-trace hypothesis states that vMMN is the result of bottom-up processes only. For many years, the memory-trace hypothesis was the dominant explanation for MMN and vMMN (for review, see Näätänen et al., 2007). However, there is growing evidence against this account. For example, Kimura, Katayama, and Murohashi (2006) found that vMMN is elicited only when a deviant is preceded by a sequence of at least four standards; sequences consisting of fewer than four standards do not elicit vMMN. This result is inconsistent with a memory-trace explanation of vMMN, because according to this hypothesis, vMMN should be elicited when a previous event is different to the current event.

Another interpretation of vMMN is the adaptation hypothesis, which states that vMMN is the result of different states of adaptation between standards and deviants. That is, because the standards are more frequent
than the deviants, they are presumably processed by neurons that are more adapted than neurons processing the deviant (Jääskeläinen et al., 2004; May & Tiitinen, 2010). However, there is considerable evidence against this interpretation as the sole contributor to vMMN. For example, Kimura et al. (2009) showed differences between physically identical deviants and controls from the combined oddball-equiprobable paradigm (for review, see Figure 2.1). These differences cannot be explained by adaptation, because these stimuli are equally adapted by the visual system. Therefore, these differences must be caused by another mechanism of deviance detection: prediction and prediction-error.

At present, predictive coding is the only hypothesis that best accounts for all of the available vMMN data (for reviews, see Garrido et al., 2009; Schröger et al., 2013; Stefanics et al., 2014; Wacongne et al., 2012; Winkler & Czigler, 2012).

2.2.2 General aim of the thesis

So far in this section, I have reviewed the general characteristics of vMMN. I will now discuss the general aim of my thesis: to investigate conscious and not-conscious processing of sequences of stimuli that give rise to vMMN. The reasons for this are:
1. vMMN is thought to be an automatic brain response—it is elicited in the absence of top-down attention (Czigler, 2007; Stefanics et al., 2007). However, attention is not the only tool for assessing automatic processing of vMMN; one can also manipulate visual consciousness. Although attention and visual consciousness are often treated as essentially the same psychological construct (e.g., Dehaene et al., 2006), there is a growing body of research that shows that they perform separate functions in the brain (e.g., Crick & Koch, 2003; Lamme, 2003) and that they can be doubly dissociated (e.g., Koch & Tsuchiya, 2007). Therefore, one reason for conducting this research is to study the automatic processing of vMMN.

2. An important component of theories of predictive coding, the current consensus explanation for vMMN (e.g., Garrido et al., 2009; Schröger et al., 2013; Stefanics et al., 2014; Wacongne et al., 2012; Winkler & Czigler, 2012), is that the brain establishes, tests, and updates predictive models of visual perception, even when visual input for those predictions does not reach conscious visual perception (e.g., Hohwy et al., 2008; Mill et al., 2011, 2013; Spratling, 2008). However, to the best of my knowledge, this has never been tested experimentally. Therefore, another reason for conducting this research is to
provide evidence confirming this assumption of theories of predictive coding and of MMN and vMMN.

I will now review each reason in more detail.

### 2.2.2.1 Reason 1: Attention and consciousness

vMMN is thought to be an automatic brain response—it is elicited in the absence of top-down attention. Indeed, there is abundant evidence for this fact (e.g., Alho et al., 1992; Amenedo et al., 2007; Cammann, 1990; Heslenfeld, 2002; Kremláček et al., 2006; Maekawa et al., 2005; Pazo-Alvarez, Amenedo, & Cadaveira, 2004; Stagg et al., 2004; Tales & Butler, 2006; Tales et al., 1999; van Rhijn et al., 2013; Winkler et al., 2005; Woods et al., 1992; for reviews, see Czigler, 2007; Stefanics et al., 2014, especially their Table 1). In general, manipulating attention or task difficulty does not influence the amplitude or latency of vMMN (e.g., Heslenfeld, 2002; Pazo-Alvarez, Amenedo, & Cadaveira, 2004; but see Kimura & Takeda, 2013), suggesting that the generation of vMMN is an automatic process. However, attention is not the only tool for assessing automatic processing of vMMN; one can also manipulate visual consciousness.

What is attention? What is consciousness? And what is their relation to each other and to visual perception? Unfortunately, these questions are difficult to resolve, even within the scholarly literature. Nevertheless, it is
often assumed that attention and consciousness are the same psychological construct (e.g., Dehaene et al., 2006). For example, when we attend to an object, such as a human face, we become conscious of its features; when we shift attention away from an object, say, toward something else, the original object fades from consciousness. I will now provide separate definitions for top-down attention and visual consciousness and explain how they can be doubly dissociated.

According to Crick and Koch (2003) and Lamme (2003), top-down attention and visual consciousness contribute to the construction of visual perception in different ways: top-down attention selects visual input for further processing; visual consciousness summarises all available visual input. To illustrate this difference, I will provide an example given by Crick and Koch (2003): imagine you are standing outside your favourite restaurant waiting for a friend. You notice that there are hundreds of people in the area, meaning that you will have to look through the crowd. However, rather than search the entire visual scene, you select a small area, say, the region directly in front you, search it with your eyes, and shift your gaze to another region. This is an example of top-down attention, because visual information is selected for further processing. Visual consciousness, on the other hand, is a summary of the entire visual scene, not just the region of the crowd you are searching. That is, even though you are searching for your friend in a region of the crowd directly in front of you, you may
become aware of your friend’s presence when he or she exits the crowd to your left. Therefore, top-down attention and visual consciousness perform separate functions in the brain.

If one accepts that top-down attention and visual consciousness perform separate functions in the brain, then one must also accept that they can be doubly dissociated. Koch and Tsuchiya (2007) proposed a model in which top-down attention and visual consciousness can be doubly dissociated (see Table 2.3; based on Koch & Tsuchiya, 2007).

<table>
<thead>
<tr>
<th>Attention</th>
<th>Conscious</th>
<th>Not-conscious</th>
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<tr>
<td>Attention with consciousness</td>
<td>Attention without consciousness</td>
<td></td>
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<tr>
<td>Consciousness without attention</td>
<td>No-attention, no-consciousness</td>
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According to Koch and Tsuchiya’s (2007) model, top-down attention and visual consciousness can be doubly dissociated into four distinct categories. These categories are (Koch & Tsuchiya, 2007, p. 17–19):

1. Attention with consciousness. For instance, when we attend to an object, we become conscious of its features. For example, participants can attend to a novel stimulus and be conscious of its features (e.g., Mack & Rock, 1998).
2. No-attention, no-consciousness. For instance, when we shift attention away from an object, it disappears from consciousness. For example, negative afterimages can be produced by stimuli that are both unattended and not-conscious (e.g., Gilroy & Blake, 2005; Tsuchiya & Koch, 2005).

3. Attention without consciousness. For instance, when we attend to an object for several seconds, under some circumstances, we can fail to become conscious of its features. For example, in heterosexuals, erotic pictures of the opposite sex attract attention, even when these images are not-conscious (e.g., Jiang, Costello, & He, 2007).

4. Consciousness without attention. For instance, when we focus intently on one object in a visual scene, we are still conscious of other objects that are not attended. For example, when an image is unexpectedly flashed on a screen, participants can report the gist of the image, even though they were unable to attend to all of its features (e.g., Kirchner & Thorpe, 2006).

Recently, Watanabe et al. (2011) used a two-by-two factorial design to doubly dissociate top-down attention and visual consciousness. In their experiment, they presented a target—a moving grating, and a suppressing annulus—a mosaic of multiple patches of smaller motion gratings. To manipulate attention, they asked participants either to attend to the target
grating (they called this their attention-to-target condition) or to identify when a specific letter was presented in a stream of letters (they called this their inattention-to-target condition). To manipulate visual consciousness, they presented their stimuli either to the same eye, such that the target was conscious (they called this their visible condition), or to different eyes, such that the target was not-conscious, yielding CFS (they called this their invisible condition; for review of CFS, see Section 2.3.2).

Watanabe et al. (2011) found that manipulating top-down attention affected blood oxygen level-dependent (BOLD) activity in V1: BOLD activity to the target grating was bigger when attention was on the target than when attention was not on the target, regardless of whether the target was conscious or not-conscious. Critically, they found that manipulating visual consciousness had no effect on BOLD activity in V1. These results show that top-down attention and visual consciousness perform separate functions in the brain, as early as V1 for visual stimuli, and that they can be successfully doubly dissociated.

If one accepts that top-down attention and visual consciousness perform separate functions in the brain, and if one accepts that top-down attention and visual consciousness can be doubly dissociated, then there are two questions that need to be addressed regarding the automaticity of the vMMN brain response:
1. Do sequences of not-conscious standards and deviants yield vMMN?

2. If so, does manipulating visual consciousness influence the processing of vMMN?

To the best of my knowledge, the answers to these questions are a mystery. Therefore, the general aim of my thesis is to conduct the research necessary to fill this gap in knowledge.

2.2.2.2 Reason 2: Not-conscious models of perception

The current consensus explanation for vMMN is predictive coding (e.g., Garrido et al., 2009; Schröger et al., 2013; Stefanics et al., 2014; Wacongne et al., 2012; Winkler & Czigler, 2012): somehow, the brain establishes, tests, and updates predictive models of visual perception (e.g., Friston, 2005; Rao & Ballard, 1999). An important component of theories of predictive coding is that the brain establishes, tests, and updates predictive models of visual perception, even when visual input for those predictions does not reach conscious visual perception (Hohwy et al., 2008; Mill et al., 2011, 2013; Spratling, 2008). Although there are several descriptive and computational models of predictive coding, for simplicity, and because this model is relevant to other parts of the thesis, I review Hohwy et al.’s (2008) predictive coding explanation for binocular rivalry.
Hohwy et al. (2008) proposed a predictive coding explanation for binocular rivalry, a powerful form of bistable perception in which visual consciousness alternates unpredictably between two dissimilar images presented one to each eye (Wheatstone, 1838; for review, see Alais & Blake, 2004; Blake & O’Shea, 2009; Miller, 2013). That is, one of the images is dominant, visible, whereas the other is suppressed, invisible. For example, when one eye is shown a picture of a face and the other eye is shown a picture of a house, rather than seeing a combination of the two (i.e., a face-house), observers typically report seeing the face for a few seconds, then the house for a few seconds, then the face again, and so on, for as long as one cares to look (for review of binocular rivalry, see Section 2.3.1).

There are two properties of binocular rivalry that need to be explained. The first is why, when the two eyes are presented with dissimilar images, we see only one of them at a time—this is called the selection problem. The second is why the image we see changes over time—this is called the alternation problem. These problems can be addressed with predictive coding.

Hohwy et al. (2008) argued that the selection problem in binocular rivalry is solved by priors, or likelihood, that a prediction is an accurate representation of visual input. That is, one of the images (i.e., a face) is selected for visual consciousness because it has a higher prior than the other image (i.e., a house) or than both images superimposed (i.e., a face-house).
In addition, Hohwy et al. (2008) solved the alternation problem using prediction-error. If one of the images accounts for half of the total visual input, then the other half of visual input is unexplained and is therefore prediction-error. According to theories of predictive coding, prediction-error is passed up the hierarchy until it is resolved by higher-level neurons (e.g., Friston, 2005; Rao & Ballard, 1999), because it is unacceptable to the predictive model that half of the visual input remains unexplained. When this happens, there is a change in visual consciousness, such that the image that was previously suppressed is now dominant and the image that was previously dominant is now suppressed. Furthermore, the image that is now suppressed is the new source of prediction-error in visual input. This pattern repeats itself for as long as one cares to look (for similar accounts, see Dayan, 1998; Sundareswara & Schrater, 2008).

Critically, Hohwy et al.’s (2008) predictive coding explanation of binocular rivalry assumes that the brain establishes, tests, and updates predictive models of visual perception, even when visual input for those predictions does not reach conscious visual perception. That is, Hohwy et al.’s (2008) predictive coding explanation of binocular rivalry states that the image that is suppressed from visual consciousness is prediction-error. If one accepts that a suppressed image contributes a source of prediction-error in the visual system, one must also accept that the brain establishes, tests, and updates predictive models of visual perception for not-conscious visual
input, because visual input cannot be prediction-error if there is no original prediction.

Although Hohwy et al.’s (2008) predictive coding explanation of binocular rivalry demonstrates that the brain establishes, tests, and updates predictive models of visual perception for not-conscious visual input, to the best of my knowledge, this claim has never been tested. Therefore, the general aim of my thesis is to conduct the research necessary to fill this gap in knowledge.

2.2.2.3 Visual mismatch negativity and consciousness

To the best of my knowledge, only three studies have investigated vMMN in the absence of visual consciousness. I review them here:

1. Czigler, Weisz, and Winkler (2007) used backward masking, a popular tool for making a brief target stimulus perceptually invisible by following it with a mask. They presented their standards and deviants, either green/black or red/black checkerboard patterns, for 14 ms, followed by a mask consisting of red and green hexagons, also for 14 ms. In their not-conscious condition, the time between the onset of the standard or deviant and the mask was 14 ms; in their conscious condition, the time between the onset of the standard or deviant
and the mask was 174 ms. Czigler et al. (2007) found a vMMN in their conscious condition, and although there was a hint of a difference between standards and deviants in their not-conscious condition, the difference was not statistically significant. They argued that their failure to find a vMMN in the not-conscious condition was likely due to the complexity of their mask: their mask differed from the standards and deviants in both shape and colour, and that these features may have prevented a reliable vMMN from being generated in the brain. This study leaves open the question of whether vMMN can be generated from not-conscious stimuli.

2. Kogai et al. (2011) also used backward masking. They presented their standards and deviants (vertical gratings that differed only in spatial frequency) for 17 ms, followed by a mask (a vertical grating that differed in spatial frequency to the standards and deviants) for 433 ms. Kogai et al. (2011) found a vMMF when deviants with a high spatial frequency were infrequently presented in a sequence of standards with a low spatial frequency (they called this their Condition 2), but not when deviants with a low spatial frequency were infrequently presented in a sequence of standards with a high spatial frequency.
vMMN and visual consciousness

frequency (they called this their Condition 1). There are at least three limitations to their conclusion:

a. Kogai et al. (2009) did not compare physically identical stimuli (e.g., Kujala et al., 2007). Rather, they report their participants’ responses to the stimuli from different conditions separately. Therefore, it is possible that this physical difference contributed a source of variability that obscured their results. Furthermore, after visual inspection of Kogai et al.’s (2009) Figure 2, I suspect that they would not have found a vMMF even if they had compared physically identical stimuli, because responses to high spatial frequency gratings as standards and as deviants are essentially identical, and because responses to low spatial frequency gratings as standards and as deviants are also essentially identical.

b. Participants were asked to detect the presentation of a deviant. Although Kogai et al. (2009) obtained a low hit ratio, suggesting that participants could not detect the difference between standards and deviants, they also obtained a low false alarm ratio. I calculated $d'$, a measure of sensitivity to the deviants from signal detection theory (Swets, 1964) and found it to be around
unity. That is, Kogai et al.’s (2009) participants were conscious of the deviants, albeit with a conservative response criterion.

c. Kogai et al. (2009) randomly sampled 100 standards from a total of 900. Therefore, it is possible that the standards they selected do not accurately reflect the nature of all of their standards. It is also possible that Kogai et al. (2009) have committed a Type-I error.

I conclude that Kogai et al.’s (2009) study does not bear on the question of whether vMMN can occur in the absence of visual consciousness.

3. Berti (2011) used the attentional blink, the tendency to ignore a second target when it is presented between 200 and 600 ms after a first target, to prevent his standards and deviants from being perceived. He presented his deviants (a slight shift upwards from the standard position) either 300 ms after the first target, such that it was not-conscious, or 700 ms after the first target, such that it was conscious. Berti (2011) found a vMMN in both conditions. However, the attentional blink does not influence visual consciousness; rather, as the name of the illusion suggests, it influences attention. That is, participants did not attend to the deviant. Therefore, Berti (2011) did not show
vMMN to not-conscious deviants; instead, he showed vMMN to unattended deviants.

I conclude from the literature that the effects of visual consciousness on the generation of vMMN are unknown, and that there is no empirical evidence supporting the notion that the brain establishes, tests, and updates predictive models of visual perception for not-conscious visual input. Therefore, I set out to investigate conscious and not-conscious processing of sequences of stimuli that give rise to vMMN.

2.3 Manipulating visual consciousness

According to Kim and Blake (2005), the following techniques can be used to render a visual stimulus invisible to visual consciousness:

- Backward and forward masking.
- Visual crowding.
- Bistable figures.
- Binocular rivalry.
- Flash suppression.
- CFS.
- Motion-induced blindness.

To manipulate conscious visual perception, I used binocular rivalry and CFS, because they have some important advantages over the other
techniques for manipulating and studying visual consciousness. In this section, I review binocular rivalry and CFS, and I discuss how they can be combined with vMMN to investigate conscious and not-conscious processing of sequences of stimuli that give rise to vMMN. The goal of this section is to outline how I will accomplish the general aim of my thesis.

2.3.1 What is binocular rivalry?

Binocular rivalry is a powerful form of bistable perception in which visual consciousness alternates unpredictably between two dissimilar images presented one to each eye (Wheatstone, 1838; for reviews, see Alais & Blake, 2004; Blake & O’Shea, 2009; Miller, 2013). That is, one of the images is dominant, visible, whereas the other is suppressed, invisible. For example, when one eye is shown a picture of a face and the other eye is shown a picture of a house, rather than seeing a combination of the two (i.e., a face-house), observers typically report seeing the face for a few seconds, then the house for a few seconds, then the face again, and so on, for as long as one cares to look (see Figure 2.3).
Binocular rivalry is a remarkable phenomenon of visual perception, because a suprathreshold visual stimulus disappears from visual consciousness for several seconds, even though that stimulus is still being presented to one eye, and because the image that we perceive changes over time. Sometimes, transitions in visual consciousness from one image to the other can be abrupt, causing a sudden change in visual consciousness, and other times, transitions can be gradual in which a dynamic, patchy, mosaic-like combination of both images are briefly perceived at the same time (Yang, Rose, & Blake, 1992). Furthermore, sometimes there are return transitions: when a patchy combination of both images returns to the previously dominant percept (Brascamp, van Ee, Noest, Jacobs, & van den
Berg, 2006). This shows that participants' experience of binocular rivalry is that of continual, unpredictable changes in visual consciousness.

Binocular rivalry can occur between any two images, provided that they are sufficiently dissimilar that they cannot be combined via binocular fusion (Blake, 1989). For example, binocular rivalry can be experienced with simple stimuli, such as when one eye views a grating and the other eye views an identical, orthogonally orientated grating (e.g., contour rivalry; Breese, 1899) or when one eye views one colour and the other eye views a different colour (e.g., colour rivalry; Dutour, 1760), or with more complex stimuli, such as when one eye views a picture of a face and the other eye views a picture of a house (e.g., complex rivalry; see Figure 2.3; Tong, Nakayama, Vaughan, & Kanwisher, 1998). Binocular rivalry can also be experienced when the two eyes view pictures that are intermingled, such as when one eye views half of a red horizontal grating and half of a green circle grating and the other eye views the reverse image (e.g., perceptual grouping; Diaz-Caneja, 1928) or when one eye views an intermingled picture of a monkey’s face and some text and the other eye views the reverse image (e.g., Kovács, Papathomas, Yang, & Fehér, 1996). During binocular rivalry of intermingled pictures, rather than always perceiving one intermingled picture or the other, observers frequently perceive one percept, such as the monkey’s face, then the other percept, such as some text, then the monkey’s face again, and so on.
Binocular rivalry is a popular field of study for vision scientists, as evidenced by the number of publications on the topic (Baker, 2010). To that end, I do not intend to review binocular rivalry exhaustively but to give an overview of it and to provide an evaluation of its merits as a tool to study visual consciousness. There are numerous, comprehensive reviews of the literature (e.g., Alais, 2012; Alais & Blake, 2004; Blake, Brascamp, & Heeger, 2014; Blake & O’Shea, 2009; Blake & Wilson, 2011; Howard & Rogers, 2012; Miller, 2013).

I will now provide a brief history of binocular rivalry, an evaluation of binocular rivalry and its merits as a tool to study visual consciousness, and two explanations for binocular rivalry.

2.3.1.1 A brief history of binocular rivalry

According to Maier, Panagiotaropoulos, Tsuchiya, and Keliris (2012), binocular rivalry was discovered by Porta (1593) when he placed one book in front of one eye and another book in front of the other eye in an attempt to increase his productivity by reading from two books at the same time. However, to his surprise, he found that he could only read from only one book, then the other, then the first again, and so on, by transferring the “visual virtue” (p. 143) between his eyes (Wade, 1998). According to Wade
Wade (1998) credited Wheatstone (1838) with conducting the first systematic study of binocular rivalry. Using his newly invented mirror stereoscope, an optical device providing independent stimulation to the two eyes (e.g., see Figure 2.3b), Wheatstone described his experiences of binocular rivalry (p. 386):

If \([S\text{ and } A]\) are each presented at the same time to a different eye, the common border will remain constant, while the letter within it will change alternately from that which would be perceived by the right eye alone to that which would be perceived by the left eye alone. At the moment of change the letter which has just been seen breaks into fragments, while fragments of the letter which is about to appear mingle with them, and are immediately after replaced by the entire letter. It does not appear to be in the power of the will to determine the appearance of either of the letters, but the duration of the appearance seems to depend on causes which are under our control: thus if the two pictures be equally illuminated, the alternations appear in general of equal duration; but if one picture be more illuminated than the other, that which is less so will be perceived during a shorter time.

That is, Wheatstone (1838) reported dominance or suppression of one or the other image, the back and forth transitions in visual consciousness from one image to the other, the inability to maintain dominance of one or the other image for a prolonged time, and the effect of increasing the luminance of one or the other image on binocular rivalry predominance, the percentage of total time a particular image is dominant. These observations
are now hallmark characteristics of binocular rivalry (for reviews, see Alais & Blake, 2004; Blake & O’Shea, 2009; Miller, 2013).

The next major contribution to the study of binocular rivalry was made by Breese (1899, 1909). He studied how numerous properties of the stimuli and of the observer affected binocular rivalry. For example, he showed that when the two images have the same luminance, the predominance of each image is about 50%, that when the luminance of each image is uniformly increased, the rate of alternation between the two images increases, even though there is no change in predominance, and that when one image was duller than the other, it tended to be dominant far less than the higher luminance image.

Breese (1899) made one other major contribution to the study of binocular rivalry: he presented orthogonal red and green gratings to one eye only, and to his surprise, they fluctuated in visibility (p. 43):

… a rivalry of the colours was perceptible. Neither disappeared entirely: but at times the red would appear very distinctly while the green would fade, or the red would fade and the green appear distinctly. The two sets of lines showed the same fluctuation, keeping pace with the changing of the intensities of the colours. Sometimes one of them would disappear altogether. This rivalry of the colours and of the lines was much slower than the rivalry in binocular vision.

That is, Breese (1899) discovered monocular rivalry, a form of bistable perception in which visual consciousness alternates irregularly between two dissimilar images when both are presented to one eye. Breese
acknowledged that if monocular rivalry is similar to binocular rivalry, then rivalry is a general phenomenon that does not rely on the rival images’ being presented to different eyes (cf. Leopold & Logothetis, 1999).

According to Blake (2004), the next major milestone in binocular rivalry research came with the completion of three PhD dissertations on the nature of binocular rivalry in two years: one by Fox (1963), one by Whittle (1963), and one by Levelt (1965).

Fox (1963) studied the depth of binocular rivalry suppression. He presented a probe to one eye, such as a flash of light, during episodes of binocular rivalry dominance or suppression, and asked participants to press keys indicating whether he or she saw the probe. He found that flashes of light are harder to detect (Wales & Fox, 1970) and letters are more difficult to identify (Fox & Check, 1972) when the probe is presented to the suppressed eye than when an identical probe is presented to the dominant eye. This allowed objective quantification of the strength of suppression, which Fox (1963) found to be about half a log unit.

Whittle (1963) studied the transitions in visual consciousness from one image to the other. He discovered that a brief, patchy percept of both images would tend to be replaced by one or the other image along the features that comprise that image. That is, as some features of a particular image become dominant, more and more aspects of that same feature become dominant, too. On the basis of these observations, Whittle (1963) asserted that
binocular rivalry occurs within local zones of the visual field, and that figural processes are partly responsible for the alternation in visual consciousness from one image to the other.

Levelt (1965) made many contributions to the study of binocular rivalry. He is best known for his use of the term “stimulus strength” (p. 74), which he defined as the properties of binocular rivalry stimuli, such as their size, luminance, blur, and so on, and its effect on predominance, which he outlined in four propositions (Blake, 2004, p. 19–20):

1. Increasing the stimulus strength in one eye will increase the predominance of that stimulus.
2. Increasing the stimulus strength in one eye will not affect the average duration of dominance of that eye.
3. Increasing the stimulus strength in one eye will increase the rate of binocular rivalry alternations.
4. Increasing the stimulus strength in both eyes will increase the rate of binocular rivalry alternations.

Levelt (1967) was also the first to document the stochastic properties of binocular rivalry and to suggest that individual durations of episodes of binocular rivalry dominance comprised a gamma distribution. The gamma distribution has become another hallmark feature of binocular rivalry (for reviews, see Alais & Blake, 2004; Blake & O’Shea, 2009; Miller, 2013), and is used to determine that binocular rivalry was experienced during binocular
rivalry experiments (Blake, 1989). Furthermore, these discoveries prompted many others to investigate the statistical properties that govern binocular rivalry (e.g., Fox & Herrmann, 1967; Lehky, 1995; Walker, 1975; Zhou, Gao, White, Merk, & Yao, 2004).

There is one more important milestone in the history of binocular rivalry that deserves to be mentioned: the assertion that the importance of binocular rivalry, while an interesting phenomenon in its own right, is in its potential to tease apart the neural mechanisms that contribute to visual consciousness (Crick, 1996). Indeed, binocular rivalry’s potential as a tool for studying the neural correlates of visual consciousness had been recognised before (e.g., Myerson, Miezen, & Allman, 1981); however, according to Baker (2010), Crick’s (1996) commentary on binocular rivalry caught the attention of the cognitive neuroscience community.

### 2.3.1.2 Evaluation of binocular rivalry

Why is binocular rivalry a useful tool to study visual consciousness? Binocular rivalry is a useful tool to study visual consciousness, because a suprathreshold visual stimulus disappears from visual consciousness for several seconds, even though that stimulus is still being presented to one eye. This dissociation between visual sensation and visual consciousness offers us a window through which we can study the so-called neural
correlates of visual consciousness (Crick, 1996). Indeed, in the search for neural correlates of visual consciousness, many researchers have found fluctuations in brain activity associated with the appearance and disappearance of a stimulus (e.g., Kaernbach, Schröger, Jacobsen, & Roeber, 1999; Leopold & Logothetis, 1996; Lansing, 1964; Lumer, Friston, & Rees, 1998; Roeber et al., 2008; Tong et al., 1998; Veser, O'Shea, Schröger, Trujillo- Barreto, & Roeber, 2008; for reviews see Blake & Logothetis, 2002; Rees, Kreiman, & Koch, 2002; Tong, Meng, & Blake, 2006).

I will now evaluate binocular rivalry and its merits as a tool to study visual consciousness using the criteria set out by Kim and Blake (2005):

- Does binocular rivalry work with a broad range of visual stimuli? Yes. As discussed in Section 2.3.1, binocular rivalry can occur between any two images, provided that they are sufficiently dissimilar that they cannot be combined via binocular fusion (Blake, 1989).

- Does binocular rivalry work equally well in central and in peripheral vision? Yes. Unlike visual crowding, which is more effective in peripheral vision than in central vision (Kim & Blake, 2005), binocular rivalry is just as effective in central vision as it is in peripheral vision. However, binocular rivalry alternations are slower and local zones are larger in peripheral vision than in central vision (Blake, O’Shea, & Mueller, 1992).
• Are there constraints on the exposure duration of the stimulus? Yes. Binocular rivalry is stochastic (Levelt, 1967; Zhou et al., 2004), meaning that it produces unpredictable switches in visual consciousness. Despite this shortcoming, dominance durations in binocular rivalry can last up to several seconds, which is more than can be expected from backward masking or visual crowding (Kim & Blake, 2005; Hugrass & Crewther, 2012). Furthermore, the timing of binocular rivalry alternations can be better controlled using flash suppression: a stimulus is presented to one eye (this is called the adapting stimulus) for about a second while a blank stimulus is presented to the other eye. Then, when a new stimulus is presented to the eye viewing the blank stimulus, this stimulus becomes dominant and the adapting stimulus is immediately suppressed for at least several seconds (McDougall, 1901; Wolfe, 1984).

• Does binocular rivalry abolish all aspects of visual consciousness? Yes. As discussed in Section 2.3.1.1, binocular rivalry suppression is a powerful tool for abolishing aspects of visual consciousness. For example, flashes of light are harder to detect (Wales & Fox, 1970) and letters are more difficult to identify (Fox & Check, 1972) when the probe is presented to the suppressed eye than when an identical probe is presented to
the dominant eye. Furthermore, changes in the spatial frequency or orientation of a suppressed grating go unnoticed by a participant, even though these events are completely salient during episodes of binocular rivalry dominance (Blake & Fox, 1974a), and changes in the emotional expressions of human faces go unnoticed by participants during binocular rivalry suppression (Kim, Grossman, & Blake, 2002). These findings suggest that binocular rivalry suppression is a powerful effect.

Despite this, there are some exceptions. For example, increasing the contrast of (Wilson, Blake, & Lee, 2001) or providing abrupt transients to (O’Shea & Crassini, 1981) the suppressed stimulus, as well as presenting probes that move to the suppressed stimulus (Grindley & Townsend, 1965; Walker & Powell, 1979), tend to break binocular rivalry suppression immediately. Moreover, adaptation aftereffects to a grating can be generated, even when the adapting pattern is suppressed for large portions of the adapting period (Blake & Fox, 1974b). These findings suggest that binocular rivalry suppression does not affect all properties of visual stimuli equally, but it is certainly enough for my purposes.
• Does physical stimulation remain invariant when visual consciousness fluctuates? Yes. As discussed above, a suprathreshold visual stimulus disappears from visual consciousness for several seconds, even though that stimulus is still being presented to one eye.

To conclude, although there are some constraints on the duration of episodes of binocular rivalry dominance and suppression, binocular rivalry has many advantages that make it a useful tool for studying visual consciousness, especially for my purposes (see Section 2.3.3).

2.3.1.3 Explanations for binocular rivalry

As discussed in Section 2.2.2.2, there are two properties of binocular rivalry that need to be explained. The first is why, when the two eyes are presented with dissimilar images, we see only one of them at a time—this is called the selection problem. The second is why the image we see changes over time—this is called the alternation problem. I will now provide two explanations for these problems: adaptation and reciprocal inhibition, and predictive coding.

Adaptation and reciprocal inhibition is the theory that different populations of neurons process each image in the visual system and that when one population is active, that image is perceived (e.g., Blake &
Logothetis, 2002; McDougall, 1901; Noest, van Ee, Nijs, & van Wezel, 2007).

Reciprocal inhibition solves the selection problem, and refers to the proposal that the two populations of neurons are linked by inhibitory connections. When binocular rivalry stimuli are shown to the eyes, an observer sees both of them for the first 150 ms (Wolfe, 1983). This is thought to arise from the simultaneous activation of both populations, because excitation is a faster process than inhibition (Varela & Maturana, 1970). After the first 150 ms, one population successfully inhibits the other, resulting in only one of the images reaching visual consciousness.

Adaptation solves the alternation problem, and refers to the gradual decrease in the responsiveness of continuously active neurons. During binocular rivalry, the neurons processing the dominant image adapt, thereby reducing their excitation and the strength of inhibition they can exert on the neurons processing the suppressed image. Meanwhile, those other neurons are increasing their excitation and the strength of inhibition they can exert on the other population. Eventually, a tipping point is reached, at which the activity of the two populations is about equal, requiring only a small nudge (such as from internal noise or an eye movement), to reverse the balance of inhibition leading to an abrupt increase in the activity of the second population, leading to a change in visual consciousness. This pattern of reciprocal inhibition and adaptation continues for as long as one cares to look at binocular rivalry stimuli.
Another explanation for binocular rivalry is predictive coding (Hohwy et al., 2008). However, because I discussed this theory in Section 2.2.2.2, I will only provide a brief summary of it here. According to the predictive coding theory of binocular rivalry, the selection problem is solved by priors, or likelihood, that a prediction is an accurate representation of visual input. The alternation problem is solved using prediction-error. If one of the images accounts for half of the total visual input, then the other half of visual input is unexplained and is therefore prediction-error. Prediction-error is passed up the hierarchy until it is resolved by higher-level neurons (e.g., Friston, 2005; Rao & Ballard, 1999), because it is unacceptable to the predictive model that half of the visual input remains unexplained, leading to a change in visual consciousness.

Predictive coding is particularly attractive for explaining binocular rivalry, because it can accommodate findings that adaptation and reciprocal inhibition cannot. For example, some studies have shown that sensory input in other modalities (i.e., auditory, olfactory, and somatosensory) can influence alternations and dominance durations in binocular rivalry (e.g., Lunghi, Morrone, & Alais, 2014; Zhou, Jiang, He, & Chen, 2010). Adaptation and reciprocal inhibition are unable to explain these findings, because it does not account for multisensory inputs. Predictive coding, on the other hand, is able to explain these findings, because one of its assumptions is that
all sensory input contributes to the predictive model of perception (e.g., Jack & Hacker, 2014).

2.3.2 What is continuous flash suppression?

CFS is a powerful form of interocular suppression in which an image presented to one eye, such as a face, is suppressed from visual consciousness indefinitely by a rapidly changing sequence of Mondrian patterns presented to the other eye (Tsuchiya & Koch, 2004, 2005; Yang & Blake, 2012; for review, see Yang et al., 2014; see Figure 2.4). That is, during CFS, observers typically report seeing only the Mondrian patterns, even though a suprathreshold visual stimulus is presented to one eye. In fact, CFS has been shown to suppress an image from visual consciousness for up to 3 minutes (Tsuchiya & Koch, 2005); this time is about 100 times longer than that of binocular rivalry suppression (Yang et al., 2014). This quality of CFS makes it a more powerful tool than binocular rivalry.
CFS is a relatively new technique for studying visual consciousness. It was first reported by Tsuchiya and Koch (2004). They claimed that dynamic Mondrian patterns could suppress a broad range of images, including Gabor patches, human faces, and geometric shapes, from visual consciousness for up to 60 seconds (they used 60 second trials in their experiment).

I will now provide an evaluation of CFS and its merits as a tool to study visual consciousness, as well as two explanations for CFS.
2.3.2.1 Evaluation of continuous flash suppression

CFS is not, by itself, a useful tool to study visual consciousness, because visual consciousness does not fluctuate between two images, as in the case of binocular rivalry. Rather, CFS is a useful tool to study the neural processing of a stimulus in the absence of visual consciousness (Yang et al., 2014), because a suprathreshold visual stimulus disappears from visual consciousness for at least several minutes, even though that stimulus is still being presented to one eye. Many researchers have used CFS to investigate the neural processing of a stimulus in the absence of visual consciousness (e.g., Almeida, Mahon, Nakayama, & Caramazza, 2008; Bahrami et al., 2010; Fang & He, 2005; Jiang et al., 2007; Jiang & He, 2006; Kaunitz et al., 2011; Tsuchiya et al., 2009; Yang, Hong, & Blake, 2010; for review, see Yang et al., 2014).

How does CFS fare as a tool to study the neural processing of a stimulus in the absence of visual consciousness using the criteria set out by Kim and Blake (2005) and used in Section 2.3.1.2?

- Does CFS work with a broad range of visual stimuli? There are two aspects to this question. First, the CFS pattern: so far, only Mondrian and Mondrian-like patterns have been used in CFS experiments (Yang & Blake, 2012). That is, only a limited range of CFS patterns have been used.
Second, the image being suppressed: a broad range of simple and complex stimuli have been used, including Gabor patches, human faces, and geometric shapes (Tsuchiya & Koch, 2004, 2005). Therefore, a broad range of visual stimuli can be suppressed from visual consciousness during CFS.

- Does CFS work equally well in central and in peripheral vision? Yes. According to Yang et al. (2014), anecdotal observations suggest that CFS is just as effective in central vision as it is in peripheral vision.

- Are there constraints on the exposure duration of the stimulus? No. Unlike binocular rivalry, which is stochastic and can only suppress an image from visual consciousness for about 30 seconds (in 1 and 2 second intervals) in a 60 second trial, CFS can reliably and predictably suppress an image from visual consciousness for up to 3 minutes (Tsuchiya & Koch, 2005). This makes CFS a more reliable tool for suppressing an image from visual consciousness than binocular rivalry.

- Does CFS abolish all aspects of visual consciousness? Yes. In fact, the depth of suppression during CFS is much deeper than that of binocular rivalry suppression. For example, Tsuchiya et al. (2006) used the test-probe technique and found that visual sensitivity to a probe when it was superimposed on a CFS
pattern was approximately the same to that measured during binocular rivalry dominance and during normal monocular viewing. Critically, they found that visual sensitivity to a probe when it was superimposed on a suppressed image during CFS was considerably reduced, even more so than that measured during binocular rivalry suppression.

- Does physical stimulation remain invariant when visual consciousness fluctuates? This is an inappropriate question to ask of CFS, because during CFS, visual consciousness does not fluctuate. Rather, a visual stimulus disappears from visual consciousness for at least several minutes, even though that stimulus is still being presented to one eye. Therefore, I wish to evaluate CFS using two additional criteria/questions:

1. Does CFS have both a conscious and a not-conscious condition? It can. Obviously, CFS has a not-conscious condition, because the primary function of CFS is to prevent a stimulus from reaching visual consciousness. Nevertheless, there are at least two ways in which one can create a conscious condition. First, one can superimpose the stimulus of interest on the CFS patterns, rather than present it to the other eye, such that the stimulus of interest becomes
visible to visual consciousness (e.g., Harris, Schwarzkopf, Song, Bahrami, & Rees, 2011).

Second, one can present a blank stimulus to the eye viewing the CFS patterns whenever one presents the stimulus of interest to the other eye, such that it becomes visible to visual consciousness (e.g., Jack, Roeber, & O’Shea, 2014). That is, techniques exist which make it possible to have both a conscious and a not-conscious condition during CFS, but not without creating physical differences in the stimuli between these conditions. To date, this limitation of CFS has not been rectified.

2. Does physical stimulation remain invariant? As before, there are two aspects to this question. First, the CFS pattern: in order for CFS to suppress an image from visual consciousness, the CFS pattern must rapidly change. For example, most CFS experiments refresh the CFS patterns every 100 ms or so, because presenting individual CFS patterns for longer durations (i.e., for more than 200 ms) reduces the effectiveness of CFS (Yang et al., 2014). In any case, this is not a problem, because researchers are not interested in the processing of the CFS pattern; rather, they are interested in the processing of the suppressed image.
Second, the image being suppressed: physical stimulation can remain invariant for up to 3 minutes (Tsuchiya & Koch, 2005). Therefore, it is not a problem that physical stimulation changes for the CFS pattern, because it does not change for the image being suppressed.

To conclude, although there are some constraints on the range of CFS patterns that can be used to suppress an image from visual consciousness, and although there are physical differences in the stimuli between conscious and not-conscious conditions, CFS has many advantages that make it a useful tool for studying visual consciousness, especially for my purposes. In fact, for my purposes, CFS is an ideal tool for studying not-conscious processing of vMMN (see Section 2.3.3).

2.3.2.2 *Explanations for continuous flash suppression*

Binocular rivalry and CFS are similar in that both require the two eyes to be presented with dissimilar images. Why, then, does visual consciousness change during binocular rivalry but remain stable during CFS? At present, there is no uniformly agreed upon explanation for CFS (Yang et al., 2014). Despite this, two theories seem possible: adaptation and reciprocal inhibition and predictive coding.
As discussed in Section 2.3.1.3, adaptation and reciprocal inhibition is the theory that different populations of neurons, linked by reciprocal-inhibitory connections and adapting when active, process each rival image (e.g., Blake & Logothetis, 2002; McDougall, 1901; Noest et al., 2007). According to my understanding of adaptation and reciprocal inhibition, during CFS, because each CFS pattern is presented for a small time, and because each CFS pattern is slightly different to all the others, the neurons processing the CFS patterns are not afforded the opportunity to adapt, and each CFS pattern activates a slightly different population of neurons. Therefore, the CFS patterns remain in visual consciousness.

Similarly, as discussed in Section 2.3.1.3, predictive coding is the theory that the visual system makes predictions about visual input (Hohwy et al., 2008). During CFS, the CFS pattern is a source of prediction-error, because the CFS pattern is constantly changing and the predictive model of visual perception needs to account for this change. According to this theory, there is a higher prior, or likelihood, for the constantly changing error signal from the CFS patterns than for the static error signal from the suppressed image.
2.4 Closing remarks

My thesis is that our brains process regular and unexpected visual events, that there are systematic differences in the way that our brains process these events, and that these differences in processing occur even when an observer never consciously sees these events. The general aim of my thesis is to investigate conscious and not-conscious processing of sequences of stimuli that give rise to vMMN.

In this chapter, I have shown that vMMN is a good measure of the processing of regular and unexpected visual events, that the general aim of my thesis is a suitable avenue for research, and that binocular rivalry and CFS are suitable tools for manipulating visual consciousness. That is, in this chapter, I have accomplished what I set out to do: review the relevant literature.

In Chapters 3–6, I describe Experiments 1–4, respectively. In Chapter 7, I provide a general discussion on the outcomes of the studies reported in Chapters 3–6, I detail their contribution to the field, and I provide a direction for future research. A general summary of these chapters can be found in Section 1.2.
Chapter 3

Does the oblique effect influence early neural correlates of visual consciousness during binocular rivalry?

In this chapter, I set out to determine the better stimulus for studying conscious and not-conscious processing of visual stimuli: cardinal (horizontal and vertical) gratings or oblique (diagonal) gratings. There is good reason to suppose that cardinal gratings may be a better stimulus for studying visual consciousness than oblique gratings, because of the oblique effect—a decrease in performance for visual tasks when stimuli are oblique instead of cardinal (for reviews, see Appelle, 1972; Howard, 1982; Li, Peterson, & Freeman, 2003).

I also wanted to establish a consistent methodology for subsequent experiments. That is, I wanted to ensure that my methods and procedures were sufficient to reproduce a well-established ERP correlate of visual consciousness: diminution of the P1 component from a rivalry-to-fusion change when that change is made to the suppressed grating than when an identical change is made to the dominant grating (e.g., Roeber et al., 2008). To meet these aims:

- I measured participants’ EEG activity while presenting one grating to one eye and an identical, orthogonally oriented
grating to the other eye, yielding binocular rivalry. Gratings were either cardinal orientations or oblique orientations.

- I asked participants to press keys on a response keypad indicating which of the two gratings was dominant.

- After doing so for at least 6 seconds, I changed one of the gratings to match the grating shown to the other eye, yielding binocular fusion. Because of binocular rivalry, rivalry-to-fusion changes made to the dominant grating were conscious whereas rivalry-to-fusion changes made to the suppressed grating were not-conscious.

I found that the amplitude of the P1 component of ERPs was bigger for conscious changes than for not-conscious changes—this is a neural correlate of visual consciousness. I also found that the amplitude of the N1 component of ERPs was bigger for conscious changes than for not-conscious changes, but only for cardinal gratings. That is, changes to cardinal gratings yielded more reliable neural correlates of visual consciousness than changes to oblique gratings. These results suggest that it is easier to find neural correlates of visual consciousness with cardinal gratings than with oblique gratings, and inform the design of Experiments 3 and 4 (see Chapters 5 and 6).
3.1 Introduction

The oblique effect refers to our being more sensitive to cardinal stimuli (i.e., stimuli having orientations that are vertical, 0°, or horizontal, 90°), than to oblique stimuli (i.e., stimuli having orientations that are non-cardinal; these are often stimuli having ±45° orientations). For example, when participants are asked to judge the orientation of a visual stimulus, they are faster and more accurate when those stimuli are aligned to cardinal orientations than to oblique orientations (Bouma & Andriessen, 1968; Westheimer & Beard, 1998). As summarised by Li et al. (2003), the oblique effect is a robust phenomenon of vision: it applies to human participants and animal subjects (including the rabbit, monkey, pigeon, goldfish, rat, squirrel, cat, and octopus) for a range of visual tasks, such as spatial acuity (Berkley, Kitterle, & Watkins, 1975; Campbell & Kulikowski, 1966; Jastrow, 1893), contrast sensitivity (Campbell & Kulikowski, 1966; Mitchell, Freeman, & Westheimer, 1967), orientation selectivity (Andrews, 1965, 1967; Campbell & Kulikowski, 1966; Orban, Vandenbussche, & Vogels, 1984), and vernier acuity (Saarinen & Levi, 1995; Westheimer & Beard, 1998; for reviews, see Appelle, 1972; Howard, 1982; Li et al., 2003).

Lie et al. (2003) have argued that the oblique effect originates in V1. As summarised by Li et al. (2003), single-cell recordings of V1 from the cat (Bauer & Jordan, 1993; Kalia & Whitteridge, 1973; Kennedy & Orban, 1979;
Payne & Berman, 1983; Pettigrew, Nikara, & Bishop, 1968; Wilson & Sherman, 1976) and from the monkey (De Valois, Yund, & Hepler, 1982; Mansfield, 1974; Poggio & Fischer, 1977) have shown that fewer neurons are tuned for ±45° orientations than for cardinal orientations, and that fewer neurons are tuned for ±22.5° and ±67.5° orientations than for ±45° orientations. Furthermore, in humans, BOLD activity in V1 is higher (Furmanski & Engel, 2000) and the amplitudes of ERP components over posterior regions of the brain are bigger (Arakawa et al., 2000; Maffei & Campbell, 1970; May, Cullen, Moskowitz-Cook, & Siegfried, 1979; Moskowitz & Sokol, 1985; Proverbio, Esposito, & Zani, 2002; Skrandies, 1984; Yoshida, Iwahara, & Nagamura, 1975) when participants view cardinal orientations than when they view ±45° orientations.

I am interested in the oblique effect for at least three reasons:

1. If the oblique effect influences the way in which conscious visual stimuli are processed in the brain, then it is possible that the oblique effect may also influence the way in which not-conscious visual stimuli are processed. To the best of my knowledge, this has never been tested.

2. Similarly, if the oblique effect influences conscious and not-conscious processing of visual stimuli, then this information is critical to the design of the other experiments contained in this thesis, especially Experiments 3 and 4 (see Chapters 5 and 6).
3. Furthermore, most psychophysical studies of binocular rivalry (see below) have tended to use cardinal gratings as stimuli, whereas most neuroimaging studies have tended to use oblique gratings. If the oblique effect influences conscious and not-conscious processing of visual stimuli, then one would be forced to reinterpret what we know about binocular rivalry as well as some of the neural correlates of visual consciousness that have been discovered using binocular rivalry.

Therefore, I set out to determine the better stimulus for studying conscious and not-conscious processing of visual stimuli: cardinal gratings or oblique gratings. To study this, I used binocular rivalry and an ERP paradigm introduced by Kaernbach et al. (1999).

Binocular rivalry is a powerful form of bistable perception in which visual consciousness alternates unpredictably between two dissimilar images presented one to each eye (Wheatstone, 1838; for reviews, see Alais & Blake, 2004; Blake & O’Shea, 2009; Miller, 2013). That is, one of the images is dominant, visible, whereas the other is suppressed, invisible. For example, when one eye is shown a horizontal grating and the other eye is shown a vertical grating, rather than seeing a combination of the two (i.e., a grid), observers typically report seeing 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 one cares to look.
Kaernbach et al. (1999) developed an ERP paradigm in which they presented one grating (with an orientation of 45°) to one eye and an identical, orthogonally oriented grating to the other eye, yielding binocular rivalry, and asked participants to press keys on a response keypad indicating which of the two gratings was dominant. After doing so for at least 10–15 seconds, they changed one of the gratings to match the grating shown to the other eye, yielding binocular fusion. Because of binocular rivalry, rivalry-to-fusion changes made to the dominant grating were conscious whereas rivalry-to-fusion changes made to the suppressed grating were not-conscious. This ERP paradigm was an improvement over previous attempts to use binocular rivalry and EEG to study neural correlates of visual consciousness, because previous attempts did not contain a high-precision, time-locked event, such as a stimulus change, from which one could compute an ERP (e.g., Biersdorf & Lawwill, 1968; Cobb, Morton, & Ettlinger, 1967; Lansing, 1964).

Kaernbach et al. (1999) found that when the change was conscious, there was a bigger N1 and P3 than when an identical change was not-conscious. That is, they found two neural correlates of visual consciousness. The basic finding has been repeated with steady stimuli (Roeber & Schröger, 2004; Veser et al., 2008), flickering stimuli (Roeber & Schröger, 2004), and colour stimuli (Veser et al., 2008). Roeber et al. (2008) extended the basic finding to include the P1 component—a bigger P1 for conscious changes
than for not-conscious changes. Veser et al. (2008) reanalysed the data of Kaernbach et al. (1999) and found the same P1 result; apparently, they did not analyse for this in the original study. Furthermore, Roeber et al. (2008) used VARETA (Bosch-Bayard et al., 2001) to localise the neural generators of their P1. They placed the P1 in the ventrolateral occipito-temporal cortex. To date, this is the earliest neural correlate of visual consciousness ever discovered (Revonsuo & Koivisto, 2010)—a mere 100 ms after stimulus change.

To investigate the possibility that the oblique effect may influence the way in which conscious and not-conscious visual stimuli are processed in the brain, I repeated Kaernbach et al.’s (1999) paradigm with cardinal gratings and with oblique gratings. I compared ERPs from conscious changes with ERPs from not-conscious changes, and ERPs from cardinal gratings with ERPs from oblique gratings. I found the typical P1 result for cardinal and oblique gratings, with no difference between them, as well as the typical P3b result. I also found the typical N1 result, but only for cardinal gratings. That is, changes to cardinal gratings yielded more reliable neural correlates of visual consciousness than changes to oblique gratings. These results suggest that it is easier to find neural correlates of visual consciousness with cardinal gratings than with oblique gratings, and inform the design of Experiments 3 and 4 (see Chapters 5 and 6).
3.2 Method

3.2.1 Participants

Seventeen volunteers participated in my study. There was no reward or financial incentive offered to participate. All participants gave written informed consent prior to the experiment, had normal or corrected-to-normal visual acuity in both eyes, and showed normal binocular rivalry in a 12 minute pre-test session. Data of five participants were excluded from further analyses, because too few epochs remained after data pre-processing. Mean (SD) age of the remaining 12 participants, of whom four were male, was 21 (3) years. To determine my sample size, also conducted a power analysis prior to collecting any data. According to this analysis, to find a power of 0.8 (alpha = 0.01) with an effect size of .8, I needed a sample size of 11 participants. The study was approved by Southern Cross University’s Human Research Ethics Committee (ECN-11-149).

3.2.2 Apparatus

The experiment was conducted in the EEG Research Laboratory at Southern Cross University, Coffs Harbour, Australia, in a sound-attenuated (42 dB) room 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, ensuring that the physical and retinal orientation of the gratings were the same. Stimuli were presented on a Samsung 2233RZ monitor (1024 x 768; 60 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 Macintosh Mini running specially written Matlab scripts using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Participants responded using two keys on a response keypad.

EEG was recorded from 58 Ag/AgCl active electrodes placed according to the extended 10-20 system (AF7, AF3, AF4, AF8, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FC2, FC4, FC6, FT8, T7, C5, C3, C1, Cz, 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 FCz, with the ground at AFz. A vertical electrooculogram (EOG) was recorded by placing an electrode above (I used FP2) and below the right eye and a horizontal EOG was recorded by placing an electrode on the outer canthi of each eye. I also placed an electrode on each earlobe. The sampling rate of the EEG was 500 Hz and the online filtering of the EEG was 1,000 Hz.
3.2.3 Stimuli

I used annulus-shaped black (0.40 cd/m²) and white (86.67 cd/m²) sine-wave gratings as visual stimuli. The size of the gratings was 3.2° of visual angle and the spatial frequency was 1.6 cpd. 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 neighbour. In the centre of each grating was a red fixation cross of 0.3° with a line width of 0.1°. The gratings were presented on a medium grey (43.54 cd/m²) background and were aligned to vertical, horizontal, left-oblique (–45°), or right-oblique (45°) orientations.

3.2.4 Design and procedure

The experiment consisted of 20 blocks. In half of them, participants were presented with cardinal stimuli—a horizontal grating to one eye and a vertical grating to the other eye; in the other half, participants were presented with oblique stimuli—a left-oblique grating to one eye and a right-oblique grating to the other eye. The order of these blocks was random and different for each participant. Each block contained 24 trials.

A trial comprised a display of binocular rivalry gratings for at least 6.25–6.75 seconds and until the participant’s next key press. The display then continued for a further 300–600 ms before one of the gratings changed.
to match the grating shown to the other eye, yielding binocular fusion. The binocular fusion display lasted for 1.75–2.25 seconds, at which point one of the gratings changed, yielding binocular rivalry and the start of the next trial (see Figure 3.1).

Figure 3.1. Procedure for Experiment 1. (a) I presented binocular rivalry gratings to the eyes (in this case, a horizontal grating to the left eye and a vertical grating to the right eye) for at least 6.25–6.75 seconds and until the participant’s next key press. The display then continued for a further 300–600 ms before one of the gratings changed to match the grating shown to the other eye, yielding binocular fusion (in this case, the horizontal grating changed to a vertical grating). The binocular fusion display lasted for 1.75–2.25 seconds, at which point one of the gratings changed, yielding binocular rivalry and the start of the next trial. I used the same procedure in the oblique blocks of the experiment, except that I used oblique gratings instead of cardinal gratings. (b) The participant’s task was to press keys indicating which of the two gratings was dominant. Because of binocular rivalry, changes made to the dominant grating were conscious (c) and changes made to the suppressed grating were not-conscious.
The participant’s task was to look at the fixation cross in the centre of the grating stimuli, to report binocular rivalry dominance of one or the other grating by pressing down one or another key on the response keypad, and to refrain from pressing either key if any combination of the two gratings was perceived. This yielded two events: key presses—when a key was pressed, and key releases—when a key stopped being pressed. I used key presses and releases to determine participants’ mean binocular rivalry dominance duration and to classify rivalry-to-fusion changes as conscious or not-conscious.

3.2.5 Electrophysiological analysis

For data analyses, I re-referenced the EEG data offline to the average of the linked earlobes, and I filtered the data using a 0.1 to 35 Hz phase-shift free Butterworth filter (48 dB/Oct slope). I extracted the epochs from –100 to 600 ms, and I normalised all epochs to their mean voltage from –100 to 0 ms. I excluded all epochs with signals exceeding peak-to-peak amplitudes of 200 µV at any EEG channel, or of 60 µV at any EOG channel. I computed ERPs separately for each axis (cardinal, oblique) and for each percept (conscious, not-conscious) for each participant, and excluded data sets containing fewer than 80 epochs for any ERP.
To classify rivalry-to-fusion changes as conscious or not-conscious, I used key presses and releases. That is, if the change was made to the dominant grating, as indicated by the participant’s key press, I classified it as a conscious change; if the change was made to the suppressed grating, I classified it as a not-conscious change. However, because binocular rivalry alternations are about 450 ms ahead of a key press or release (Alais, Cass, O’Shea, & Blake, 2010), I discarded all epochs containing a key release in the first 150 ms after the rivalry-to-fusion change. I chose these times to be consistent with Kaernbach et al. (1999) and Roeber et al. (2008).

Using visual inspection of the grand-averaged ERPs, I determined the time windows of the P1 (94 to 114 ms) and N1 (170 to 200 ms) components at posterior electrodes. I analysed the mean amplitudes of the ERPs for the P1 and N1 time windows using repeated-measures ANOVA (analysis of variance; Bonferroni corrected for multiple comparisons) and the factors region (anterior, central, posterior), hemisphere (left, right), axis (cardinal, oblique), and percept (conscious, not-conscious). I also calculated voltage maps for these time windows and used sLORETA (Pascual-Marqui, 2002) to locate the current sources in the brain with a voxel-by-voxel t-test. A randomisation test based on statistical non-parametric mapping (SnPM; number of randomisations: 5,000) was used to correct for multiple comparisons (Nichols & Holmes, 2002).
3.3 Results and discussion

3.3.1 Behavioural data

The time between a key press and its release yielded the time of one episode of binocular rivalry dominance; the distribution of these times had the typical gamma shape (e.g., Levelt, 1967; Zhou et al., 2004). Mean (SD) binocular rivalry dominance duration was 1.97 (0.74) s for cardinal gratings and 1.92 (0.74) s for oblique gratings; these times were not significantly different: a one-way ANOVA on the log-transformed data did not yield a significant difference, $F(1, 11) = 1.08, p = .320, \eta_p^2 = .09$, suggesting that the oblique effect does not influence binocular rivalry dominance durations.

3.3.2 Electrophysiological data

Figure 3.2 shows the grand-averaged ERPs—time-locked to the onset of the rivalry-to-fusion change. The traces are for cardinal gratings (solid traces), oblique gratings (dotted traces), conscious changes (red traces), and not-conscious changes (green traces), and are averaged over left anterior (AF3, F5, F3, F1, FC3), right anterior (AF4, F2, F4, F6, FC4), left central (C5, C3, CP5, CP3, CP1), right central (C4, C6, CP2, CP4, CP6), left posterior (P7, PO9, PO7, PO3, O1), and right posterior (O2, PO4, PO8, PO10, P8) electrodes.
Figure 3.2. Grand-Averaged ERPs for Experiment 1. Each graph represents ERPs averaged over anterior, central, or posterior electrodes for the left or right hemispheres. The graphs show time on the x-axis and voltage on the y-axis. Time 0 on the x-axis is the onset of the stimulus (in this case, when the rivalry-to-fusion change took place), and I plot positive voltages above 0 on the y-axis and negative voltages below. There are four ERPs per graph: the solid traces are for cardinal gratings, the dotted traces are for oblique gratings, the red traces are for conscious changes, and the green traces are for not-conscious changes. The ERPs at posterior electrodes show the P1 at about 100 ms, the N1 at about 180 ms, and the P3b at about 400 ms. The grey bars show the analysed time windows.

The ERPs at posterior electrodes show a typical pattern of activity for visual stimuli: a peak at about 100 ms—the P1, a trough at about 180 ms—
The N1, and a positive deflection starting at about 300 ms and peaking at about 400 ms—the P3b (O’Shea et al., 2009; Odom et al., 2010). I report the results of critical statistical tests below; I give full details in Appendix A:

- The P1, which was maximal at about 100 ms, is associated with sensory and perceptual processing (Pratt, 2012; Woodman, 2010). At the P1, conscious changes from cardinal and oblique gratings yielded bigger amplitudes than not-conscious changes, $F(1, 11) = 4.08, p = .038, \eta^2 = .27$—this is a neural correlate of visual consciousness, and is consistent with Roeber et al. (2008). Crucially, there was no difference between cardinal and oblique gratings, $F(1, 11) < 0.01, p = .948, \eta^2 < .01$.

- The N1, which was maximal at about 180 ms, is associated with perceptual and attentional processing (Pratt, 2012; Woodman, 2010). At the N1, planned $t$-tests (they were planned, because Kaernbach et al., 1999, conducted similar analyses on their data) showed that the amplitudes of cardinal gratings were bigger for conscious changes than for not-conscious changes at right posterior electrodes, $t(11) = 2.82, p = .020$, but not at left posterior electrodes, $t(11) = 0.80, p = .441$. There was no difference between conscious and not-conscious changes from oblique gratings at left posterior electrodes, $t(11) = 1.54, p = .151$, or at right posterior electrodes, $t(11) = 1.64, p = 130$. Crucially, there
was no difference between cardinal and oblique gratings, $F(1, 11) < 0.01$, $p = .948$, $\eta^2_p < .01$.

- The P3b, which started at about 300 ms and was maximal at about 400 ms, can also be seen at anterior and central electrodes and is associated with the detection of task-relevant events (Polich, 2007). In this experiment, the P3b is probably due to neural activity associated with the release of one key and the press of the other key. These events would be required when a rivalry-to-fusion change yields a change in visual consciousness. Because I am interested in the oblique effect and its effects on early neural correlates of visual consciousness, I do not analyse or elaborate further on the P3b.

Figure 3.3 shows the voltage maps for the P1 and N1 time windows for conscious not-conscious changes from cardinal and oblique gratings. I include these maps for comparison with Kaernbach et al. (1999) and Roeber et al. (2008).
Figure 3.3. Voltage Maps for Experiment 1. At the P1, there are positive voltages in posterior regions of the brain for cardinal and oblique gratings. There is more activity for conscious changes than for not-conscious changes. At the N1, there are negative voltages in posterior regions of the brain and positive voltages in anterior and central regions of the brain.

Similar to Roeber et al. (2008), at the P1, there are positive voltages in posterior regions of the brain, especially in the right hemisphere, $F(1, 11) = 6.30, p = .029, \eta^2_p = .36$, for cardinal and oblique gratings, with conscious changes yielding more activity than not-conscious changes (see above and Table A-1). Similar to Kaernbach et al. (1999), at the N1, there are negative voltages in posterior regions of the brain and positive voltages in anterior and central regions of the brain. For cardinal gratings, there is more activity for conscious changes than for not-conscious changes (see above and Table A-1); for oblique gratings, there is no difference in activity for conscious and not-conscious changes (see above and Table A-1).
To locate the differences in the brain between conscious and not-conscious changes for cardinal and oblique gratings, I used sLORETA (Pascual-Marqui, 2002). According to sLORETA, for cardinal and oblique gratings at the P1, the best matches for current sources were in parietal and frontal areas of the brain; for cardinal and oblique gratings at the N1, the best matches for current sources were in frontal and limbic areas of the brain. Despite this, sLORETA was unable to locate brain areas with statistically significant differences ($p < .01$ or $p < .05$) between neural activities for conscious and not-conscious changes. This was disappointing for my hope of localising conscious and not-conscious changes in the brain.

### 3.4 General discussion

I set out to determine the better stimulus for studying conscious and not-conscious processing of visual stimuli: cardinal gratings or oblique gratings, using an ERP paradigm developed by Kaernbach et al. (1999). The ERP data show that conscious and not-conscious changes yield the P1 and N1 components, suggesting that not-conscious changes are processed by the brain, even though participants do not perceive the rivalry-to-fusion change. Furthermore, I found that the amplitude of the P1 from cardinal and oblique gratings and the amplitude of the N1 from cardinal gratings is bigger for conscious changes than for not-conscious changes—these are
neural correlates of visual consciousness. Surprisingly, I did not find any
differences at the N1 from oblique gratings between conscious and not-
conscious changes. These results suggest that it is easier to find neural
correlates of visual consciousness with cardinal gratings than with oblique
gratings.

In general, during the P1 time window, there is no sign of an
advantage for cardinal gratings compared to oblique gratings. However,
during the N1 time window, I found a neural correlate of visual
consciousness from cardinal gratings but not from oblique gratings.
Although it is tempting to think of this difference as the oblique effect, I
argue that it is not the oblique effect and that it is instead a failure to
replicate the typical N1 result with oblique gratings. There are at least two
reasons for this:

1. According to Li et al. (2003), in humans, the oblique effect can
   be seen in the amplitudes of ERP components: ERPs over
   posterior regions of the brain are bigger when participants view
   cardinal orientations than when they view ±45° orientations
   (e.g., Arakawa et al., 2000; Maffei & Campbell, 1970; May et al.,
   1979; Moskowitz & Sokol, 1985; Proverbio et al., 2002;
   Skrandies, 1984; Yoshida et al., 1975). In this experiment, there
   was no difference in the amplitudes of ERPs between cardinal
and oblique gratings at the P1 or at the N1. Therefore, my ERPs do not show evidence for the oblique effect.

2. I am not the first to fail to replicate the typical N1 result with oblique gratings. For example, Roeber et al. (2008) did not find the typical N1 result with oblique gratings (although they did not analyse it, after visual inspection of their Figure 2, I suspect that there was no difference between conscious and not-conscious changes at the N1). If so, my failure to replicate the typical N1 result with oblique gratings is consistent with Roeber et al. (2008), suggesting that that the typical N1 result may not be as reliable as the typical P1 result. Further evidence for the fragility of the N1 result compared to the P1 result can be seen in the ERPs from cardinal gratings: I found the typical P1 result at left and right posterior electrodes for cardinal and oblique gratings, whereas I could only find the typical N1 result at right posterior electrodes for cardinal gratings. Although this is not conclusive, it shows that more research is needed to investigate the possibility that the typical N1 result is not as reliable as the typical P1 result.

Because I found no evidence for the oblique effect in the ERPs during the P1 and N1 time windows, and because the voltage maps look essentially identical for cardinal and oblique gratings, I conclude that I found no
evidence for the oblique effect in my data. If one accepts this, then it is important to ask: why did I fail to replicate the oblique effect? I can think of at least two reasons:

1. According to Arakawa et al. (2000), a critical parameter for eliciting the oblique effect with grating stimuli is the spatial frequency of the grating. In particular, low spatial frequencies (i.e., less than 1 cpd, the number of cycles in a grating per degree of visual angle) yield bigger ERPs from cardinal gratings than from oblique gratings—the oblique effect, whereas high spatial frequencies (i.e., more than 1 cpd) yield essentially identical ERPs. Because the spatial frequency of my gratings was 1.6 cpd, which I used to be consistent with Roeber and Schröger (2004), it is possible that my failure to find the oblique effect is because my gratings were not optimal for revealing it.

2. I am not the first to fail to replicate the oblique effect during binocular rivalry (e.g., Abadi, 1976; Blake, Yu, Lokey, & Norman, 1998; Borra, Hooge, & Verstraten, 2010; Fahle, 1982; Wade, de Weert, & Swanston, 1984). One possible reason for binocular rivalry’s disrupting the oblique effect could be that the oblique effect may occur only after the inputs from each eye are combined—binocular fusion, and during binocular rivalry,
the inputs from each eye do not combine. Nevertheless, in my experiment, I recorded ERPs from the onset of binocular fusion. So, why did I fail to find the oblique effect? Some studies (e.g., Leopold & Logothetis, 1996; Tong & Engel, 2001; Tong et al., 1998) have shown that the effects of binocular rivalry can continue to be observed in V1, the same neural site as binocular fusion (Anzai, Ohzawa, & Freeman, 1997) and the oblique effect (Li et al., 2003), for a short time after the onset of binocular fusion. Therefore, it is possible that the lingering effects of binocular rivalry during the early stages of binocular fusion prevented me from finding the oblique effect in my data.

Therefore, which is the better stimulus for studying conscious and not-conscious processing of visual stimuli: cardinal gratings or oblique gratings? Even though I found no difference between cardinal and oblique gratings in any of my analyses, I found two neural correlates of visual consciousness from cardinal gratings but only one neural correlate of visual consciousness from oblique gratings. This suggests that it is easier to find neural correlates of visual consciousness with cardinal gratings than with oblique gratings. Despite this, these results leave open the question of whether the oblique effect influences not-conscious processing of visual stimuli. This is an avenue for future research.
Recently, Railo, Koivisto, and Revonsuo (2011) have argued that a bigger P1 for conscious changes than for not-conscious changes is not a genuine neural correlate of visual consciousness, because the rivalry-to-fusion change is confounded with attention. They argue that when a change is made to the dominant grating, it is the attended and conscious grating that changes; when an identical change is made to the suppressed grating, it is the unattended and not-conscious grating that changes. Therefore, it is possible that the enhanced P1 is for differences in attention and visual consciousness.

Railo et al. (2011) make a potentially valid argument, because the P1 is known to be enhanced by increased attention (Hillyard & Anllo-Vento, 1998; Vogel & Luck, 2000; Zhang & Luck, 2009), and because it is important to control for the effects of attention when studying visual consciousness (Crick & Koch, 2003; Lamme, 2003). Despite this, there are at least three limitations to Railo et al.’s (2011) argument:

1. It is not true to say that the suppressed grating is not attended. The participants’ task in all of the studies using the ERP paradigm developed by Kaernbach et al. (1999) was to press down a particular key when that grating was conscious. That means that both gratings are attended, even though one of them is not-conscious. In this, binocular rivalry dominance is identical to the case of attention with consciousness described
by Koch and Tsuchiya (2007), whereas binocular rivalry suppression is identical to the case of attention without consciousness (for review, see Section 2.2.2.1).

2. Recently, Roeber, Veser, Schröger, and O’Shea (2011) showed that the amplitude of the P1 elicited by a rivalry-to-fusion change is essentially the same whether or not attention is on the gratings. This suggests that, even if attention is present during conscious changes and not present during not-conscious changes, its influence on the amplitude of the P1 is not statistically significant. Therefore, the bigger P1 from cardinal and oblique gratings must be a neural correlate of visual consciousness.

3. Railo et al. (2011) argue that Veser et al.’s (2008) failure to find a P1 for not-conscious changes is consistent with their claim that visual consciousness is confounded with attention. Indeed, they are correct. But this is to ignore the reanalysis of the results of Kaernbach et al. (1999) by Veser et al. (2008), the results of Roeber and Schröger (2004), the results of Roeber et al. (2008, 2011), and my experiment: all show that the P1 is elicited by not-conscious changes, but smaller than for conscious changes. Railo et al. (2011) cannot use the results from one study to
justify their argument when there are five other studies that oppose their claim.

Unfortunately, sLORETA was unable to locate brain areas with statistically significant differences between neural activities for conscious and not-conscious changes. This was disappointing for my hope of localising conscious and not-conscious changes in the brain. These results are dissimilar to those of Roeber et al. (2008) who found significant activity in occipital areas and at the junction connecting the occipital, parietal, and temporal lobes. Although it is beyond the scope of my thesis to discuss the reasons why I did not find significant differences whereas Roeber et al. (2008) did, an obvious explanation is that I used sLORETA whereas Roeber et al. (2008) used VARETA (Bosch-Bayard et al., 2001). VARETA and sLORETA use different algorithms for localising EEG and ERP sources, neither of which offer an unambiguous solution to the inverse problem (Grech et al., 2008). In any case, I am not too worried that Roeber et al. (2008) found significant differences and I did not, because it does not affect my conclusion: that it is easier to find neural correlates of visual consciousness with cardinal gratings than with oblique gratings.

There is one final issue to discuss: can these results be used to inform the design of the other experiments contained in this thesis? Yes and no. Yes, because if I use the gratings that I used in this experiment in my other experiments, then I should not find any differences in ERPs between
cardinal and oblique gratings. This means that I do not need to use both sets of stimuli, which will reduce the duration of each experiment for each participant. This is a good thing. However, because I could not find any evidence for the oblique effect, these results leave open the question of whether the oblique effect influences not-conscious processing of visual stimuli. This is an avenue for future research.

In conclusion, I set out to determine the better stimulus for studying conscious and not-conscious processing of visual stimuli: cardinal gratings or oblique gratings, using an ERP paradigm developed by Kaernbach et al. (1999). I found the typical P1 result from cardinal and oblique gratings and the typical N1 result from cardinal gratings. Surprisingly, I did not find any differences at the N1 from oblique gratings between conscious and not-conscious changes. These results suggest that it is easier to find neural correlates of visual consciousness with cardinal gratings than with oblique gratings.
Chapter 4

Visual mismatch negativity is sensitive to eye-of-origin information

In this chapter, I set out to demonstrate that a source of information about which we are not-conscious, eye-of-origin (utrocular) information (Blake & Cormack, 1979; Logothetis, et al., 1996), can be used to elicit vMMN. To study this:

- I measured participants’ EEG activity while presenting standards comprising a grating to one eye and an identical, orthogonally oriented grating to the other eye, yielding binocular rivalry, and deviants in which gratings were swapped between the eyes—an eye-swap deviant. I also had a control condition that I expected to give a typical vMMN in which I presented orientation deviants. These involved changing the orientation of both eye’s gratings by 45°.
- I asked participants to press keys on a response keypad indicating which of the two gratings was dominant.

I found that eye-of-origin information can be used to elicit vMMN (I call this an eye-swap vMMN) at about 380 ms after stimulus onset. However, the behavioural data suggested that participants were aware of when an eye-swap deviant was presented. Although this does not necessarily limit
my conclusion that swapping binocular rivalry stimuli between the eyes yields a vMMN from information of which observers are unaware (i.e., observers are unaware of which eye is viewing which stimulus; Blake & Cormack, 1979), I went on to use different techniques for hiding the deviants (see Experiment 3) and the standards and deviants (see Experiment 4) from visual consciousness.

4.1 Introduction

When an unexpected visual event occurs in our field of view, there is a sudden change in the electrical activity of our brains as measured from electrodes on the scalp (EEG), called the vMMN (for reviews, see Czigler, 2007; Kimura, 2012; Kimura et al., 2011; Pazó-Alvarez et al., 2003; Winkler & Czigler, 2012). vMMN is typically observed in the oddball paradigm: an infrequent visual stimulus—a deviant, is randomly and unpredictably presented in a sequence of more frequent visual stimuli—the standards. vMMN is seen most clearly in the difference wave: the ERP for the deviant minus the ERP for the standard, between 150 and 400 ms after stimulus onset (Kimura et al., 2009; Kimura, Ohira, & Schröger, 2010; Kimura, 2012).

The current consensus explanation of vMMN is predictive coding (e.g., Friston, 2005; Rao & Ballard, 1999): that our brains construct a model of the regularities in our visual environment (i.e., the standards) and that when
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This model is violated by an unexpected event (i.e., a deviant), extra processing is required to update the model. The extra processing is thought to reflect prediction and prediction-error of visual information (e.g., Garrido et al., 2009; Schröger et al., 2013; Stefanics et al., 2014; Wacongne et al., 2012; Winkler & Czigler, 2012).

vMMN is elicited by any unexpected change in visual input (Czigler, 2014; Kimura, 2012). So far, vMMN has been found in response to deviant stimuli for low-level features of vision, such as changes in colour, direction of motion, orientation, spatial frequency, location, shape, size, and contrast/luminance, as well as to deviant stimuli for high-level features of vision, such as human facial expression, gender of human faces, lateralization of human hands, and bilateral symmetry (for a thorough list of papers on vMMN, see Section 2.2.1.1). What all of these features have in common is that a deviant is noticeably different to that of the standards, and such differences automatically attract attention, even when attention is not on the standards and deviants (i.e., the deviant “pops out”), and come, in some way, to visual consciousness. I set out to confirm a new, low-level, visual stimulus for eliciting vMMN that does not necessarily recruit visual consciousness: eye-of-origin (utrocular) information.

To vary eye-of-origin, I presented standards comprising a grating to one eye and an identical, orthogonally oriented grating to the other eye, and deviants in which the gratings were swapped between the eyes (I call this
an eye-swap deviant). That is, the orientation information presented to the
two eyes is identical for standards and eye-swap deviants; the only
difference is the eye-of-origin of the orientations. I also had a control
condition for which I expected a vMMN from deviants comprising gratings
rotated in both eyes by 45° (I call this an orientation deviant). Changes in
orientation information are well known to elicit vMMN (e.g., Astikainen et
al., 2004, 2008; Czigler & Pató, 2009; Kimura et al., 2009; Sulykos et al., 2013;
for review, see Kimura, 2012).

Indeed, simply looking at dissimilar images presented one to each eye
leads to binocular rivalry: continual, unpredictable changes in visual
consciousness between the image viewed by one eye, the image viewed by
the other eye, and some dynamic, patchy combination of both images
(Wheatstone, 1838; for recent reviews, see Alais & Blake, 2004; Blake, &
O’Shea, 2009; Miller, 2013). We already know from psychophysical studies
that observers cannot tell which eye is viewing which stimulus during
binocular rivalry—a failure of utrocular discrimination (Blake & Cormack,
1979). Furthermore, Logothetis et al. (1996) have shown that swapping
grating stimuli between the eyes does not lead to any change in the
experience of binocular rivalry, which would also rule out any role for
visual consciousness in processing eye-of-origin information. Despite this,
eye-of-origin is vitally important to us for telling how close things are to
us—depth perception. For example, a hungry lion behind a thick sheet of
glass projects images into each eye that if swapped between the eyes would show the lion as dangerously in front of the glass (Howard & Rogers, 2012; Wheatstone, 1838). From a functional perspective, it makes sense to process such information without requiring visual consciousness, because this takes time away from our escaping the lion in the latter case.

This prompts me to pose two questions about vMMN:

1. Is visual consciousness necessary for vMMN to be generated?

   There is a clear difference in conscious experience from typical oddball sequences, say, with standards in which both eyes view a grating of one orientation and deviants in which those gratings are rotated by 90°, and the ones I used, because the stochastic nature of binocular rivalry (e.g., Levelt, 1967; Zhou et al., 2004) by itself would seem to rule out any role for visual consciousness in generating vMMN. That is, if vMMN can be elicited to eye-swap deviants during binocular rivalry, then this would mean that visual consciousness of sequences of stimuli is not necessary to yield vMMN.

2. What regions of the brain are involved in the generation of vMMN? This question can be answered by neuroimaging, which I have done in this study. Kimura (2012) summarised four studies showing that the neural generators of vMMN can be found in visual extrastriate areas (both hemispheres) and
prefrontal areas of the brain (right hemisphere bias). But one can also find converging evidence for neuroimaging by taking a psychoanatomical approach (Blake, 1995): by showing whether the binocular rivalry mechanism is serially earlier than the vMMN mechanism or after it. Simply put, if the binocular rivalry mechanism has resolved the differences between the images viewed by the two eyes prior to neural input to the vMMN mechanism, then there should be no vMMN. But if the differences between the two eyes are conveyed to the vMMN mechanism, then there should be a vMMN. The locations of the brain areas responsible for the processing of binocular rivalry have been extensively studied via neuroimaging (for reviews, see Blake & Logothetis, 2002; Tong et al., 2006). Moreover, binocular rivalry’s dependence on, and independence of, other visual mechanisms has also been extensively studied (e.g., Blake, 1995, 1997).

van Rhijn et al. (2013) have taken a first step to showing that eye-of-origin information can be used to elicit vMMN. They presented 80% of standards comprising a horizontal grating to one eye and a vertical grating to the other eye, 10% of eye-swap deviants, and 10% of orientation deviants. In half of the blocks, participants tracked their ever-changing percept of binocular rivalry using two keys on a response keypad (they called this
their attend-to-rivalry condition); in the remaining blocks, participants performed an attention-demanding task at fixation (they called this their reduced-attention condition). van Rhijn et al. (2013) found a vMMN from about 140 ms to about 290 ms after stimulus onset in the attend-to-rivalry condition and from about 140 ms to about 220 ms in the reduced-attention condition. Otherwise, the pattern of activity was essentially the same for eye-swap and orientation deviants. van Rhijn et al. (2013) concluded that eye-of-origin information can elicit vMMN.

van Rhijn et al. (2013) conceded that their results are only a first step in establishing eye-of-origin information as a stimulus feature that can be used to elicit vMMN. In this experiment, I take two additional steps:

1. van Rhijn et al. (2013) used physically identical stimuli for their eye-swap vMMN, but they did not for their orientation vMMN. That is, in their control condition, their standards were gratings aligned to cardinal orientations, whereas their orientation deviants were aligned to oblique orientations. It is possible that this physical difference contributed a source of variability in their results that obscured differences between their eye-swap and orientation vMMNs (e.g., Kujala et al., 2007). In this experiment, I ensured that I computed vMMNs from physically identical standards, eye-swap deviants, and orientation
deviants; the stimuli differed only in their frequency and in their unpredictability.

van Rhijn et al. (2013) measured their ERPs with 26 electrodes, preventing them from conducting any detailed analysis of the sources of the vMMNs they found. In this experiment, I used 58 electrodes, allowing me to localise vMMN activity in the brain using sLORETA (Pascual-Marqui, 2002).

Similar to the results of van Rhijn et al. (2013), I found an eye-swap vMMN and an orientation vMMN, but unlike their results, my eye-swap vMMN peaked about 100 ms later than my orientation vMMN. However, because my behavioural data suggested that participants were aware of when an eye-swap deviant was presented, I cannot conclude that vMMN occurs in the absence of visual consciousness.

4.2 Method

4.2.1 Participants

Fifteen volunteers participated in my study. There was no reward or financial incentive offered to participate. All participants gave written informed consent prior to the experiment, had normal or corrected-to-normal visual acuity in both eyes, and showed normal binocular rivalry in a 12 minute pre-test session. Data of three participants were excluded from
further analyses, because too few epochs remained after data pre-
processing. Mean (SD) age of the remaining 12 participants, of whom seven 
were male, was 30 (12) years. The study was approved by Southern Cross 
University’s Human Research Ethics Committee (ECN-11-149).

4.2.2 Apparatus

The apparatus was identical to the one used in Experiment 1 (for review, see Section 3.2.2).

4.2.3 Stimuli

The stimuli were identical to the ones used in Experiment 1 (for review, see Section 3.2.3).

4.2.4 Design and procedure

The experiment consisted of 16 blocks. In half of them, participants 
were presented with cardinal standards—a horizontal grating to one eye 
and a vertical grating to the other eye; in the other half, participants were 
presented with oblique standards—a left-oblique grating to one eye and a 
right-oblique grating to the other eye. Furthermore, in half of the blocks 
factorially, participants were presented with eye-swap deviants; in the 
other half, participants were presented with orientation deviants. Therefore,
there were four different types of blocks: cardinal standards with eye-swap deviants (see Figure 4.1a), cardinal standards with oblique orientation deviants, oblique standards with eye-swap deviants, and oblique standards with cardinal orientation deviants (see Figure 4.1b). Each block type was presented four times. The order of these blocks was counterbalanced within participants and the starting block type was counterbalanced between participants.

![Diagram](https://via.placeholder.com/150)

**Figure 4.1.** Procedure for Experiment 2. I presented 80% of binocular rivalry standards—one grating to one eye and an identical, orthogonally orientated grating to the other eye, and 20% of deviants—either by swapping the gratings between the eyes to change the eye-of-origin of the gratings or by rotating the gratings by 45° to change the orientation of the gratings, shown in each sequence as the fifth display of the stimuli. (a) A sequence of cardinal standards (in this case, a horizontal grating to the left eye and a vertical grating to the right eye) and an eye-swap deviant (in this case, a vertical grating to the left eye and a horizontal grating to the right eye). (b) A sequence of oblique standards (in this case, a left-oblique grating to the left eye and a right-oblique grating to the right eye) and an orientation
deviant (in this case, a vertical grating to the left eye and a horizontal grating to the right eye). Note that the deviants in both sequences are identical; this allowed me to compare physically identical standards, eye-swap deviants, and orientation deviants.

Each block contained 480 trials. An individual trial comprised a presentation of grating stimuli for 500 ms. Following this, the gratings shifted 180° in phase; this change marked the end of one trial and the beginning of the next, allowing us to time-lock the EEG signal. Eighty percent of all trials within a block were standards; 20% of all trials were either eye-swap deviants or orientation deviants. The order of trials within a block was random for each participant with the constraints that the first three and last two trials had to display standard stimuli, and that any two deviants had to be separated by at least three standards.

The participant’s task was identical to the one used in Experiment 1 (for review, see Section 3.2.4). I used key presses and releases to determine participants’ mean binocular rivalry dominance duration and to assess the intrusiveness of deviants on visual consciousness.

4.2.5 Electrophysiological analysis

I treated the EEG data in the same way as in Experiment 1, except that I re-referenced the EEG data offline to the average of all scalp electrodes, I extracted the epochs from –100 to 500 ms, and I excluded all standards that immediately followed a deviant. I computed ERPs separately for each axis
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(cardinal, oblique) and for each stimulus (standard, eye-swap deviant, orientation deviant) for each participant, and excluded data sets containing fewer than 250 epochs for any ERP.

To assess vMMN, I computed difference waves by subtracting the grand-averaged ERPs for standards from the grand-averaged ERPs for either eye-swap deviants or orientation deviants. This yields four difference waves: cardinal eye-swap difference waves (cardinal eye-swap deviants minus cardinal standards), cardinal orientation difference waves (cardinal orientation deviants minus cardinal standards), oblique eye-swap difference waves (oblique eye-swap deviants minus oblique standards), and oblique orientation difference waves (oblique orientation deviants minus oblique standards).

Using visual inspection of the difference waves, I determined the time windows of the orientation vMMN (240 to 290 ms) and eye-swap vMMN (350 to 400 ms) components at posterior electrodes. I analysed the mean amplitudes of the ERPs for the orientation and eye-swap vMMN time windows using repeated-measures ANOVA and the factors region (anterior, central, posterior), hemisphere (left, right), axis (cardinal, oblique), and stimuli (standards, eye-swap deviants or orientation deviants). I also calculated voltage maps for these time windows and used sLORETA (Pascual-Marqui, 2002).
4.3 Results and discussion

4.3.1 Behavioural data

The time between a key press and its release yielded the time of one episode of binocular rivalry dominance; the distribution of these times had the typical gamma shape (e.g., Levelt, 1967; Zhou et al., 2004). Mean (SD) binocular rivalry dominance duration was 1.43 (1.04) s for cardinal standards and eye-swap deviants, 1.59 (1.17) s for cardinal standards and orientation deviants, 1.47 (0.94) s for oblique standards and eye-swap deviants, and 1.61 (1.08) s for oblique standards and orientation deviants; these times were not significantly different. I assessed significance with a repeated-measures ANOVA on the log-transformed data using the factors axis (cardinal, oblique) and block (eye-swap block, orientation block). I give the ANOVA table in Table B-1. I found no significant main effects or interactions, suggesting that participants’ experiences of binocular rivalry did not differ between blocks.

To assess the intrusiveness of eye-swap and orientation deviants on binocular rivalry, I compared binocular rivalry dominance durations containing standards with binocular rivalry dominance durations containing either an eye-swap deviant or an orientation deviant. However, because binocular rivalry alternations are about 450 ms ahead of a key press
or release (Alais et al., 2010), I classified dominance durations as containing a deviant only if a key was pressed at least 1 ms before the onset of the deviant and only if the key continued to be pressed for the duration of the deviant. I chose this time because any before the onset of the deviant means that the participant’s percept started at least about 450 ms beforehand. Approximately 80% of all deviants had no preceding key press, meaning that I am unsure if these deviants were conscious or not.

Mean binocular rivalry dominance duration was 1.73 (0.69) s for cardinal standards, 2.21 (1.36) s for cardinal eye-swap deviants, 2.17 (1.63) s for cardinal orientation deviants, 1.79 (0.40) s for oblique standards, 2.08 (1.26) s for oblique eye-swap deviants, and 1.65 (0.58) s for oblique orientation deviants; these times are not significantly different: repeated-measures ANOVA on the log transformed data using the factors axis (cardinal, oblique) and stimuli (standards, eye-swap deviants, orientation deviants) found no significant main effects or interactions (see Table B-2). This suggests that eye-swap and orientation deviants did not influence binocular rivalry dominance durations.

However, I also found that the mean time for a key release after an eye-swap deviant was 0.70 (0.06) s for cardinal gratings and 0.70 (0.05) s for oblique gratings; these times are essentially identical to those after an orientation deviant, of which participants must have been conscious: 0.68 (0.04) s for cardinal gratings and 0.68 (0.04) s for oblique gratings. These
results show that even though dominance durations containing standards and eye-swap deviants did not differ, the onset of a deviant caused a change in participants’ experience of binocular rivalry that led uniformly to a key release. I conclude that participants were conscious of the eye-swap deviants. This was disappointing for my hope that eye-swap deviants might not recruit visual consciousness.

4.3.2 Electrophysiological data

Figure 4.2 shows the grand-averaged ERPs—time-locked to the onset of the phase-shift in the stimuli, as well as their difference waves. Because I found no differences between cardinal and oblique gratings (see below; see also Chapter 3), I collapsed the axis factor. The traces are for standards (black traces), eye-swap deviants (red traces), and orientation deviants (green traces), eye-swap difference waves (red dotted trace), and orientation difference waves (green dotted trace), and are averaged over left anterior, right anterior, left central, right central, left posterior, and right posterior electrodes.
Figure 4.2. Grand-Averaged ERPs for Experiment 2. There are three ERPs and two difference waves per graph: the black traces are for standards, the red traces are for eye-swap deviants, the green traces are for orientation deviants, the red-dotted traces are for the eye-swap difference waves, and the green-dotted traces are for the orientation difference waves. The difference waves at posterior electrodes show a small peak at about 90 ms and a small trough at about 110 ms—I call this the P1 difference. The orientation difference waves show an orientation vMMN at about 250 ms and the eye-swap difference waves show an eye-swap vMMN at about 380 ms. The grey bars show the analysed time windows.

The ERPs at posterior electrodes show a typical pattern of activity for phase-reversal stimuli: a peak at about 110 ms—the P1, and a negativity starting at about 200 ms (O’Shea et al., 2009; Odom et al., 2010). At the P1,
standards yield bigger peaks than eye-swap and orientation deviants; from about 200 ms onwards, eye-swap and orientation deviants yield bigger troughs than standards.

The difference waves at posterior electrodes show:

- A small peak at about 90 ms—deviants started to go positive for the P1 before the standards did, a negative trough at about 110 ms—standards gave a bigger voltage than deviants, and a return to baseline by about 150 ms. van Rhijn et al. (2013) found a similar positivity at about 100 ms, but then their difference waves went negative to a trough at about 150 ms with no subsequent, quick return to baseline. They called their trough the “early vMMN” (p. 6). I call the complex from 90 to 120 ms the P1 difference between standards and deviants, because these differences are in the time range of the P1. Because this activity is outside the time range of the vMMN I do not analyse it further.

- A trough at about 250 ms for the orientation difference waves—orientation deviants gave a bigger voltage than standards, $F(1, 11) = 56.43, p < .001, \eta^2_p = .84$. This activity is similar to the “late vMMN” (p. 6) found by van Rhijn et al. (2013) at about 210 ms. Similar to Astikainen et al. (2008), orientation deviants also gave a bigger voltage than standards at anterior electrodes, $F(1,$
11) = 17.79, \( p = .001, \eta^2_p = .62 \), and at central electrodes, \( F(1, 11) = 32.85, \ p < .001, \eta^2_p = .75 \) (see Table B-3). I call this the orientation vMMN.

- A trough at about 380 ms for the eye-swap difference waves—eye-swap deviants gave a bigger voltage than standards, \( F(1, 11) = 36.18, \ p < .001, \eta^2_p = .77 \). This activity is later than the “late vMMN” (p. 6) found by van Rhijn et al. (2013) at about 210 ms. Similar to orientation deviants, eye-swap deviants also gave a bigger voltage than standards at anterior electrodes, \( F(1, 11) = 11.00, \ p = .007, \eta^2_p = .50 \), and at central electrodes, \( F(1, 11) = 14.62, \ p = .003, \eta^2_p = .57 \) (see Table B-3). I call this the eye-swap vMMN.

- A sustained negativity for both difference waves following the vMMN from each difference wave to at least 500 ms after stimulus onset (my epochs ended at 500 ms). van Rhijn et al. (2013) found no evidence of this negativity. I call this the sustained negativity. I do not analyse this time window.

Figure 4.3 shows the voltage maps for the orientation and eye-swap vMMN components. I include these maps for comparison with van Rhijn et al. (2013).
Similar to van Rhijn et al. (2013), the maps for orientation and eye-swap vMMN show negative voltages in posterior regions of the brain, especially in the right hemisphere, $F(1, 11) = 7.76, p = .018, \eta^2_p = .41$, and positive voltages in anterior and central regions of the brain. In general, the maps show that the two sorts of deviants yield similar voltages in the brain, but at different times after stimulus onset.

To locate the differences in the brain between standards and orientation deviants or eye-swap deviants, I used sLORETA (Pascual-Marqui, 2002). Figure 4.4 shows the sLORETA maps for the orientation and eye-swap vMMN components.
Figure 4.4. sLORETA Maps for Experiment 2. Areas coloured in red represent the voxels where statistically significant differences ($p_s < .01$) between standards and deviants were found. For orientation vMMN, the best matches for current sources were in occipital, parietal, and frontal areas of the brain; for eye-swap vMMN, the best matches for current sources were in occipital, temporal, and frontal areas of the brain.

According to sLORETA, for orientation vMMN, the best matches for current sources were in occipital, parietal, and frontal areas of the brain—this is mostly consistent with Kimura, Ohira, and Schröger (2010), who found significant differences in brain activity between deviants and controls (they used the combined oddball-equiprobable paradigm) in occipital and frontal areas of the brain. For eye-swap vMMN, the best matches for current sources were in occipital, temporal, and frontal areas of the brain (see Table B-4). These results show that orientation and eye-swap vMMN share similar, but not identical, neural generators.

4.4 General discussion

I set out to demonstrate that a source of information about which we are not-conscious, eye-of-origin information (Blake & Cormack, 1979; Logothetis, et al., 1996), can be used to elicit vMMN. I presented 80% of
binocular rivalry standards—one grating to one eye and an identical, orthogonally orientated grating to the other eye, and 20% of deviants—either in some blocks by swapping the gratings between the eyes to change the eye-of-origin of the gratings or in other, control blocks, by rotating the gratings by 45° to change the orientation of the gratings. I found an orientation vMMN at about 250 ms and an eye-swap vMMN at about 380 ms. However, the behavioural data suggested that participants were aware of when an eye-swap deviant was presented. Although this does not necessarily limit my conclusion that swapping binocular rivalry stimuli between the eyes yields a vMMN from information of which observers are unaware (i.e., observers are unaware of which eye is viewing which stimulus; Blake & Cormack, 1979), these results leave open the question of whether vMMN can be generated by sequences of stimuli that are not-conscious.

Before I can accept that eye-of-origin information can act as a deviant, I need to address one possible objection. If we consider each eye separately, an eye-swap deviant is essentially the same as an orientation deviant, except that the rotation is 90° instead of 45°. Could it be that vMMN elicited by changes in eye-of-origin information is nothing more than an orientation vMMN? I argue not for the following reasons:

1. Czigler and Sulykos (2010) found similar vMMNs to 30° and 60° changes in orientation information, suggesting that the size and
timing of vMMN does not correspond to the size of the change between standards and deviants. Furthermore, different stimulus features (e.g., colour, direction of motion, orientation, spatial frequency, and so on) yield vMMN at different times after stimulus onset (e.g., see Table 3 in Pazo-Alvarez et al., 2003). In this experiment, the timing of vMMN to 45° changes in orientation information (i.e., an orientation deviant) was dissimilar to the timing of vMMN to 90° changes in orientation information (i.e., an eye-swap deviant). This suggests that an eye-swap deviant is not simply a change in orientation information.

2. Although it is logically possible to consider what is happening in each eye separately, this does not mean that the normal human visual system operates in this way. The normal human visual system is fundamentally binocular (Blake & Wilson, 2011; Howard & Rogers, 2012). An eye-swap deviant presents exactly the same orientations to the visual system as done by a standard, so any adaptation to those orientations from repeated viewing of the standards will continue, because adaptation to one orientation in one eye partially transfers to the other eye (Blakemore & Campbell, 1969)—the only non-adapted neurons to be stimulated by an eye-swap deviant will be those sensitive
to eye-of-origin. An orientation deviant, however, presents new orientations to both eyes, so that all new neurons will be stimulated, yielding bigger voltages. Therefore, if eye-swap deviants do not stimulate new neurons that process stimulus orientation, whereas orientation deviants do, it is unlikely that the visual system would treat an eye-swap deviant as being the same as an orientation deviant.

If it can be accepted that eye-of-origin information can yield a vMMN, then there are some features of it that deserve special mention, as well as some theoretical implications.

First, it is perhaps not all that surprising that eye-of-origin information can be used to elicit vMMN, because it is a basic feature of binocular vision that, when the inputs from each eye are combined, yields depth perception via stereopsis (Howard & Rogers, 2012). Wheatstone (1838) found that a horizontal disparity between two otherwise identical two-dimensional images presented one to each eye yields the illusion of depth, and that swapping the images between the eyes reverses the perception of depth. He also noted that if the images were sufficiently different, such as I have done in this experiment by presenting one grating to one eye and an identical, orthogonally orientated grating to the other eye, they would engage in binocular rivalry. Although my gratings did not provide any depth cues, the fact that my participants experienced binocular rivalry highlights the
important role of eye-of-origin information as a basic, low-level feature of binocular vision.

From a functional perspective, one might think that it is surprising that eye-swap vMMN peaks at about 380 ms—about 100 ms later than orientation vMMN, because it would make sense to process eye-of-origin information without requiring visual consciousness. For instance, in the case of a hungry lion and a thick sheet of glass, the processing of visual consciousness takes time away from escaping the lion if it is in front of the glass, yet we need not escape if the lion is behind the glass. Indeed, as shown with random-dot stereograms, depth perception precedes any analysis of the form of the objects in each eye (Julesz, 1960); this analysis happens within 120 ms (Over & Long, 1973).

I suspect that the long latency for my eye-swap vMMN is because my eye-swap deviants did not reverse the perception of depth; rather, they continued to alternate in visual consciousness. Therefore, my eye-swap vMMN is due to a change in eye-of-origin information instead of a change in depth perception information. I suspect that infrequently swapping stimuli that contain depth cues between the eyes might yield a vMMN for changes in depth perception information—a stereopsis vMMN. I also suspect that the timing of a stereopsis vMMN would be earlier than 250 ms. I look forward to conducting this experiment in the future.
It is important to point out that eye-swap difference waves did yield an effect at about 110 ms: the P1 difference. An eye-swap deviant involves identical orientations to those of the standards, so it is likely that the neurons processing the deviant are already highly adapted from viewing the standards (Blakemore & Campbell, 1969). However, the P1 difference for eye-swap deviants is essentially identical to that from orientation deviants, which are processed by neurons that are not adapted by the standards. This suggests early deviance-related processing of eye-of-origin information, even if it does not qualify as a typical vMMN.

Second, in Section 4.1, I argued that eye-swap deviants are a useful stimulus for showing that visual consciousness is not necessary for the generation of vMMN. Despite this, my behavioural data indicates that the onset of an eye-swap deviant caused a change in participants’ experience of binocular rivalry that led uniformly to a key release. That is, participants were conscious of the eye-swap deviants (or at least, they were conscious of some sort of change in stimulation, even if they did not consciously know anything about the change) when they were presented during an episode of binocular rivalry dominance. This was disappointing for my hope that eye-swap deviants might not recruit visual consciousness, and contradicts the work of Logothetis et al. (1996). One reason for my failure to replicate Logothetis et al.’s (1996) results is because their effect occurs within a small range of stimulus parameters (Lee & Blake, 1999), and my stimuli were
outside these parameters. Future studies that investigate eye-swap vMMN should consider this issue.

Although the behavioural data suggest that participants were aware of when an eye-swap deviant was presented, this does not necessarily limit my conclusion that swapping binocular rivalry stimuli between the eyes yields a vMMN from information of which observers are unaware, because observers are unaware of which eye is viewing which stimulus during binocular rivalry (Blake & Cormack, 1979). Nevertheless, these results leave open the question of whether vMMN can be generated by sequences of stimuli that are not-conscious. In Experiments 3 and 4 (see Chapters 5 and 6), I use different techniques for hiding the deviants and the standards, deviants, and controls, respectively, from visual consciousness.

Third, these results provide converging operations showing an eye-swap vMMN with those of van Rhijn et al. (2013). They defined their trials by inserting a 100 ms blank interval between presentations; I defined my trials by phase-shifting the stimuli. They mixed up their two types of deviants within each block of trials; I presented only a single sort of deviant within a block of trials. They did not use physically identical stimuli for all of their vMMN analyses; I did. The fact that both approaches yielded rather similar results, an eye-swap vMMN, is testimony to its robustness. For this reason, I argue that eye-of-origin information can be added to the list of stimulus features that yield vMMN.
I also set out to extend upon the results of van Rhijn et al. (2013) by using sLORETA to localise vMMN activity in the brain. My results show that orientation vMMN originated in occipital, parietal, and frontal areas of the brain and that eye-swap vMMN originated in occipital, temporal, and frontal areas of the brain. These results are mostly consistent with Kimura, Ohira, and Schröger (2010), who localised their orientation vMMN to occipital and frontal areas of the brain. One explanation for the subtle differences in current sources between my results and those of Kimura, Ohira, and Schröger (2010) could be that they used the combined oddball-equiprobable paradigm (see below) and I did not.

Testing eye-of-origin information with the combined oddball-equiprobable paradigm would be the final, crucial step for showing that eye-of-origin information can reliably produce a vMMN. In the oddball sequence, deviants are randomly and unpredictably presented in a sequence of standards; in the equiprobable sequence, a stimulus that is physically identical to the deviant from the oddball sequence—a control, is embedded in a sequence with many other sorts of stimuli, all of which are as frequent as the deviant from the oddball sequence. Because there are no standards or deviants in the equiprobable sequence, and because controls are as frequent as the deviant, control minus standard comparisons yield differences in adaptation—an adaptation-based mechanism of deviance detection, and deviant minus control comparisons yield differences in
prediction and prediction-error—a prediction-error-based mechanism of deviance detection (e.g., Astikainen et al., 2008; Czigler et al., 2002; Kimura et al., 2009; Pazo-Alvarez, Amenedo, & Cadaveira, 2004; for review, see Schröger & Wolff, 1996). However, as pointed out by van Rhijn et al. (2013), the combined oddball-equiprobable paradigm is not practical with eye-of-origin information, because one would need five eyes to equate eye-swap deviants with a frequency of 20%! I am designing other approaches to address this limitation.

Finally, my experiment allowed me to assess the influence of the oblique effect on vMMN. The oblique effect is a decrease in performance for visual tasks when stimuli are oblique (diagonal) instead of cardinal (horizontal and vertical; for reviews, see Appelle, 1972; Howard, 1982; Li et al., 2003). Recently, Takács, Sulykos, Czigler, Barkaszi, and Balázs (2013) reported an oblique effect for orientation vMMN. They found a bigger and more sustained vMMN for changes from horizontal standards to vertical deviants (and vice versa) than for changes from left-oblique standards to right-oblique deviants (and vice versa). However, I found no evidence of the oblique effect in my behavioural data or in my ERP data—this is consistent with the results of Chapter 3. I must confess that I am not sure if this is because the spatial frequency of my gratings were not optimal for revealing it (Arakawa et al., 2000), or if this is because binocular rivalry prevented me from finding it (e.g., Abadi, 1976; Blake et al., 1998; Borra et
al., 2010; Fahle, 1982; Wade et al., 1984; for review, see Section 3.4). In any case, I am not too worried that Takács et al. (2013) observed the oblique effect and I did not, because it does not affect my conclusion: that eye-of-origin information can be used to elicit vMMN.

In conclusion, I set out to demonstrate that a source of information about which we are not-conscious, eye-of-origin information, can be used to elicit vMMN. I found an eye-swap vMMN at about 380 ms; however, I suspect that my participants were aware of when an eye-swap deviant was presented. Although this does not necessarily limit my conclusion that swapping binocular rivalry stimuli between the eyes yields a vMMN from information of which observers are unaware, these results leave open the question of whether vMMN can be generated by sequences of stimuli that are not-conscious.
Chapter 5
Not-conscious deviants yield the visual mismatch negativity

In this chapter, I set out to compare vMMN from deviants that were conscious with vMMN from deviants that were not-conscious during binocular rivalry. To study this:

- I measured participants’ EEG activity while presenting standards comprising a grating to one eye and an identical, orthogonally oriented grating to the other eye, yielding binocular rivalry, and deviants in which I reduced the contrast and luminance of the grating presented to either the left eye or the right eye (I call these monocular deviants), or the gratings presented to both eyes (I call this a binocular deviant).

- I 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.

- I asked participants to press keys on a response keypad indicating which of the two gratings was dominant.

- Because of binocular rivalry dominance and suppression, monocular deviants were either conscious or not-conscious, respectively. Binocular deviants were always conscious,
because either the left or right eye would be dominant, or because a patchy combination of stimuli from both eyes would be perceived.

I found two vMMNs for each deviant: one at about 130 ms—an early vMMN, and another at about 240 ms—a late vMMN. I also found that conscious and not-conscious deviants yielded a similar early vMMN, and that conscious deviants yielded a bigger late vMMN than not-conscious deviants. These results show that vMMN occurs in the absence of visual consciousness, that visual consciousness enhances the processing of late vMMN, and that predictive models of visual perception are tested and updated, even when visual input for those predictions does not reach conscious visual perception.

5.1 Introduction

According to theories of predictive coding, the human brain establishes predictive models for the efficient coding of regularities in visual input (e.g., Friston, 2005; Rao & Ballard, 1999). That is, neural networks learn statistical regularities from incoming visual input and reduce redundant processing by ignoring the predicted inputs and by processing only what is not predicted—prediction-error. An important component of theories of predictive coding is that the brain establishes, tests,
and updates predictive models of visual perception, even when visual input for those predictions goes unattended and/or does not reach conscious visual perception (e.g., Hohwy et al., 2008; Mill et al., 2011, 2013; Spratling, 2008). Although there are hundreds of papers showing that predictions are established, tested, and updated in the absence of top-down attention (for reviews, see Näätänen et al., 2007; Winkler & Czigler, 2012), to the best of my knowledge, there is no evidence to suggest that predictions are established, tested, and updated in the absence of visual consciousness (for review, see Section 2.2.2.2 and 2.2.2.3). In this experiment, I provide evidence for this assumption of predictive coding by combining vMMN with binocular rivalry.

vMMN is a well-established brain signature of prediction and prediction-error (e.g., Garrido et al., 2009; Schröger et al., 2013; Stefanics et al., 2014; Wacongne et al., 2012; Winkler & Czigler, 2012), it is typically observed in the oddball paradigm: an infrequent visual stimulus—a deviant, is randomly and unpredictably presented in a sequence of more frequent visual stimuli—the standards, and is seen most clearly in the difference wave: the deviant minus the standard (Kimura et al., 2009; Kimura, Ohira, & Schröger, 2010; Kimura, 2012; see Section 2.2). Binocular rivalry refers to a powerful form of bistable perception in which visual consciousness alternates unpredictably between two dissimilar images
presented one to each eye (Wheatstone, 1838; for reviews, see Alais & Blake, 2004; Blake & O’Shea, 2009; Miller, 2013; see Section 2.3.1).

In this experiment, I 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 as the standards except that the contrast and luminance of one or both were reduced (I 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). Because of binocular rivalry, monocular deviants presented to the dominant eye were conscious and monocular deviants presented to the suppressed eye were not-conscious. Binocular deviants were always conscious, because either the left or right eye would be dominant or because a combination of both eyes would be perceived (I included this deviant because I was sure it would yield a vMMN). I chose to use luminance decrements for three reasons:

1. Infrequent and unpredictable decreases in the luminance of stimuli yield a reliable vMMN (e.g., Kimura et al., 2008b, 2008c; Kimura, Widmann, & Schröger, 2010a, 2010b; Stagg et al., 2004). Moreover, luminance decrements yield smaller exogenous components—ERP components and neural processes sensitive to the physical characteristics of the stimulus, such as visual N1 and adaptation, than full contrast and luminance stimuli (e.g.,
Spekreijse, van der Twell, & Zuidema, 1973; for discussion, see Kimura, 2012); thus, I am under-estimating, rather than over-estimating, and differences between standards and deviants.

2. Luminance decrements are easily detected when presented to the dominant eye during binocular rivalry (e.g., Blake, 1977). That is, these deviants are conscious.

3. Luminance decrements are rarely, if ever, detected when presented to the suppressed eye during binocular rivalry (e.g., Blake & Fox, 1974a). That is, these deviants are not-conscious.

Given that conscious luminance decrements are known to yield a reliable vMMN (e.g., Kimura et al., 2008b, 2008c; Kimura, Widmann, & Schröger, 2010a, 2010b; Stagg et al., 2004), I expected to find a vMMN from conscious deviants. However, I must confess that I did not know what to expect from not-conscious deviants. Four outcomes seemed possible:

1. Conscious and not-conscious deviants yield identical ERPs, meaning that there is no difference between conscious and not-conscious vMMNs. This is consistent with theories of predictive coding proposed by Hohwy et al. (2008), Mill et al. (2011, 2013), and Spratling (2008), and suggests that vMMN is independent of visual consciousness.
2. Conscious deviants yield bigger amplitudes than not-conscious deviants, meaning that not-conscious vMMN is smaller than conscious vMMN.

3. Alternatively, conscious deviants yield smaller amplitudes than not-conscious deviants, meaning that not-conscious vMMN is bigger than conscious vMMN.

4. Finally, not-conscious deviants do not differ from the standards. This is inconsistent with theories of predictive coding proposed by Hohwy et al. (2008), Mill et al. (2011, 2013), and Spratling (2008), and suggests that visual consciousness is necessary to elicit vMMN.

I found two vMMNs for each deviant: one at about 130 ms—an early vMMN, and another at about 240 ms—a late vMMN. I also found that conscious and not-conscious deviants yielded a similar early vMMN, and that conscious deviants yielded a bigger late vMMN than not-conscious deviants. These results are consistent with outcomes 1 and 2, and suggest that vMMN occurs in the absence of visual consciousness, that visual consciousness enhances the processing of late vMMN, and that predictive models of visual perception are tested and updated, even when visual input for those predictions does not reach conscious visual perception.
5.2 Method

5.2.1 Participants

Fifteen volunteers participated in my study for course credit or payment (6 €/h). All participants gave written informed consent prior to the experiment, had normal or corrected-to-normal visual acuity in both eyes, and showed normal binocular rivalry in a 12 minute pre-test session. Data of five participants were excluded from further analyses: one due to technical problems, the others because too few epochs remained after data pre-processing. Mean (SD) age of the remaining 10 participants, of whom three were male, was 26 (11) years. The study was performed in accordance with the ethical standards laid down in the Declaration of Helsinki (World Medical Association, 2000) and with the ethics guidelines of the German Psychological Association.

5.2.2 Apparatus

The experiment was conducted in the EEG Research Laboratory at the University of Leipzig, Leipzig, Germany, in a sound-attenuated (42 dB) 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 SonicView G90fB monitor (1024 x 768; 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; Pelli, 1997). Participants responded using two keys on a response keypad connected via an ActiveWire USB I/O board.

EEG was recorded from 59 Ag/AgCl active electrodes 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, CP7, 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 EOG was recorded by placing an electrode above (FP2) and below the right eye and a horizontal EOG was recorded by placing an electrode on the outer canthi of each eye. I also placed an electrode on each earlobe. The sampling rate was 500 Hz and the online filtering was 0.1 to 250 Hz. In general, the apparatus is similar to the one used in Experiment 1 (for review, see Section 3.2.2).
5.2.3 Stimuli

I used three types of stimuli: standard stimuli, deviant stimuli, and blank stimuli. Standards were identical to the gratings used in Experiment 1 (for review, see Section 3.2.3), with the following exceptions:

- Standards were presented on a black background (0.40 cd/m²), instead of on a medium grey (43.54 cd/m²) background.
- Standards were aligned to horizontal and vertical orientations only (i.e., I did not use oblique gratings; for review of cardinal versus oblique gratings, see Chapters 3 and 4).

I used three types of deviants: binocular deviants, left-eye deviants, and right-eye deviants. Deviants were identical to standards, except that deviants had a lower contrast and luminance:

- For binocular deviants, both gratings had a mean luminance of 21.96 cd/m² and a Michelson contrast of .98.
- For monocular deviants, one eye viewed a grating with a mean luminance of 21.96 cd/m² and a Michelson contrast of .98 (i.e., a luminance decrement), and the other eye viewed a grating with a mean luminance of 43.53 cd/m² and a Michelson contrast of .99. For left-eye deviants, the left eye viewed the luminance decrement; for right-eye deviants, the right eye viewed the luminance decrement.
Blank stimuli consisted only of the fixation rings and the fixation cross only (i.e., there was no grating).

5.2.4 Design and procedure

I used two types of blocks: experimental blocks and control blocks. In experimental blocks, participants were presented with binocular deviants (randomly on 2% of trials), left-eye deviants (also randomly on 2% of trials), right-eye deviants (also randomly on 2% of trials), and standards (on the remaining 94% of trials). There were 12 of these blocks in my experiment, each of which contained 900 trials. An individual trial comprised a display of binocular rivalry gratings—a horizontal grating to one eye and a vertical 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, each onset marking the beginning of a new trial (see Figure 5.1). According to Wolfe (1983), this time is easily enough for binocular rivalry to survive from one display to the next (if anything, rivalry is slightly enhanced by this; O’Shea & Crassini, 1984). The order of trials within a block was random for each participant with the constraint that any two deviants had to be separated by at least 10 standards.
I also included control blocks in my experiment so that I could assess vMMN using physically identical standards and deviants. That is, I used standards in the control blocks that were the same as deviants in the experimental blocks and deviants in the control blocks that were the same as standards in the experimental blocks. However, I found that the difference waves between physically identical stimuli had a pronounced 10-
Hz periodicity, even in the pre-stimulus onset period. This made my difference waves impossible to interpret. I do not report any further data from my control blocks.

The participant’s task, to track his or her experience of rivalry with key presses, was identical to the one used in Experiment 1 (for review, see Section 3.2.4). I used key presses and releases to determine participants’ mean binocular rivalry dominance duration, to classify left- and right-eye deviants as conscious or not-conscious, and to assess the intrusiveness of deviants on visual consciousness.

5.2.5 Electrophysiological analysis

I treated the EEG data in the same way as in Experiment 2, with the following exceptions:

- The phase-shift free Butterworth filter was from 0.1 to 40 Hz instead of 0.1 to 35 Hz.
- I extracted the epochs from –100 to 400 ms.
- I excluded all epochs that contained a key press or release from –300 to 150 ms.
- I computed ERPs separately for each stimulus (standard, binocular deviant, conscious deviant, not-conscious deviant)
for each participant, and excluded data sets containing fewer than 100 epochs for any ERP.

To classify left- and right-eye deviants as conscious or not-conscious, I used key presses and releases. That is, if a left- or right-eye deviant was presented, and if the left or right eye was dominant, respectively, I classified it as a conscious deviant. If, however, a left- or right-eye deviant was presented, and if the right or left eye was dominant, respectively, I classified it as a not-conscious deviant. However, because binocular rivalry alternations are about 450 ms ahead of a key press or release (Alais et al., 2010), I classified left- and right-eye deviants as conscious or not-conscious 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. I chose these times to be consistent with Kaernbach et al. (1999) and Roeber et al. (2008).

To assess vMMN, I computed difference waves by subtracting the grand-averaged ERPs for standards from the grand-averaged ERPs for binocular deviants, conscious deviants, or not-conscious deviants. This yields three difference waves: binocular difference waves (binocular deviants minus standards), conscious difference waves (conscious deviants minus standards), and not-conscious difference waves (not-conscious deviants minus standards). To assess visual consciousness, I subtracted not-
conscious difference waves from conscious difference waves. This yields the awareness difference waves.

Using visual inspection of the binocular, conscious, and not-conscious difference waves, I determined the time windows of the early vMMN (126 to 146 ms) and late vMMN (236 to 256 ms) components at posterior electrodes. I analysed the mean amplitudes of the ERPs for the early and late vMMN time windows using repeated-measures ANOVA and the factors region (anterior, central, posterior), hemisphere (left, right), and stimuli (standards, binocular deviants, conscious deviants, not-conscious deviants). Similarly, using visual inspection of the awareness difference waves, I determined the time windows of the P1 difference (66 to 86 ms), the late vMMN difference (306 to 356 ms), and the late negativity difference (306 to 256 ms). I analysed the mean amplitudes of the ERPs for these time windows using repeated-measures ANOVA and the factors region, hemisphere, and difference wave (conscious difference waves, not-conscious difference waves). I also calculated voltage maps for these time windows and used sLORETA (Pascual-Marqui, 2002).
5.3 Results and discussion

5.3.1 Behavioural data

The time between a key press and its release yielded the time of one episode of binocular rivalry dominance; the distribution of these times had the typical gamma shape (e.g., Levelt, 1967; Zhou et al., 2004). Mean (SD) binocular rivalry dominance duration was 1.96 (0.49) s; this time is about 10 presentations of my stimuli, and is consistent with what we know about binocular rivalry during 5 Hz on-off flicker (O’Shea & Crassini, 1984; Wolfe, 1983). That is, visual consciousness of one or the other grating survived the 5 Hz on-off flicker.

To assess the intrusiveness of deviants on binocular rivalry, I compared binocular rivalry dominance durations containing standards with binocular rivalry dominance durations containing binocular deviants, conscious deviants, or not-conscious deviants. Mean binocular rivalry dominance duration was 1.66 (0.27) s for standards, 2.35 (0.74) s for binocular deviants, 2.25 (0.72) s for conscious deviants, and 2.27 (0.63) s for not-conscious deviants. One-way ANOVAs on the log-transformed data found that dominance durations containing standards were shorter than those containing binocular deviants, $F(1, 9) = 37.83, p < .001, \eta^2_p = .81$, those containing conscious deviants, $F(1, 9) = 29.64, p < .001, \eta^2_p = .77$, and those
containing not-conscious deviants, $F(1, 9) = 46.98, p < .001, \eta_p^2 = .84$. There were no significant differences among binocular deviants, conscious deviants, and not-conscious deviants. These results are consistent with Levelt’s (1965) third and fourth propositions: that decreasing the stimulus strength (i.e., contrast and luminance) in one eye or in both eyes will decrease the rate of binocular rivalry alternations, consequently increasing the mean dominance duration.

Furthermore, I found that the mean time for a key release was 0.86 (0.24) s after binocular deviants, 0.89 (0.24) s after conscious deviants, and 0.87 (0.26) s after not-conscious deviants; one-way ANOVAs on the log-transformed data found that these times were not significantly different (see Table C-1). Because reaction times during binocular rivalry are about 450 ms (Alais et al., 2010), and because the times for a key release after a deviant are about twice that, it is unlikely that my binocular, conscious, and not-conscious deviants led to a change in visual consciousness. This is consistent with what we know about binocular rivalry and luminance decrements (Blake, 1977; Blake & Fox, 1974a).

5.3.2 Electrophysiological data

I averaged the grand-averaged ERPs over left anterior, right anterior, left central, right central, left posterior, and right posterior electrodes. I do
not show the grand-averaged ERPs, because they show a pronounced 10 Hz periodicity. For instance, at posterior electrodes, I found a peak at about – 50, 50, 150, 250, and 350 ms, and a trough at about 0, 100, 200, and 300 ms, for all ERPs. I also found a similar pattern of activity at anterior and central electrodes. I suspect that this activity reflects the rapid onsets and offsets of my stimuli (see Figure C-1).

Figure 5.2 shows the binocular difference waves (blue traces), the conscious difference waves (red traces), the not-conscious difference waves (green traces), and the awareness difference waves (black traces) averaged over left anterior, right anterior, left central, right central, left posterior, and right posterior electrodes.
Figure 5.2. Difference Waves for Experiment 3. There are four difference waves per graph: the blue traces are for the binocular difference waves, the red traces are for the conscious difference waves, the green traces are for the not-conscious difference waves, and the black dotted traces are for the awareness difference waves. The grey bars show the analysed time windows. The deviant minus standard difference waves at posterior electrodes show an early vMMN at about 130 ms, a deviance-related positivity at about 200 ms, a late vMMN at about 240 ms, and a positive-going deflection starting at about 260 ms. For the binocular difference waves, the deflection peaks for the P3a at about 330 ms, for the conscious difference waves, the deflection turned into a sustained negativity at about 280 ms, and for the not-conscious difference waves, the deflection returned to baseline at about 280 ms—I call this the late deviance-related activity. The awareness difference waves at posterior electrodes show a P1 difference at about 75 ms, and a negative-going deflection starting at about 200 ms and continuing to at least 400 ms.
I perform two types of comparisons on the electrophysiological data: deviant minus standard comparisons and visual consciousness comparisons. For readability, I report these comparisons separately.

5.3.2.1 Deviant minus standard comparisons

The binocular, conscious, and not-conscious difference waves at posterior electrodes show:

- A trough at about 130 ms—binocular, conscious, and not-conscious deviants are more negative than standards, $F_{s}(1, 9) = 27.78, 19.96, \text{ and } 15.55$ respectively, all $p_s < .005$, all $\eta_p^2 s > .60$, with essentially no difference among the three deviants (see Table C-2). The timing of this activity is similar to that found by Kimura et al. (2008b) at about 130 ms and by Kimura et al. (2008c) at about 150 ms.

- A peak at about 200 ms—standards have a bigger voltage than deviants. I did not analyse this component statistically because its being positive means it does not qualify as part of the vMMN, but it is quite clear that the binocular difference wave is more positive than the conscious and not-conscious difference waves which do not differ. Because I am interested
in vMMN, and because this activity is beyond the scope of my thesis, I do not analyse it further.

- Another trough at about 240 ms for all three deviants that I call the late vMMN—binocular, conscious, and not-conscious deviants are more negative than standards, $F_{s}(1, 9) = 6.82, 18.86, 6.20, ps = .028, .002, .034, \eta_{p}^{2} = .43, .68, .41$. There were no differences in amplitudes among the deviant types (Table C-2). The timing of this activity is similar to that found by Kimura, Widmann, and Schröger (2010a) at about 200 ms, by Kimura, Widmann, and Schröger (2010b) at about 250 ms, and by Stagg et al. (2004) at about 250 ms.

- A positive-going deflection starting at about 260 ms that I call the late deviance-related activity. For the binocular difference waves, there is a peak at about 330 ms—the P3a. The P3a is associated with the novelty of a stimulus (Polich, 2007); in this experiment, it is probably due to the frequency of deviants—binocular deviants were rarer (2%) than monocular deviants (4%; 2% for left-eye deviants and 2% for right-eye deviants). For the conscious difference waves, the deflection turned into a sustained negativity at about 280 ms. For the not-conscious difference waves, the deflection returned to baseline. Because I
am interested in vMMN, and because this activity is beyond the scope of my thesis, I do not analyse it further.

Figure 5.3 shows the voltage maps for the early and late vMMN time windows for the binocular, conscious, and not-conscious difference waves. I include these maps for comparison with Kimura et al. (2008b, 2008c), Kimura, Widmann, and Schröger (2010a, 2010b), and Stagg et al., (2004).

![Voltage Maps for Deviant Minus Standard Comparisons for Experiment 3.](image)

**Figure 5.3. Voltage Maps for Deviant Minus Standard Comparisons for Experiment 3.** The maps are essentially identical for binocular, conscious, and not-conscious early and late vMMNs: there are negative voltages in posterior regions of the brain and positive voltages in anterior and central regions of the brain.

Similar to previous research (e.g., Kimura et al., 2008b, 2008c; Kimura, Widmann, & Schröger, 2010a, 2010b; Stagg et al., 2004), for early and late vMMN, there are negative voltages in posterior regions of the brain and
positive voltages in anterior and central regions of the brain. In general, the voltage maps for early and late vMMN are identical, regardless of the type of deviant, except that the maps for early vMMN are symmetrical whereas the maps for late vMMN show a hint of a right hemisphere bias.

To locate the differences in the brain between standards and binocular deviants, conscious deviants, and not-conscious deviants during the early vMMN time window, I used sLORETA (Pascual-Marqui, 2002). Figure 5.4a shows the sLORETA maps for the early vMMN components.

According to sLORETA, for early binocular vMMN, the best matches for current sources were in parietal and frontal areas of the brain; for early conscious vMMN, the best matches for current sources were in parietal,
limbic, and frontal areas of the brain; for early not-conscious vMMN, the best matches for current sources were in parietal, sub-lobar, and temporal areas of the brain (see Table C-3). These results show that early binocular, early conscious, and early not-conscious vMMNs share similar neural generators.

I also used sLORETA to locate the differences in the brain between standards and binocular deviants, conscious deviants, and not-conscious deviants during the late vMMN time window. However, sLORETA was unable to locate brain areas with statistically significant differences ($p_s < .01$ or $p_s < .05$) between neural activities for standards and binocular deviants, conscious deviants, and not-conscious deviants. This was disappointing for my hope of localising late vMMN in the brain.

### 5.3.2.2 Visual consciousness comparisons

The awareness difference waves at posterior electrodes show:

- A small peak at about 75 ms—conscious difference waves yielded more activity than not-conscious difference waves at right hemisphere electrodes, $F(1, 9) = 6.56, p = .031, \eta^2_p = .42$ (see Table C-4); this is the earliest neural correlate of visual consciousness ever discovered (cf. Revonsuo & Koivisto, 2010)—a mere 75 ms after stimulus onset. I call this the P1
difference between conscious and not-conscious difference waves. To confirm the latency of this difference, I used a peak detection technique. I found that the mean (SD) latency of the P1 difference was 72 (18) ms.

- Critically, during the early vMMN time window, there is essentially no activity—the awareness difference wave is at baseline, suggesting that visual consciousness does not influence the processing of early vMMN (see Table C-4).

- A negative-going deflection starting at about 200 ms—conscious difference waves yielded more activity than not-conscious difference waves. This deflection continued during the time window for the late vMMN, $F(1, 9) = 7.26, p = .025, \eta^2_p = .45$ (see Table C-5); this is another neural correlate of visual consciousness, and shows visual consciousness enhances the processing of late vMMN. I call this the late vMMN difference between conscious and not-conscious difference waves.

- The negative-going deflection continued during the time window of the late deviance-related activity, wave, $F(1, 9) = 6.46, p = .032, \eta^2_p = .42$ (see Table C-5). I call this the late negativity difference between conscious and not-conscious difference waves.
Figure 5.5 shows the voltage maps for the P1 difference, the late vMMN difference, and the late negativity difference time windows.

For the P1 difference, there are positive voltages in the right hemisphere of the brain and negative voltages in the left hemisphere of the brain. For the late vMMN difference and the late negativity difference, there are negative voltages in posterior regions of the brain (with a hint of a right hemisphere bias) and positive voltages in anterior and central regions of the brain—this activity is a neural correlate of visual consciousness.

For the P1 difference, there are positive voltages in the right hemisphere of the brain and negative voltages in the left hemisphere of the brain. For the late vMMN and the late negativity difference, there are negative voltages in posterior regions of the brain (with a hint of a right hemisphere bias) and positive voltages in anterior and central regions of the brain. These maps show differences between conscious and not-conscious difference waves; thus, these maps show neural activity that is correlated with visual consciousness.

To locate the differences in the brain between conscious and not-conscious difference waves for the P1 difference, the late vMMN difference,
and the late negativity difference, I used sLORETA (Pascual-Marqui, 2002). However, sLORETA was unable to locate brain areas with statistically significant differences ($p < .01$ or $p < .05$) between neural activities for conscious difference waves and not-conscious difference waves during the P1 difference, the late vMMN difference, and the late negativity difference time windows. This was disappointing for my hope of localising visual consciousness in the brain.

5.4 General discussion

I set out to compare vMMN from deviants that were conscious with vMMN from deviants that were not-conscious during binocular rivalry. I 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 as the standards except that the contrast and luminance of one or both were reduced. Because of binocular rivalry, monocular deviants presented to the dominant eye were conscious and monocular deviants presented to the suppressed eye were not-conscious. I found two vMMNs for each deviant: one at about 130 ms—an early vMMN, and another at about 240 ms—a late vMMN. I also found that conscious and not-conscious deviants yielded a similar early vMMN, and that conscious deviants yielded a bigger late
vMMN than not-conscious deviants. These results show that vMMN occurs in the absence of visual consciousness, that visual consciousness enhances the processing of late vMMN, and that predictive models of visual perception are tested and updated, even when visual input for those predictions does not reach conscious visual perception.

However, there is at least one limitation for my conclusion: I did not use physically identical stimuli for my deviant minus standard comparisons. That is, I did not compare deviants from the experimental blocks with standards from the control blocks. Therefore, it is possible that any differences in ERPs between standards and deviants could be explained by differences in stimulus contrast and luminance, rather than prediction and prediction-error (e.g., Kujala et al., 2007). Despite my intention to assess vMMN using physically identical stimuli, I was forced to abandon this comparison after visual inspection of the data. Specifically, the difference waves (i.e., deviants from the experimental blocks minus standards from the control blocks) had a pronounced 10 Hz periodicity, even in the pre-stimulus onset period. This made my difference waves impossible to interpret. Nevertheless, I am confident that this limitation does not affect my conclusion, because my deviants had lower contrast and luminance than that of my standards. It is well known that stimuli with reduced contrast and luminance yield smaller ERPs than stimuli with full contrast and luminance (e.g., Spekreijse et al., 1973), meaning that I should have
found smaller ERPs for deviants than for standards. Instead, I found bigger ERPs for deviants than for standards, indicating that my difference waves are due to a process other than sensory processing; I suspect prediction and prediction-error: the vMMN mechanism.

I can think of at least two other reasons to suppose that the deviance-related negativities at about 130 ms and again at about 240 ms are early and late vMMNs, respectively. They are:

1. Binocular, conscious, and not-conscious difference waves yielded a similar pattern of results in the analysed time windows, at least until about 300 ms. Indeed, I included binocular deviants in this experiment because I was sure they would yield a vMMN (e.g., Kimura et al., 2008b, 2008c; Kimura, Widmann, & Schröger, 2010a, 2010b; Stagg et al., 2004). The fact that all three difference waves yielded rather similar waveforms, at least for negativities, suggests that my deviants elicited a similar pattern of responses in the brain, presumably the vMMN brain response.

2. The timing of early vMMN is consistent with others who have used changes in contrast and luminance information to elicit vMMN. For example, Kimura et al. (2008b) found a vMMN at about 130 ms and Kimura et al. (2008c) found a vMMN at about 150 ms. Similarly, Kimura, Widmann, and Schröger (2010a)
found a vMMN at about 200 ms and Kimura, Widmann, and Schröger (2010b) found a vMMN at about 250 ms; these times are consistent with my late vMMN. Furthermore, Stagg et al. (2004) found a vMMN at about 250 ms and a sustained negativity until about 400 ms; this pattern of activity is consistent with my conscious difference waves. Therefore, it is unlikely that my deviance-related negativities are something other than vMMNs.

If it can be accepted that my deviance-related negativities are early and late vMMNs, then there are some features of these components that deserve special mention, as well as some theoretical implications.

First, I am the first to show that vMMN can occur in the absence of visual consciousness (for review, see Section 2.2.2.3). I presented left- and right-eye deviants during episodes of binocular rivalry dominance and suppression, such that the deviants were either conscious or not-conscious, respectively. At the early vMMN, the size of the difference waves was essentially identical for conscious and not-conscious difference waves. That is, I found that not-conscious deviants yield an early vMMN, and that visual consciousness does not influence its processing. However, at the late vMMN, conscious difference waves yielded more activity than not-conscious difference waves—this is a neural correlate of visual consciousness, and suggests that visual consciousness enhances the
processing of late vMMN. Even though visual consciousness influences the processing of late vMMN, the fact that I found two vMMNs from not-conscious deviants suggests that visual consciousness is not necessary to elicit vMMN.

Furthermore, to the best of my knowledge, these results are the first to provide evidence for one aspect of the theories of predictive coding proposed by Hohwy et al. (2008), Mill et al. (2011, 2013), and Spratling (2008), namely that predictive processing occurs even when visual input causing prediction error does not reach visual consciousness. In this experiment, although I did not find evidence for the establishing of predictive models (see below), the fact that I found an early and a late vMMN from not-conscious deviants shows that predictive models are tested and updated, even in the absence of visual consciousness.

So, why is it that these results do not provide any evidence for the establishing of predictive models in the absence of visual consciousness? The answer is quite simple: in this experiment, the standards were similar to binocular deviants in that they always evoked some consciousness, because they were always presented to both eyes. Therefore, I do not have any evidence for the establishing of predictions in the absence of visual consciousness. One way to provide this evidence is to combine vMMN with CFS, a powerful form of interocular suppression in which an image presented to one eye is suppressed from visual consciousness indefinitely.
by a rapidly changing sequence of Mondrian patterns presented to the other eye (Tsuchiya & Koch, 2004, 2005; Yang & Blake, 2012; for review, see Yang et al., 2014). That is, CFS could be used to suppress standards and deviants to test if predictions can be established, tested, and updated in the absence of visual consciousness. I describe the details of this experiment in Chapter 6.

Second, although these results do not show that top-down attention and visual consciousness perform separate functions in the brain (e.g., Crick & Koch, 2003; Lamme, 2003), they are consistent with this notion. For instance, in general, manipulating attention does not influence the amplitude or latency of vMMN (for reviews, see Czigler, 2007; Stefanics et al., 2014), suggesting that vMMN does not require attentional resources. However, in this experiment, I found that conscious processing of the deviants enhances the amplitude of the late vMMN compared to not-conscious processing of the deviants. That is, it appears as though attention and visual consciousness have opposing effects on vMMN, which means that they must perform separate functions in the brain.

Of course, the only way to show convincingly that top-down attention and visual consciousness have opposing effects on vMMN is to conduct another experiment that doubly dissociates attention and visual consciousness. Recently, Watanabe et al. (2011) used a two-by-two factorial design to doubly dissociate attention and visual consciousness. They found
that reducing attention to a target stimulus reduced the BOLD signal in V1, but that manipulating visual consciousness had no effect (for review, see Section 2.2.2.1). At present, I am designing another experiment to determine the effects of attention and visual consciousness on vMMN using a similar paradigm to that used by Watanabe et al. (2011). I look forward to conducting this experiment.

Third, if one accepts that reduced contrast and luminance stimuli elicit smaller ERPs than full contrast and luminance stimuli, then one must also accept that the early and late vMMNs in this experiment are incompatible with the adaptation hypothesis of vMMN. According to the adaptation hypothesis, vMMN is the result of different states of adaptation between standards and deviants. That is, because the standards are more frequent than the deviants, they are presumably processed by neurons that are more adapted than neurons processing the deviant (Jääskeläinen et al., 2004; May & Tiitinen, 2010). However, in this experiment, my deviants did not stimulate a new population of neurons, as is the case in other vMMN experiments (for review, see Kimura, 2012), because different populations of neurons do not process high-contrast/luminance and low-contrast/luminance stimuli (e.g., Spekreijse et al., 1973). Instead, my standards and deviants stimulated the same population of neurons. Therefore, these results cannot be explained by the adaptation hypothesis of vMMN.
Fourth, my sLORETA analyses on early vMMN are mostly consistent with Kimura, Ohira, and Schröger (2010). They used the combined oddball-equiprobable paradigm and localised their orientation vMMN to occipital and frontal areas of the brain; I used luminance decrements and localised my early vMMN to parietal and frontal areas of the brain. One explanation for the subtle differences in current sources between my results and those of Kimura, Ohira, and Schröger (2010) could be that they changed the orientation of their stimuli to elicit vMMN, and orientation is processed in V1 (e.g., Livingstone & Hubel, 1988), whereas I reduced the contrast and luminance of my stimuli. My sLORETA analyses on early vMMN are also consistent with Urakawa et al. (2010) and Yucel et al. (2007), who used MEG and fMRI, respectively, to localise colour vMMN to occipital, parietal, and frontal areas of the brain. Surprisingly, sLORETA was unable to locate brain areas with statistically significant differences between neural activities for standards and binocular deviants, conscious deviants, and not-conscious deviants during the late vMMN time window. Although I am unable to provide an adequate explanation for this, it was disappointing for my hope of localising late vMMN in the brain.

The results of this experiment also revealed something about deviance-related components other than vMMN, about some previously unreported neural correlates of visual consciousness, and about the nature of binocular rivalry. I discuss these findings here.
First, I found two other deviance-related components: the deviance-related positivity at about 200 ms and the late deviance-related activity at about 300 ms. The deviance-related positivity is likely involved with memory-comparison-based visual change detection. For instance, Kimura et al. (2008b) found a similar positivity at about 180 ms to infrequent contrast and luminance decrements. They argued that it was due to memory-comparison-based visual change detection. Likewise, Kimura et al. (2006) found a similar positivity (they called it a change-related positivity) that occurred whenever the current stimulus was dissimilar to the previous stimulus, even when a stimulus change was not a rare or infrequent event; this is consistent with a memory-comparison-based account of visual change detection. Furthermore, Fonteneau and Davidoff (2007) have shown that the amplitude of change-related positivity is influenced by the magnitude of the change; again, this is consistent with a memory-comparison-based account of visual change detection. My results are consistent with those of Fonteneau and Davidoff (2007), because my binocular deviants yielded a deviance-related positivity that was about twice the size of that from conscious and not-conscious deviants, and because binocular deviants involved a change in the contrast and luminance of both eyes’ gratings, whereas left- and right-eye deviants involved a change in only one eyes’ grating. If one accepts that my deviance-related positivity is due to memory-comparison-based visual change detection,
then one must also accept that it is an exogenous component, and therefore unrelated to the vMMN mechanism.

I also found a late deviance-related activity at about 300 ms. In particular, there was a positive-going deflection starting at about 260 ms for the binocular, conscious, and not-conscious difference waves. For the binocular difference waves, there is a peak at about 330 ms—the P3a. The P3a is associated with the novelty of a stimulus (Polich, 2007); in this experiment, it is probably due to the frequency of deviants—binocular deviants were rarer (2%) than monocular deviants (4%; 2% for left-eye deviants and 2% for right-eye deviants). For the conscious difference waves, the deflection turned into a sustained negativity at about 280 ms. This is similar to my sustained negativity for my orientation and eye-swap difference waves in Chapter 4. I suspect that the sustained negativity has something to do with visual consciousness, because conscious orientation deviants (Chapter 4), conscious eye-swap deviants (Chapter 4), and conscious luminance decrements (this Chapter) all yielded a sustained negativity, whereas not-conscious luminance decrements did not. Instead, not-conscious deviants returned to baseline at about 280 ms—I called this difference between conscious and not-conscious deviants the late negativity difference. Although it is difficult to say why visual consciousness influences the processing of stimuli during the late deviance-related activity time window, I suspect that teasing apart the relation between late vMMN
and the late deviance-related activity may be a profitable avenue for future research.

Second, I found two other neural correlates of visual consciousness: the P1 difference and the late negativity difference. Undoubtedly, the more exciting of these two components is the P1 difference, because it occurs a mere 75 ms after stimulus onset. According to Revonsuo and Koivisto (2010), this time is 25 ms faster than the previous earliest correlate found by Roeber et al. (2008; in Chapter 3, I used the same paradigm as Roeber et al., 2008, and I found the same result). Therefore, my neural correlate of visual consciousness is now the earliest neural correlate of visual consciousness ever discovered! Although I am not entirely sure why my neural correlate of visual consciousness is earlier than Roeber et al.’s (2008), I suspect it has something to do with the effects of visual consciousness on the processing of prediction and prediction-error.

To find their neural correlate of visual consciousness, Roeber et al. (2008) used an ERP paradigm developed by Kaernbach et al. (1999): they presented one grating to one eye and an identical, orthogonally oriented grating to the other eye, yielding binocular rivalry, and asked participants to press keys on a response keypad indicating which of the two gratings was dominant. After doing so for at least 6 seconds, they changed one of the gratings to match the grating shown to the other eye, yielding binocular fusion. Because of binocular rivalry, rivalry-to-fusion changes made to the
dominant grating were conscious whereas rivalry-to-fusion changes made to the suppressed grating were not-conscious. Roeber et al. (2008) found that when the change was conscious, there was more activity at about 100 ms after stimulus onset—the P1, than when an identical change was not-conscious.

Roeber et al.’s (2008) experiment differs from my experiment in one crucial way: they compared conscious changes with not-conscious changes, whereas I compared conscious deviants with not-conscious deviants. Although the distinction between changes and deviants is a subtle one, because my standards established a pattern of regularity in the brain that was predicted by the visual system and because my deviants violated that prediction, and because Roeber et al.’s (2008) stimuli did not, it is possible that my P1 difference is an early component of visual change detection, similar to vMMN, that is enhanced by visual consciousness. Indeed, there is some evidence for this possibility from the auditory modality. Recently, Grimm (2014) showed that differences between auditory deviants and controls can be found as early as 50 ms after stimulus onset; this time, albeit 25 ms earlier, is not too dissimilar to that of my P1 difference. Furthermore, because my results show that visual consciousness enhances the processing of late vMMN, it is possible that visual consciousness may also influence this early component of visual change detection. I look forward to exploring this idea in the future.
Finally, my results confirmed some facts about the dynamics of binocular rivalry. For instance, consistent with O’Shea and Crassini (1984) and Wolfe (1983), participant’s experience of binocular rivalry survived the 5 Hz on-off flicker of the stimuli. Additionally, binocular rivalry dominance durations containing deviants were longer than dominance durations containing only standards. This is consistent with Levelt’s (1965) third and fourth propositions: that decreasing the stimulus strength (in this experiment, contrast and luminance) in one eye or in both eyes will decrease the rate of binocular rivalry alternations, consequently increasing the mean binocular rivalry dominance duration. Similarly, reducing the contrast and luminance of stimuli during binocular rivalry did not break binocular rivalry suppression; this is consistent with previous research investigating the depth of suppression (e.g., Blake, 1977; Blake & Fox, 1974a).

These results also tell us that predictability of visual input survives binocular rivalry suppression. Although binocular rivalry suppression is a powerful effect, some properties of visual stimuli are still processed by the brain. For example, adaptation aftereffects to a grating can be generated, even when the adapting pattern is suppressed for large portions of the adapting period (Blake & Fox, 1974b; Sweeny, Grabowecky, & Suzuki, 2011). Because I found an early and a late vMMN, this experiment shows that predictability of visual input can be added to the list of features that survive binocular rivalry suppression.
In conclusion, I compared vMMN from deviants that were conscious with vMMN from deviants that were not-conscious during binocular rivalry. I found two vMMNs: an early vMMN at about 130 ms and a late vMMN at about 240 ms. For early vMMN, there were no differences between deviants; for late vMMN, conscious deviants yielded a bigger vMMN than not-conscious deviants—this is a neural correlate of visual consciousness. These results show that vMMN occurs in the absence of visual consciousness, that visual consciousness enhances the processing of late vMMN, and that predictive models of visual perception are tested and updated, even when visual input for those predictions does not reach conscious visual perception.
Chapter 6
Prediction of vision from invisible stimuli

In this chapter, I set out to show vMMN from not-conscious standards and deviants during CFS. To study this:

- In not-conscious oddball blocks, I measured participants’ EEG activity while presenting standards and deviants to one eye and a rapidly changing sequence of Mondrian patterns to the other eye, yielding CFS.

- In conscious oddball blocks, I measured participants’ EEG activity to the same standards and deviants and the same sequence of Mondrians, except that I presented a blank stimulus to the eye viewing the Mondrians whenever I presented a grating to the other eye (I included these blocks as a control).

- In other sorts of blocks, some of which were conscious and some of which were not-conscious, I presented the same gratings along with others of different orientations so that all were equiprobable.

- I asked participants to press keys on a response keypad indicating when either one of two target letters in a continuous stream of other letters appeared at fixation.
I found a vMMN from standards and deviants that were not-conscious; surprisingly, I did not find a vMMN from standards and deviants that were conscious. Despite this, these results show that vMMN occurs in the absence of attention and visual consciousness. When I compared deviants with equiprobable gratings, I found that prediction-error-based mechanisms of deviance detection were processed earlier and longer when the gratings were not-conscious than when the gratings were conscious. These results show that vMMN occurs in the absence of visual consciousness, that predictive models of visual perception are established, tested, and updated, even when visual input for those predictions does not attract attention or reach conscious visual perception, and that visual consciousness slows the processing of predictability of visual input.

6.1 Introduction

In Chapter 5, I showed that vMMN occurs in the absence of visual consciousness and that predictive models of visual perception are tested and updated, even when visual input for those predictions does not reach conscious visual perception. To do this, I used binocular rivalry to make some deviants not-conscious, yet I found vMMN at about 130 ms that was identical to when the deviants were conscious. I also found vMMN at about
240 ms that was larger for conscious deviants than for not-conscious deviants.

There are two more final, crucial steps for showing that vMMN occurs in the absence of visual consciousness:

1. Make the standards and deviants invisible to visual consciousness. In Chapter 5, because my standards were always presented to both eyes, participants were always conscious of one or both rival gratings. That is, for my not-conscious vMMN, I compared conscious standards with not-conscious deviants. To ensure that vMMN occurs in the absence of visual consciousness, one would need to compare not-conscious standards with not-conscious deviants. In the experiment I report here, I addressed this issue with CFS, a powerful form of interocular suppression in which an image presented to one eye is suppressed from visual consciousness indefinitely by a rapidly changing sequence of Mondrian patterns presented to the other eye (Tsuchiya & Koch, 2004, 2005; Yang & Blake, 2012; for review, see Yang et al., 2014). That is, unlike binocular rivalry, during which visual consciousness alternates back and forth between two images, during CFS, observers typically report seeing only the Mondrian patterns. In fact, CFS has been shown to suppress an image from visual
consciousness for up to 3 minutes (Tsuchiya & Koch, 2005). This quality of CFS makes it possible to present not-conscious sequences of stimuli to participants.

2. Dissociate the mechanisms that give rise to vMMN. At least two mechanisms of deviance detection are responsible for vMMN (Schröger & Wolff, 1996): an adaptation-based mechanism, because standards are more adapted than deviants (Jääskeläinen et al., 2004; May & Tiitinen, 2010), and a prediction-error-based mechanism, because standards are predicted and deviants are not (e.g., Garrido et al., 2009; Schröger et al., 2013; Stefanics et al., 2014; Wacongne et al., 2012; Winkler & Czigler, 2012). In Chapter 5, I used the oddball paradigm, meaning that I could not dissociate adaptation and prediction-error. In the experiment I report here, I addressed this issue using the combined oddball-equiprobable paradigm (Schröger & Wolff, 1996): in the oddball sequence, deviants are randomly and unpredictably presented in a sequence of standards; in the equiprobable sequence, a stimulus that is physically identical to the deviant from the oddball sequence—a control, is embedded in a sequence with many other sorts of stimuli, all of which are as frequent as the deviant from the oddball sequence. Because there are no standards or deviants
in the equiprobable sequence, and because controls are as frequent as the deviant, control minus standard comparisons yield differences in adaptation, and deviant minus control comparisons yield differences in prediction and prediction-error (e.g., Astikainen et al., 2008; Czigler et al., 2002; Kimura et al., 2009; Pazo-Alvarez, Amenedo, & Cadaveira, 2004).

The purpose of this experiment is to take the final, crucial steps for showing that vMMN occurs in the absence of visual consciousness. I found a not-conscious vMMN from about 154 to 274 ms, a not-conscious adaptation-based mechanism of deviance detection from about 194 to 244 ms, and a not-conscious prediction-error-based mechanism of deviance detection from about 162 to 262 ms. Consistent with Chapter 5, these results confirm that vMMN occurs in the absence of visual consciousness and that predictive models of visual perception are established, tested, and updated, even when visual input for those predictions does not attract attention or reach conscious visual perception.

6.2 Method

6.2.1 Participants

Eighteen volunteers participated in my study. There was no reward or financial incentive offered to participate. All participants gave written
informed consent prior to the experiment and had normal or corrected-to-normal visual acuity in both eyes. Data of six participants were excluded from further analyses: two due to technical problems, the others because too few epochs remained after data pre-processing. Mean (SD) age of the remaining 12 participants, of whom nine were male, was 25 (7) years. The study was approved by Southern Cross University’s Human Research Ethics Committee (ECN-13-070).

6.2.2 Apparatus

The apparatus was identical to the one used in Experiment 1 (for review, see Section 3.2.2).

6.2.3 Stimuli

I used three types of stimuli: grating stimuli, CFS patterns, and blank stimuli. I used grating stimuli as standards, deviants, and controls. They and other stimuli were identical to those used in Experiment 1 (for review, see Section 3.2.3), with the following exceptions:

- The gratings were enveloped by a Gaussian centred on the grating (1.6° at half height; SD = 1.01° of visual angle). I did this because I discovered during pilot testing that the edges of the gratings would sometimes break CFS, briefly revealing the
orientation of the grating; the Gaussian blurs the edges of the grating, thus ensuring that they were not-conscious in not-conscious blocks of the experiment and that they were conscious in conscious blocks of the experiment. Because of the Gaussian, the contrast of the gratings was less than that of the gratings in Experiments 1–3; the Michelson contrast of the gratings in this experiment was .85.

- I replaced the fusion rings with a black (0.40 cd/m²), square, frame concentric to the gratings and Mondrian patterns; this served to lock vergence. One side of the frame was 6.4° of visual angle; its thickness was 0.3°. I made this change from previous experiments to accommodate the size of the CFS patterns; the CFS patterns needed to be bigger than the gratings to ensure that they were reliably suppressed.

- I replaced the red fixation cross in the centre of each grating with a continuous stream of red letters, because rather than tracking rivalry as in Experiments 1–3, participants pressed keys to indicate the presence of one or another target letter. The font style of the letters was Courier size 18 (height of 0.5°, width of 0.3°, and line width of 0.08°).

- Standard gratings were either vertical (0°) or horizontal (90°); deviants had orthogonal orientations.
• Control gratings (shown in the equiprobable blocks) were either vertical or horizontal, and were presented equally alongside gratings of four other orientations: right-vertical-oblique (30°), right-horizontal-oblique (60°), left-horizontal-oblique (120°; also seen as –60°), and left-vertical-oblique (150°; also seen as –30°).

CFS patterns consisted of 200, different, square Mondrians, each of which consisted of 5,000 overlapping, random-sized, monochromatic quadrangles on a medium grey (43.54 cd/m²) background. The Mondrians had a side of 6.4° of visual angle, and their mean (SD) Michelson contrast was .91 (.03). That is, the Mondrians had a higher contrast than that of the gratings, and the Mondrians comprised many horizontal and vertical contours. I used these patterns because I was sure they would suppress the gratings from visual consciousness (for review, see Section 2.3.2).

Blank stimuli consisted only of a display of a medium grey background and the black frame.

6.2.4 Design and procedure

The experiment consisted of 24 blocks. In half of them, gratings were not-conscious; in the other half, gratings were conscious (I included these blocks as a control from which one would expect vMMN). Furthermore, I
used two types of sequences for each type of block: oddball sequences and equiprobable sequences. In not-conscious oddball blocks, participants were presented with deviants (randomly on 16.67% of trials) and standards (on the remaining 83.33% of trials). There were eight of these blocks in my experiment, each of which contained 240 trials. An individual trial comprised a grating stimulus to one eye—either a horizontal grating or a vertical grating, and a Mondrian to the other eye, for 100 ms, and four presentations of randomly chosen (without replacement) Mondrians, identical to both eyes, for 100 ms each. The order of trials within a block was random for each participant with the constraints that any two deviants had to be separated by at least three standards. Conscious oddball blocks were identical to not-conscious oddball blocks, except that participants were presented with a blank stimulus to the eye viewing the Mondrians whenever the other eye viewed a grating. The purpose of the blank stimulus was to ensure that the grating was visible (see Figure 6.1).
Figure 6.1. Procedure for Experiment 4. Each trial comprised a grating to one eye and either a Mondrian or a blank stimulus to the other eye for 100 ms, then four 100-ms-presentations of random Mondrians to both eyes. I show three trials. (a) In not-conscious oddball blocks, 83.33% of gratings were standards—either horizontal or vertical (in this case, horizontal) and a Mondrian to the other eye, and 16.67% of orthogonally oriented deviants (in this case, vertical). (b) Conscious oddball blocks were identical to not-conscious oddball blocks, except that gratings were accompanied by a blank stimulus to the other eye. (c) Not-conscious equiprobable blocks were identical to (a) except that the deviant served as a control and the standards were replaced by gratings of 0°, ±30°, and ±60°, all with equal probability. (d) Conscious equiprobable blocks were identical to not-conscious equiprobable blocks, except that a blank stimulus replaced the Mondrian as in (b).
Not-conscious equiprobable blocks were identical to conscious oddball blocks except that deviant gratings served as control stimuli and the standards were replaced by gratings of 0°, ±30°, or ±60°, all with equal probability. There were four of these blocks in my experiment, each of which contained 240 trials. Conscious equiprobable blocks were identical to not-conscious equiprobable blocks, except that participants were presented with a blank stimulus to the eye viewing the Mondrians whenever the other eye viewed a grating (see Figure 6.1).

Participants performed a demanding target-detection task at fixation. Participants looked at the ever-changing fixation letter in the centre of the stimuli, they pressed one key on the response keypad when the letter “O” appeared and another key when the letter “X” appeared, and they refrained from pressing either key if any other letter was presented. The letters changed every 730 ms, and were presented in a randomised, continuous stream with no repetitions. At the end of each block, participants received feedback on the number of correct responses, the number of false alarms, and the number of misses on the task.

To ensure that the gratings in not-conscious blocks and in conscious blocks were, in fact, not-conscious and conscious, respectively, participants performed a post-test (see Figure 6.2). The post-test consisted of 4 blocks, each of which contained 40 trials. An individual trial comprised four presentations of random Mondrians to both eyes, for 100 ms each, a test
stimulus, for 100 ms, and four more presentations of random Mondrians to both eyes, for 100 ms each. In not-conscious post-test trials, the test stimulus was either a horizontal grating or a vertical grating, and a Mondrian to the other eye. Conscious post-test trials were identical, except that the grating was accompanied in the other eye by a Mondrian. I asked participants to indicate which grating had been presented, and to rate their confidence from 1 (guess) to 3 (sure) on a 3-point Likert scale. This provided me with a measure of participant’s visual consciousness.

6.2.5 Electrophysiological analysis

I treated the EEG data in the same way as in Experiment 2. I computed ERPs separately for each percept (not-conscious, conscious) and for each
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stimulus (standard, deviant, control) for each participant, and excluded data sets containing fewer than 200 epochs for any ERP.

To assess vMMN, I computed difference waves by subtracting the grand-averaged ERPs for standards from the grand-averaged ERPs for deviants. This yields two difference waves: not-conscious deviance-based difference waves (not-conscious deviants minus not-conscious standards) and conscious deviance-based difference waves (conscious deviants minus conscious standards). To assess adaptation, I computed difference waves by subtracting the grand-averaged ERPs for standards from the grand-averaged ERPs for controls. This yields two difference waves: not-conscious adaptation-based difference waves (not-conscious controls minus not-conscious standards) and conscious adaptation-based difference waves (conscious controls minus conscious standards). Finally, to assess prediction-error, I computed difference waves by subtracting the grand-averaged ERPs for controls from the grand-averaged ERPs for deviants. This yields two difference waves: not-conscious prediction-error-based difference waves (not-conscious deviants minus not-conscious controls) and conscious prediction-error-based difference waves (conscious deviants minus conscious controls).

Using visual inspection of the not-conscious difference waves, I determined the time windows of the not-conscious early deviance-based negativity, adaptation-based mechanism, and prediction-error-based
mechanism (60 to 80 ms), the not-conscious vMMN (154 to 274 ms), the not-conscious late adaptation mechanism (194 to 244 ms), and the not-conscious late prediction-error mechanism (162 to 262 ms) components at right posterior electrodes. Similarly, using visual inspection of the conscious difference waves, I determined the time windows of the conscious early deviance-based negativity, adaptation-based mechanism, and prediction-error-based mechanism (60 to 80 ms), the conscious late adaptation mechanism (178 to 218 ms), the conscious late prediction-error mechanism (190 to 260 ms), the first conscious vMMN (230 to 260 ms), and the second conscious vMMN (324 to 344 ms) components at right posterior electrodes. I analysed the mean amplitudes of the ERPs for the different time windows using repeated-measures ANOVA and the factors region (anterior, central, posterior), hemisphere (left, right), percept (not-conscious, conscious), and stimuli (deviance-based difference wave: standards, deviants; adaptation-based difference wave: standards, controls; prediction-error-based difference wave: deviants, controls). I also calculated voltage maps for these time windows and used sLORETA (Pascual-Marqui, 2002).
6.3 Results and discussion

6.3.1 Behavioural data

In the experiment proper, I defined a target as being detected when participants pressed the correct key between 150 and 750 ms after its occurrence. On average (SD), participants detected 75% (16%) of the targets and committed 0.3% (0.2%) false alarms. This yielded a mean $d'$ of 3.54 (0.48). Repeated-measures ANOVA using the factors percept (not-conscious, conscious) and block (oddball, equiprobable) found no differences in performance (see Table D-1). These results show that participants performed the target detection task quite well, but not perfectly, suggesting that the task was demanding and that it occupied participants’ attention.

To verify successful manipulation of visual consciousness, I analysed the data from the post-test. I found that accuracy was lower in not-conscious trials ($M = 57\%, SD = 13\%$) than in conscious trials ($M = 70\%, SD = 15\%$). Critically, accuracy in not-conscious trials was not significantly different from chance, $t(11) = 2.00, p = .070$, whereas accuracy in conscious trials was significantly better than chance, $t(11) = 2.82, p = .017$. Furthermore, I found that confidence ratings were lower in not-conscious trials ($M = 1.56, SD = 0.35$) than in conscious trials ($M = 2.18, SD = 0.67$), $F(1, 11) = 11.72, p = .006, \eta^2_p = .52$. These results show that participants were objectively (i.e., the
orientation task) and subjectively (i.e., the confidence task) not-conscious of the gratings in not-conscious post-test trials and conscious of the gratings in conscious post-test trials, and are consistent with others (e.g., Raio, Carmel, Carrasco, & Phelps, 2012) who concluded that their stimuli were invisible to visual consciousness.

### 6.3.2 Electrophysiological data

I averaged the grand-averaged ERPs over left anterior, right anterior, left central, right central, left posterior, and right posterior electrodes. I do not show the grand-averaged ERPs, because, as in Chapter 5, they show a pronounced 10 Hz periodicity. I suspect that this activity reflects the rapid onsets and offsets of my stimuli (see Figure D-1).

I perform two types of comparisons on the electrophysiological data: not-conscious comparisons and conscious comparisons. For readability, I report these comparisons separately, and then I report the ANOVAs for the visual consciousness comparisons.

#### 6.3.2.1 Not-conscious comparisons

Figure 6.3 shows the deviance-based difference waves (black traces), the adaptation-based difference waves (red traces), and the prediction-error-based difference waves (green traces) for not-conscious stimuli
averaged over left anterior, right anterior, left central, right central, left posterior, and right posterior electrodes.

Figure 6.3. Difference Waves for Not-Conscious Comparisons for Experiment 4. There are three difference waves per graph: the black traces are for the deviance-based difference waves (deviant minus standard), the red traces are for adaptation-based difference waves (control minus standard), and the green traces are for prediction-error-based difference waves (deviant minus standard). The light grey bars show the analysed time window for the deviance-based difference waves, the dark grey bars above 0 on the y-axis show the analysed time windows for the adaptation-based difference waves, and the dark grey bars below 0 on the y-axis show the analysed time windows for the prediction-error-based difference waves. Effects are most pronounced for right posterior electrodes. Note: ABM, Adaptation-Based
In general, the not-conscious deviance-based, adaptation-based, and prediction-error-based difference waves show bigger amplitudes at posterior electrodes than at anterior and central electrodes, bigger amplitudes at right posterior electrodes than at left posterior electrodes, and a reversal in polarity between posterior and anterior electrodes. Furthermore, the difference waves at right posterior electrodes show:

- A trough at about 70 ms for the deviance-based difference wave, but it was not significant, $F(1, 11) = 1.61, p = .230, \eta^2_p = .13$ (see Table D-2). Although I did not expect to find this negativity, which I call the not-conscious early deviance-based negativity, I am surprised that it is not significant, because I also found a peak for the adaptation-based difference wave—not-conscious controls gave a bigger voltage than not-conscious standards, $F(1, 11) = 6.42, p = .028, \eta^2_p = .37$ (see Table D-3), and a trough for the prediction-error-based difference wave—not-conscious deviants gave a bigger voltage than not-conscious controls, $F(1, 11) = 6.63, p = .026, \eta^2_p = .38$ (see Table D-4). I call the peak in the adaptation-based difference wave the not-conscious early adaptation-based mechanism, and I call the trough in the
prediction-error-based difference wave the not-conscious early prediction-error-based mechanism.

- A negative deflection starting at about 100 ms, most negative at about 230 ms, and returning to baseline at about 280 ms, for the deviance-based difference wave—not-conscious deviants gave a bigger voltage than not-conscious standards, $F(1, 11) = 4.43, p = .049, \eta_p^2 = .29$ (see Table D-2). I call this the not-conscious vMMN. During this time window, there is also a peak for the adaptation-based difference wave—not-conscious controls gave a bigger voltage than not-conscious standards, $F(1, 11) = 6.81, p = .024, \eta_p^2 = .38$ (see Table D-3), and a trough for the prediction-error-based difference wave—not-conscious deviants gave a bigger voltage than not-conscious controls, $F(1, 11) = 11.71, p = .006, \eta_p^2 = .52$ (see Table D-4). I call the peak in the adaptation-based difference wave the not-conscious late adaptation-based mechanism, and I call the trough in the prediction-error-based difference wave the not-conscious late prediction-error-based mechanism.

Figure 6.4 shows the voltage maps for the not-conscious early and late components. For the early deviance-based negativity, the early prediction-error-based mechanism, the vMMN, and the late prediction-error-based mechanism, there are negative voltages in posterior regions of the brain and
positive voltages in anterior and central regions of the brain. For the early and late adaptation-based mechanisms, there are positive voltages in posterior regions of the brain, negative voltages in anterior regions of the brain, and essentially no activity in central regions of the brain. These maps show that vMMN and its underlying mechanisms occur in the absence of visual consciousness.

Figure 6.4. Voltage Maps for Not-Conscious Comparisons for Experiment 4.
To locate the differences in the brain between not-conscious standards, deviants, and controls, I used sLORETA (Pascual-Marqui, 2002). Figure 6.5 shows the sLORETA maps for the not-conscious early adaptation-based mechanism, for the not-conscious vMMN, and for the not-conscious late adaptation-based mechanism.

![sLORETA Maps for Not-Conscious Comparisons for Experiment 4. Areas coloured in red represent the voxels where statistically significant differences ($p < .01$) between deviants and standards and between controls and standards were found.](image)

According to sLORETA, for the not-conscious early adaptation-based mechanism, for the not-conscious vMMN, and for the not-conscious late adaptation-based mechanism, the best matches for current sources were in temporal and limbic areas of the brain. sLORETA also found significant differences in brain activity for these components in occipital and frontal areas of the brain (see Table D-5).
I also used sLORETA to locate the differences in the brain between not-conscious deviants and not-conscious controls during the early and late prediction-error-based mechanism time windows. However, sLORETA was unable to locate brain areas with statistically significant differences ($p < .01$ or $p < .05$) between neural activities for not-conscious deviants and not-conscious controls. This was disappointing for my hope of localising not-conscious prediction-error-based mechanisms in the brain.

6.3.2.2 Conscious comparisons

Figure 6.6 shows the deviance-based difference waves (black traces), the adaptation-based difference waves (red traces), and the prediction-error-based difference waves (green traces) for conscious stimuli averaged over left anterior, right anterior, left central, right central, left posterior, and right posterior electrodes.
Figure 6.6. Difference Waves for Conscious Comparisons for Experiment 4. There are three difference waves per graph: the black traces are for the deviance-based difference waves (deviant minus standard), the red traces are for adaptation-based difference waves (control minus standard), and the green traces are for prediction-error-based difference waves (deviant minus standard). The light grey bars show the analysed time window for the deviance-based difference waves, the dark grey bars above 0 on the y-axis show the analysed time windows for the adaptation-based difference waves, and the dark grey bars below 0 on the y-axis show the analysed time windows for the prediction-error-based difference waves. Effects are most pronounced for right posterior electrodes. Note: ABM, Adaptation-Based Mechanism; DBN, Deviance-Based Negativity; PEBM, Prediction-Error-Based Mechanism.
In general, and similar to the not-conscious difference waves, the conscious difference waves show bigger amplitudes at posterior electrodes than at anterior and central electrodes, bigger amplitudes at right posterior electrodes than at left posterior electrodes, and a reversal in polarity between posterior and anterior electrodes. Furthermore, the difference waves at right posterior electrodes show:

- A trough at about 70 ms for the deviance-based difference wave, but it was not significant, $F(1, 11) = 1.42, p = .259, \eta^2_p = .11$ (see Table D-6). Similar to the not-conscious condition, although I did not expect to find this negativity, which I call the conscious early deviance-based negativity, I am surprised that it is not significant, because I also found a peak for the adaptation-based difference wave—conscious controls gave a bigger voltage than conscious standards, $F(1, 11) = 13.67, p = .004, \eta^2_p = .55$ (see Table D-7), and a trough for the prediction-error-based difference wave—conscious deviants gave a bigger voltage than conscious controls, $F(1, 11) = 8.23, p = .015, \eta^2_p = .43$ (see Table D-8). I call the peak in the adaptation-based difference wave the conscious early adaptation-based mechanism, and I call the trough in the prediction-error-based difference wave the conscious early prediction-error-based mechanism.
• A positive deflection starting at about 180 ms, most positive at about 200 ms, and returning to baseline at about 250 ms, for the adaptation-based difference wave—conscious controls gave a bigger voltage than conscious standards, $F(1, 11) = 6.81, p = .024$, $\eta^2_p = .38$ (see Table D-7). I call this the conscious late adaptation-based mechanism. During this time window, there is also a trough for the prediction-error-based difference wave—conscious deviants gave a bigger voltage than conscious controls, $F(1, 11) = 12.79, p = .004$, $\eta^2_p = .54$ (see Table D-8). I call this the conscious late prediction-error-based mechanism.

• A trough at about 250 ms for the deviance-based difference wave, but it was not significant, $F(1, 11) = 1.49, p = .248$, $\eta^2_p = .12$ (see Table D-9). There was also another trough at about 330 ms for the deviance-based difference wave; again, it was not significant, $F(1, 11) = 1.12, p = .312$, $\eta^2_p = .09$ (see Table D-9). For readability, I call the trough at about 250 ms the first conscious vMMN and I call the trough at about 330 ms the second conscious vMMN. These results show that I failed to find a vMMN from conscious gratings.

Figure 6.7 shows the voltage maps for the conscious components.
For the early deviance-based negativity, there are negative voltages in the right hemisphere of the brain and positive voltages in the left hemisphere of the brain; for the first and second vMMN components, there
are negative voltages in left and right posterior regions of the brain, and there are positive voltages in central posterior regions of the brain as well as in anterior and central regions of the brain. For the early and late adaptation-based mechanisms, there are positive voltages in posterior regions of the brain and negative voltages in anterior regions of the brain. For the early and late prediction-error-based mechanisms, there are negative voltages in posterior regions of the brain and positive voltages in anterior and central regions of the brain.

To locate the differences in the brain between standards, deviants, and controls, I used sLORETA (Pascual-Marqui, 2002). Figure 6.8 shows the sLORETA maps for the conscious early and late adaptation-based mechanisms.

According to sLORETA, for the conscious early adaptation-based mechanism, the best matches for current sources were in frontal and sub-
lobar areas of the brain; for the conscious late adaptation-based mechanism, the best matches for current sources were in temporal and limbic areas of the brain. sLORETA also found significant differences in brain activity for these components in occipital and frontal areas of the brain (see Table D-10).

I also used sLORETA to locate the differences in the brain between conscious deviants and conscious controls during the early and late prediction-error-based mechanism time windows. However, sLORETA was unable to locate brain areas with statistically significant differences ($p < .01$ or $p < .05$) between neural activities for not-conscious deviants and not-conscious controls. This was disappointing for my hope of localising conscious prediction-error-based mechanisms in the brain. I did not use sLORETA to locate the differences in the brain between conscious deviants and conscious standards, because I did not find any significant components for the conscious deviance-based difference wave.

### 6.3.2.3 Visual consciousness comparisons

The left-most graph of Figure 6.9 shows the difference waves for not-conscious stimuli averaged over right posterior electrodes; the right-most graph of Figure 6.9 shows the difference waves for conscious stimuli averaged over right posterior electrodes.
The not-conscious and conscious difference waves at right posterior electrodes show:

- There is essentially no difference between the not-conscious and conscious early deviance-based negativity, $F(1, 11) = 1.91$, $p = .195$, $\eta^2_p = .15$, between the not-conscious and conscious early adaptation-based mechanism, $F(1, 11) = 3.37$, $p = .100$, $\eta^2_p = .27$, or between the not-conscious and conscious early prediction-error-based mechanism, $F(1, 11) = 2.45$, $p = .146$, $\eta^2_p = .18$. Therefore, there were no neural correlates of visual consciousness during the early time windows.

- The not-conscious late adaptation-based mechanism is bigger than the conscious late adaptation based mechanism, $F(1, 11) = 9.28$, $p = .011$, $\eta^2_p = .46$, and the not-conscious late prediction-
error-based mechanism is bigger than the conscious late prediction-error-based mechanism, $F(1, 11) = 41.85, p < .001, \eta^2_p = .79$—these are neural correlates of visual consciousness.

- Finally, the not-conscious vMMN is bigger than the first conscious vMMN, $F(1, 11) = 21.08, p = .001, \eta^2_p = .66$, and the second conscious vMMN, $F(1, 11) = 29.38, p < .001, \eta^2_p = .73$—these are neural correlates of visual consciousness. This is not surprising, because the not-conscious vMMN was significant whereas the conscious vMMNs were not.

6.4 General discussion

I set out to show vMMN from not-conscious sequences of stimuli. To suppress my stimuli from visual consciousness, I presented them to one eye and a rapidly changing sequence of Mondrian patterns to the other eye, yielding CFS. I found a not-conscious vMMN from about 154 to 274 ms. I also found that not-conscious adaptation-based mechanism of deviance detection and not-conscious prediction-error-based mechanism of deviance detection occur at about 70 ms after stimulus onset and again at about 230 ms. These results show that vMMN and its underlying mechanisms, adaptation and prediction-error, occur in the absence of visual consciousness, and that predictive models of visual perception are
established, tested, and updated, even when visual input for those predictions does not reach conscious visual perception.

Before I can accept my conclusions, I have to highlight at least two puzzling aspects of my data:

1. Why was there no vMMN when the stimuli were conscious? I expected to find a vMMN from this condition because it is superficially similar to previous vMMN studies in which participants see the standards and deviants. One explanation could be that participants experienced an abrupt change from the high-contrast Mondrians to a lower-contrast grating in one eye and a blank field in the other in conscious blocks of the experiment, causing contrast adaptation (Heinrich & Bach, 2001) that meant that participants could not even see the monocular gratings, especially when combined with a grey field in the other eye (Baker, Wallis, Georgeson, & Meese, 2012). Basically, it is possible that the visual system may have been processing the regular transition from high-contrast, binocularly fused Mondrians to effectively zero-contrast, rival displays in both eyes (and then, of course, the return to a high-contrast, fused pattern 100 ms later). Although this would engender massive activity in the visual system, such stimuli would not give prediction-error. This is sufficiently different to
not-conscious blocks of the experiment, when such a change occurred only in one eye, leading to less change in contrast between displays of fused Mondrians and an unfused Mondrian plus a grating. This would reveal the grating to the visual system (although it would still be suppressed by CFS), allowing the vMMN to be revealed. To rule out such influences would require a differently designed experiment, something I am keen to do.

2. Why were the amplitudes of the prediction-error-based mechanisms so much bigger than that of vMMN, and why were the amplitudes of the adaptation-based mechanisms approximately equal and opposite in polarity to those of the prediction-error-based mechanisms? One explanation could be that because the ERPs to controls are different to the ERPs to standards and deviants (see Figure D-1), when they are entered into difference waves as the minuend, they yield positive values, and when they are entered as the subtrahend, they yield negative values. However, this merely pushes the question back to why the control stimuli yielded different ERPs from that of standards and deviants. One possible explanation comes from Ruhnau, Herrmann, and Schröger (2012). They argue that the combined oddball-equiprobable paradigm underestimates
adaptation, because the frequency distribution of controls in the equiprobable sequence is typically wider than that of deviants in the oddball sequence, and because the oddball sequence contains a repeating pattern whereas the equiprobable sequence does not. To address this limitation, Ruhnau et al. (2012) proposed using an equiprobable sequence in which stimuli are ordered in a regular, cascading pattern (they called this a “cascadic control”, p. 509). In my experiment, this could be implemented by presenting a vertical grating, then a right-vertical-oblique grating, then a right-horizontal-oblique grating, then a horizontal grating, and so on, such that the gratings appear to rotate clockwise (i.e., a clockwise cascadic control; the gratings could also rotate anti-clockwise, i.e., an anti-clockwise cascadic control). I look forward to adopting this methodology in the future.

If one can accept that the results from not-conscious stimuli are reasonable, the fact that I found vMMN from not-conscious standards and not-conscious deviants means that I am the first to show, but not the first to try to show, that vMMN occurs in the absence of visual consciousness. So, why is it that I was able to show vMMN in the absence of visual consciousness and others were not? I can think of several reasons:
1. Czigler et al. (2007) used backward masking to hide their standards and deviants from visual consciousness. Although there was a hint of a difference between their stimuli, the difference was not statistically significant. In this experiment, I used CFS to hide my standards and deviants, and I found a not-conscious vMMN. One explanation for these different results could be that backward masking and CFS may disrupt visual consciousness at different stages of the visual pathways, such that backward masking disrupts visual consciousness serially earlier than the vMMN mechanism whereas CFS disrupts visual consciousness after the vMMN mechanism. This is an idea I would like to explore in the future.

2. Kogai et al. (2011) used backward masking and found a vMMF. Despite this, they did not compare physically identical stimuli, even though their experiment allowed them to do so. Moreover, their participants said that they could identify some of their standards and deviants, so it is questionable as to whether their stimuli were not-conscious or not. In this experiment, I compared physically identical standards, deviants, and controls. Furthermore, in this experiment, my stimuli were not-conscious: in not-conscious post-test trials, accuracy in the orientation task was at chance and confidence ratings in the
confidence task were low, indicating that my stimuli were not-conscious (see below).

3. Berti (2011) used the attentional blink to hide his deviants. Although he found a vMMN, the attentional blink does not influence visual consciousness; rather, as the name of the illusion suggests, it influences attention. That is, Berti (2011) found a vMMN to deviants that were unattended. In this experiment, I used CFS, a technique that reliably suppresses an image from visual consciousness, and I found a vMMN.

4. Finally, in Chapter 5, I used binocular rivalry suppression to hide my deviants from visual consciousness. I found a not-conscious vMMN at about 130 ms and again at about 240 ms. However, because my standards were always presented to both eyes, there was always consciousness of something about them. That is, for my not-conscious vMMN, I compared conscious standards with not-conscious deviants. In this experiment, to compare not-conscious standards with not-conscious deviants, I used CFS, and I found a not-conscious vMMN from about 154 to 274 ms.

In this experiment, there are two crucial pieces of evidence that allow me to conclude that vMMN occurs in the absence of visual consciousness, and to conclude that predictive models of visual perception are established,
tested, and updated, even when visual input for those predictions does not reach conscious visual perception:

1. I used the combined oddball-equiprobable paradigm to dissociate the underlying mechanisms, adaptation and prediction-error, responsible for the elicitation of vMMN. I found that comparing not-conscious controls and not-conscious standards yielded an adaptation-based mechanism of deviance detection at about 70 ms and again at about 230 ms, and I found that comparing not-conscious deviants and not-conscious controls yielded a prediction-error-based mechanism of deviance detection, also at about 70 ms and again at about 230 ms. These results provide the first crucial piece of evidence for my conclusions, because if vMMN occurs in the absence of visual consciousness, then its underlying mechanisms should also be observed in the absence of visual consciousness. That is exactly what I found.

2. I showed in the post-test that my stimuli were, in fact, invisible to visual consciousness. In particular, I found that accuracy in the orientation task was at chance for not-conscious trials and above chance for conscious trials, and I found that confidence ratings in the confidence task were low in not-conscious trials and high in conscious trials. Therefore, results show that
participants were objectively and subjectively not-conscious of
the gratings in not-conscious post-test trials, presumably
because of CFS, and that they were objectively and subjectively
conscious of the gratings in conscious post-test trials.

If it can be accepted that I have found a not-conscious vMMN, as well
as its underlying mechanisms, then there are some features of these
components (as well as their conscious counterparts) that deserve special
mention, as well as some theoretical implications.

First, not only do my results show that vMMN occurs in the absence
of visual consciousness; they also show that vMMN occurs in the absence
of both top-down attention and visual consciousness. In this experiment, I
ensured participants did not attend to the orientation of the gratings by
asking them to perform a target-detection task at fixation, and I ensured
that participants were not-conscious of the orientation of the gratings by
using CFS. That is, this situation is identical to the no-attention, no-
consciousness situation described by Koch and Tsuchiya (2007; for review,
see Section 2.2.2.1). Because vMMN occurs in the absence of both top-down
attention and visual consciousness, I conclude that vMMN is an automatic
brain response.

Indeed, there is already abundant evidence for vMMN being an
automatic brain response (e.g., Alho et al., 1992; Amenedo et al., 2007;
Cammann, 1990; Heslenfeld, 2002; Kremláček et al., 2006; Maekawa et al.,
vMMN and visual consciousness

2005; Pazo-Alvarez, Amenedo, & Cadaveira, 2004; Stagg et al., 2004; Tales & Butler, 2006; Tales et al., 1999; van Rhijn et al., 2013; Winkler et al., 2005; Woods et al., 1992; for reviews, see Czigler, 2007; Stefanics et al., 2014, especially their Table 1). However, what all of these studies have in common is that standards and deviants, even when presented in the absence of attention, come, in some way, to visual consciousness. In this experiment, my standards, deviants, and controls were unattended and invisible to visual consciousness. Therefore, the fact that I found a vMMN to both unattended and not-conscious stimuli further demonstrates that vMMN is an automatic brain response.

Second, if it can be accepted that I have found a vMMN to both unattended and not-conscious stimuli, then I must also conclude that my results are consistent with the notion that predictive models of visual perception are established, tested, and updated, even when visual input for those predictions goes unattended and does not reach conscious visual perception (Hohwy et al., 2008; Mill et al., 2011, 2013; Spratling, 2008). The key finding in this experiment is that visual consciousness is not necessary for the establishing of predictive models, because in Chapter 5, I showed that visual consciousness is not necessary for the testing and updating (i.e., from the deviants) of predictive models. Therefore, these results show that visual consciousness is not necessary for the establishing of predictive
models, and confirms that visual consciousness is not necessary for the testing and updating of predictive models.

Third, puzzlingly, my sLORETA analyses on the not-conscious difference waves are inconsistent with those of Kimura, Ohira, and Schröger (2010). They used the combined oddball-equiprobable paradigm and localised their adaptation-based mechanism to occipital areas of the brain; I localised my adaptation-based mechanisms to occipital, temporal, and limbic areas of the brain. Furthermore, they localised their prediction-error-based mechanism to occipital and frontal areas of the brain; I could not localise my prediction-error-based mechanisms, because sLORETA was unable to find any significant voxels between not-conscious deviants and not-conscious controls. One reason for these dissimilar results could be that the Mondrian patterns introduced a source of variability in this experiment that was not present in Kimura, Ohira, and Schröger’s (2010) data, because the time of onset and duration of display for the Mondrians was identical to that of the gratings.

More importantly: why did I fail to localise my prediction-error-based mechanisms in the brain? Similar to Ruhnau et al.’s (2012) argument that the combined oddball-equiprobable paradigm underestimates adaptation, it is possible that it also underestimates prediction-error, because the oddball sequence contains a repeating pattern of standards whereas the equiprobable sequence is random. If this is true, then underestimating
prediction-error-based mechanisms may have partly concealed these components, preventing sLORETA from localising them in the brain. As discussed above, to address this issue, I recommend that future experiments use a “cascadic control” (Ruhnau et al., 2012, p. 509).

So far, the majority of this discussion has been limited to the not-conscious difference waves. This is because the aim of this experiment was to show vMMN from not-conscious sequences of stimuli, and because I only included conscious stimuli as a control. I will now discuss the results of the conscious difference waves.

Surprisingly, I failed to find a conscious vMMN. I must confess that I am not entirely sure why I failed to find a conscious vMMN, but it could have something to do with the blank stimulus. In this experiment, to allow participants to perceive the gratings, I presented a blank stimulus to the eye viewing the Mondrian patterns whenever I presented a grating to the other eye. Although there is a hint of a difference between standards and deviants at about 250 ms and again at about 330 ms, it is possible that the visual system treated the blank stimulus and the grating as a change in the regularity established by the repeating Mondrian patterns, irrespective of the orientation of the grating. This idea requires further testing (for more discussion, see above).

In any case, I am not too worried that I did not find a conscious vMMN, because I found two conscious adaptation-based mechanisms and two
conscious prediction-error-based mechanisms. These components suggest that the underlying mechanisms of vMMN were present in my data, even though my vMMNs were not significant. Furthermore, I was able to localise the adaptation-based mechanisms to occipital, temporal, and limbic areas of the brain; these are the same regions involved in not-conscious adaptation-based mechanisms of deviance detection. However, sLORETA was unable to find any significant voxels in the brain for conscious prediction-error-based mechanisms. I encountered the same difficulties when attempting to localise not-conscious prediction-error-based mechanisms.

Are there any similarities between not-conscious and conscious difference waves? Yes. For instance, the early deviance-based negativity, the early adaptation-based mechanism, and the early prediction-error-based mechanism are essentially identical for not-conscious and conscious difference waves. However, not-conscious and conscious difference waves differ in at least three ways:

1. I found a not-conscious vMMN, whereas I failed to find a conscious vMMN. This result is the opposite to that found in Chapter 5 (I found that visual consciousness enhances the processing of vMMN), suggesting that visual consciousness can also reduce the processing of vMMN.
2. I found that the late adaptation-based mechanism is bigger for not-conscious gratings than for conscious gratings. This is surprising, because the adaptation-based mechanism is an exogenous component; therefore, it should not be affected by visual consciousness. One explanation for this could be that because I used the combined oddball-equiprobable paradigm, it is possible that there are differences in processing between the not-conscious control and the conscious control, yielding a bigger adaptation-based mechanism for not-conscious gratings than for conscious gratings.

3. I found that the late prediction-error-based mechanism was processed earlier and longer when the gratings were not-conscious than when the gratings were conscious. I suspect that the extra processing has something to do with the absence of visual consciousness. Recently, Dehaene (2014) claimed that conscious processing engages more brain regions throughout the visual system than not-conscious processing, meaning that not-conscious processing can occur earlier than conscious processing, because some stages of the processing stream can be skipped by not-conscious stimuli, but that conscious processing, once started, can finish earlier than not-conscious processing, because several brain regions are working in
unison to process the stimulus. This account is consistent with my results, because I found that the not-conscious late prediction-error-based mechanism was processed earlier and longer than the conscious late prediction-error-based mechanism. These results show that visual consciousness slows the processing of predictability of visual input.

In conclusion, I set out to show vMMN from not-conscious standards and not-conscious deviants during CFS. I found a not-conscious vMMN from about 154 to 274 ms, a not-conscious adaptation-based mechanism of deviance detection from about 194 to 244 ms, and a not-conscious prediction-error-based mechanism of deviance detection from about 162 to 262 ms. These results show that vMMN occurs in the absence of visual consciousness, that predictive models of visual perception are established, tested, and updated, even when visual input for those predictions does not attract attention or reach conscious visual perception, and that visual consciousness slows the processing of predictability of visual input.
Chapter 7
General Discussion

To repeat the example I gave at the beginning of Chapter 1, imagine you are sitting in a car at a busy intersection waiting for the traffic light to turn green, and you notice that the left indicator light of the car in front is blinking regularly. Instead of attending to the blinking light, you might pay attention to the traffic light, or to the song playing on the radio, or to pedestrians crossing from one side of the street to the other. Now, imagine that one of the blinks from the indicator light changes from yellow to blue. Regardless of whether you notice this change, there will be a sudden change in the electrical activity of your brain, because something unexpected happened. This change in electrical activity is our brain’s way of processing unexpected changes.

Although the story I have told above is not particularly likely, it is an example of the sorts of processes I dealt with in this thesis. In particular, I set out to discover the answers to the following questions:

1. What happens in our brains when we see something that repeats regularly, such as a blinking indicator light? In my thesis, I show that rather than process every new blink as a new object of visual input, our brains form the prediction that the indicator light will continue to exist and to blink in the same
way. That is, our brains establish predictive models of visual perception.

2. What happens in our brains when that regular something changes unexpectedly, such as when one of the blinks from the indicator light changes from yellow to blue? In my thesis, I show that when a prediction is violated, the predictive model is no longer an accurate representation of visual input and therefore needs to be updated. That is, our brains are constantly testing the predictive model against visual input, and updating the model when it is incongruent with visual input.

3. What happens in our brains if we do not notice something that repeats regularly, or if that regular something changes unexpectedly without our noticing? In my thesis, I show for the very first time that the processes of establishing, testing, and updating predictive models of visual perception are independent of visual consciousness.

To reach the answers for the first two questions, in Chapter 2, I reviewed the relevant literature. To reach the answer to the third question, I conducted four EEG/ERP experiments. In Experiment 1 (Chapter 3), I established a consistent methodology for subsequent experiments, and in Experiments 2–4 (Chapters 4–6), I investigated conscious and not-conscious processing of vMMN by combining it with either binocular rivalry or CFS.
I will now provide a general discussion on the outcomes of the studies reported in Chapters 3–6, I will detail their contribution to the field, and I will provide a direction for future research.

7.1 General discussion of Experiments 1–4

In Experiment 1, I set out to determine the better stimulus for studying conscious and not-conscious processing of visual stimuli: cardinal (horizontal and vertical) gratings or oblique (diagonal at ±45°) gratings, using an ERP paradigm developed by Kaernbach et al. (1999). There is good reason to suppose that cardinal gratings may be a better stimulus for studying visual consciousness than oblique gratings, because of the oblique effect—a decrease in performance for visual tasks when stimuli are oblique instead of cardinal (for reviews, see Appelle, 1972; Howard, 1982; Li et al., 2003), and I was concerned that the orientation of my gratings may influence some of the processes discussed in my thesis, such as neural correlates of visual consciousness—differences in brain activity between conscious and not-conscious visual stimuli.

As it turns out, the oblique effect does not influence neural correlates of visual consciousness: I found that conscious and not-conscious rivalry-to-fusion changes yielded the P1 and N1 components, and I found no differences between cardinal and oblique gratings for these times.
Furthermore, I found that the amplitude of the P1 from cardinal and oblique gratings and the amplitude of the N1 from cardinal gratings is bigger for conscious changes than for not-conscious changes—these are neural correlates of visual consciousness, and are consistent with, and extend, the findings of Kaernbach et al. (1999) and Roeber et al. (2008). Unlike Kaernbach et al. (1999), I did not find any differences at the N1 from oblique gratings between conscious and not-conscious changes, but I showed that the P1 and N1 differences occurred for cardinal gratings, that Kaernbach et al. (1999) did not study. Although these results suggest that it is easier to find neural correlates of visual consciousness with cardinal gratings than with oblique gratings, they do not show differences in processing for cardinal and oblique stimuli. Therefore, I did not find any evidence for the oblique effect.

In many ways, the goal of this experiment was to establish a consistent methodology for subsequent experiments. For example, I used essentially the same apparatus, stimuli, and data analysis procedures in Experiment 1 as in Experiments 2–4. Furthermore, because I concluded from this experiment that it is easier to find neural correlates of visual consciousness with cardinal gratings than with oblique gratings, in Experiments 3 and 4, my test stimuli were cardinal gratings.

In Experiment 2, I set out to demonstrate that a source of information about which we are not-conscious, eye-of-origin (utrocular) information,
vMMN and visual consciousness
can be used to elicit vMMN. Eye-of-origin information is considered to be not-conscious for at least two reasons:

1. We already know from psychophysical studies that observers cannot tell which eye is viewing which stimulus during binocular rivalry—a failure of utrocular discrimination (Blake & Cormack, 1979).

2. Logothetis et al. (1996) have shown that swapping grating stimuli between the eyes during binocular rivalry does not lead to any change in the experience of binocular rivalry, which would also rule out any role for visual consciousness in processing eye-of-origin information.

I found that eye-of-origin information can be used to elicit vMMN—I call this an eye-swap vMMN, at about 380 ms after stimulus onset. However, the behavioural data suggested that participants were aware of when an eye-swap deviant was presented. In particular, I found that the onset of an eye-swap deviant caused a change in participants’ experience of binocular rivalry that led uniformly to a key release. That is, participants were conscious of some sort of change in stimulation, even if they did not consciously know anything about the change. Although this does not necessarily limit my conclusion that swapping binocular rivalry stimuli between the eyes yields a vMMN from information of which observers are unaware, because observers are unaware of which eye is viewing which
stimulus (Blake & Cormack, 1979), these results leave open the question of whether vMMN can be generated by sequences of stimuli that are not-conscious. In Experiments 3 and 4, I went on to use different techniques for hiding my stimuli from visual consciousness.

In Experiment 3, I set out to compare vMMN from deviants that were conscious with vMMN from deviants that were not-conscious during binocular rivalry. I 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 as the standards except that the contrast and luminance of one or both were reduced. Because of binocular rivalry, monocular deviants presented to the dominant eye were conscious and monocular deviants presented to the suppressed eye were not-conscious.

I found two vMMNs for each deviant: one at about 130 ms—an early vMMN, and another at about 240 ms—a late vMMN. I also found that conscious and not-conscious deviants yielded a similar early vMMN, and that conscious deviants yielded a bigger late vMMN than not-conscious deviants. These results show that vMMN occurs in the absence of visual consciousness, that visual consciousness enhances the processing of late vMMN, and that predictive models of visual perception are tested and updated, even when visual input for those predictions does not reach conscious visual perception.
Despite these encouraging results, there was at least one limitation for my conclusion: because my standards were always presented to both eyes, they were always conscious. That is, for my not-conscious vMMN, I compared conscious standards with not-conscious deviants. To ensure that vMMN occurs in the absence of visual consciousness, I would need to compare not-conscious standards with not-conscious deviants. Furthermore, I realised that binocular rivalry is not a suitable tool for suppressing a sequence of stimuli from visual consciousness for a long period of time, because binocular rivalry is characterised by brief (about 1 or 2 seconds), continual, and unpredictable changes in visual consciousness. To address this limitation, in Experiment 4, I used CFS.

In my fourth and final experiment, I set out to show vMMN from not-conscious standards and not-conscious deviants during CFS. To study this, I presented standards and deviants to one eye and a rapidly changing sequence of Mondrian patterns to the other eye, and I asked participants to perform an attention demanding task at fixation. The Mondrians performed as intended: they dominated visual consciousness, meaning that my test stimuli were not-conscious. Critically, when I compared not-conscious standards and not-conscious deviants, I found a vMMN from about 154 to 274 ms after stimulus onset. That is, I found a vMMN to unattended and not-conscious stimuli, meaning that vMMN is an automatic brain response.
Furthermore, in this experiment, I used an equiprobable sequence, which allowed me to dissociate the underlying mechanisms, adaptation and prediction-error, responsible for the elicitation of vMMN, and I used conscious stimuli, which allowed me to compare not-conscious and conscious mechanisms of deviance detection. I found that prediction-error-based mechanisms of deviance detection were processed earlier and longer when the gratings were not-conscious than when the gratings were conscious. These results show that vMMN occurs in the absence of visual consciousness, that predictive models of visual perception are established, tested, and updated, even when visual input for those predictions does not attract attention or reach conscious visual perception, and that visual consciousness slows the processing of predictability of visual input.

7.2 Contribution to the field

The general aim of my thesis was to investigate conscious and not-conscious processing of sequences of stimuli that yield vMMN. My thesis accomplished this general aim, and in the process, made at least three important contributions. In particular, my thesis shows that:

1. Visual consciousness is not necessary to elicit vMMN, showing that vMMN is an automatic brain response. Although vMMN is already thought to be an automatic brain response, because
it is elicited in the absence of top-down attention (Czigler, 2007; Stefanics et al., 2014), in three experiments, I found that vMMN is elicited without various forms of visual consciousness of the stimuli. In Experiment 2, I found a vMMN elicited in the absence of consciousness of the source of deviance—eye-of-origin information (Blake & Cormack, 1979). In Experiment 3, I found two vMMNs from not-conscious deviants presented during binocular rivalry suppression: one at about 130 ms—an early vMMN, and another at about 240 ms—a late vMMN. And in Experiment 4, I found a vMMN from not-conscious standards and not-conscious deviants presented during CFS. These results show that visual consciousness is not necessary to elicit vMMN, meaning that vMMN is an automatic brain response.

2. If it can be accepted that visual consciousness is not necessary to elicit vMMN, then it must also be accepted that visual consciousness is not necessary for the brain to establish, test, and update predictive models of visual perception. This finding is consistent with theories of predictive coding proposed by Hohwy et al. (2008), Mill et al. (2011, 2013), and Spratling (2008).
3. Not-conscious processing of predictability of visual inputs is not simply a weaker version of conscious processing of predictability of visual inputs. In Experiment 3, I found that conscious deviants yielded a bigger late vMMN than not-conscious deviants, meaning that visual consciousness enhances the processing of late vMMN; in Experiment 4, I found that prediction-error-based mechanisms of deviance detection were processed earlier and longer when the stimuli were not-conscious than when the stimuli were conscious, meaning that visual consciousness slows the processing of predictability of visual input. One reason for the different effects of visual consciousness on vMMN could be that attention was on the test stimuli in Experiment 3 but not in Experiment 4, and it is possible that top-down attention and visual consciousness may have opposing effects on vMMN (for a similar argument, see Koch & Tsuchiya, 2007). In any case, the fact that I found more activity in Experiment 4 for not-conscious prediction-error-based mechanisms than for conscious prediction-error-based mechanisms shows that not-conscious processing of predictability of visual inputs is not simply a weaker version of conscious processing of predictability of visual inputs.
7.3 Future research

Throughout my thesis, I have proposed suggestions for future research. For example, I suggested exploring the reliability of the typical N1 result (see Experiment 1), I suggested testing eye-of-origin information with the combined oddball-equiprobable paradigm (see Experiment 2), I suggested that teasing apart the relation between late vMMN and the late deviance-related activity (see Experiment 3), and I suggested that future experiments using the equiprobable sequence should consider using the “cascadic control” (Ruhnau et al., 2012, p. 509; see Experiment 4). However, there is one direction for future research that I think could be especially profitable: to dissociate the influences of top-down attention and visual consciousness on the vMMN brain response.

In Chapter 2, I discussed the concepts of top-down attention and visual consciousness and I explained how they are theorised to perform separate functions in the brain (e.g., Crick & Koch, 2003; Lamme, 2003). My thesis provides some results that are consistent with this notion. For example, in Experiment 3, I found that attended and conscious deviants yielded a bigger late vMMN than attended and not-conscious deviants, and in Experiment 4, I found that prediction-error-based mechanisms of deviance detection were processed earlier and longer when the stimuli were
unattended and not-conscious than when the stimuli were unattended and conscious. These results hint at top-down attention and visual consciousness having opposing effects on vMMN.

Of course, the only way to show beyond reasonable doubt that top-down attention and visual consciousness have opposing effects on vMMN is to conduct another experiment that doubly dissociates attention and visual consciousness. To test the possibility that attention and visual consciousness have opposing effects on vMMN, I propose that participants complete an experiment similar to that described by Watanabe et al. (2011).

Watanabe et al. (2011) used a two-by-two factorial design to doubly dissociate top-down attention and visual consciousness. In their experiment, they presented a target—a moving grating, and a suppressing annulus—a mosaic of multiple patches of smaller motion gratings. To manipulate attention, they asked participants to either attend to the target grating (they called this their attention-to-target condition) or to identify when a specific letter was presented in a stream of letters (they called this their inattention-to-target condition). To manipulate visual consciousness, they presented their stimuli to either the same eye, such that the target was conscious (they called this their visible condition), or different eyes, such that the target was not-conscious, yielding CFS (they called this their invisible condition). They found that there was more BOLD activity in V1
when attention was on the target than when attention was not on the target, whereas manipulating visual consciousness had no effect.

I suspect that an experiment similar to Watanabe et al. (2011), except that the target is replaced by standards and deviants, would meet the criteria for doubly dissociating top-down attention and visual consciousness, as defined by Koch and Tsuchiya (2007), and would therefore allow researchers to evaluate the influences of attention and visual consciousness on vMMN. Moreover, if using ERPs, it would come with much better temporal resolution than that provided by fMRI. I look forward to conducting this experiment.

7.4 Conclusion

In conclusion, I set out to investigate conscious and not-conscious processing of sequences of stimuli that yield vMMN. To study this, I conducted four EEG/ERP experiments: in Experiment 1 (Chapter 3), I established a consistent methodology for subsequent experiments, and in Experiments 2–4 (Chapters 4–6), I investigated conscious and not-conscious processing of vMMN by combining it with either binocular rivalry or CFS. My results are consistent with the notions that our brains establish predictive models of visual perception about regular visual input, that our brains are constantly testing the reliability of these models, and that our
brains update these models when something unexpected occurs. My results also show that these processes are independent of visual consciousness. I conclude from my results that visual consciousness is not necessary to elicit vMMN, confirming that vMMN is an automatic brain response.
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Appendix

Appendix A: Experiment 1

Here, I provide supplementary information for Experiment 1 (Chapter 3). In particular, in Table A-1, I provide the results of a repeated-measures ANOVA using the factors region (anterior, central, posterior), hemisphere (left, right), axis (cardinal, oblique), and percept (conscious, not-conscious) on the mean amplitudes of the ERPs for the P1 (94 to 114 ms) and N1 (170 to 200 ms) time windows.

Table A-1
Results of the Statistical Analysis of the ERP Data for the P1 (94 to 114 ms) and N1 (170 to 200 ms) Time Windows

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>P1</th>
<th>N1</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td>Region (R)</td>
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<td>.176</td>
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<tr>
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<td>6.73</td>
<td>.025</td>
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<td>.866</td>
</tr>
<tr>
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<td>1.19</td>
<td>.299</td>
</tr>
<tr>
<td>R x H</td>
<td>2, 22</td>
<td>2.29</td>
<td>.125</td>
</tr>
<tr>
<td>R x A</td>
<td>2, 22</td>
<td>0.03</td>
<td>.972</td>
</tr>
<tr>
<td>H x A</td>
<td>1, 11</td>
<td>0.33</td>
<td>.577</td>
</tr>
<tr>
<td>R x H x A</td>
<td>2, 22</td>
<td>1.56</td>
<td>.232</td>
</tr>
<tr>
<td>R x P</td>
<td>2, 22</td>
<td>7.38</td>
<td>.004</td>
</tr>
<tr>
<td>H x P</td>
<td>1, 11</td>
<td>0.94</td>
<td>.353</td>
</tr>
<tr>
<td>R x H x P</td>
<td>2, 22</td>
<td>2.59</td>
<td>.097</td>
</tr>
<tr>
<td>A x P</td>
<td>1, 11</td>
<td>0.14</td>
<td>.712</td>
</tr>
<tr>
<td>R x A x P</td>
<td>2, 22</td>
<td>0.66</td>
<td>.529</td>
</tr>
<tr>
<td>H x A x P</td>
<td>1, 11</td>
<td>0.06</td>
<td>.819</td>
</tr>
<tr>
<td>R x H x A x P</td>
<td>2, 22</td>
<td>0.36</td>
<td>.705</td>
</tr>
</tbody>
</table>
Appendix B: Experiment 2

Here, I provide supplementary information for Experiment 2 (Chapter 4). In particular, I provide the ANOVA tables for the binocular rivalry dominance duration data (Table B-1), for the intrusiveness of deviants on binocular rivalry dominance duration data (Table B-2), and for the orientation (240 to 290 ms) and eye-swap (350 to 400 ms) vMMN time windows (Table B-3), and I report the results of the sLORETA analyses (Table B-4).

In Table B-1, I provide the results of a repeated-measures ANOVA using the factors axis (cardinal, oblique) and block (eye-swap block, orientation block) on the log-transformed binocular rivalry dominance duration data.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>F</th>
<th>p</th>
<th>η²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Axis (A)</td>
<td>1, 11</td>
<td>0.14</td>
<td>.720</td>
<td>.01</td>
</tr>
<tr>
<td>Block (B)</td>
<td>1, 11</td>
<td>0.63</td>
<td>.443</td>
<td>.05</td>
</tr>
<tr>
<td>A x B</td>
<td>1, 11</td>
<td>&lt;0.01</td>
<td>.969</td>
<td>&lt;.01</td>
</tr>
</tbody>
</table>
In Table B-2, I provide the results of a repeated-measures ANOVA using the factors axis (cardinal, oblique) and stimuli (standards, eye-swap deviants, orientation deviants) on the log-transformed intrusiveness of deviants on the binocular rivalry dominance duration data.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>F</th>
<th>p</th>
<th>ηp²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Axis (A)</td>
<td>1, 11</td>
<td>0.20</td>
<td>.663</td>
<td>.02</td>
</tr>
<tr>
<td>Stimuli (S)</td>
<td>2, 22</td>
<td>0.58</td>
<td>.569</td>
<td>.06</td>
</tr>
<tr>
<td>A x S</td>
<td>2, 22</td>
<td>0.54</td>
<td>.590</td>
<td>.05</td>
</tr>
</tbody>
</table>
In Table B-3, I provide the results of a repeated-measures ANOVA using the factors region (anterior, central, posterior), hemisphere (left, right), axis (cardinal, oblique), and stimuli (standards, eye-swap deviants or orientation deviants) on the mean amplitudes of the ERPs for the orientation and eye-swap vMMN time windows.

Table B-3
Results of the Statistical Analysis of the ERP Data for the Orientation (240 to 290 ms) and Eye-Swap (350 to 400 ms) vMMN Time Windows

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>Orientation vMMN</th>
<th>Eye-Swap vMMN</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td>Region (R)</td>
<td>2, 22</td>
<td>9.19</td>
<td>.001</td>
</tr>
<tr>
<td>Hemisphere (H)</td>
<td>1, 11</td>
<td>5.22</td>
<td>.043</td>
</tr>
<tr>
<td>Axis (A)</td>
<td>1, 11</td>
<td>4.10</td>
<td>.068</td>
</tr>
<tr>
<td>Stimuli (S)</td>
<td>1, 11</td>
<td>46.49</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>R x H</td>
<td>2, 22</td>
<td>5.14</td>
<td>.015</td>
</tr>
<tr>
<td>R x A</td>
<td>2, 22</td>
<td>0.24</td>
<td>.786</td>
</tr>
<tr>
<td>H x A</td>
<td>1, 11</td>
<td>0.35</td>
<td>.564</td>
</tr>
<tr>
<td>R x H x A</td>
<td>2, 22</td>
<td>2.59</td>
<td>.098</td>
</tr>
<tr>
<td>R x S</td>
<td>2, 22</td>
<td>41.85</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>H x S</td>
<td>1, 11</td>
<td>3.22</td>
<td>.100</td>
</tr>
<tr>
<td>R x H x S</td>
<td>2, 22</td>
<td>5.37</td>
<td>.013</td>
</tr>
<tr>
<td>A x S</td>
<td>1, 11</td>
<td>0.84</td>
<td>.380</td>
</tr>
<tr>
<td>R x A x S</td>
<td>2, 22</td>
<td>3.05</td>
<td>.068</td>
</tr>
<tr>
<td>H x A x S</td>
<td>1, 11</td>
<td>0.22</td>
<td>.647</td>
</tr>
<tr>
<td>R x H x A x S</td>
<td>2, 22</td>
<td>1.68</td>
<td>.209</td>
</tr>
</tbody>
</table>
In Table B-4, I report the results of the sLORETA analyses for the orientation and eye-swap vMMN time windows.

<table>
<thead>
<tr>
<th>Anatomical Region</th>
<th>BA</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>t</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Orientation vMMN</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PL, superior parietal lobule</td>
<td>7</td>
<td>-30</td>
<td>-60</td>
<td>50</td>
<td>8.60</td>
</tr>
<tr>
<td>PL, inferior parietal lobule</td>
<td>40</td>
<td>50</td>
<td>-35</td>
<td>35</td>
<td>8.43</td>
</tr>
<tr>
<td>PL, precuneus</td>
<td>7</td>
<td>-25</td>
<td>-60</td>
<td>50</td>
<td>8.37</td>
</tr>
<tr>
<td>PL, postcentral gyrus</td>
<td>2</td>
<td>45</td>
<td>-35</td>
<td>60</td>
<td>8.36</td>
</tr>
<tr>
<td>OL, superior occipital gyrus</td>
<td>19</td>
<td>-40</td>
<td>-80</td>
<td>25</td>
<td>8.09</td>
</tr>
<tr>
<td>OL, middle temporal gyrus</td>
<td>19</td>
<td>-55</td>
<td>-65</td>
<td>15</td>
<td>8.01</td>
</tr>
<tr>
<td>FL, paracentral lobule</td>
<td>5</td>
<td>-15</td>
<td>-40</td>
<td>55</td>
<td>7.98</td>
</tr>
<tr>
<td><strong>Eye-Swap vMMN</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TL, fusiform gyrus</td>
<td>20</td>
<td>-40</td>
<td>-35</td>
<td>-20</td>
<td>10.70</td>
</tr>
<tr>
<td>OL, lingual gyrus</td>
<td>19</td>
<td>20</td>
<td>-70</td>
<td>-5</td>
<td>10.20</td>
</tr>
<tr>
<td>OL, lingual gyrus</td>
<td>18</td>
<td>15</td>
<td>-65</td>
<td>-5</td>
<td>9.92</td>
</tr>
<tr>
<td>PL, postcentral gyrus</td>
<td>3</td>
<td>35</td>
<td>-25</td>
<td>45</td>
<td>9.53</td>
</tr>
<tr>
<td>OL, cuneus</td>
<td>30</td>
<td>5</td>
<td>-65</td>
<td>5</td>
<td>9.49</td>
</tr>
<tr>
<td>OL, fusiform gyrus</td>
<td>19</td>
<td>25</td>
<td>-80</td>
<td>-20</td>
<td>9.45</td>
</tr>
<tr>
<td>FL, superior frontal gyrus</td>
<td>8</td>
<td>15</td>
<td>30</td>
<td>55</td>
<td>9.02</td>
</tr>
</tbody>
</table>

Notes: PL, Parietal Lobe; OL, Occipital Lobe; FL, Frontal Lobe; TL, Temporal Lobe. The critical t-value for p < .01 was 4.08 for orientation vMMN and 4.82 for eye-swap vMMN.
Appendix C: Experiment 3

Here, I provide supplementary information for Experiment 3 (Chapter 5). In particular, I provide the ANOVA table for the intrusiveness of deviants on binocular rivalry dominance duration data (Table C-1), I show the grand-averaged ERPs for the stimuli (Figure C-1), I provide the ANOVA tables for the early (126 to 146 ms) and late (236 to 256 ms) vMMN time windows (deviant minus standard comparisons: Table C-2), I report the results of the sLORETA analyses on the early vMMN components (Table C-3), and I provide the ANOVA tables for the P1 difference (66 to 86 ms) and for the early vMMN difference (126 to 146 ms) time windows (visual consciousness comparisons: Table C-4) and for the late vMMN difference (236 to 256 ms) and late negativity difference (306 to 356 ms) time windows (visual consciousness comparisons: Table C-5).
In Table C-1, I provide the results of three one-way ANOVAs on the log-transformed intrusiveness of deviants on the binocular rivalry dominance duration data.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>F</th>
<th>p</th>
<th>η²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Binocular vs Conscious</td>
<td>1, 9</td>
<td>3.29</td>
<td>.103</td>
<td>.27</td>
</tr>
<tr>
<td>Binocular vs Not-Conscious</td>
<td>1, 9</td>
<td>0.37</td>
<td>.561</td>
<td>.04</td>
</tr>
<tr>
<td>Conscious vs Not-Conscious</td>
<td>1, 9</td>
<td>2.04</td>
<td>.187</td>
<td>.19</td>
</tr>
</tbody>
</table>
Figure C-1 shows the grand-averaged ERPs for standards, binocular deviants, conscious deviants, and not-conscious deviants averaged over left anterior, right anterior, left central, right central, left posterior, and right posterior electrodes.

*Figure C-1.* Grand-Averaged ERPs for Experiment 3. There are four ERPs per graph: the black traces are for the standards, the blue traces are for the binocular deviants, the red traces are for the conscious deviants, and the green traces are for the not-conscious deviants. The grey bars show the analysed time windows. The ERPs show a pronounced 10 Hz periodicity. I suspect that this activity reflects the rapid onsets and offsets of my stimuli.
In Table C-2, I provide the results of a repeated-measures ANOVA using the factors region (anterior, central, posterior), hemisphere (left, right), and stimuli (standards, binocular deviants, conscious deviants, not-conscious deviants) on the mean amplitudes of the ERPs for the deviant minus standard comparisons for the early and late vMMN time windows.

Table C-2
Results of the Statistical Analysis of the ERP Data for the Deviant minus Standard Comparisons for the Early (126 to 146 ms) and Late (236 to 256 ms) vMMN Time Windows

<table>
<thead>
<tr>
<th>Factor</th>
<th>$df$</th>
<th>Early vMMN</th>
<th>Late vMMN</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$F$</td>
<td>$p$</td>
</tr>
<tr>
<td>Region (R)</td>
<td>2, 18</td>
<td>1.02</td>
<td>.381</td>
</tr>
<tr>
<td>Hemisphere (H)</td>
<td>1, 9</td>
<td>8.52</td>
<td><strong>.017</strong></td>
</tr>
<tr>
<td>Stimuli (S)</td>
<td>3, 27</td>
<td>1.63</td>
<td>.206</td>
</tr>
<tr>
<td>R x H</td>
<td>2, 18</td>
<td>1.05</td>
<td>.372</td>
</tr>
<tr>
<td>R x S</td>
<td>6, 54</td>
<td>7.83</td>
<td><strong>&lt;.001</strong></td>
</tr>
<tr>
<td>H x S</td>
<td>3, 27</td>
<td>0.12</td>
<td>.946</td>
</tr>
<tr>
<td>R x H x S</td>
<td>6, 54</td>
<td>1.87</td>
<td>.103</td>
</tr>
</tbody>
</table>
In Table C-3, I report the results of the sLORETA analyses for the early vMMN components.

<table>
<thead>
<tr>
<th>Anatomical Region</th>
<th>BA</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>t</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Binocular Early vMMN</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PL, precuneus</td>
<td>7</td>
<td>15</td>
<td>-45</td>
<td>50</td>
<td>4.46</td>
</tr>
<tr>
<td>FL, superior frontal gyrus</td>
<td>6</td>
<td>10</td>
<td>30</td>
<td>60</td>
<td>4.41</td>
</tr>
<tr>
<td>PL, postcentral gyrus</td>
<td>3</td>
<td>35</td>
<td>-25</td>
<td>45</td>
<td>4.34</td>
</tr>
<tr>
<td>PL, inferior parietal lobule</td>
<td>40</td>
<td>65</td>
<td>-30</td>
<td>40</td>
<td>4.26</td>
</tr>
<tr>
<td><strong>Conscious Early vMMN</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LL, cingulate gyrus</td>
<td>31</td>
<td>15</td>
<td>-30</td>
<td>45</td>
<td>4.19</td>
</tr>
<tr>
<td>PL, inferior parietal lobule</td>
<td>40</td>
<td>-45</td>
<td>-30</td>
<td>30</td>
<td>4.16</td>
</tr>
<tr>
<td>FL, cingulate gyrus</td>
<td>32</td>
<td>10</td>
<td>20</td>
<td>40</td>
<td>3.95</td>
</tr>
<tr>
<td>FL, inferior frontal gyrus</td>
<td>45</td>
<td>-50</td>
<td>25</td>
<td>20</td>
<td>3.82</td>
</tr>
<tr>
<td>FL, sub-gyral</td>
<td>6</td>
<td>35</td>
<td>-5</td>
<td>45</td>
<td>3.78</td>
</tr>
<tr>
<td><strong>Not-Conscious Early vMMN</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PL, inferior parietal lobule</td>
<td>40</td>
<td>-45</td>
<td>-30</td>
<td>30</td>
<td>4.03</td>
</tr>
<tr>
<td>PL, precuneus</td>
<td>7</td>
<td>10</td>
<td>-45</td>
<td>50</td>
<td>3.94</td>
</tr>
<tr>
<td>FL, inferior frontal gyrus</td>
<td>45</td>
<td>-50</td>
<td>25</td>
<td>20</td>
<td>3.91</td>
</tr>
<tr>
<td>FL, paracentral lobule</td>
<td>31</td>
<td>0</td>
<td>-35</td>
<td>45</td>
<td>3.82</td>
</tr>
<tr>
<td>LL, cingulate gyrus</td>
<td>31</td>
<td>10</td>
<td>-45</td>
<td>40</td>
<td>3.77</td>
</tr>
<tr>
<td>SL, insula</td>
<td>13</td>
<td>-30</td>
<td>20</td>
<td>15</td>
<td>3.62</td>
</tr>
</tbody>
</table>

Notes: PL, Parietal Lobe; FL, Frontal Lobe; LL, Limbic Lobe; SL, Sub-Lobar. The critical t-value for $p < .01$ was 4.23 for binocular early vMMN, and the critical t-value for $p < .05$ was 3.76 for conscious early vMMN and 3.46 for not-conscious early vMMN.
In Table C-4, I provide the results of a repeated-measures ANOVA using the factors region (anterior, central, posterior), hemisphere (left, right), and difference wave (conscious difference waves, not-conscious difference waves) on the mean amplitudes of the difference waves for the visual consciousness comparisons for the P1 difference and for the early vMMN difference time windows.

Table C-4

Results of the Statistical Analysis of the Difference Wave Data for the Visual Consciousness Comparisons for the P1 Difference (66 to 86 ms) and for the Early vMMN (126 to 146 ms) Time Windows

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>P1 Difference</th>
<th>Early vMMN</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td>Region (R)</td>
<td>2, 18</td>
<td>0.16</td>
<td>.853</td>
</tr>
<tr>
<td>Hemisphere (H)</td>
<td>1, 9</td>
<td>0.97</td>
<td>.350</td>
</tr>
<tr>
<td>Diff. Wave (DW)</td>
<td>1, 9</td>
<td>0.75</td>
<td>.410</td>
</tr>
<tr>
<td>R x H</td>
<td>2, 18</td>
<td>0.75</td>
<td>.485</td>
</tr>
<tr>
<td>R x DW</td>
<td>2, 18</td>
<td>0.47</td>
<td>.632</td>
</tr>
<tr>
<td>H x DW</td>
<td>1, 9</td>
<td>6.64</td>
<td>.030</td>
</tr>
<tr>
<td>R x H x DW</td>
<td>2, 18</td>
<td>1.13</td>
<td>.344</td>
</tr>
</tbody>
</table>
In Table C-5, I provide the results of a repeated-measures ANOVA using the factors region (anterior, central, posterior), hemisphere (left, right), and difference wave (conscious difference waves, not-conscious difference waves) on the mean amplitudes of the difference waves for the visual consciousness comparisons for the late vMMN difference and for the late negativity difference time windows.

Table C-5
Results of the Statistical Analysis of the Difference Wave Data for the Visual Consciousness Comparisons for the Late vMMN Difference (236 to 256 ms) and for the Late Negativity Difference (306 to 356 ms) Time Windows

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>P1 Difference</th>
<th>Late Negativity Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td>Region (R)</td>
<td>2, 18</td>
<td>10.91</td>
<td>.001</td>
</tr>
<tr>
<td>Hemisphere (H)</td>
<td>1, 9</td>
<td>1.04</td>
<td>.334</td>
</tr>
<tr>
<td>Diff. Wave (DW)</td>
<td>1, 9</td>
<td>8.03</td>
<td>.020</td>
</tr>
<tr>
<td>R x H</td>
<td>2, 18</td>
<td>1.80</td>
<td>.194</td>
</tr>
<tr>
<td>R x DW</td>
<td>2, 18</td>
<td>4.25</td>
<td>.031</td>
</tr>
<tr>
<td>H x DW</td>
<td>1, 9</td>
<td>.17</td>
<td>.687</td>
</tr>
<tr>
<td>R x H x DW</td>
<td>2, 18</td>
<td>2.65</td>
<td>.098</td>
</tr>
</tbody>
</table>
Appendix D: Experiment 4

Here, I provide supplementary information for Experiment 4 (Chapter 6). I provide the ANOVA table for the target detection task (Table D-1), I show the grand-averaged ERPs for not-conscious and conscious stimuli (Figure D-1), I provide the ANOVA tables for the not-conscious early deviance-based negativity (60 to 80 ms) and for the not-conscious vMMN (154 to 274 ms; Table D-2), for the not-conscious early adaptation-based mechanism (60 to 80 ms) and for the not-conscious late adaptation-based mechanism (194 to 244 ms; Table D-3), and for the not-conscious early prediction-error-based mechanism (60 to 80 ms) and for the not-conscious late prediction-error-based mechanism (162 to 262 ms; Table D-4), I report the results of the sLORETA analyses on the not-conscious components (Table D-5), I provide the ANOVA tables for the conscious early deviance-based negativity (60 to 80 ms; Table D-6), for the conscious early adaptation-based mechanism (60 to 80 ms) and for the conscious late adaptation-based mechanism (178 to 218 ms; Table D-7), for the conscious early prediction-error-based mechanism (60 to 80 ms) and for the conscious late prediction-error-based mechanism (190 to 260 ms; Table D-8), and for the first (230 to 260 ms) and second (324 to 344 ms) conscious vMMN components (Table D-9), and I report the results of the sLORETA analyses on the conscious components (Table D-10).
In Table D-1, I provide the results of a repeated-measures ANOVA using the factors percept (not-conscious, conscious) and block (oddball, equiprobable) on $d'$ for the target detection task.

**Table D-1**

*Results of the Statistical Analysis of $d'$ for the Target Detection Task*

<table>
<thead>
<tr>
<th>Factor</th>
<th>$d_f$</th>
<th>$F$</th>
<th>$p$</th>
<th>$\eta^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percept (P)</td>
<td>1, 11</td>
<td>0.19</td>
<td>.669</td>
<td>.02</td>
</tr>
<tr>
<td>Block (B)</td>
<td>1, 11</td>
<td>0.05</td>
<td>.825</td>
<td>.01</td>
</tr>
<tr>
<td>P x B</td>
<td>1, 11</td>
<td>0.70</td>
<td>.420</td>
<td>.06</td>
</tr>
</tbody>
</table>
Figure D-1 shows the grand-averaged ERPs for not-conscious and conscious standards, deviants, and controls averaged over left anterior, right anterior, left central, right central, left posterior, and right posterior electrodes.

*Figure D-1.* Grand-Averaged ERPs for Experiment 4. There are six ERPs per graph: the black traces are for the standards, the red traces are for the deviants, the green traces are for the controls, the solid traces are for not-conscious stimuli, and the dotted traces are for conscious stimuli. Similar to Figure C-1, the ERPs show a pronounced 10 Hz periodicity. I suspect that this activity reflects the rapid onsets and offsets of my stimuli.
In Table D-2, I provide the results of a repeated-measures ANOVA using the factors region (anterior, central, posterior), hemisphere (left, right), and stimuli (standards, deviants) on the mean amplitudes of the ERPs for the not-conscious early deviance-based negativity and for the not-conscious vMMN.

Table D-2

*Results of the Statistical Analysis of the ERP Data for the Not-Conscious Early Deviance-Based Negativity (60 to 80 ms) and for the Not-Conscious vMMN (154 to 274 ms) Time Windows*

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>Early DBN</th>
<th></th>
<th></th>
<th>vMMN</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>p</td>
<td>η²</td>
<td>F</td>
<td>p</td>
<td>η²</td>
</tr>
<tr>
<td>Region (R)</td>
<td>2, 22</td>
<td>19.289</td>
<td>&lt;.001</td>
<td>.64</td>
<td>29.56</td>
<td>&lt;.001</td>
<td>.73</td>
</tr>
<tr>
<td>Hemisphere (H)</td>
<td>1, 11</td>
<td>0.98</td>
<td>.343</td>
<td>.08</td>
<td>10.28</td>
<td>.008</td>
<td>.48</td>
</tr>
<tr>
<td>Stimuli (S)</td>
<td>1, 11</td>
<td>1.91</td>
<td>.194</td>
<td>.15</td>
<td>2.02</td>
<td>.183</td>
<td>.16</td>
</tr>
<tr>
<td>R x H</td>
<td>2, 22</td>
<td>0.30</td>
<td>.746</td>
<td>.03</td>
<td>1.74</td>
<td>.200</td>
<td>.14</td>
</tr>
<tr>
<td>R x S</td>
<td>2, 22</td>
<td>3.03</td>
<td>.069</td>
<td>.22</td>
<td>3.32</td>
<td>.055</td>
<td>.23</td>
</tr>
<tr>
<td>H x S</td>
<td>1, 11</td>
<td>0.11</td>
<td>.743</td>
<td>.01</td>
<td>0.10</td>
<td>.756</td>
<td>.01</td>
</tr>
<tr>
<td>R x H x S</td>
<td>2, 22</td>
<td>0.84</td>
<td>.447</td>
<td>.07</td>
<td>0.46</td>
<td>.635</td>
<td>.04</td>
</tr>
</tbody>
</table>

Notes: DBN, Deviance-Based Negativity.
In Table D-3, I provide the results of a repeated-measures ANOVA using the factors region (anterior, central, posterior), hemisphere (left, right), and stimuli (standards, controls) on the mean amplitudes of the ERPs for the not-conscious early and late adaptation-based mechanisms.

Table D-3

Results of the Statistical Analysis of the ERP Data for the Not-Conscious Early Adaptation-Based Mechanism (60 to 80 ms) and for the Not-Conscious Late Adaptation-Based Mechanism (194 to 244 ms) Time Windows

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>Early ABM</th>
<th>Late ABM</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Region (R)</td>
<td>2, 22</td>
<td>4.61</td>
<td>.021 .30</td>
</tr>
<tr>
<td>Hemisphere (H)</td>
<td>1, 11</td>
<td>10.26</td>
<td>.008 .48</td>
</tr>
<tr>
<td>Stimuli (S)</td>
<td>1, 11</td>
<td>0.20</td>
<td>.667 .02</td>
</tr>
<tr>
<td>R x H</td>
<td>2, 22</td>
<td>0.51</td>
<td>.606 .04</td>
</tr>
<tr>
<td>R x S</td>
<td>2, 22</td>
<td>1.75</td>
<td>.197 .14</td>
</tr>
<tr>
<td>H x S</td>
<td>1, 11</td>
<td>0.02</td>
<td>.897 &lt; .01</td>
</tr>
<tr>
<td>R x H x S</td>
<td>2, 22</td>
<td>2.26</td>
<td>.128 .17</td>
</tr>
</tbody>
</table>

Notes: ABM, Adaptation-Based Mechanism.
In Table D-4, I provide the results of a repeated-measures ANOVA using the factors region (anterior, central, posterior), hemisphere (left, right), and stimuli (deviants, controls) on the mean amplitudes of the ERPs for the not-conscious early and late prediction-error-based mechanisms.

Table D-4

Results of the Statistical Analysis of the ERP Data for the Not-Conscious Early Prediction-Error-Based Mechanism (60 to 80 ms) and for the Not-Conscious Late Prediction-Error-Based Mechanism (162 to 262 ms) Time Windows

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>Early PEBM</th>
<th>Late PEBM</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Region (R)</td>
<td>2, 22</td>
<td>7.93</td>
<td>.003</td>
</tr>
<tr>
<td>Hemisphere (H)</td>
<td>1, 11</td>
<td>0.68</td>
<td>.428</td>
</tr>
<tr>
<td>Stimuli (S)</td>
<td>1, 11</td>
<td>4.89</td>
<td>.049</td>
</tr>
<tr>
<td>R x H</td>
<td>2, 22</td>
<td>0.07</td>
<td>.929</td>
</tr>
<tr>
<td>R x S</td>
<td>2, 22</td>
<td>11.69</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>H x S</td>
<td>1, 11</td>
<td>0.01</td>
<td>.945</td>
</tr>
<tr>
<td>R x H x S</td>
<td>2, 22</td>
<td>0.10</td>
<td>.909</td>
</tr>
</tbody>
</table>

Notes: PEBM, Prediction-Error-Based Mechanism.
In Table D-5, I report the results of the sLORETA analyses for the not-conscious components.

<table>
<thead>
<tr>
<th>Brain Areas Where Significant Differences Between Standards and Controls (60 to 80 ms; Not-Conscious Early Adaptation-Based Mechanism), Standards and Deviants (154 to 274 ms; Not-Conscious vMMN), and Standards and Controls (194 to 244 ms; Not-Conscious Late Adaptation-Based Mechanism) Were Shown by sLORETA, Giving Anatomical Region, BA, the x-, y-, and z-Coordinates of the Brain According to the MNI, and the t-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Early Adaptation-Based Mechanism</strong></td>
</tr>
<tr>
<td>Anatomical Region</td>
</tr>
<tr>
<td>LL, parahippocampal gyrus</td>
</tr>
<tr>
<td>TL, fusiform gyrus</td>
</tr>
<tr>
<td>TL, superior temporal gyrus</td>
</tr>
<tr>
<td>FL, superior frontal gyrus</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td><strong>Not-Conscious vMMN</strong></td>
</tr>
<tr>
<td>Anatomical Region</td>
</tr>
<tr>
<td>LL, parahippocampal gyrus</td>
</tr>
<tr>
<td>TL, fusiform gyrus</td>
</tr>
<tr>
<td>TL, superior temporal gyrus</td>
</tr>
<tr>
<td>OL, lingual gyrus</td>
</tr>
<tr>
<td>OL, fusiform gyrus</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td><strong>Late Adaptation-Based Mechanism</strong></td>
</tr>
<tr>
<td>Anatomical Region</td>
</tr>
<tr>
<td>TL, fusiform gyrus</td>
</tr>
<tr>
<td>LL, parahippocampal gyrus</td>
</tr>
<tr>
<td>TL, superior temporal gyrus</td>
</tr>
<tr>
<td>OL, lingual gyrus</td>
</tr>
</tbody>
</table>

Notes: LL, Limbic Lobe; TL, Temporal Lobe; FL, Frontal Lobe; OL, Occipital Lobe. The critical t-value for p < .01 was 4.00 for the early adaptation-based mechanism, 5.41 for the not-conscious vMMN, and 4.73 for the late adaptation-based mechanism.
In Table D-6, I provide the results of a repeated-measures ANOVA using the factors region (anterior, central, posterior), hemisphere (left, right), and stimuli (standards, deviants) on the mean amplitudes of the ERPs for the conscious early deviance-based negativity.

Table D-6
Results of the Statistical Analysis of the ERP Data for the Conscious Early Deviance-Based Negativity (60 to 80 ms) Time Window

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>Early DBN</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>p</td>
<td>ηp²</td>
</tr>
<tr>
<td>Region (R)</td>
<td>2, 22</td>
<td>18.10</td>
<td>&lt; .001</td>
<td>.62</td>
</tr>
<tr>
<td>Hemisphere (H)</td>
<td>1, 11</td>
<td>8.91</td>
<td>.012</td>
<td>.45</td>
</tr>
<tr>
<td>Stimuli (S)</td>
<td>1, 11</td>
<td>&lt; 0.01</td>
<td>.972</td>
<td>&lt; .01</td>
</tr>
<tr>
<td>R x H</td>
<td>2, 22</td>
<td>3.58</td>
<td>.045</td>
<td>.25</td>
</tr>
<tr>
<td>R x S</td>
<td>2, 22</td>
<td>0.09</td>
<td>.913</td>
<td>.01</td>
</tr>
<tr>
<td>H x S</td>
<td>1, 11</td>
<td>0.81</td>
<td>.389</td>
<td>.07</td>
</tr>
<tr>
<td>R x H x S</td>
<td>2, 22</td>
<td>0.75</td>
<td>.483</td>
<td>.06</td>
</tr>
</tbody>
</table>

Notes: DBN, Deviance-Based Negativity.
In Table D-7, I provide the results of a repeated-measures ANOVA using the factors region (anterior, central, posterior), hemisphere (left, right), and stimuli (standards, controls) on the mean amplitudes of the ERPs for the conscious early and late adaptation-based mechanisms.

Table D-7
Results of the Statistical Analysis of the ERP Data for the Conscious Early Adaptation-Based and Prediction-Error-Based Mechanism (60 to 80 ms) Time Windows

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>Early ABM</th>
<th></th>
<th>Late ABM</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>p</td>
<td>η²</td>
<td>F</td>
</tr>
<tr>
<td>Region (R)</td>
<td>2, 22</td>
<td>11.47</td>
<td>&lt; .001</td>
<td>.51</td>
<td>9.37</td>
</tr>
<tr>
<td>Hemisphere (H)</td>
<td>1, 11</td>
<td>2.73</td>
<td>.127</td>
<td>.20</td>
<td>15.08</td>
</tr>
<tr>
<td>Stimuli (S)</td>
<td>1, 11</td>
<td>0.18</td>
<td>.677</td>
<td>.02</td>
<td>0.72</td>
</tr>
<tr>
<td>R x S</td>
<td>2, 22</td>
<td>12.14</td>
<td>&lt; .001</td>
<td>.53</td>
<td>7.28</td>
</tr>
<tr>
<td>H x S</td>
<td>1, 11</td>
<td>0.62</td>
<td>.447</td>
<td>.05</td>
<td>0.07</td>
</tr>
<tr>
<td>R x H x S</td>
<td>2, 22</td>
<td>0.16</td>
<td>.851</td>
<td>.02</td>
<td>0.37</td>
</tr>
</tbody>
</table>

Notes: ABM, Adaptation-Based Mechanism.
In Table D-8, I provide the results of a repeated-measures ANOVA using the factors region (anterior, central, posterior), hemisphere (left, right), and stimuli (deviants, controls) on the mean amplitudes of the ERPs for the conscious early and late prediction-error-based mechanisms.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>Early PEBM</th>
<th>Late PEBM</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F  p</td>
<td>ηp²</td>
</tr>
<tr>
<td>Region (R)</td>
<td>2, 22</td>
<td>11.37 &lt; .001</td>
<td>.51</td>
</tr>
<tr>
<td>Hemisphere (H)</td>
<td>1, 11</td>
<td>6.60 .026</td>
<td>.38</td>
</tr>
<tr>
<td>Stimuli (S)</td>
<td>1, 11</td>
<td>0.05 .821</td>
<td>.01</td>
</tr>
<tr>
<td>R x H</td>
<td>2, 22</td>
<td>3.01 .821</td>
<td>.01</td>
</tr>
<tr>
<td>R x S</td>
<td>2, 22</td>
<td>5.53 .011</td>
<td>.33</td>
</tr>
<tr>
<td>H x S</td>
<td>1, 11</td>
<td>0.90 .364</td>
<td>.08</td>
</tr>
<tr>
<td>R x H x S</td>
<td>2, 22</td>
<td>0.33 .721</td>
<td>.03</td>
</tr>
</tbody>
</table>

Notes: PEBM, Prediction-Error-Based Mechanism.
In Table D-9, I provide the results of a repeated-measures ANOVA using the factors region (anterior, central, posterior), hemisphere (left, right), and stimuli (standards, deviants) on the mean amplitudes of the ERPs for the first and second conscious vMMN components.

Table D-9

Results of the Statistical Analysis of the ERP Data for the First (230 to 260 ms) and Second (324 to 344 ms) Conscious vMMN Time Windows

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>First vMMN</th>
<th>Second vMMN</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td>Region (R)</td>
<td>2, 22</td>
<td>28.89</td>
<td>&lt; .001</td>
</tr>
<tr>
<td>Hemisphere (H)</td>
<td>1, 11</td>
<td>7.10</td>
<td>.022</td>
</tr>
<tr>
<td>Stimuli (S)</td>
<td>1, 11</td>
<td>1.62</td>
<td>.230</td>
</tr>
<tr>
<td>R x H</td>
<td>2, 22</td>
<td>9.37</td>
<td>.001</td>
</tr>
<tr>
<td>R x S</td>
<td>2, 22</td>
<td>0.26</td>
<td>.777</td>
</tr>
<tr>
<td>H x S</td>
<td>1, 11</td>
<td>0.27</td>
<td>.612</td>
</tr>
<tr>
<td>R x H x S</td>
<td>2, 22</td>
<td>5.48</td>
<td>.012</td>
</tr>
</tbody>
</table>
In Table D-10, I report the results of the sLORETA analyses for the conscious components.

Table D-10

<table>
<thead>
<tr>
<th>Anatomical Region</th>
<th>BA</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>T</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Early Adaptation-Based Mechanism</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SL, insula</td>
<td>13</td>
<td>-40</td>
<td>-5</td>
<td>15</td>
<td>8.79</td>
</tr>
<tr>
<td>FL, superior frontal gyrus</td>
<td>9</td>
<td>30</td>
<td>45</td>
<td>40</td>
<td>7.93</td>
</tr>
<tr>
<td>FL, middle frontal gyrus</td>
<td>9</td>
<td>25</td>
<td>45</td>
<td>40</td>
<td>7.91</td>
</tr>
<tr>
<td>FL, precentral gyrus</td>
<td>44</td>
<td>50</td>
<td>0</td>
<td>5</td>
<td>7.84</td>
</tr>
<tr>
<td><strong>Late Adaptation-Based Mechanism</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TL, fusiform gyrus</td>
<td>20</td>
<td>-40</td>
<td>-35</td>
<td>-20</td>
<td>9.53</td>
</tr>
<tr>
<td>LL, parahippocampal gyrus</td>
<td>36</td>
<td>-40</td>
<td>-30</td>
<td>-15</td>
<td>8.71</td>
</tr>
<tr>
<td>TL, superior temporal gyrus</td>
<td>22</td>
<td>45</td>
<td>-25</td>
<td>-5</td>
<td>8.27</td>
</tr>
<tr>
<td>FL, precentral gyrus</td>
<td>4</td>
<td>35</td>
<td>-20</td>
<td>45</td>
<td>7.03</td>
</tr>
<tr>
<td>OL, lingual gyrus</td>
<td>18</td>
<td>-10</td>
<td>-60</td>
<td>0</td>
<td>7.02</td>
</tr>
</tbody>
</table>

Notes: SL, Sub-Lobar; FL, Frontal Lobe; TL, Temporal Lobe; LL, Limbic Lobe; OL, Occipital Lobe. The critical $t$-value for $p < .01$ was 4.73 for the early adaptation-based mechanism, 6.35 for the late adaptation-based mechanism, 4.64 for the first conscious vMMN, and 4.52 for the second conscious vMMN.