

Human Visual System Automatically Encodes Sequential Regularities of Discrete Events

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Abstract

■ For our adaptive behavior in a dynamically changing environment, an essential task of the brain is to automatically encode sequential regularities inherent in the environment into a memory representation. Recent studies in neuroscience have suggested that sequential regularities embedded in discrete sensory events are automatically encoded into a memory representation at the level of the sensory system. This notion is largely supported by evidence from investigations using auditory mismatch negativity (auditory MMN), an event-related brain potential (ERP) correlate of an automatic memory-mismatch process in the auditory sensory system. However, it is still largely unclear whether or not this notion can be generalized to other sensory modalities. The purpose of the present study was to investigate the contribution of the visual sensory system to the automatic encoding of sequential regularities using visual mismatch negativity (visual MMN), an ERP correlate of an automatic memory-mismatch process in the visual sensory system. To this end, we conducted a sequential analysis of visual MMN in an oddball sequence con-

sisting of infrequent deviant and frequent standard stimuli, and tested whether the underlying memory representation of visual MMN generation contains only a sensory memory trace of standard stimuli (trace-mismatch hypothesis) or whether it also contains sequential regularities extracted from the repetitive standard sequence (regularity-violation hypothesis). The results showed that visual MMN was elicited by first deviant (deviant stimuli following at least one standard stimulus), second deviant (deviant stimuli immediately following first deviant), and first standard (standard stimuli immediately following first deviant), but not by second standard (standard stimuli immediately following first standard). These results are consistent with the regularity-violation hypothesis, suggesting that the visual sensory system automatically encodes sequential regularities. In combination with a wide range of auditory MMN studies, the present study highlights the critical role of sensory systems in automatically encoding sequential regularities when modeling the world. ■

INTRODUCTION

An external environment is dynamically changing. For our adaptive behavior in such a changing environment, an essential task of the brain is to automatically encode what is regular in a sequence of sensory events into a memory representation, even when the sequence is irrelevant for the current task, as such a memory representation forms the basis of predictions for future events, which enables us to minimize the processing resources for redundant events and to maximize the processing resources for novel events (e.g., Sokolov, 1963).

When a sequence of sensory events is irrelevant for the current task, an automatically formed memory representation has traditionally been understood in terms of a sensory store, which was originally described as a memory register in the multistore model proposed by Atkinson and Shiffrin (1968). According to this model, the sensory store is sensory-specific and plays an impor-

tant role in the automatic encoding of a large amount of sensory information. However, its contents are rather literal, in the sense that it is involved in encoding static information rather than dynamic information, such as sequential regularities embedded in a sequence of sensory events.

In contrast to this traditional notion, recent neuroscience studies have provided evidence which supports the notion that not only static information but also dynamic information, such as sequential regularities, is, in fact, automatically encoded into a memory representation at the level of the sensory system. This evidence is largely obtained from investigations using auditory mismatch negativity (auditory MMN; Näätänen, Gaillard, & Mäntysalo, 1978; for reviews, see e.g., Näätänen, Paavilainen, Rinne, & Alho, 2007; Näätänen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001; Näätänen, 1990, 1992) event-related brain potential (ERP). A series of auditory MMN studies have shed new light on the involvement of the auditory sensory system in higher cognitive processes than previously thought (e.g., “primitive intelligence”; Näätänen et al., 2001) and provide important insight into recent theories on the brain which state that, rather than passively waiting

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to be activated by sensory events, the brain is constantly predicting future events (e.g., “proactive brain,” Bar, 2007; “predictive coding,” Friston, 2005; “predictive modeling,” Denham & Winkler, 2006).

Although auditory MMN studies have provided evidence which supports this new notion, it is still largely unclear whether this notion can be generalized to other sensory modalities. The aim of the present study was to investigate the contribution of the visual sensory system to the automatic encoding of sequential regularities using a visual analogue of MMN, visual mismatch negativity (visual MMN; e.g., Kimura, Katayama, Ohira, & Schröger, 2009; Czigler, Balázs, & Winkler, 2002; for reviews, see Czigler, 2007; Pazo-Alvarez, Cadaveira, & Amenedo, 2003).

Mismatch Negativity

Auditory MMN is a negative-going ERP component that peaks at around 150–250 msec after the onset of deviant stimulation with a fronto-central scalp distribution, and has been typically observed in response to infrequent “deviant” compared to frequent “standard” stimuli in the auditory oddball sequence. For example, it is elicited by infrequent deviations in several stimulus dimensions such as frequency (Näätänen et al., 1978), intensity (Näätänen et al., 1978), duration (Näätänen, Paavilainen, & Reinikainen, 1989), and location (Paavilainen, Karlsson, Reinikainen, & Näätänen, 1989) (for reviews, see e.g., Näätänen, 1990, 1992). Auditory MMN has generators in the auditory (and probably frontal) areas (for a review, see Deouell, 2007) and is largely unaffected by various attentional manipulations (for a review, see Sussman, 2007), which suggests that auditory MMN generation is an automatic brain process in the auditory sensory system.

It has long been unclear whether or not MMN occurs in other sensory modalities. Over the past few decades, however, several studies have tried to identify a visual analogue of MMN and have reported that infrequent deviant compared to frequent standard stimuli in the visual oddball sequence elicited a posterior negativity that peaked at around 150–250 msec after stimulus onset and is usually called visual MMN. For example, it is elicited by infrequent deviations in several stimulus dimensions such as color (Kimura, Katayama, & Murohashi, 2006c; Mazza, Turatto, & Sarlo, 2005; Czigler, Balázs, & Pató, 2004; Czigler et al., 2002), shape (Mazza et al., 2005; Stagg, Hindley, Tales, & Butler, 2004; Tales, Newton, Troscianko, & Butler, 1999; Alho, Woods, Algazi, & Näätänen, 1992), motion direction (Amenedo, Pazo-Alvarez, & Cadaveira, 2007; Pazo-Alvarez, Amenedo, & Cadaveira, 2004; Pazo-Alvarez, Amenedo, Lorenzo-López, & Cadaveira, 2004), orientation (Kimura et al., 2009; Astikainen, Lillstrang, & Ruusuvirta, 2008), spatial frequency (Heslenfeld, 2003; Kenemans, Jong, & Verbaten, 2003), luminance (Kimura, Katayama, & Murohashi, 2008c, 2008d; Stagg et al., 2004), size (Kimura, Katayama, & Murohashi, 2008a), spatial location (Berti & Schröger, 2001, 2004, 2006), and conjunction of color and orientation (Winkler, Czigler, Sussman, Horváth,

& Balázs, 2005). Visual MMN has generators in visual areas (Amenedo et al., 2007; Yucel, McCarthy, & Belger, 2007; Czigler et al., 2004; Pazo-Alvarez, Amenedo, Lorenzo-López, et al., 2004) and is largely unaffected by several attentional manipulations (Pazo-Alvarez, Amenedo, & Cadaveira, 2004; Heslenfeld, 2003), which suggests that visual MMN generation is an automatic brain process in the visual sensory system.

MMN and the Involvement of Memory Representation

With regard to the processes that underlie MMN generation, two contrasting hypotheses have been proposed: the memory-mismatch hypothesis and the refractoriness hypothesis. The memory-mismatch hypothesis assumes that MMN is an ERP correlate of a memory-mismatch process and is elicited when a current stimulus input mismatches the memory representation formed by the preceding stimulus sequence (Näätänen, 1990, 1992). In contrast, the refractoriness hypothesis assumes that MMN is not an ERP correlate of a memory-mismatch process and fully or partly reflects a lower refractoriness level (or a lower adaptation level) of afferent N1 neurons that specifically respond to a feature value of infrequent deviant stimuli compared to those that specifically respond to a feature value of frequent standard stimuli. Thus, MMN may result from the small amplitude of N1 elicited by frequent standard stimuli and the large amplitude of N1 elicited by infrequent deviant stimuli (Jääskeläinen et al., 2004).

Concerning this issue, several studies have shown that although it is often overlapped by N1, reflecting the refractory effect, MMN has several characteristics that are different from those of N1 and cannot be explained in terms of the refractoriness hypothesis. For example, unlike auditory N1, auditory MMN is elicited even by infrequent intensity decrements (Woldorff, Hackley, & Hillyard, 1991; Näätänen, Paavilainen, Alho, Reinikainen, & Sams, 1989), infrequent duration decrements (Kaukoranta, Sams, Hari, Hämäläinen, & Näätänen, 1989; Näätänen, Paavilainen, & Reinikainen, 1989), and sudden stimulus omission (Yabe et al., 1998; Yabe, Tervaniemi, Reinikainen, & Näätänen, 1997; for a review, see Näätänen, Jacobsen, & Winkler, 2005). Also, unlike visual N1, visual MMN is elicited even by infrequent luminance decrements (Kimura et al., 2008c; Stagg et al., 2004), infrequent size decrements (Kimura et al., 2008a), and sudden stimulus omission (Czigler, Winkler, et al., 2006; see also Czigler, Weisz, & Winkler, 2006, 2007; Winkler et al., 2005). These results are highly consistent with the memory-mismatch hypothesis and suggest that MMN is an ERP correlate of a memory-mismatch process.¹

MMN and the Nature of Underlying Memory Representation

As described above, MMN has been confirmed to be an ERP correlate of an automatic memory-mismatch process

in the sensory system. If we consider the underlying process of MMN generation, MMN can be used as a tool that taps into the contents of an automatically formed memory representation at the level of the sensory system (Schröger, 2007).

In early auditory MMN studies, auditory MMN was typically observed in response to infrequent deviant compared to frequent standard stimuli in the auditory oddball sequence. Based on these findings, it was originally proposed that auditory MMN is based on a sensory memory trace of standard stimuli (or stimulus feature) and is elicited by a mismatch between the sensory memory trace of standard stimuli (or stimulus feature) and the current deviant stimulus (or stimulus feature) (trace-mismatch hypothesis) (e.g., Näätänen, 1990, 1992). The trace-mismatch hypothesis implies that the auditory sensory system automatically encodes the standard stimulus (or stimulus feature), which is similar to the traditional notion of the sensory store (Atkinson & Shiffrin, 1968) regarding the point that only static information is assumed to be automatically encoded into a memory representation at the level of the sensory system.

In more recent auditory MMN studies, however, it has been reported that auditory MMN can be elicited not only by infrequent deviant stimuli in the oddball sequence but also by several types of regularity-violating events in more complex stimulus sequences (Paavilainen, Saarinen, Tervaniemi, & Näätänen, 1995; Alain, Woods, & Ogawa, 1994; Saarinen, Paavilainen, Schröger, Tervaniemi, & Näätänen, 1992; Nordby, Roth, & Pfefferbaum, 1988; for a review, see e.g., Näätänen et al., 2001). For example, Nordby et al. (1988) used a stimulus sequence in which two stimuli were presented regularly in an ABABABAB... order and found that irregular repetitions (i.e., ABABABABB...) elicited auditory MMN. Because the trace-mismatch hypothesis was not sufficient for explaining the generation of such auditory MMN, the trace-mismatch hypothesis has been updated, and the most widely accepted hypothesis is that auditory MMN is based on sequential regularities inherent in the sequential presentation of discrete events, and MMN is elicited when regularity is violated by incoming stimuli (regularity-violation hypothesis) (e.g., Schröger, 2007; Winkler, 2007). The regularity-violation hypothesis implies that the auditory sensory system automatically encodes sequential regularities among repetitive standard stimuli. Thus, in contrast to the trace-mismatch hypothesis, the regularity-violation hypothesis supports the notion that not only static information but also dynamic information, such as sequential regularities, is, in fact, automatically encoded into a memory representation at the level of the sensory system.²

As in early studies of auditory MMN, visual MMN has typically been observed in response to infrequent deviant compared to frequent standard stimuli in a visual oddball sequence. Thus, the trace-mismatch hypothesis of visual MMN is now widely accepted. However, one recent study showed that visual MMN was elicited by regularity-violating

events in more complex stimulus sequences (Czigler, Weisz, et al., 2006). They used a stimulus sequence in which two stimuli were presented regularly in an AABBAABB... order and found that irregular repetitions (i.e., AABBAABBB...) elicited visual MMN. Based on this finding, they noted that the trace-mismatch hypothesis should be updated and suggested a regularity-violation hypothesis for visual MMN.

Present Study

As reviewed above, previous auditory MMN studies have provided converging evidence to support the notion that not only static information but also dynamic information, such as sequential regularities, is, in fact, automatically encoded into a memory representation at the level of the auditory sensory system. However, this notion has not been extensively tested in other sensory modalities and it is still largely unclear whether or not it can be generalized to other sensory modalities.

With regard to this issue, Czigler, Weisz, et al. (2006) provided important results which supported the regularity-violation hypothesis for visual MMN. The notion, however, would need more consideration because the visual MMN observed in their study might reflect modality-non-specific activities rather than modality-specific activities (see Czigler, 2007, p. 226). In fact, unlike visual MMN in oddball studies (Kimura et al., 2009; Astikainen et al., 2008; Berti & Schröger, 2006; Stagg et al., 2004; Czigler et al., 2002), which has been confirmed to be generated in visual areas (Amenedo et al., 2007; Yucel et al., 2007; Czigler et al., 2004; Pazo-Alvarez, Amenedo, Lorenzo-López, et al., 2004), visual MMN in their study had a central scalp distribution and seemed to be more similar to another modality-non-specific deviance-related ERP component, N2b (Ferdinand, Mecklinger, & Kray, 2008; Rüsseler, Hennighausen, Münte, & Rösler, 2003; Eimer, Goschke, Schlaghecken, & Stürmer, 1996).

The purpose of the present study was to investigate whether or not visual MMN obtained in the oddball sequence, which has been confirmed to have generators in visual areas, can be interpreted in terms of the regularity-violation hypothesis. On this end, we used a typical oddball sequence consisting of four types of stimuli (standard nontarget, deviant nontarget, standard target, and deviant target stimuli; Figure 1), and tested the elicitation of visual MMN by (1) deviant nontarget stimuli following at least one standard nontarget stimulus (first deviant), (2) deviant nontarget stimuli immediately following first deviant (second deviant), (3) standard nontarget stimuli immediately following first deviant (first standard), and (4) standard nontarget stimuli immediately following first standard (second standard) (Figure 2A).

We hypothesized that if visual MMN is based on sequential regularities extracted from the preceding repetitive standard sequence (regularity-violation hypothesis), then visual MMN would be elicited by first deviant, second

	Nontarget stimuli					Target stimuli				
Oddball 1	30 (Deviant)	—	—	—	120 (Standard)	3 (Deviant)	—	—	—	12 (Standard)
Oddball 2	30 (Deviant)	120 (Standard)	—	—	—	3 (Deviant)	12 (Standard)	—	—	—
Oddball 3	120 (Standard)	30 (Deviant)	—	—	—	12 (Standard)	3 (Deviant)	—	—	—
Oddball 4	—	30 (Deviant)	120 (Standard)	—	—	—	3 (Deviant)	12 (Standard)	—	—
Oddball 5	—	120 (Standard)	30 (Deviant)	—	—	—	12 (Standard)	3 (Deviant)	—	—
Oddball 6	—	—	30 (Deviant)	120 (Standard)	—	—	—	3 (Deviant)	12 (Standard)	—
Oddball 7	—	—	120 (Standard)	30 (Deviant)	—	—	—	12 (Standard)	3 (Deviant)	—
Oddball 8	—	—	—	30 (Deviant)	120 (Standard)	—	—	—	3 (Deviant)	12 (Standard)
Oddball 9	—	—	—	120 (Standard)	30 (Deviant)	—	—	—	12 (Standard)	3 (Deviant)
Oddball 10	120 (Standard)	—	—	—	30 (Deviant)	12 (Standard)	—	—	—	3 (Deviant)
Equiprobable	30 (Control)	30 (Control)	30 (Control)	30 (Control)	30 (Control)	3 (Control)	3 (Control)	3 (Control)	3 (Control)	3 (Control)

(Times/Block)

Figure 1. Four types of stimuli in the oddball sequence and their probabilities (standard nontarget 120 times/block, deviant nontarget 30 times/block, standard target 12 times/block, and deviant target 3 times/block) and 10 types of stimuli in the equiprobable sequence and their probabilities (5 types of control nontarget 30 times/block each and 5 types of control target 3 times/block each).

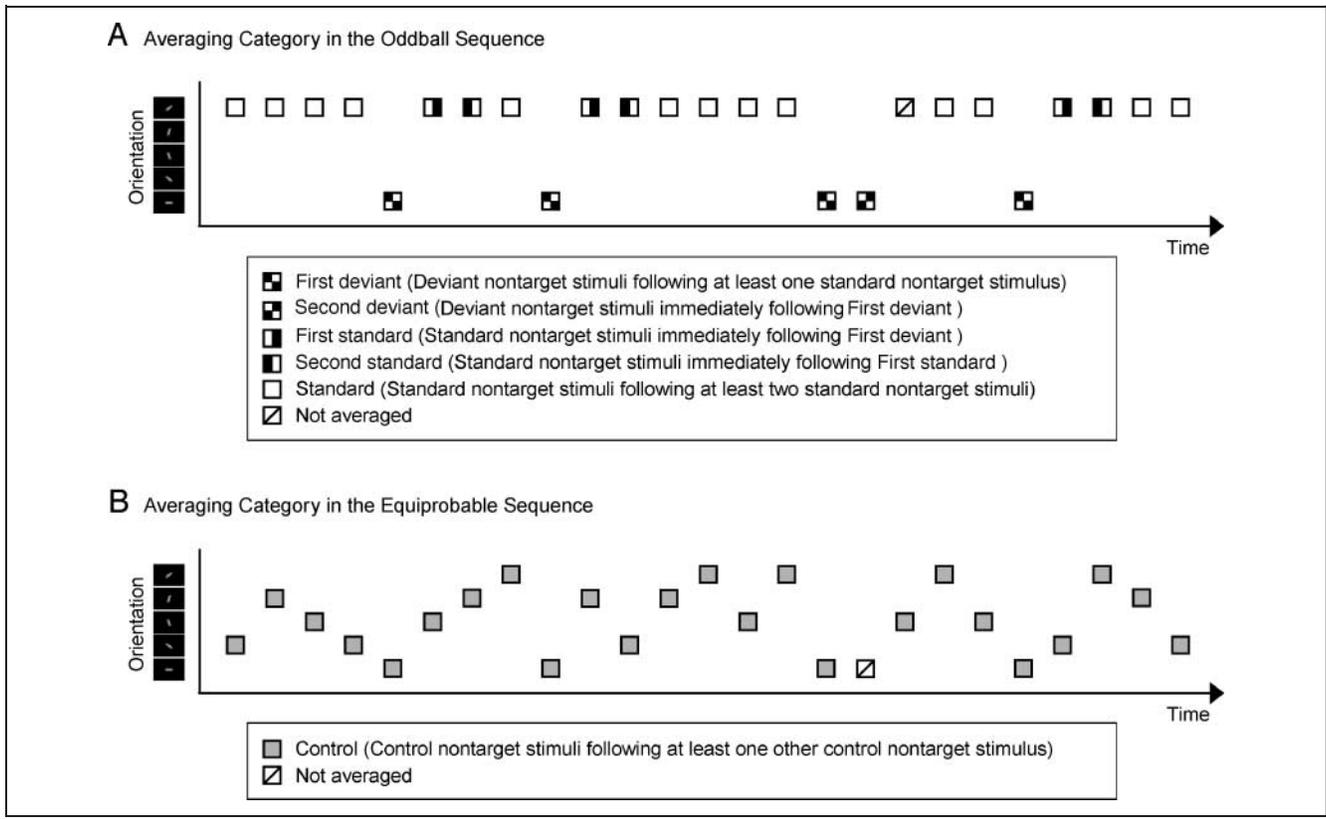


Figure 2. (A) Schematic illustration of five averaging categories in the oddball sequence (first deviant, second deviant, first standard, second standard, and standard). (B) Schematic illustration of one averaging category in the equiprobable sequence (control).

deviant, and first standard, but not by second standard, as first deviant (i.e., standard is followed by deviant), second deviant (deviant is followed by deviant), and first standard (deviant is followed by standard) violate sequential regularities extracted from the repetitive standard sequence (standard is followed by standard), whereas second standard (standard is followed by standard) does not. In contrast, if visual MMN is based only on a sensory memory trace of standard stimuli (trace-mismatch hypothesis), then visual MMN would be elicited by first deviant and second deviant, but not by first standard and second standard, because first deviant and second deviant mismatch the sensory memory trace of standard stimuli, whereas first standard and second standard do not (Table 1) (for a similar argument in the auditory modality, see Winkler, 2007).³

To estimate visual MMN, we first compared ERPs elicited by traditional standard nontarget stimuli following at least two standard nontarget stimuli (standard) (Figure 2A) and those elicited by the four types of stimulus in the oddball sequence (first deviant, second deviant, first standard, and second standard). However, as mentioned above, visual MMN in the oddball sequence is often overlapped by a visual N1 refractory effect caused by the different overall probabilities of infrequent deviant stimuli and frequent standard stimuli (e.g., Kimura et al., 2008a, 2008c, 2009). Therefore, to estimate “genuine” visual MMN without the overlap of a visual N1 refractory effect, we additionally used an equiprobable sequence consisting of 10 types of stimuli (5 types of control nontarget and 5 types of control target stimuli; Figure 1) and compared ERPs elicited by control nontarget stimuli that followed at least one other control nontarget stimulus (control; Figure 2B) and those elicited by the four types of stimuli in the oddball sequence (first deviant, second deviant, first standard, and second standard). Note that ERPs elicited by control nontarget stimuli that followed at least one presentation of the same control

nontarget stimulus were not used in the comparisons due to the possibility of visual MMN elicited by infrequent stimulus repetition (Czigler, Weisz, et al., 2006; but see an additional comparison in the Discussion section).

Because the overall probability of control nontarget stimuli is the same as that of deviant nontarget stimuli and is lower than that of standard nontarget stimuli, the state of refractoriness for control should be the same as those for first and second deviant and lower than those for first and second standard. Thus, visual N1 elicited by control should be the same as those elicited by first and second deviant and larger than those elicited by first and second standard (Table 1). Also, because the control nontarget stimuli do not violate any regularity, control should not elicit visual MMN. Thus, this protocol can provide a strict control condition for estimating visual MMN (see Kimura et al., 2009; Astikainen et al., 2008; Pazo-Alvarez, Amenedo, & Cadaveira, 2004; Czigler et al., 2002; for similar arguments in the auditory modality, see Horváth et al., 2008; Maess, Jacobsen, Schröger, & Friederici, 2007; Opitz, Schröger, & von Cramon, 2005; Jacobsen, Horenkamp, & Schröger, 2003; Jacobsen & Schröger, 2001, 2003; Jacobsen, Schröger, Horenkamp, & Winkler, 2003; Schröger & Wolff, 1996, 1998; Näätänen & Alho, 1997; Schröger, 1997).

METHODS

Participants

Twelve students (5 women, 7 men; age range = 20–30 years, $M = 24.5$ years) participated in this experiment. All participants were right-handed, had normal or corrected-to-normal vision, and were free of neurological or psychiatric disorders. Written informed consent was obtained from each participant after the nature of the study had been explained.

Table 1. Expected Effects of Memory-mismatch and Refractoriness in Difference Waves under the Regularity-violation and Trace-mismatch Hypotheses

Hypothesis	Difference Wave							
	First Deviant Minus		Second Deviant Minus		First Standard Minus		Second Standard Minus	
	Standard	Control	Standard	Control	Standard	Control	Standard	Control
<i>Regularity Violation</i>								
Memory mismatch	Visual MMN	Visual MMN	Visual MMN	Visual MMN	Visual MMN	Visual MMN	–	–
Refractory	Visual N1	–	Visual N1	–	–	Reversed visual N1	–	Reversed visual N1
<i>Trace Mismatch</i>								
Memory mismatch	Visual MMN	Visual MMN	Visual MMN	Visual MMN	–	–	–	–
Refractory	Visual N1	–	Visual N1	–	–	Reversed visual N1	–	Reversed visual N1

Stimuli and Procedure

Figure 1 illustrates the stimuli and their probabilities (times/block). Ten gray bars at a central location against a black background [luminance of 42 cd/m² and visual angle of 3.0° (length) × 0.5° (width) from a viewing distance of 70 cm] that were defined by five types of orientation (0°, 36°, 72°, 108°, 144° to the right from the horizontal) and two types of shape for the opposite ends of the bar (square and round) were used as stimuli. The durations of the stimuli were 100 msec, and the interstimulus interval (onset-to-onset) was 500 msec in all conditions.

To evaluate visual MMN without contamination by the effects of physical differences in eliciting stimuli, we used 11 types of stimulus sequence: 10 oddball sequences and 1 equiprobable sequence. In the oddball sequences, four types of stimuli (standard nontarget 120 times/block, deviant nontarget 30 times/block, standard target 12 times/block, and deviant target 3 times/block) were presented in random order. Standard nontarget and deviant nontarget stimuli were two bars of square edge with the closest orientation, and standard target and deviant target stimuli were two bars of round edge with the same orientations as the corresponding nontarget stimuli. In the equiprobable sequence, 10 types of stimuli (5 types of control nontarget 30 times/block each and 5 types of control target 3 times/block each) were presented in random order.

This experiment consisted of 20 blocks (10 blocks for the oddball and 10 blocks for the equiprobable sequences), each of which consisted of 165 trials. The order of these blocks was randomized across participants. In all blocks, the participant was seated in a reclining chair in a sound-attenuated and electrically shielded room and instructed to press a button with the right thumb as quickly and accurately as possible when target stimuli (i.e., bars of round edge) were presented. The participant was also asked to focus on the center of the display, and to minimize any eye movement during each block.

Recordings

The electroencephalogram (EEG) was recorded from 25 silver–silver chloride cup electrodes attached to an electrocap (EasyCap), with electrodes placed at Fp1, Fp2, F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6, PO7, PO3, POz, PO4, PO8, O1, Oz, and O2 according to the extended International 10–20 System. All electrodes were referenced to the nose tip. Blinks and eye movements were monitored with electrodes above and below the right eye (vertical electrooculogram, VEOG) and at the right and left outer canthi of the eyes (horizontal electrooculogram, HEOG). The impedance of the electrodes was kept below 5 kΩ. EEG and EOG signals were amplified from DC to 120 Hz at a sampling rate of 500 Hz and digitally low-pass filtered off-line at 30 Hz with a finite impulse response filter.

Figure 2A shows the averaging categories in the oddball sequences. The EEG in the oddball sequences was aver-

aged for five categories across 10 types of oddball sequence: (1) deviant nontarget stimuli following at least one standard nontarget stimulus (first deviant), (2) deviant nontarget stimuli immediately following first deviant (second deviant), (3) standard nontarget stimuli immediately following first deviant (first standard), (4) standard nontarget stimuli immediately following first standard (second standard), and (5) standard nontarget stimuli following at least two standard nontarget stimuli (standard). Figure 2B shows the averaging categories in the equiprobable sequence. The EEG in the equiprobable sequence was averaged for one category: control nontarget stimuli following at least one other control nontarget stimulus (control).

Averaging epochs were 500 msec featuring a 100-msec prestimulus baseline. In the averaging procedure, the first three epochs in each block, two epochs preceded by target stimuli, epochs in which the signal amplitudes exceeded ± 100 μ V on any of the electrodes, and epochs with erroneous responses to nontarget stimuli were excluded. As a result, the averaging number for each stimulus was, on average, 201 (first deviant), 34 (second deviant), 133 (first standard), 90 (second standard), 793 (standard), and 1003 (control), respectively.

Data Analysis

Behavioral Performance

Behavioral performance was measured in terms of reaction time, hit rate, and false alarm rate. Responses were scored as hits if the button was pressed within 100–800 msec after target stimulus onset. Incorrect responses during this period were classified as false alarms. These measures were subjected to repeated measures ANOVAs with one factor: 3 stimulus types (standard, deviant, control). The Greenhouse–Geisser ϵ correction was used to reduce the positive bias of the F test due to possible violations of the assumption of sphericity. Post hoc comparisons were made using the Bonferroni procedure. Effect sizes were presented as f values.

Event-related Potentials

To estimate visual MMN, eight types of grand-averaged difference wave were calculated: first-deviant-minus-standard, first-deviant-minus-control, second-deviant-minus-standard, second-deviant-minus-control, first-standard-minus-standard, first-standard-minus-control, second-standard-minus-standard, and second-standard-minus-control difference waves. Based on the results of the first-deviant-minus-control difference waves, mean amplitudes of visual MMN were calculated as the mean amplitudes of the difference waves within the 200–250 msec time window. To test the significance of the elicitation of visual MMN, the mean amplitudes of the difference waves within the corresponding 50-msec time windows at 13 posterior electrodes (T5, P3, Pz, P4, T6, PO7, PO3, POz, PO4, PO8, O1,

Oz, and O2) were subjected to two-tailed paired *t* tests. Effect sizes were presented as *d* values.

A significant elicitation of visual MMN was seen for first deviant, second deviant, and first standard. To compare the amplitudes of visual MMN, the mean amplitudes of the difference waves within the corresponding 50-msec time windows at 13 posterior electrodes were subjected to repeated measures ANOVAs with two factors: 3 difference waves (first-deviant-minus-control, second-deviant-minus-control, first-standard-minus-control) and 13 electrodes (T5, P3, Pz, P4, T6, PO7, PO3, POz, PO4, PO8, O1, Oz, and O2). Further, to compare the scalp topographies of visual MMN, the same analysis was performed on amplitude values that were normalized by vector length, where each amplitude value was divided by the square root of the sum of the squared amplitudes over the 13 electrode locations for each difference wave, as recommended by McCarthy and Wood (1985).⁴ The Greenhouse–Geisser ϵ correction was used to reduce the positive bias of the *F* test due to possible violations of the assumption of sphericity. Post hoc comparisons were made using the Bonferroni procedure. Effect sizes were presented as *f* values.

In addition to visual MMN, three ERP effects were observed in the grand-averaged difference waves: a negativity that peaked at around 50–100 msec (early negativity), a negativity that peaked at around 100–150 msec (visual N1), and a positivity that peaked at around 100–150 msec (polarity-reversed visual N1). To test the significance of the elicitation of these effects, the mean amplitudes of the difference waves within the corresponding 50-msec time windows at an electrode (electrodes), where each effect had maximum amplitudes, were subjected to two-tailed paired *t* tests. Effect sizes were presented as *d* values.

RESULTS

Behavioral Performance

The mean reaction time was 484 msec (*SD* = 42) for deviant target, 505 msec (26) for standard target, and 496 msec (37) for control target stimuli. One-way ANOVAs (3 stimulus types) revealed no significant effects. The hit rate was 88.9% (14.8) for deviant target, 93.1% (6.2) for standard target, and 90.2% (8.3) for control target stimuli. One-way ANOVAs revealed no significant effects. The false alarm rate was 0.67% (0.82) for deviant nontarget, 0.06% (0.16) for standard nontarget, and 0.10% (0.20) for control nontarget stimuli. One-way ANOVAs revealed a significant main effect of stimulus type [$F(2, 22) = 6.35, p < .05, \epsilon = .53, f = 0.55$], which was due to higher false alarm rates in response to deviant nontarget than standard nontarget stimuli ($p < .10, f = 0.53$).

Event-related Potentials

Figure 3A shows the grand-averaged ERPs. At posterior electrodes (i.e., Pz, POz, and Oz), compared to ERPs elicited by

standard, ERPs elicited by first deviant were shifted to a negative polarity at around 90–300 msec (left panel), ERPs elicited by second deviant were shifted to a negative polarity at around 50–350 msec (second panel), ERPs elicited by first standard were shifted to a negative polarity at around 180–250 msec (third panel), and ERPs elicited by second standard were similar to those elicited by standard (right panel). In contrast, compared to ERPs elicited by control, ERPs elicited by first deviant were shifted to a negative polarity at around 180–300 msec (left panel), ERPs elicited by second deviant were shifted to a negative polarity at around 50–120 msec and 200–350 msec (second panel), ERPs elicited by first standard were shifted to a positive polarity at around 90–180 msec and to a negative polarity at around 180–250 msec (third panel), and ERPs elicited by second standard were shifted to a positive polarity at around 90–180 msec (right panel).

Figure 3B shows the grand-averaged difference waves. At the posterior electrodes, the first-deviant-minus-standard difference waves showed a negativity that peaked at around 100–150 msec (visual N1) and a negativity that peaked at around 200–250 msec (visual MMN), whereas the first-deviant-minus-control difference waves showed a negativity that peaked at around 200–250 msec (visual MMN) (left panel). The second-deviant-minus-standard difference waves showed a negativity that peaked at around 50–150 msec (early negativity and visual N1) and a negativity that peaked at around 200–250 msec (visual MMN), whereas the second-deviant-minus-control difference waves showed a negativity that peaked at around 50–100 msec (early negativity) and a negativity that peaked at around 200–250 msec (visual MMN) (second panel). The first-standard-minus-standard difference waves showed a negativity that peaked at around 200–250 msec (visual MMN), whereas the first-standard-minus-control difference waves showed a positivity that peaked at around 100–150 msec (reversed visual N1) and a negativity that peaked at around 200–250 msec (visual MMN) (third panel). Finally, the second-standard-minus-standard difference waves showed no effects, whereas the second-standard-minus-control difference waves showed a positivity that peaked at around 100–150 msec (reversed visual N1) (right panel).

Figure 4 shows topographical maps of the grand-averaged difference waves within the 50–100 msec (top), 100–150 msec (middle), and 200–250 msec time windows (bottom). In the 50–100 msec time window, the early negativity observed in the second-deviant-minus-standard and second-deviant-minus-control difference waves had a left parietal (P3) maximum wide scalp distribution over the occipital to frontal areas. In the 100–150 msec time window, visual N1 observed in the first-deviant-minus-standard and second-deviant-minus-standard difference waves and reversed visual N1 observed in the first-standard-minus-control and second-standard-minus-control difference waves had an occipito-temporal (PO7 and PO8) maximum scalp distribution. In the 200–250 msec time window, although visual MMN elicited by three types of stimuli

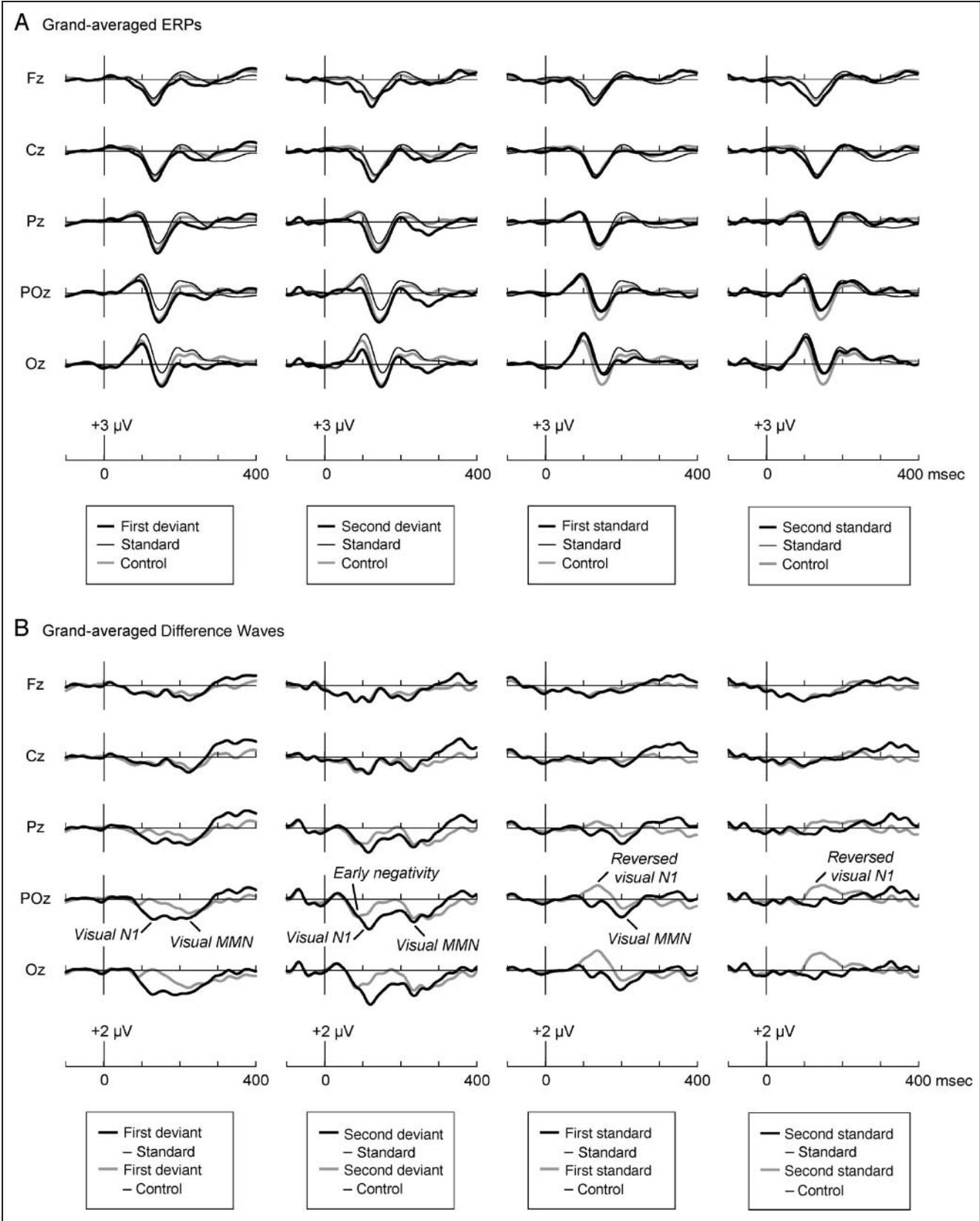


Figure 3. (A) Grand-averaged ERPs elicited by first deviant, standard, and control (left panel); second deviant, standard, and control (second panel); first standard, standard, and control (third panel); and second standard, standard, and control (right panel). (B) Grand-averaged first-deviant-minus-standard and first-deviant-minus-control (left panel); second-deviant-minus-standard and second-deviant-minus-control (second panel); first-standard-minus-standard and first-standard-minus-control (third panel); and second-standard-minus-standard and second-standard-minus-control difference waves (right panel).

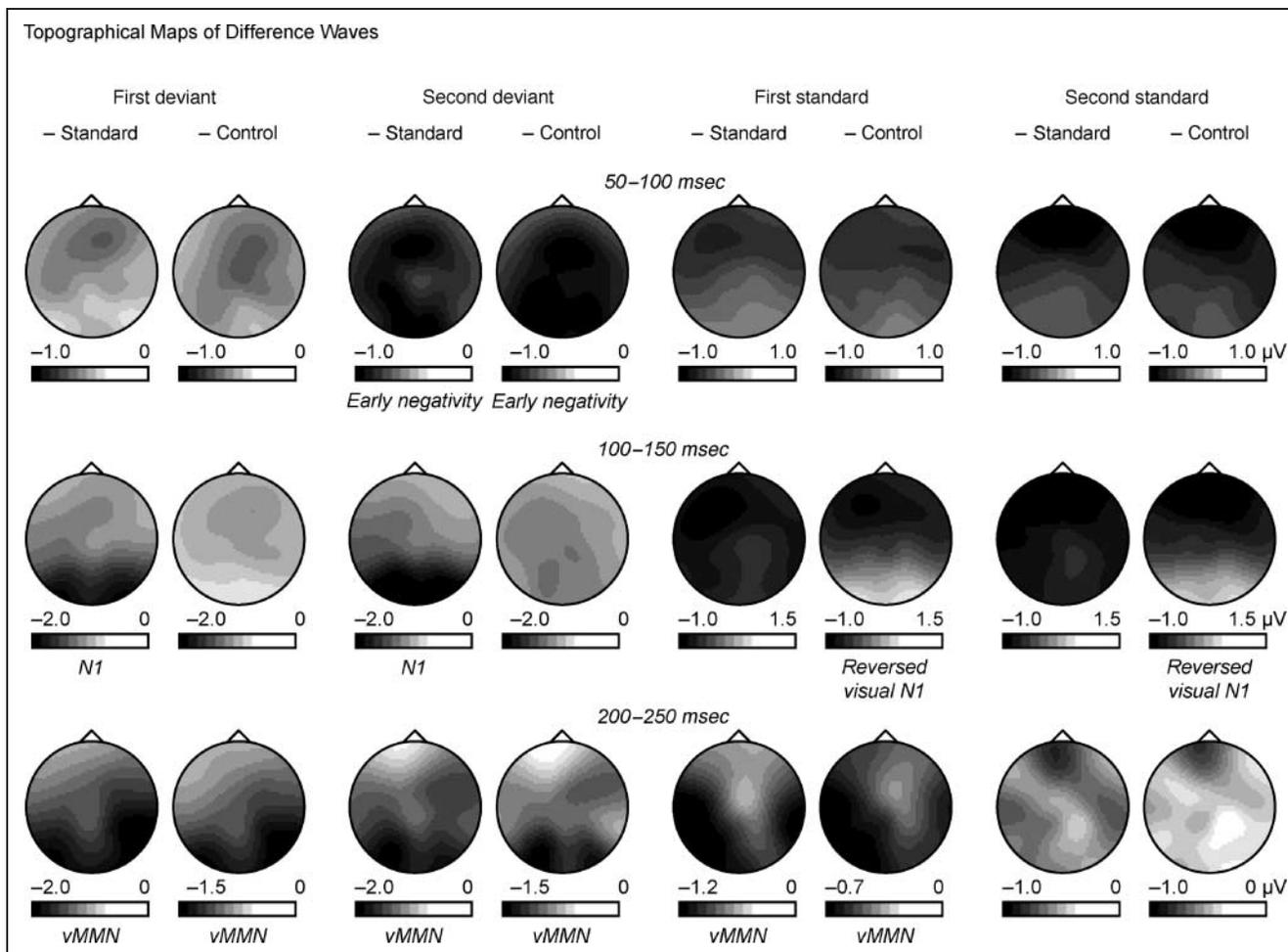


Figure 4. Topographical maps of the grand-averaged difference waves within the 50–100 msec (top), 100–150 msec (middle), and 200–250 msec time windows (bottom).

had a relatively similar bilateral posterior scalp distribution, visual MMN observed in the first-deviant-minus-standard and first-deviant-minus-control difference waves had a right temporal (T6) maximum scalp distribution, visual MMN observed in the second-deviant-minus-standard and second-deviant-minus-control difference waves had a left occipitoparietal (PO3) maximum scalp distribution, and visual MMN observed in the first-standard-minus-standard and first-standard-minus-control difference waves had a left occipitotemporal (PO7) maximum scalp distribution.

Table 2 shows the mean amplitudes of difference waves within the 200–250 msec time window at 13 posterior electrodes and a summary of two-tailed paired t tests performed on the amplitudes. The t tests revealed that visual MMN was elicited in the first-deviant-minus-standard [$ts(11) = -5.88$ to -3.15 , $ps < .01$, $ds = 0.91$ – 1.70], first-deviant-minus-control [$ts(11) = -7.37$ to -2.92 , $ps < .05$ – $.01$, $ds = 0.85$ – 2.13], second-deviant-minus-standard [$ts(11) = -3.55$ to -2.48 , $ps < .05$ – $.01$, $ds = 0.72$ – 1.08], second-deviant-minus-control [$ts(11) = -2.55$ to -2.43 , $ps < .05$, $ds = 0.70$ – 0.73], first-standard-minus-standard [$ts(11) = -4.97$ to -2.68 , $ps < .05$ – $.01$, $ds = 0.77$ – 1.44], and first-standard-minus-control difference

waves [$ts(11) = -3.54$ to -2.26 , $ps < .05$ – $.01$, $ds = 0.65$ – 1.02], but not in the second-standard-minus-standard and second-standard-minus-control difference waves.

Two-way ANOVAs (3 Difference waves \times 13 Electrodes) performed on the amplitudes of the first-deviant-minus-control, second-deviant-minus-control, and first-standard-minus-control difference waves within the 200–250 msec time window revealed the significant interaction of Difference waves \times Electrodes [$F(24, 264) = 2.94$, $p < .05$, $\epsilon = .19$, $f = 0.09$], which was due to enhanced negative amplitudes of visual MMN in the first-deviant-minus-control compared to the first-standard-minus-control difference waves at the T6 ($p < .10$, $f = 0.71$) and PO8 electrodes ($p < .10$, $f = 0.74$). However, the same two-way ANOVAs performed on the normalized amplitudes revealed no significant effects, which implies that the significant interaction of Difference waves \times Electrodes revealed in the two-way ANOVAs performed on the nonnormalized data arises from the differences in the strength of visual MMN generation.

Two-tailed paired t tests performed on the amplitudes of the early negativity within the 50–100 msec time window revealed that the early negativity was elicited in the

Table 2. Mean Amplitudes (μV) of the Difference Waves within the 200–250 msec Time Window at 13 Posterior Electrodes (Standard Errors in Parentheses) and Summary of Two-tailed Paired t Tests (All d 's were 11)

Electrode	Difference Wave							
	First Deviant Minus		Second Deviant Minus		First Standard Minus		Second Standard Minus	
	Standard	Control	Standard	Control	Standard	Control	Standard	Control
T5	-1.83 (0.31)**	-1.22 (0.25)**	-1.50 (0.42)**	-0.90 (0.52)	-1.29 (0.26)**	-0.69 (0.24)*	-0.08 (0.46)	0.52 (0.52)
P3	-1.45 (0.37)**	-0.97 (0.32)*	-1.65 (0.50)**	-1.17 (0.56)	-1.10 (0.34)**	-0.62 (0.28)*	-0.13 (0.42)	0.35 (0.49)
Pz	-1.22 (0.39)**	-0.85 (0.29)*	-1.21 (0.55)	-0.83 (0.60)	-0.79 (0.39)	-0.42 (0.33)	-0.17 (0.48)	0.54 (0.52)
P4	-1.67 (0.35)**	-1.24 (0.25)**	-1.39 (0.56)*	-0.97 (0.63)	-0.61 (0.40)	-0.19 (0.37)	0.26 (0.49)	0.69 (0.54)
T6	-2.27 (0.41)**	-1.59 (0.26)**	-1.38 (0.55)*	-0.70 (0.64)	-1.06 (0.37)*	-0.38 (0.31)	-0.04 (0.44)	0.64 (0.50)
PO7	-1.97 (0.37)**	-1.47 (0.32)**	-1.88 (0.50)**	-1.38 (0.56)*	-1.30 (0.30)**	-0.80 (0.23)**	-0.18 (0.44)	0.32 (0.51)
PO3	-1.62 (0.36)**	-1.18 (0.33)**	-1.87 (0.53)**	-1.43 (0.56)*	-1.15 (0.39)*	-0.71 (0.26)*	-0.03 (0.45)	0.41 (0.50)
POz	-1.47 (0.35)**	-1.03 (0.26)**	-1.50 (0.53)*	-1.06 (0.57)	-0.90 (0.44)	-0.46 (0.33)	0.14 (0.48)	0.58 (0.50)
PO4	-1.65 (0.35)**	-1.23 (0.24)**	-1.60 (0.59)*	-1.18 (0.61)	-0.74 (0.44)	-0.32 (0.36)	0.13 (0.48)	0.55 (0.53)
PO8	-2.07 (0.39)**	-1.58 (0.22)**	-1.77 (0.56)**	-1.29 (0.64)	-0.79 (0.42)	-0.31 (0.33)	0.18 (0.48)	0.66 (0.52)
O1	-1.82 (0.39)**	-1.39 (0.32)**	-1.84 (0.55)**	-1.41 (0.58)*	-1.10 (0.35)**	-0.67 (0.21)**	-0.09 (0.42)	0.33 (0.48)
Oz	-1.81 (0.34)**	-1.29 (0.25)**	-1.63 (0.54)*	-1.11 (0.60)	-1.07 (0.40)*	-0.55 (0.30)	-0.05 (0.46)	0.47 (0.50)
O2	-1.95 (0.36)**	-1.39 (0.22)**	-1.81 (0.61)*	-1.24 (0.61)	-0.87 (0.45)	-0.31 (0.33)	0.18 (0.48)	0.74 (0.50)

* $p < .05$.

** $p < .01$.

second-deviant-minus-standard [P3: $t(11) = -3.21, p < .01, d = 0.93$] and second-deviant-minus-control difference waves [P3: $t(11) = -4.00, p < .01, d = 1.15$]. Also, the same t tests performed on the amplitudes of visual N1 and reversed visual N1 within the 100–150 msec time window revealed that visual N1 was elicited in the first-deviant-minus-standard [PO7 and PO8: $t_s(11) = -8.11$ and $-9.04, p_s < .01, d_s = 2.34$ and 2.61] and second-deviant-minus-standard difference waves [PO7 and PO8: $t_s(11) = -5.76$ and $-5.36, p_s < .01, d_s = 1.66$ and 1.55], whereas polarity-reversed N1 was elicited in the first-standard-minus-control [PO7 and PO8: $t_s(11) = 4.31$ and $6.02, p_s < .01, d_s = 1.24$ and 1.74] and second-standard-minus-control difference waves [PO7 and PO8: $t_s(11) = 2.79$ and $2.66, p_s < .05, d_s = 0.80$ and 0.77].

DISCUSSION

In the present study, we investigated whether visual MMN that emerged in the oddball sequence, an ERP correlate of an automatic memory-mismatch process in the visual sensory system, is based only on a sensory memory trace of standard stimuli (trace-mismatch hypothesis) or is also based on sequential regularities extracted from the repetitive standard sequence (regularity-violation hypothesis). To this end, we conducted a sequential analysis of visual MMN in the oddball sequence and tested the elicitation

of visual MMN by first deviant, second deviant, first standard, and second standard.

Visual MMN and the Nature of Underlying Memory Representation

Compared to standard, first deviant, second deviant, and first standard elicited visual MMN that peaked at around 200–250 msec with a posterior scalp distribution. The peak latency and scalp distribution are consistent with those of visual MMN in previous visual oddball studies (Kimura et al., 2009; Astikainen et al., 2008; Berti & Schröger, 2006; Stagg et al., 2004), which has been confirmed to have generators in visual areas (Amenedo et al., 2007; Yucel et al., 2007; Czigler et al., 2004; Pazo-Alvarez, Amenedo, Lorenzo-López, et al., 2004). Importantly, visual MMN was still observed even when these stimuli were compared to control. Although the electrode location of the maximal visual MMN amplitudes was slightly different in the three stimulus types, there was no statistically significant difference in the scalp distribution of visual MMN. This result indicates that the visual MMN elicited by the three types of stimuli were qualitatively similar and related to a brain process in the visual sensory system.

In the present study, the physical attributes of the eliciting stimulus were not different from each other. Furthermore, the state of refractoriness for control should be the same as those for first deviant and second deviant

and lower than those for first and second standard because the probability of control nontarget stimuli was the same as that of deviant nontarget stimuli and lower than that of standard nontarget stimuli. Furthermore, control should not elicit visual MMN because each control nontarget stimulus did not violate any regularity. Consequently, visual MMN observed in the present study could be considered to reflect an automatic memory-mismatch process in the visual sensory system.

Concerning the main question of the present study, the present finding that first deviant, second deviant, and first standard elicited visual MMN supports the regularity-violation hypothesis, but cannot be fully explained by the trace-mismatch hypothesis. If visual MMN was solely based on a sensory memory trace of standard stimuli (trace-mismatch hypothesis), then visual MMN would have been observed with first deviant and second deviant, but not first standard. In contrast, if visual MMN was based on the memory representation of sequential regularities (regularity-violation hypothesis), then visual MMN should be seen with first deviant, second deviant, and first standard, as all of these stimuli violate the sequential regularity extracted from the repetitive standard sequence. Thus, the present results indicate that visual MMN in the oddball sequence can be interpreted in terms of the regularity-violation hypothesis, as previously suggested based on visual MMN generation in a more complex stimulus sequence (Czigler, Weisz, et al., 2006), and support the notion that the visual sensory system automatically encodes the sequential regularities inherent in the sequential presentation of discrete events beyond the simple storage of sensory memory trace.

However, it would also be necessary to emphasize that the regularity-violation and trace-mismatch hypotheses are not mutually exclusive (e.g., Schröger, 2007; Winkler, 2007). In the present study, first standard elicited visual MMN with relatively small amplitudes compared to first deviant and second deviant. Based on the regularity-violation hypothesis, first deviant, second deviant, and first standard violate the sequential regularity extracted from the repetitive standard sequence. In addition, based on the trace-mismatch hypothesis, first deviant and second deviant mismatch the sensory memory trace of standard stimuli, which is not the case for first standard. Thus, one possible interpretation of the relatively small visual MMN elicited by first standard is that visual MMN elicited by first deviant and second deviant is elicited by both the regularity violation and trace mismatch, whereas visual MMN elicited by first standard is elicited only by the regularity violation.

In the present study, the amplitudes of visual MMN elicited by first deviant and second deviant were not significantly different. However, previous auditory MMN studies have reported that the amplitude of auditory MMN elicited by second deviant was smaller than that of auditory MMN elicited by first deviant (e.g., Müller, Widmann, & Schröger, 2005; Noursak, Deacon, Ritter, & Vaughan, 1996; Sams, Alho, & Näätänen, 1984). This result has been considered

to reflect the fact that a single presentation of a deviant stimulus strongly interrupts the memory representation formed by the preceding standard sequence. According to this account, the present result suggests that the extent of such interruption may be different among sensory modalities. Although it would be interesting to determine whether or not an interruption effect occurs in response to third deviant (i.e., deviant nontarget stimuli immediately following second deviant), a reliable estimation was not possible due to the constraint of the averaging number. Further studies on this issue will be necessary.

Early Negativity, Visual N1, and Reversed Visual N1

Within the 100–150 msec time window, first deviant and second deviant compared to standard elicited a negativity with an occipito-temporal scalp distribution, whereas first standard and second standard compared to control elicited a positivity with a similar occipito-temporal scalp distribution. A reasonable explanation is that these negative and positive ERPs are visual N1 and polarity-reversed visual N1 refractory effects, respectively, because the state of refractoriness for first and second deviant was considerably lower than that for standard, whereas the state of refractoriness for first and second standard was considerably higher than that for control (see Kimura et al., 2009; Astikainen et al., 2008; Pazo-Alvarez, Amenedo, & Cadaveira, 2004; Czigler et al., 2002). The peak latency and scalp distribution are also consistent with the visual N1 refractory interpretation (e.g., Kimura et al., 2008a, 2008c, 2009).

Within the 50–100 msec time window, second deviant compared to standard and control elicited an early negativity that peaked at around 50–100 msec with a wide scalp distribution over the occipital to frontal areas. This early negativity seems to be difficult to be interpreted in terms of a visual N1 refractory effect because the state of refractoriness for control is assumed to be the same as that for deviant. This interpretation is also inconsistent with the result that first deviant, the refractoriness state of which should be the same as (or possibly lower than) that of second deviant, did not elicit a comparable negativity. Another possible explanation is that the negativity reflects the polarity-reversed change-related positivity (Kimura, Katayama, & Murohashi, 2005b), which has been observed in response to visual stimulus changes (e.g., Kimura, Katayama, & Murohashi, 2005a, 2006a, 2006b, 2008b; Kimura et al., 2005b, 2006c, 2008a, 2008c, 2008d; Fonteneau & Davidoff, 2007; Fu, Fan, & Chen, 2003; Wang et al., 2003). This component has typically been obtained by subtracting ERPs elicited by a stimulus that is the same as the immediately preceding stimulus from those elicited by a stimulus that differs from the immediately preceding stimulus (i.e., change-minus-no-change difference waves). It has an earlier latency than the visual N1 refractory effect (e.g., Kimura et al., 2006c; Fu et al., 2003) and sometimes has a broad scalp distribution over the occipital to frontal areas (e.g., Kimura et al., 2008a, 2008c, 2008d). From the

2001). This provides some important implications in the field of neuroscience.

An automatically formed memory representation in the sensory systems has traditionally been understood in terms of the sensory store that plays an important role in encoding static information (Atkinson & Shiffrin, 1968). For the auditory modality, such a memory representation is generally considered to be worth while, as most stimuli in the auditory modality are transient. In contrast, for the visual modality, the worth of such a memory representation is debated, as the visual world is usually available permanently as an external memory (e.g., O'Regan & Noë, 2001; Haber, 1983). However, if the automatically formed memory representation can maintain dynamic information such as sequential regularities, as the present and previous MMN studies have suggested, the existence of such a memory representation even in the visual modality seems to be reasonable because it would play a critical role in predicting events encountered in the immediate future (e.g., Czigler, 2007).

Also, the present and previous MMN studies suggest that sensory systems substantially contribute to the encoding of sequential regularities embedded in the sequence of sensory events. However, there is a discrepancy with previous neuroscience studies which support the notion that dynamic information, such as sequential regularities, is mainly processed in sensory-non-specific systems rather than sensory-specific systems. For example, several ERP studies have reported that sensory-non-specific ERP components, such as N2b (e.g., Ferdinand et al., 2008; Rüsseler et al., 2003; Eimer et al., 1996) and/or P300 (e.g., Rüsseler et al., 2003; Jentzsch & Sommer, 2001; Duncan-Johnson, Roth, & Kopell, 1984; Ford, Duncan-Johnson, Pfefferbaum, & Kopell, 1982; Squires, Wickens, Squires, & Donchin, 1976), are elicited by violations of sequential regularities. Moreover, several fMRI studies have reported that prefrontal cortex (e.g., Bubic, von Cramon, Jacobsen, Schröger, & Schubotz, 2008; Turner et al., 2004; Huettel, Mack, & McCarthy, 2002) and/or premotor cortex (e.g., Bubic et al., 2008; Schubotz, 2007; Schubotz & von Cramon, 2002) are critical for the encoding of sequential regularities. However, in these studies, the sequential regularities were either directly task-relevant, because participants were required to monitor them, or indirectly task-relevant, because participants were required to respond to the stimuli, and the extraction of sequential regularities embedded in a stimulus sequence can be used to improve their behavioral performance, which might lead to activations in these higher processing areas (e.g., Bendixen, Prinz, Horváth, Trujillo-Barreto, & Schröger, 2008). The fact that MMN has been observed regardless of the relevance of sequential regularities to the current task supports the notion that not only sensory-non-specific systems but also sensory-specific systems substantially contribute to these cognitive operations.

Finally, several behavioral studies have suggested that the encoding of sequential regularities is considerably auto-

matic and obligatory. For example, when presented with visual stimuli that alternate between the left and right sides of a display, even 3-month-old infants can make anticipatory eye movements to the next event (e.g., Canfield & Haith, 1991; Haith & McCarty, 1990). Also, studies of sequential learning have shown that even when they are not aware of the existence of sequential regularities embedded in a sequence of sensory events, participants can improve their behavioral performance by using sequential regularities (e.g., Cohen, Ivry, & Keele, 1990; Nissen & Bullemer, 1987). This automatic nature of anticipatory behavior seems to be consistent with that of MMN generation (e.g., Czigler, 2007; Sussman, 2007). Although the automatic nature of visual MMN generation is still an important issue that should be investigated more carefully in future studies (Czigler, 2007), it is reasonable to assume that sequential regularities that are automatically encoded into a memory representation at the level of the sensory system may, at least to some extent, subserve such anticipatory behavior (e.g., Mayr, 1996).

Conclusion

The present study showed that the memory representation that underlies visual MMN generation in the oddball sequence involves not only a sensory memory trace of standard stimuli but also sequential regularities extracted from the preceding repetitive standard sequence. The present results suggest that the visual sensory system automatically encodes sequential regularities. In combination with a wide range of auditory MMN studies, the present results highlight the critical role of sensory systems in automatically encoding sequential regularities when modeling the world.

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Notes

1. In a strict sense, N1 is also related to memory functions because N1 indirectly contains information about previous stimulation (e.g., Grill-Spector, Henson, & Martin, 2006). However, N1 is simply related to adaptation to the repeated physical aspects of a stimulus and is not directly related to the encoding of dynamic information such as sequential regularities (e.g., Schröger, 2007). Also, note that visual MMN is called "posterior N2" and visual N1 is called "change-related negativity" in two studies by Kimura et al. (2008a, 2008c).
2. The regularity-violation and trace-mismatch hypotheses are not necessarily mutually exclusive and the regularity-violation hypothesis does not rule out the trace-mismatch hypothesis. The regularity-violation hypothesis stands for the assumption

that a memory representation maintains not only static information but also dynamic information (see, e.g., Schröger, 2007; Winkler, 2007).

3. It is not necessary to take into account the sensory memory trace of deviant stimuli because postdeviant stimuli (i.e., second deviant, first standard, and second standard) are preceded by a single presentation of a deviant stimulus (first deviant), which is known to be insufficient to form a strong sensory memory trace of the deviant stimulus required for the elicitation of visual MMN (see, e.g., Kimura et al., 2005a, 2005b, 2006a, 2006b, 2006c, 2008b; Mazza et al., 2005).

4. Differences between scalp distributions are typically established by the finding of a statistically significant interaction between condition and electrode in a repeated measures ANOVA (i.e., in the present experiment, 3 difference waves and 13 electrodes). However, McCarthy and Wood (1985) showed that the interaction between condition and electrode is not sufficient for inferring that the spatial configurations of scalp distribution differs between conditions, as such an interaction can result when a dipolar generator in a fixed spatial location varies only with regard to strength. To protect against drawing this unwarranted conclusion, McCarthy and Wood proposed a vector scaling procedure.

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