Binocular Rivalry: A Key Phenomenon to understand Temporal Dynamics of Conscious Perception

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Abstract- When dissimilar images are presented to corresponding retinal areas of each eye, fusion fails and brief intermittent periods of exclusive visibility of only one of the images is experienced. This is known as binocular rivalry. To address how and what regions of the brain is involved in binocular rivalry, we used functional magnetic resonance imaging (fMRI) and compared brain activities during binocular rivalry, stereopsis and fusion. Significant increases in blood oxygenation level dependent (BOLD) signals were observed along the dorsal visual pathway and V4 in the occipital area, in the parietal area adjacent to the intraparietal sulcus and in the prefrontal area both in binocular rivalry and stereopsis conditions compared with those in a fusion condition. On the other hand, no significant difference was found between BOLD signals in binocular rivalry and stereopsis conditions. Furthermore, right hemisphere dominance was observed both in binocular rivalry and stereopsis conditions. These findings suggest that a distributed network of brain activities in the extrastriate, parietal and prefrontal cortical areas dominantly in the right hemisphere is commonly associated with both binocular rivalry and stereopsis.

1. Introduction

The processes within the brain associated with visual awareness have become an important research topic in the field of cognitive neuroscience. Interest has recently been shown in visual awareness as it is thought that it may be a clue for revealing aspects of consciousness [1, 2]. The elucidation of brain mechanisms of visual awareness is expected not only to contribute to the advancement of cognitive neuroscience, but also to provide valuable knowledge for a variety of fields, such as biomedical engineering and information science.

When the left and right eyes are separately shown dissimilar images at the same time, perception changes depending on the dissimilarity of the two images. The phenomenon of two dissimilar images being perceived alternately is known as binocular rivalry as illustrated in Fig. 1, whereas the phenomenon of two images with disparity being fused and their 3-D structures being perceived is known as stereopsis.

Binocular rivalry is thought to be a promising phenomenon for understanding temporal dynamics of conscious perception. Since conscious perception in binocular rivalry changes over time while the stimuli remain constant, this phenomenon offers a means for distinguishing neural activity related to physical features of the stimuli and neural activity directly related to conscious experience.

However, despite extensive studies on binocular rivalry, it is still not clear precisely what region of the brain is involved in binocular rivalry [3]. In contrast, it is well known that the dorsal (magnocellular) visual pathway is involved in stereopsis [4, 5]. Results of psychophysical experiments [6, 7] have shown that stereopsis and rivalry can coexist in the same location, suggesting parallel processing of the two phenomena.

In this paper, we first describe the temporal characteristics of binocular rivalry. Then, we show an fMRI evidence for common neural substrates of binocular rivalry and stereopsis.



Fig. 1. The phenomenon of binocular rivalry. When different two visual stimuli are presented to the right and left eyes independently, the two stimuli are perceived alternately.

2. Temporal Characteristics of Binocular Rivalry

Binocular rivalry is a kind of "multistable perceptions". In multistable perceptions an observer who is presented with an unchanging visual stimulus experiences two or three different percepts alternately and repetitively. This provides a very easy-to-understand objective phenomenon for an empirical investigation to try to determine the kind of mechanism in the brain accounts for what is seen or noticed, i.e., conscious perception.

The total observation duration T of the binocular rivalry is

$$T = \sum_{i=1}^{n_L} d_{Li} + \sum_{i=1}^{n_R} d_{Ri}$$
(1)

where n_L and n_R are numbers of dominance durations, and d_{Li} and d_{Ri} are the durations of the binocular rivalry for left and right eyes, respectively.

Temporal characteristics of multiple perceptions including binocular rivalry have been the subject of experimental studies. In the studies, gamma distributions defined by the following equation are commonly fitted to the data and are found to fit reasonably well [8].

$$f(t) = \frac{\lambda^{\gamma} t^{\gamma-1} e^{-\lambda t}}{\Gamma(\gamma)}$$
(2)

where $\Gamma(\gamma)$ is the gamma function. The mean μ and variance σ^2 of dominance durations obtained by experiments are used to estimate the parameters as:

$$\gamma = \mu^2 / \sigma^2$$
 and $\lambda = \mu / \sigma^2$. (3)

Nevertheless, it must be emphasized that the selection of a gamma distribution is empirical. Although a number of models have been proposed to explain why such a theoretical significance is obtained, the reasons are still controversial.

3. Neural Substrates of Binocular Rivalry

One of controversial issues regarding binocular rivalry is what is competing during this phenomenon [3, 9]. Binocular rivalry was originally thought to reflect competition between inputs from each eye, either in the lateral geniculate nucleus or primary visual area (V1) [10]. Several recent studies, however, have indicated that perceptual competition in binocular rivalry might occur between two stimulus representations, suggesting the involvement of higher visual areas [11-13].

Possible involvement of regions outside the visual cortex has been suggested by results of several EEG and MEG studies [14-16]. In an fMRI study, Tong et al. [17] found that competitive neural interactions underlying binocular rivalry might be resolved by the time visual information reaches the fusiform face area and the parahippocampal place area in the extrastriate cortex. Lumer et al. [18] reported that the frontoparietal cortex is specifically associated with perceptual alternation in binocular rivalry. On the other hand, results of several studies indicated the involvement of V1 during rivalry [9, 19, 20].

In this section, we show brain activities during binocular rivalry, stereopsis and fusion measured by using fMRI. By comparing brain activities during these three perceptual conditions under the same experimental conditions, we are able to determine whether cooperative (stereopsis) processing and competitive (rivalry) processing of dissimilar images are based on the same neural substrates.

3.1. Methods

3.1.1. Subjects

Twelve right-handed healthy subjects (21-32 years old) with normal and corrected-to-normal visual acuity participated in the 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.

3.1.2. Experimental Procedures and Stimuli

Experimental paradigms were designed to compare brain activities between two of the three conditions of binocular rivalry, stereopsis and fusion. The visual stimuli presented in each condition are shown in Fig. 2. We performed three experiments using diferrent combinations of two of these three different conditions. The time courses of stimulus presentation in all experiments carried out under rivalry and fusion conditions were the same. Each block consisted of presentations of a fixation point for 5 s, a cue (circle or cross) fro 5 s, a fixation point for 5 s and a stimulus for 30 s. Appearance of stimulus for 2s and disappearance for 1 s were repeated 10 times during a 30-s period of stimulus presentation in order to keep the subject's attention on the stimuli. The pre-presentation of a cue (circle or cross) enabled the subject to prepare for the subsequent presentation of a stimulus. One experiment consisted of 10 blocks.



Fig. 2. Visual stimuli used in the experiments for binocular rivalry (A), for stereopsis (B), and for fusion (C).

In the rivalry block, red vertical and green horizontal circular gratings, each subtending 1.3° of the visual angle, were presented by superposition of the two gratings as shown on the right in Fig. 2A. When viewed through red and green filter glasses, only the vertical or horizontal gratings could be seen through one eye. In the stereopsis and fusion blocks, identical vertical gratings with and without disparity (Fig. 2B, C) were presented. In order to provide a base surface for depth perception in stereopsis, a square frame was placed around each circular grating. Gratings used in other conditions also had the same square frame to minimize the physical difference in stimuli. Subjects were requested to gaze at a small fixation point presented in the center of the stimuli. Subjects were requested to gaze at a small fixation point presented in the center of the stimuli. Stimuli were projected onto a screen by means of an LCD projector.

Blood oxygenation level dependent (BOLD) functional images under the two different conditions were compared in each experiment.

3.1.3. Acquisition of MRI and Data Analysis

A Signa Horizon (GE) operated at 1.5 T was used with the standard fMRI procedure (gradient echo EPI; TR = 3 s, TE = 40 ms, FA = 90°, FOV = 22 cm, 25 5-mm-thick slices, spacing = 1 mm, image matrix = 64 x 64). A total of 155 functional images for each slice were obtained during one session.

Analysis was carried out using Statistical Parametric Mapping software (SPM99). The imaging time series was 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.

3.2. Results and Discusion

Functional MR images from 12 subjects were analyzed as a group to identify brain areas in which increases in BOLD signals commonly occurred. No significant difference was found between BOLD signals in the rivalry and stereopsis blocks, suggesting that brain activities in the two blocks are the same. On the other hand, significant increases in BOLD signals were found along the dorsal visual pathway (Brodmann's Area (BA) 18 and 19) and visual area 4 (V4) in the occipital area, in the parietal area (BA7) adjacent to the intraparietal sulcus and in the prefrontal area (BA44, 9, 8, 46, 10) in the rivalry block compared with those in the fusion block as shown in Fig.3A. In this figure, differential activations during rivalry and fusion conditions are plotted in the 3-D space of the MNI template of SPM99. Four representative areas showing significant increases (p < p0.001, uncorrected) in BOLD signals were also superposed on coronal anatomical images.

Significant differential activations between stereopsis and fusion (Fig.3B) were observed along the dorsal visual pathway (BA 18 and 19) and V4 in the occipital area, in the parietal area (BA7 and 40), including the intraparietal sulcus (IPS), in the prefrontal area (BA44, 9, 8, 46, 10) and in the anterior cingulate gylus (BA32). Right hemisphere dominance was also observed in those areas in the rivalry and stereopsis blocks.

The results of the present study indicated that brain activities in the extrastriate, parietal and prefrontal areas are commonly associated with rivalry and stereopsis. Since the parietal and prefrontal areas are known as association corticies, which integrate sensory information to coordinate a variety of cognitive behaviors, it is possible that the integration process of visual information is involved not only in cooperative processing of incongruent visual stimuli to produce depth but also in perceptual competition in binocular rivalry.

We could not detect any significant activation in V1. This might be because only a small percentage of neurons in V1 might be associated with rivalry as suggested by results of cell recording studies [21, 22]. Therefore, V1 might not be activated sufficiently detected by block design paradigms performed in the present study.



Fig. 3. Differential activations observed in the experiments in binocular rivalry (A) and stereopsis (B) are plotted in the 3-D space of the MNI template. Shown are loci where the BOLD signals were significantly larger (p < 0.001, uncorrected) than those in the control conditions in the group analysis.

4. Conclusion

Differential brain activations found in the three different perceptual conditions of binocular rivalry, stereopsis and fusion suggest that brain activity and activated loci in binocular rivalry are similar to those in stereopsis. It therefore seems reasonable to conclude that common neural substrates such as a distributed network of multiple extrastriate, parietal and prefrontal cortical areas found in this study are associated with binocular rivalry and stereopsis.

Recently, it has suggested that feedback from higher visual areas including IPS to V1 is necessary for visual awareness by a couple of TMS studies [23]. Taken together, temporal dynamics of binocular rivalry, i.e., alternation of dominant and suppressed percepts, may be governed by an integration process of both feedforward information from the right and left retinas and feedback information from a right hemisphere dominant distributed network of multiple cortical areas. It is plausible to consider that the integration process is carried out mainly at V1. It will thus be a challenge for the future studies to clarify the integration process itself.

Acknowledgments

The author would like to thank Mr. H. Futakawa, Ms. S. Tokita, Dr. T. Katsura and Dr. J. Jung for their cooperation during fMRI experiments on multistable perceptions.

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