

Cortical Neural Activities Associated with Binocular Rivalry: An EEG-fMRI Integrative Study*

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Abstract—Binocular rivalry occurs over time when each eye is simultaneously presented with different visual stimuli. We have addressed which brain regions are and the mechanisms involved in binocular rivalry using EEG and fMRI measurements of cortical activities during observations of competitive (rivalry) and cooperative (fusion) drifting vertical gratings. By applying an EEG-fMRI integrative method, we analyzed the time courses of multiple cortical sources of event-related potentials obtained under rivalry or fusion conditions. We detected significant cortical activities at bilateral MT+/V5 and the right prefrontal eye field in the rivalry condition; however, this may not reflect intrinsic alternation in binocular rivalry. Our findings suggest that novel integrative methods are necessary to investigate the distributed cortical network associated with binocular rivalry, through analysis of multiple cortical sources of event-related desynchronization and/or synchronization in certain frequency bands.

I. INTRODUCTION

When the left and right eyes are shown different images simultaneously, perception changes depending on the degree of dissimilarity between the images; this is known as binocular rivalry when it results in the dissimilar images being perceived alternately (Fig. 1; [1]). Binocular rivalry is a type of multi-stable perceptions, i.e., when presented with an unchanging visual stimulus, the observer experiences two or three different perceptions alternately and repetitively. This provides a very easy-to-understand objective phenomenon for empirical investigation for determining the type of mechanism in the brain that accounts for what is seen or consciously perceived. Hence, binocular rivalry holds a promise as a model for understanding the temporal dynamics of conscious perception. Because conscious perception in binocular rivalry changes over time even though the stimuli remain constant, this phenomenon offers a means for distinguishing neural activity related to the physical features of the stimuli from neural activity directly related to conscious experience. However, despite extensive studies on binocular rivalry, the brain regions involved in binocular rivalry have not been mapped precisely [2].

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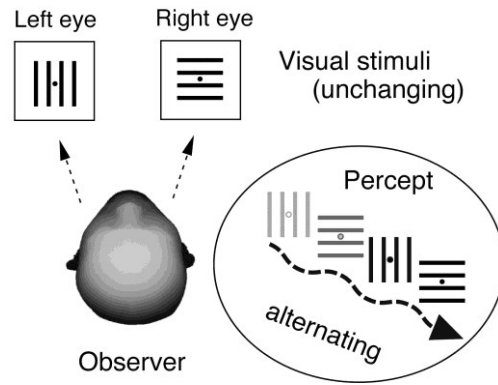


Figure 1. The phenomenon of binocular rivalry

One of the controversial issues regarding binocular rivalry is the nature of the competition [3]. Although binocular rivalry was originally considered to reflect competition in either the lateral geniculate nucleus or primary visual area (V1) [4], several recent studies indicate that perceptual competition may involve higher visual areas [5, 6]. The possible involvement of regions outside the visual cortex is suggested by several EEG and MEG studies [7-9]. In an fMRI study, Tong et al. [10] found that competitive neural interactions underlying binocular rivalry may be resolved by the time the visual information reaches the fusiform face area and the parahippocampal place area in the extrastriate cortex. Lumer et al. [11] reported that the frontoparietal cortex is specifically associated with perceptual alternation in binocular rivalry. Alternatively, V1 during rivalry may also be involved [2, 12, 13].

Here, we have used an EEG-fMRI integrative approach to address whether the temporal dynamics of binocular rivalry are governed by the integration of feedforward and feedback information from a distributed network of multiple cortical areas.

II. METHODS

A. Subjects

Nine right-handed healthy males (mean age 22.3 yrs; range, 21-26 yrs) with normal or corrected-to-normal visual acuity participated in EEG and fMRI experiments. All subjects gave written informed consent after the purpose and procedure of the experiments had been explained to them. The present study was approved by the local institutional ethics committee.

B. Stimuli

The visual stimuli used in this study (Fig. 2a) were square-shaped sinusoidal six gratings (3.0 degree of visual

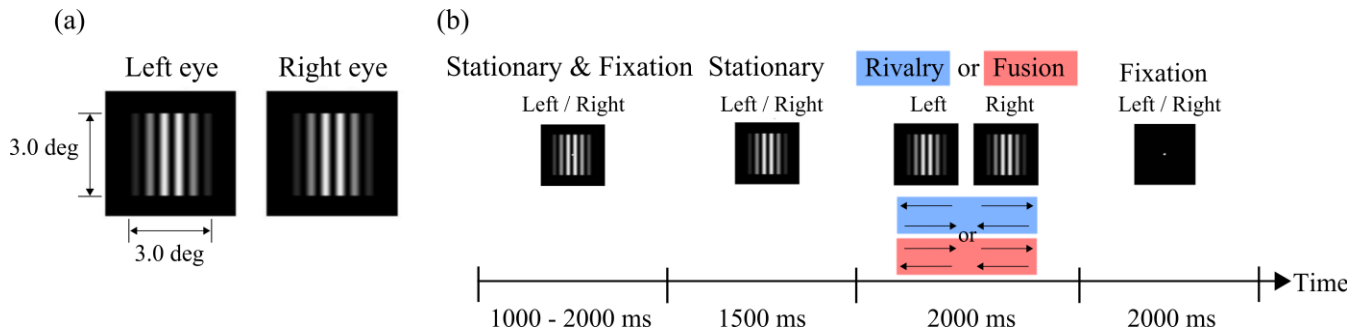


Figure 2. (a) Drifting visual stimuli presented to left and right eyes independently. (b) Experimental paradigm in EEG measurements.

angle on each side), with the same in spatial frequency (2 cycle/deg), maximum luminance (30 cd/m^2), minimum luminance (0.1 cd/m^2), and drifting velocity (3.2 deg/s). In EEG experiments, stimuli were viewed through a mirror stereoscope placed between the eyes and the display to allow the separation of the stimuli. Prior to the experiment, two presented stimuli were required to be in the same spatial position. In the rivalry experiments, the left stimulus was set to drift to the left, and the right one drifted to the right. As a control, we performed a fusion experiment consisting of stimuli presented to the left and right eyes drifting in the same directions, but alternating in direction at particular intervals.

C. EEG and eye movement measurements

The EEG experiments were conducted according to the paradigm shown in Fig. 2b. Visual stimuli were presented in the following order: stationary grating with a fixation point in the center, stationary grating only, rivalry or fusion drifting gratings, and fixation point only all with dark background. These were presented in order for 1–2 s, 1.5 s, 2 s and 2 s, respectively.

EEGs were recorded at 256 Hz from 128 locations (extended 10–20 system) using a 128-channel digital high-density EEG system (Active Two System; BioSemi, Inc.). The left mastoid electrode was used as a reference.

After off-line filtering at 0.5–55 Hz band, each trial was averaged to obtain ERPs of -400 – 0 ms as base line. Zero milliseconds was defined as the onset of drifting of the gratings. Data was smoothed using a low-pass filter (40 Hz).

The trials were selected based on the absence of artifacts as blinks. The trial number of each subject was equalized to the lowest. This process was applied to the rivalry and fusion conditions. With the fusion stimuli, the direction of eye movement following the drift and alternated immediately.

Optokinetic nystagmus (OKN) movements of the right eye were acquired at 1,000 Hz using an eye tracker (T. K. K. 2930a; Takei Scientific Instruments Corporation, Japan) based on the limbus tracking method. Slow phases occur in tracing a moving matter, whereas rapid phases occur in pulling back the position of eyes at the edge. The time of perceptual alternation were defined change in the slope of the slow movement phases from positive to negative or negative to positive. These switching times were used as triggers for perceptual alternations in the EEG analysis.

D. fMRI experiments

A Vantage (TOSHIBA) operated at 1.5 T was used with the standard fMRI procedure (gradient echo EPI; $TR = 3 \text{ s}$, $TE = 40 \text{ ms}$, $FA = 90^\circ$, $FOV = 22 \text{ cm}$, 25 5-mm-thick slices, spacing = 1 mm, image matrix = 64×64) obtaining 155 functional images per slice per session. Experimental paradigms were designed to compare brain activities between four conditions (blocks) of binocular rivalry, fusion, pause (stationary) and one-direction drifting. Each block consisted of stimuli presented for 21 s. One experiment consisted of 5×4 blocks.

Visual stimuli with red and green gratings (Fig.2) were presented by superposition of the two gratings; when viewed through red and green filter glasses, only a single grating was visible to each eye.

Data was analyzed using Statistical Parametric Mapping software (SPM8). The imaging time series were realigned, spatially normalized to the stereoscopic space of Montreal Neurological Institute (MNI) template, and smoothed with a Gaussian kernel of 6-mm full width half maximum. At the end of each experimental session, T1-weighted anatomical images were acquired for coregistration with the functional images.

E EEG–fMRI integrative analyses

To understand the dynamic multiple cortical neural activities associated with higher brain functions including binocular rivalry, we developed multimodal integrative techniques, in particular MEG–fMRI [14, 15].

In this paper, we describe the results obtained by an EEG–fMRI integrative source analysis method based on a parametric empirical Bayesian technique [16, 17]. To estimate multiple cortical activities from EEG data, cortical areas detected by fMRI were used as spatial constrains.

III. RESULTS AND DISCUSSION

Figure 3a shows grand mean event-related potentials (ERPs) obtained from all 9 subjects by averaging 990 epochs for rivalry and fusion conditions. ERPs at 128 electrode locations were superimposed in each figure. Topographical brain maps at peaks of prominent ERP components are also shown.

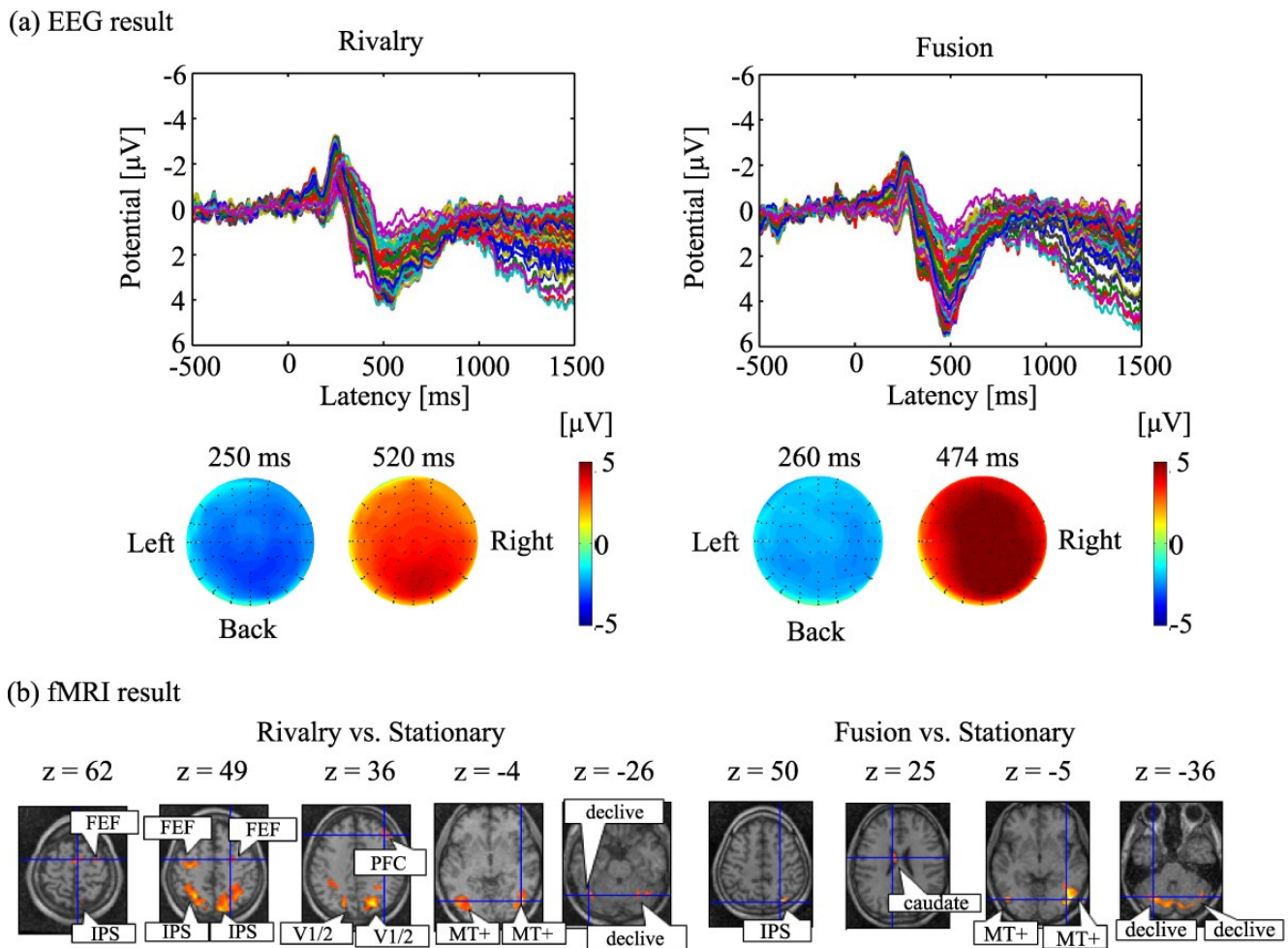


Figure 3. (a) Grand mean ERPs in rivalry and fusion conditions (upper low). Topographical maps on the head at two prominent peaks of ERP components (lower low). (b) Differential activations observed between rivalry (left) and fusion (right) conditions. Loci with significant increased BOLD signals relative to the stationary condition are shown (uncorrected, $p < 0.001$ for rivalry; $p < 0.01$ for fusion).

FMRI images from all 9 subjects were analyzed as a group to identify the brain areas where increases in BOLD signals were common. Under rivalry vs. stationary stimulation, BOLD signals were significantly increased along the dorsal visual pathway, including bilateral V1, V2 and MT+/V5 in the occipital area, bilateral frontal eye field (FEF), right prefrontal cortex (PFC), bilateral intraparietal sulcus (IPS) in the parietal area. In contrast, fusion vs. stationary conditions significantly increases BOLD signals in the bilateral MT+/V5 and the right IPS (Fig. 3b).

Figure 4 shows the time courses of ERP source activations observed in rivalry and fusion conditions at loci where source activations were significantly larger than those in pre-trigger period of -100 -0 ms. Source activations were larger (uncorrected, $p < 0.1$) at bilateral MT+/V5 of 100-600 ms, the right frontal FEF from 200-500 ms. Because these areas have important roles on eye movements, the differential brain activations observed in our EEG-fMRI integrative

study may not reflect cortical activities associated with binocular rivalry.

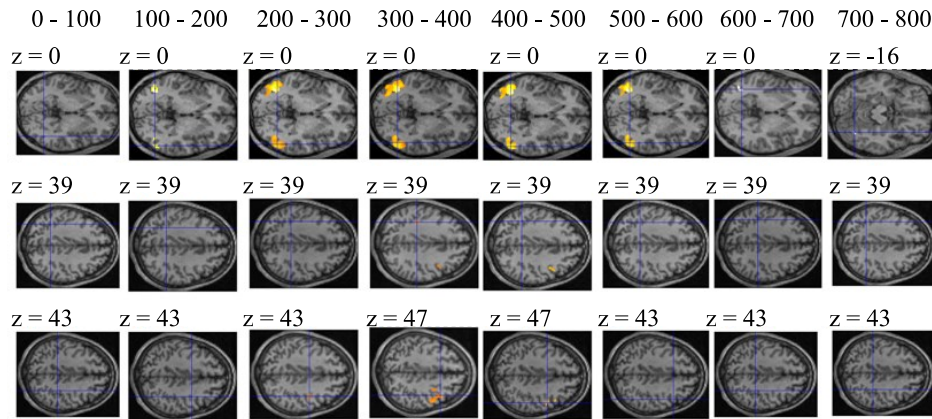
Although we have used an EEG-fMRI integrative method to analyze temporal activities of ERP sources in the brain, this was not sufficient to determine if binocular rivalry was associated a distributed network of multiple extrastriate, parietal, and prefrontal cortical activities.

Because the cortical neural activities associated with intrinsic perceptual alternation in binocular rivalry may not be highly synchronized, integrative methods need to be developed to simultaneously examine event-related desynchronizations and/or synchronizations in certain frequency bands in multiple cortical areas.

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(a) Rivalry



(b) Fusion

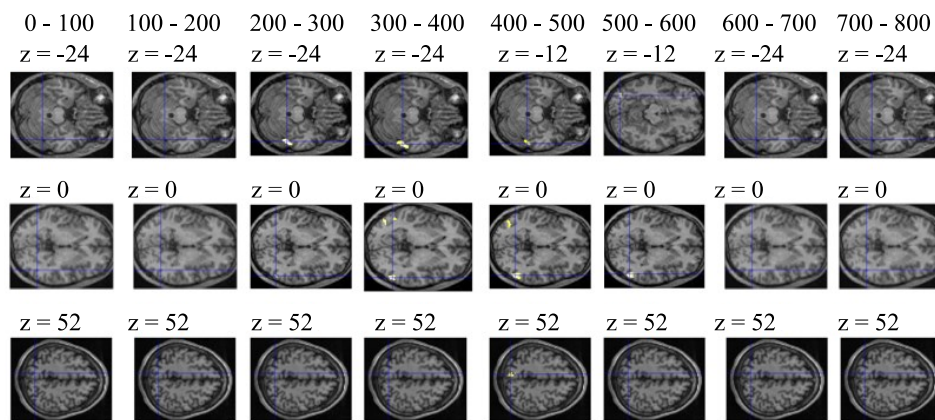


Figure 4. Time courses of ERP source activations observed in (a) rivalry and (b) fusion conditions. Loci where source activations was larger (uncorrected, $p < 0.1$) than the pre-trigger period (-100–0 ms) are shown.

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