

Interocular interactions evoked by asynchronous checkerboard pattern reversals to each eye

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Abstract

To examine interocular interactions in normal subjects, we recorded EEG activity from channel O1 and O2 on 14 healthy subjects while checkerboard pattern reversals were presented to each eye with different inter-stimulus intervals (ISIs) ranging from 0 to 218 ms. When pattern reversals were presented asynchronously to each eye, P-1 activity evoked by each reversal was significantly suppressed compared to the activation evoked by synchronous reversals. Furthermore, when there was time delay between pattern reversals to each eye, theta (4-10 Hz) band power was also significantly decreased, whereas beta (10-30 Hz) band power was relatively preserved. Our results suggest that neural activity evoked by sustained but not yet reversed checkerboard from one eye might inhibit upcoming neural response evoked by reversed checkerboard from the other eye. Decreased P-1 activity might reflect such inhibitory interaction between two eyes. Also, decreased theta and preserved beta band power might reflect engagement of different neural circuit for binocular / monocular vision.

Introduction

The visual evoked potential (VEP) has been used to investigate the relationship between the monocular VEP and the binocular VEP (Shawkat, 1997). In particular, pattern reversal visual evoked potentials (VEPs) have proved to be a useful objective technique for the evaluation of visual function (Tobimatsu, 1996). The amplitude of the P-100 wave is the measure most often used when binocular function is evaluated with the pattern-reversal visual evoked potential (McKerral, 1996).

Previous reports on the electrophysiological evaluation of binocular function in human subject identified at least three forms of binocular interaction: facilitation (or summation), suppression and averaging. For example, a number of studies have compared pattern VEPs to binocular and monocular stimulation and most have found that in normal subjects, the binocular pattern VEP is of greater amplitude than either of the monocular

responses (Wanger and Nelsson, 1978).

Interocular integration is important for intact vision. In animal research, Roelfsema et al. (1994) suggested that disturbed temporal co-ordination of cortical responses, such as reduced synchrony, may be one of the neuronal correlates of the amblyopic deficit. They found that in area 17 of strabismic cats, the synchronization between single cells subserving the amblyopic eye and normal eye was severely impaired. However, how asynchronous visual input affects neuronal response of human visual system is not yet investigated systematically. Thus, in this study, using EEG, we examine how interocular interactions are modulated when checkerboard pattern reversals are presented asynchronously to each eye.

Materials and Methods

Participants

Fourteen healthy subjects without any known history of neurological disorders participated in the experiment after giving written informed consent according to the Declaration of Helsinki. All participants had normal or

corrected-to-normal vision.

Stimuli, design and procedure

For visual stimulation, alternating black and white checkerboard were presented on two CRT monitor screen at a frame rate of 85 Hz and a resolution of 1024 X 768 pixels. Monocular presentation of the two checkerboard was assured by placing a mirror in front of each eye. There were three different stimulus presentation conditions; ‘synchronous binocular’, ‘blank monocular’, and ‘asynchronous binocular’ condition (Fig. 1). During ‘synchronous binocular’ condition, two checkerboard pattern reversal was presented to each eye synchronously. During ‘blank monocular’ condition, checkerboard pattern reversal was presented to one of two eyes, whereas blank screen was presented to the other one. During ‘asynchronous binocular’ condition, checkerboard pattern reversal was presented to each eye asynchronously. SOAs (stimulus onset asynchrony) between to reversal were four steps; 35 ms (3 frames), 58 ms (5 frames), 117 ms (10 frames), and 234 ms (20 frames).

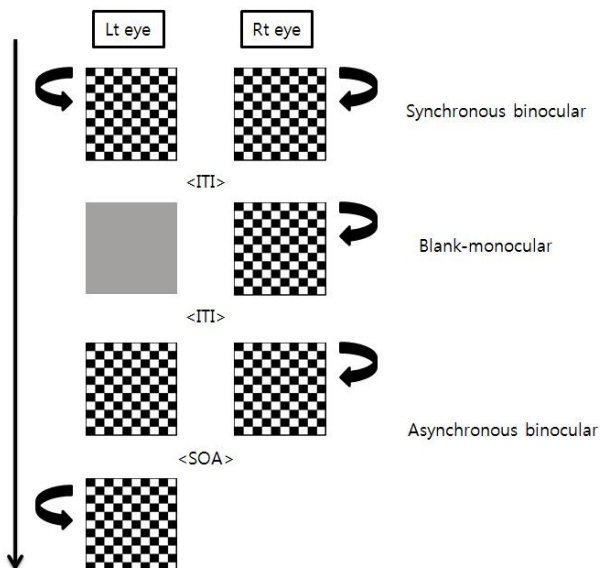


Figure. 1

EEG recording

EEG was performed using 5 Ag-AgCl electrodes according to the international 10-20 system (BRAINTRONICS, Netherlands). All the signals from each electrode were referenced to electrode Fz. Vertical and horizontal EOGs were also recorded to monitor eye movements. Impedance of each electrode was kept below 10 K Ω , and sampling rate was 256 Hz.

Data processing and analysis

All the data analyses were performed using the EEGLAB and Fieldtrip toolboxes. Preprocessing was conducted using the EEGLAB toolbox (Delorme and Makeig, 2004). For ERP and time-frequency analysis, we used the Fieldtrip toolbox. EEG epochs were obtained from 100 ms before to 400 ms after the first stimulus onset.

For ERP analysis, the raw EEG signals were band-pass filtered at 0.1~30 Hz with a finite impulse response (FIR) filter. Trials that contained voltage fluctuations exceeding $\pm 100 \mu\text{V}$ were rejected. The baseline for ERP analysis was designated from -100 to 0 ms.

For time-frequency analysis, a FIR band-pass filter (1~30Hz) was applied. For the theta and beta bands, time-frequency representations (TFRs) of the spectral power were computed using a multi-tapered approach (Jokisch and Jensen, 2007; Osipova et al., 2006; Percival and Walden, 1993). For these lower frequency bands (4~30 Hz), we applied an adaptive time window of three cycles for each frequency ($\Delta T = 3/f$) and an adaptive smoothing of $\Delta f = 1/\Delta T$ (Osipova et al., 2006). The mean power value of the prestimulus (-150 ~ -50 ms) was considered to be the baseline and divided from the poststimulus power value. This correction was done for the individual frequencies (Jokisch and Jensen, 2007). This time window was chosen to avoid temporal smearing of the poststimulus activity into the baseline

Results

ERP: P-100 amplitude

The changes in VEP waveform which occurred as a function of experimental conditions were quantified by measuring VEP amplitude, in reference to a baseline (the average voltage during the 100 ms before stimulation). As shown in Fig. 2A, P-1 amplitude peak was not different between ‘synchronous binocular’ condition and ‘blank monocular’ condition. In ‘asynchronous binocular’ conditions, two separate P-1 peaks are seen, which are evoked by successive pattern reversals to each eye with different SOAs (Fig.2 B-E).

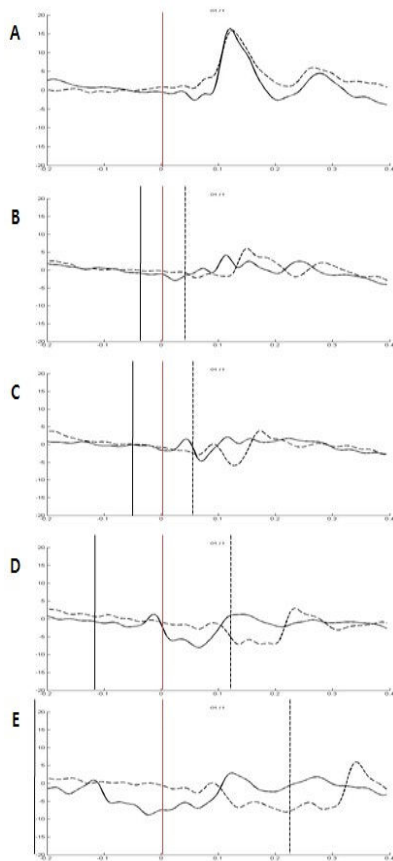


Figure. 2

The red vertical lines in Fig. 2 B-E indicate the timing when a pattern reversal is presented to the left eye. The black vertical solid and dashed lines indicate the timing when the pattern reversal is presented to the right eye.

For instance, in Fig. 2B, for solid waveforms, the right eye is stimulated first (-35 ms), and then the left eye is stimulated (0 ms). On the contrary for dashed waveforms, the left eye is stimulated first (0 ms), and then the right eye is stimulated (+35 ms).

Thin solid lines in Fig. 3A show VEP waveforms of ‘asynchronous binocular’ conditions that right eye is stimulated with various SOAs by pattern reversal first, and then left eye is stimulated (at 0 ms). Thick solid and dashed lines in Fig. 3A show VEP waveforms of ‘synchronous binocular’ condition and ‘blank monocular’ condition, respectively. Thin solid lines in Fig. 3B show VEP waveforms of ‘asynchronous binocular’ conditions that left eye is stimulated (at 0 ms) first, and then right eye is stimulated. Thick solid and dashed lines in Fig. 3B show VEP waveforms of ‘synchronous binocular’ condition and ‘blank monocular’ condition, respectively. These wave forms of VEP show that in ‘asynchronous binocular’ condition, P-1 amplitude is suppressed compared to ‘synchronous binocular’ and ‘blank monocular’ conditions.

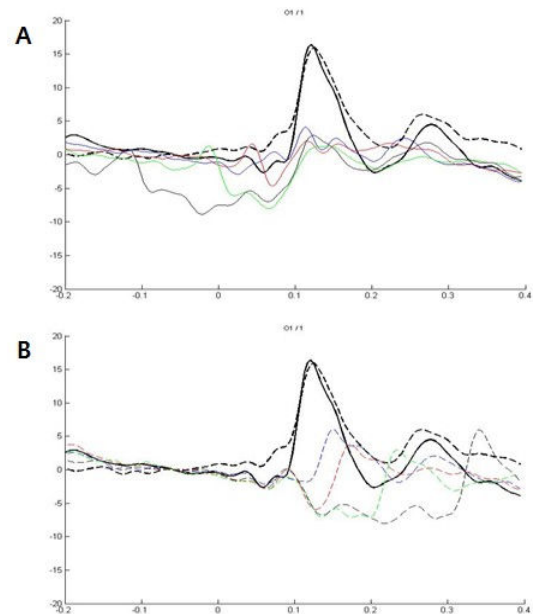


Figure.3

Time-frequency analysis

Time-frequency representations of power (TFRs) were calculated for the ‘synchronous binocular’, ‘blank monocular’, and ‘asynchronous binocular’ conditions (Fig. 4). As shown in Fig. 4A, in ‘synchronous binocular’ condition, increased 7 Hz centered activity were observed from 100 ms to 200 ms after stimulus onset. Also, enhanced oscillatory activity were found in beta band (10 ~ 30 Hz) around 100 ms after the stimulus onset. In ‘blank monocular’ condition, 7 Hz centered oscillatory activity and beta activity were also observed, however beta activity was reduced compared to ‘synchronous binocular’ condition. In ‘asynchronous binocular’ condition, enhanced beta activities which are time locked to the first stimulus onset were observed. However, enhanced 7 Hz centered oscillations were not found in ‘asynchronous binocular’ conditions.

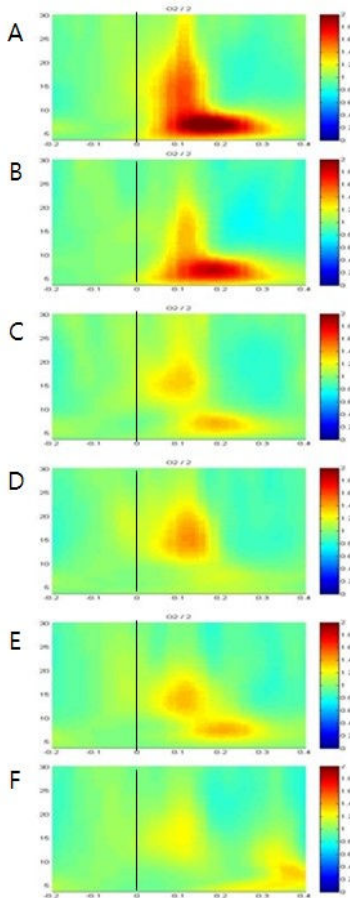


Figure.4

Discussion

When pattern reversals were presented asynchronously to each eye, P-1 activity evoked by each reversal was significantly suppressed compared to the activation evoked by synchronous reversals. These results suggest that neural activity evoked by sustained but not yet reversed checkerboard from one eye might inhibit upcoming neural response evoked by reversed checkerboard from the other eye. For example, in animal research, Walker et al. (1998) observed that when optimal grating was presented to one eye and the orthogonal mask was viewed by the other eye, response of a cortical cell activated by optimal grating could be suppressed (binocular cross orientation suppression). Similarly, Harter et al. found that orientation-specific interocular suppression effect in human visual system: the more similar the orientation of the flashed grid to one eye and the continuously presented grid to the other eye, the smaller the amplitude of the VEP components (Harter et al., 1980).

Furthermore, when there was time delay between pattern reversals to each eye, theta (4-10 Hz) band power was also significantly decreased, whereas beta (10-30 Hz) band power was relatively preserved. These results suggest that decreased alpha and preserved beta band power might reflect engagement of different neural circuit for binocular / monocular vision. It has been suggested that cortical interactions may occur on different scales, and that the complexity of interaction influences the temporal dynamics evolving within the integrating network (VonStein et al., 2000). Relatively slow oscillatory activity in theta band might reflect activation of relatively long ‘neuronal loop’ associated with synchronous binocular vision. On the contrary, beta activity might reflect activation of relatively short ‘neuronal loop’, may be required for both of monocular and binocular vision.

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