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Top-down attention affects sequential regularity representation in the human visual system

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ABSTRACT

Recent neuroscience studies using visual mismatch negativity (visual MMN), an event-related brain potential (ERP) index of memory-mismatch processes in the visual sensory system, have shown that although sequential regularities embedded in successive visual stimuli can be automatically represented in the visual sensory system, an existence of sequential regularity itself does not guarantee that the sequential regularity will be automatically represented. In the present study, we investigated the effects of top-down attention on sequential regularity representation in the visual sensory system. Our results showed that a sequential regularity (SSSSD) embedded in a modified oddball sequence where infrequent deviant (D) and frequent standard stimuli (S) differing in luminance were regularly presented (SSSSDSSSSDSSSSD…) was represented in the visual sensory system only when participants attended the sequential regularity in luminance, but not when participants ignored the stimuli or simply attended the dimension of luminance per se. This suggests that top-down attention affects sequential regularity representation in the visual sensory system and that top-down attention is a prerequisite for particular sequential regularities to be represented.

1. Introduction

The encoding of sequential regularities embedded in successive sensory events is an important issue in computational and behavioral neuroscience, as it is a prerequisite for establishing predictions for future sensory events (e.g., Bubic et al., 2010; Denham and Winkler, 2006; Kiebel et al., 2009; Schubotz, 2007). For the auditory modality, recent neuroscience studies using auditory mismatch negativity (auditory MMN; Näätänen et al., 1978) event-related brain potential (ERP) have suggested that sequential regularities embedded in a successive auditory stimulus sequence can be represented in memory at the level of the auditory sensory system, even when the stimulus sequence is irrelevant for the current task (for reviews, see e.g., Näätänen et al., 2001; Schröger, 2007; Sussman, 2007; Winkler, 2007).

For the visual modality, such an automatically formed memory representation of sequential regularities has not attracted as much scientific interest as for the auditory modality, probably because the processing of temporal information in the visual domain was not thought to be as important as in the auditory domain. However, recent neuroscience studies share the idea that representing sequential regularities and predicting future sensory events are important cognitive functions regardless of the sensory modalities (e.g., Schubotz, 2007). In particular, the contributions of the visual sensory system for automatically representing sequential regularities embedded in a successive visual stimulus sequence have been highlighted by recent studies using a visual analogue of auditory MMN, namely, visual mismatch negativity (visual MMN, e.g., Czigler et al., 2002; Kimura et al., 2009; Kimura et al., 2010a; for reviews, see Czigler, 2007; Pazo-Alvarez et al., 2003).

1.1. Mismatch negativity (MMN)

MMN is a negative-going ERP component that peaks at around 150-250 ms after the onset of deviant stimulation with an anterior (auditory MMN) and a posterior (visual MMN) scalp distribution, and it has been typically observed in response to infrequent "deviant" stimuli randomly inserted among frequent "standard" stimuli (i.e., an oddball sequence). MMN has its main generator in sensory areas (for auditory MMN, e.g., Alho, 1995; Deouell, 2007; for visual MMN, e.g., Czigler et al., 2004; Yucel et al., 2007), which suggests that MMN reflects a brain process at the level of the sensory system. Importantly, MMN is an ERP correlate of memory-mismatch processes and is elicited when a current stimulus input mismatches a memory representation in the sensory system formed by the preceding stimulus sequence (for auditory MMN, e.g., Näätänen and Alho, 1997; Schröger, 1997; Schröger and Wolff, 1996; for visual MMN, e.g., Czigler et al., 2002; Kimura et al., 2009; Kimura et al., 2010a).

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Therefore, auditory and visual MMN can be used as a tool that taps into the nature of the memory representation in the sensory system ("a microphone into memory", Schröger, 2007).

1.2. Automatically-formed sequential regularity representation

Auditory MMN studies have suggested that sequential regularities embedded in a successive auditory stimulus sequence can be automatically represented in the auditory sensory system. For example, Sussman and Gumenyuk (2005) and Sussman et al. (1998) used a modified oddball sequence where deviant (D) and standard stimuli (S) that differed in tonal frequency (e.g., 494 and 440 Hz, respectively) were regularly presented (i.e., SSSSDSSSSDSSSSD…) and asked participants to ignore tonal frequency. They hypothesized that if the sequential regularity of five stimuli (i.e., SSSSD) can be automatically represented in the auditory sensory system, then auditory MMN should not be elicited by the deviant stimuli, since the deviant stimulus is a part of the sequential regularity represented in the auditory sensory system and the deviant stimulus does not mismatch the content of memory representation. They found that auditory MMN was not elicited by the deviant stimuli when relatively short SOAs were used (160 ms in Sussman et al., 1998; 200 ms in Sussman and Gumenyuk, 2005), whereas auditory MMN was elicited when relatively long SOAs were used (1300 ms in Sussman et al., 1998; 400, 600, and 800 ms in Sussman and Gumenyuk, 2005; see also Scherg et al., 1989). These results imply that the sequential regularity of five stimuli (SSSSD) was automatically represented in the auditory sensory system when the relatively fast presentation rates were used, while it was not when the relatively slow presentation rates were used (for a review, see Sussman, 2007).

It was largely unknown whether or not sequential regularities embedded in a successive visual stimulus sequence can also be automatically represented in the visual sensory system and whether or not the automatically formed memory representation shares the basic characteristics between sensory modalities. This motivated Kimura et al. (2010b) to adopt the auditory paradigm developed by Sussman and colleagues (1998, 2005) to the visual domain. They used the modified oddball sequence where deviant and standard stimuli that differed in luminance (low- and high-luminance, respectively) were regularly presented (SSSSDSSSSDSSSSD…) and asked participants to ignore luminance. Visual MMN was not elicited by the deviant stimuli when 160-ms SOA was used, whereas visual MMN was elicited when 480- and 800-ms SOAs were used. These results indicate that the sequential regularity of five stimuli (SSSSD) was automatically represented in the visual sensory system when the fast presentation rate was used, while it was not when the slow presentation rates were used. These results are highly consistent with those of Sussman and colleagues (1998, 2005) and support the notion that the automatically formed sequential regularity representation shares the basic characteristics between the visual and auditory sensory modalities.

1.3. Top-down effects on sequential regularity representation

The results from the auditory MMN studies (Sussman and Gumenyuk, 2005; Sussman et al., 1998) and the comparable visual MMN study (Kimura et al., 2010b) suggest that although sequential regularities can be automatically represented in the sensory system, an existence of sequential regularity itself does not guarantee that the sequential regularity will be automatically represented in the sensory system. It can be limited by several stimulus-driven factors such as the temporal proximity of stimulus presentation. In the auditory modality, however, it has also been shown that such a limitation can be overcome by directing top-down attention to the sequential regularities (Sussman et al., 2002). The authors used a modified oddball sequence where deviant and standard stimuli that differed in tonal frequency (494 and 440 Hz, respectively) were regularly represented (SSSSDSSSSDSSSSD…) at a relatively long SOA (1000 ms, at which it has been shown that the sequential regularity of five stimuli, SSSSD, could not be automatically represented in the auditory sensory system, Sussman and Gumenyuk, 2005; Sussman et al., 1998), of which the standard stimuli were occasionally replaced by target stimuli (392 Hz).

They tested the elicitation of auditory MMN by the deviant stimuli under three attention conditions: (1) "Ignore condition" where participants were instructed to ignore tonal frequency, (2) "Attend-Pitch condition" where participants were instructed to detect a particular change in tonal frequency (i.e., the 392 Hz target stimuli), and (3) "Attend-Pattern condition" where participants were instructed to detect violations of the sequential regularity in tonal frequency (SSSSD) by the 392 Hz target stimuli. Thus, although the target stimuli were the same in the Attend-Pitch and Attend-Pattern conditions, the instructions promoted different ways of detecting the target stimuli. As in Sussman and Gumenyuk (2005) and Sussman et al. (1998), the authors hypothesized that if the sequential regularity in tonal frequency (SSSSD) can be represented in the auditory sensory system, then auditory MMN should not be elicited by the deviant stimuli. Results showed that auditory MMN was elicited by the deviant stimuli in the Ignore and Attend-Pitch conditions, while auditory MMN was not elicited in the Attend-Pattern condition. These results indicate that the sequential regularity in tonal frequency (SSSSD) was represented in the auditory sensory system when participants attended the sequential regularity in tonal frequency (Attend-Pattern condition), while the regularity was not represented when participants ignored the stimuli (Ignore condition) or simply attended the dimension of tonal frequency per se (Attend-Pitch condition).

1.4. Present study

The results of Sussman et al. (2002) demonstrated that top-down attention affects sequential regularity representation in the auditory sensory system. In the present study, we investigated whether or not top-down attention also affects sequential regularity representation in the visual sensory system. For this purpose, we presented stimuli consisting of peripheral circles and a central letter at a relatively long SOA (600 ms, at which it has been shown that the sequential regularity of five stimuli, SSSSD, could not be automatically represented in the visual sensory system, Kimura et al., 2010b) in a similar modified oddball sequence to that used in Sussman et al. (2002) (see Fig. 1). In this sequence, deviant and standard peripheral circles that differed in luminance (low- and high-luminance) were regularly presented (SSSSDSSSSDSSSSD…), of which the standard peripheral circles were occasionally replaced by medium-luminance circles, while several types of central letter were randomly presented. We tested the elicitation of visual MMN by the deviant peripheral circles under three attention conditions: (1) "Ignore condition" where participants were instructed to ignore luminance and detect a particular central letter, (2) "Attend condition" where participants were instructed to detect a particular change in luminance (i.e., the medium-luminance circles), and (3) "Attend-Pattern condition" where participants were instructed to detect violations of the sequential regularity in luminance (SSSSD) by the medium-luminance circles.

2. Methods

2.1. Participants

Fifteen volunteers (12 women, 3 men; age range = 19-28 years, mean age = 21.7 years) participated in this experiment for course credit. All participants were right-handed, had normal or corrected-