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NEURAL PROCESSES IN PSEUDO PERCEPTUAL RIVALRY: AN ERP AND TIME–FREQUENCY APPROACH

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Abstract—Necker cube is one of the ambiguous figures that is physically a static image but can be alternately perceived in two different perspectives. A great deal of debate exists regarding ambiguous figures that induce spontaneous switching between rival percepts. To investigate the time course of neural processes underlying such perceptual rivalry, we recorded electroencephalograms associated with participants' perceptions of a Necker cube under ambiguous and unambiguous conditions, using a modified discontinuous-presentation method. Each condition consisted of two stimuli presented consecutively, starting with an unambiguous stimulus in both conditions. The second stimulus was either ambiguous (ambiguous condition) or unambiguous (control condition). We compared endogenous reversal activity of ambiguous stimuli with exogenous reversals. As a result, we found that the right-occipital beta-band activity (16–26 Hz) increased 100–150 ms and 350–450 ms after the onset of the ambiguous stimulus only when the perception of the ambiguous stimulus differed from that of the first stimulus. These results indicate that activity in the right-occipital total beta band reflects endogenous switching between rivaling percepts.

Key words: beta-band activity, EEG, Necker cube, perceptual rivalry.

INTRODUCTION

As observed in binocular rivalry and the perception of ambiguous figures, perceptual rivalry exemplifies the flexibility of the brain by producing fluctuating perceptions of an unchanging stimulus. In the former case, the eyes are presented with incongruent images that compete for conscious perception, while in the latter case, two possible percepts of the same figure spontaneously alternate. Common ambiguous figures include bistable apparent motion stimuli, the Rubin's vase (Rubin, 1951), Boring's young/old woman (Boring, 1930), and the Necker cube (Necker, 1832). For example, the Necker cube consists of a regular hexahedron, but can be alternately perceived in two different perspectives (Fig. 1). Although a physical aspect of the Necker cube stays unchanged, the prolonged viewing leads to spontaneous perceptual switching. Several methods have been used to examine spontaneous perceptual switching, and recent functional magnetic resonance imaging (fMRI) studies have shown that multiple cortical regions, including visual, parietal, and frontal areas, are associated with perceptual alternations in both binocular rivalry (Lumer et al., 1998; Tong et al., 1998; Polonsky et al., 2000) and ambiguous figure perception (Kleinschmidt et al., 1998; Sterzer et al., 2002). For example, using apparent motion stimuli, spontaneous perceptual switching was correlated with right-inferior frontal cortex activation (Sterzer and Kleinschmidt, 2007). Using fMRI allowed researchers to detect the activated regions related to perceptual rivalry with a high degree of spatial resolution. However, magnetoencephalographic/electroencephalographic (MEG/EEG) techniques provide a higher degree of temporal resolution and are therefore more useful than fMRI for the study of temporal characteristics of perceptual switching.

Highly variable and unpredictable timing of perceptual switching is one problem often encountered when studying perceptual rivalry. In several event-related potential (ERP) studies, participants have pressed a button to report perceptual-switch onsets of continuously presented multi-stable figures (Gaddis and Gaddis, 1990; Isoglu-Alkac et al., 1998). These studies suggested that a P300-like component affects perceptual changes. However, variations in trial-by-trial reaction times make it difficult to precisely determine the time of onset. In order to resolve this problem, Kornmeier and Bach (2004) used a different approach. They presented a Necker cube twice, with a blank interval separating the two presentations (stimuli-blank-stimuli). This method led to time referencing that was more precise than was found in the participants' own reports. Studies employing similar discontinuous presentations have shown that an early

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Abbreviations: EEG, electroencephalographic; ERP, event-related potential; fMRI, functional magnetic resonance imaging; RN, reversal-negativity.

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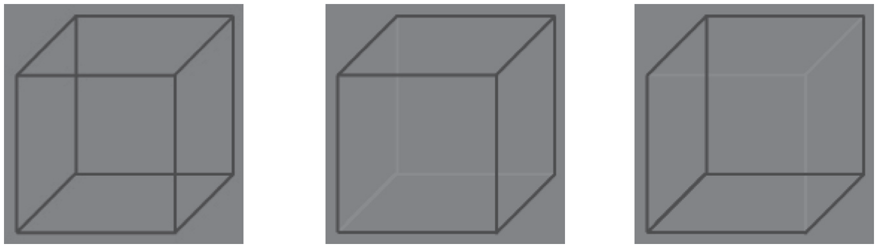

Fig. 1. Experimental stimuli. (A) ambiguous Necker cube, (B) unambiguous cube 1, (C) unambiguous cube 2.

ERP component (P1, N1) and a reversal-negativity (RN) component reflect perceptual switching (Kornmeier and Bach, 2005, 2006; Pitts et al., 2007). P1 and N1 amplitudes were enhanced for perceptual reversal compared with perceptual stability, which reflected changes in visual early spatial attention to perceptual reversals (Pitts et al., 2007). RN is a negative potential observed in the occipital region 200–400 ms after stimulus onset, and has been reported to be associated with binocular and perceptual rivalry (Kornmeier and Bach, 2004, 2005, 2006; Pitts et al., 2007; Britz and Pitts, 2011). Its amplitude is larger for perceptual reversal compared with stability (Pitts et al., 2007; Britz and Pitts, 2011), and was elicited more strongly in response to exogenous perceptual switching than to endogenous switching (Pitts et al., 2008). However, in above procedure, participants are required to disambiguate the two successive Necker cubes, and brain activity correlated with that process might occur during either of the presentations. Therefore, contamination during the blank period is likely if subjects cannot disambiguate the first stimulus. Additionally, incomplete disambiguation may delay the next perceptual switch.

Here, we employed a modified discontinuous procedure to obtain less variable time latencies. Specifically, perceptual disambiguation of the first stimulus was controlled by using an unambiguous first stimulus followed by an ambiguous second stimulus. Although this method has been used once before, authors focused on the relationship between unilateral/bilateral endogenous reversals and RN, but did not discuss the time course of neural activity correlated with ambiguous reversal (Intaite et al., 2010). Additionally, because the first stimulus is not repeated, our method can suppress the effect of priming repetition between first and second stimuli, resulting in more precise reversal-time onsets.

In order to reveal the neural activity related to the perceptual rivalry, it is important to investigate oscillatory activity of EEG. In the ERP analysis, the averaged ERP allowed us to detect activity phase-locked to stimulus onset. However, it is difficult to detect integrative functions such as perceptual inference, decision-making, and top-down attention through ERP analysis, presumably because they are typically reflected in the sustained non-phase-locked activity component (Donner and Siegel, 2011). Spectral analysis to detect the non-phase-locked activity is an extremely important method to employ when addressing the problem of perceptual rivalry. Therefore, this paper focused on oscillatory activity related to ambiguous perceptual switching in addition to ERP activity.

Oscillatory activity has been reported to reflect various biological significances within a certain frequency range. It has been recognized that various oscillatory activities are involved in endogenous switching of ambiguous figures such as the Necker cube. Some previous studies using the procedure of continuous viewing procedure showed that the enhancement of low-frequency oscillations such as delta and alpha bands was related to perceptual switching (Nakatani and van Leeuwen, 2005; Mathes et al., 2006; Shimaoka et al., 2010; Nakatani et al., 2011). For example, the study used EEG and fMRI to investigate neural dynamics of perceptual switching and reported that the delta-band activity (3–4 Hz) increased in the left-frontal and the right-occipital channels from 750 to 350 ms before the switching, which suggests a neural network from frontal to parietal-occipital regions triggers switching (Ozaki et al., 2012). Moreover, it has been reported that the enhancement of occipital alpha-band predicts the saccade to promote perceptual switching (Nakatani and van Leeuwen, 2013). However, few studies using the discontinuous procedure investigated the oscillatory activity, while many studies have been made on the ERP activity related to perceptual switching (Kornmeier and Bach, 2004, 2005, 2006; Pitts et al., 2007, 2008). For example, gamma modulation preceding perceptual switching has been reported (Ehm et al., 2010), however, gamma band activity was suggested to reflect signature of local encoding in the cortex (Donner and Siegel, 2011). In contrast, beta band activity reflects long-range cortical interactions to mediate integrative functions such as top-down control (Engel and Fries, 2010, Donner and Siegel, 2011). Therefore we predicted that perceptual switching of ambiguous figures due to a change of dynamics in the brain is reflected in the modulation of beta band activity.

Beta-band activity reflects not only the motor system (Pfurtscheller and Aranibar, 1977; Pfurtscheller, 1981) but also long-range cortical interactions which mediate integrative functions such as top-down control (Engel and Fries, 2010, Donner and Siegel, 2011). It was reported that enhancement of beta band activity is associated with the change of visual perception in bistable figures (Okazaki et al., 2008). In addition, the study on psudo-motion perception suggested the relationship between beta-band power and perceptual switching