

学位論文

**A study on brain response of binocular rivalry
using magnetoencephalography**

（脳磁図を用いた視野闘争誘発反応の研究）

東京大学大学院新領域創成科学研究科

複雑理工学専攻

篠崎 隆志

Abstract

Binocular rivalry is a spontaneous perceptual alternation when different images are independently presented to the two eyes. We studied the relationship between binocular rivalry and neural activity with psychophysical and magnetoencephalogram (MEG) measurements.

Chapter 1 introduced an overview of binocular rivalry and its previous studies by psychophysical and non-invasive measurements. We also discussed the objective of the experiments conducted with regard to previous studies. Recently, the neural mechanism of binocular rivalry were clarified gradually by non-invasive measurements. Many previous studies focused on steady state responses of binocular rivalry, but transient responses, which is caused by the process of perceptual transition in binocular rivalry, have not been clarified yet. This study focused on the transient responses of binocular rivalry, and performed psychophysical and MEG measurements.

Chapter 2 presents the first experiment, performed psychophysical measurements to investigate the temporal property of transient responses of binocular rivalry. In this study, we mainly used a binocular rivalry of motion direction as a visual stimulus. A binocular rivalry stimulus of motion direction induce two perceptual interpretations. One is “pattern motion” that forms a superimposed pattern moving with a single direction, equivalent to the vector sum of the two motion directions. The other is “component motion” that forms two independent motion directions followed by monocular dominance in which one eye’s motion is perceived alone. This perceptual process involves not only interocular rivalry but also motion-type rivalry. We studied this double rivalry process during binocular rivalry of motion direction in terms of the temporal order of each rivalry using psychophysical methods. We measured reaction times (RTs) using a visual stimulus for which the probability of each perceptual interpretation was approximately equal. RTs to perceive a consistent motion direction in pattern and component motion conditions were 400 ms and 750 ms slower, respectively, than that in the

condition when identical motion stimuli were presented to the two eyes. This results suggested that the transient response of binocular rivalry could be measured by comparison of brain responses between pattern and component motions using pattern onset stimuli.

Chapter 3 presents the second experiment, performed to MEG measurements to investigate transient brain responses of binocular rivalry. The transient process of perceptual alternation in binocular rivalry could be said to be most primitive decision process, and understanding those brain activity would be very important to neuroscience. In the chapter, based on the results of Chapter 2, we used a onset stimulus of drifting grating patterns which cause binocular rivalry. Visual evoked fields (VEFs) elicited by onsets of rivalry stimuli were recorded using a MEG system. Perceptions for the stimuli were further recorded at the same time. We classified trials to pattern and component motion conditions, and averaged across each condition. However, at about 200 ms latency after stimulus onset, there was no significant difference in the peak intensity and latency, which were generally used to analysis EEG and MEG responses. On the other hand, although there was no distinct peak of MEG response, the difference of responses between two perceptual conditions was observed at the long latency after 400 ms. Because these responses had slow temporal property, we calculated time averages of root mean square (RMS) values for every 100 ms in each condition, and compared between two perceptual conditions. As a result, the time average of RMS values of component motion condition was significantly larger than those of pattern motion condition after 400 ms stimulus onset. These results suggested that the perceptual transition in binocular rivalry increased the late MEG component.

Chapter 4 presents the third experiment, performed to further MEG measurements using various types of rivalry stimuli; orientations, colors and motion directions. Some functional magnetic resonance imaging (fMRI) studies reported modulations of BOLD signal on the cortices where the corresponding visual attribute were processed in binocular rivalry. Electrophysiological measurements also reported similar results in which firing rate in middle temporal (MT) and inferior temporal (IT) lobes was modulated by the perceptual condition in binocular rivalry. However, both results were related to steady-state responses in binocular rivalry, and transient responses about various types of rivalry stimuli have not been clarified. In this chapter, we acquired source locations of brain responses in binocular rivalry for various types of stimuli using dipole estimation, and compared them. As a result, sources of orientation, color and motion direction were estimated at parietal, IT and MT lobes, respectively. Those areas were corresponded

to the cortices where the visual information was processed in non-rivalry condition. Thus, it was suggested that transient responses of binocular rivalry activated cerebral cortices where the corresponding visual information was processed.

Chapter 5 presents the last experiment, investigated to the brain responses of color motion using transient response of binocular rivalry as a tool. Although most of previous studies about motion perception have reported that motion perception largely depended on the luminance information, we could also perceived motion only by other visual information. Previous studies of electrophysiological methods reported that luminance and color information were separated from the level of photo receptor cell in retina, and processed separately in the lower level visual cortex. However, because both luminance and color motion could be perceived similarly, these motions should be integrated somewhere in the brain. Although, non-invasive measurements are required to clarify the neural mechanism of motion integration between different attributes, the response of color motion is weak to measure and analyze with conventional methods. We found that binocular rivalry amplifies brain responses at long latency in Chapter 3. Hence, we investigated the neural mechanism of color motions using rivalry responses of binocular rivalry of color motion direction. We used luminance motion stimuli that were formed drifting sinusoidal grating with white and black color, and color motion stimuli that were formed with isoluminance red and green color and have no luminance information. In preliminary measurements of psychophysics, perceptions of motion types for various angles of motion directions were significantly differed between luminance and color motion. This results suggested that two motions mutually differed in the lower level visual process before integrating motion directions. VEFs elicited by onsets of these stimuli, luminance and color motion, were recorded using a MEG system, and calculated subtractions of the RMS values between rivalry and control conditions. The subtractions showed similar responses at long latency after 300 ms motion onset. Source estimation of responses at the latency also suggested that those responses were identical between luminance and color motion. On the other hand, the subtractions differed at short latency. These results suggested that luminance and color motions were processed in different pathway before the level in which motions presented two eyes were integrated, and in same pathway at higher level.

Chapter 6 gives general discussions. The results of Chapter 2 suggested that the transient response of binocular rivalry could be measured by comparison of brain responses between pattern and component motion using onset stimuli. In combination with results of Chapter 2 and 3, the psychological model of binocu-

lar rivalry processing was specified. The model could not be only applicable for rivalry condition, but also for ordinary condition. The results of MEG measurements in Chapter 3 and 4 demonstrated that the transient response of binocular rivalry amplified the activity in cerebral cortices corresponded to the visual attribute of rivalry stimuli. Because it is established that occurrence of MEG signals needs a synchronous firing for many neuron groups, the process which resolved rivalry information would elicited synchronized firing in the cortical columns, corresponding to the visual attribute. From the experiments of color motion rivalry in Chapter 5, we demonstrated an application of binocular rivalry to other measurements of brain responses with a new viewpoint. As a result, with both psychophysical and MEG measurements, it is suggested that the process of luminance and color motion was separated in low level visual cortices and unified after the integration of motions of the two eyes.

Acknowledgement

I would like to thank my supervisor Prof. Tsunehiro Takeda for supporting me through my master and Ph.D studies. He gave me many constructive comments for a wide range of my studies. I would also like to thank him for installing and running MEG equipment that is very expensive but indispensable for this study. I am also thankful to Prof. Mitsuo Tonoike, Prof. Masato Okada, Prof. Tomoyuki Nishita, and Assoc. Prof. Sunao Murashige for giving me several comments on the manuscript of this thesis. Especially, I would like to thank Prof. Masato Okada for giving me concrete advice and several ideas on my work. I am also thankful to Dr. Yoichi Miyawaki in RIKEN Brain Science Institute. He taught me many techniques necessary for this study, including the basics of psychophysics, and gave me several invaluable comments on the study presented in Chapter 2. I would like to thank, from the bottom of my heart, Assoc. Prof. Takashi Owaki, who took the trouble to keep the MEG equipment running and kindly gave several pieces of advice concerning my study. I would like to express my gratitude to Assoc. Prof. Ayumu Matani for empathically supporting me from my master in several respects. I am indebted to Mr. Hideshige Odajima for teaching me computing skills that helped me in a wide variety of ways. Finally, I would like to thank the members of the Laboratory for Biological Complex Systems for their support, since most of them kindly participated in the experiments.

Takashi Shinozaki
December 16, 2005.

Contents

Acknowledge	i
1 Introduction	1
1.1 Binocular Rivalry	1
1.2 Objectives of the study	3
1.2.1 Two rivalries for motion rivalry stimuli	3
1.2.2 Brain responses of rivalry stimuli	4
1.2.3 Various types of binocular rivalry	5
1.2.4 Application of binocular rivalry	6
1.3 Previous studies on binocular rivalry	7
1.3.1 Early studies	7
1.3.2 Duration of perceptual dominance	7
1.3.3 Spatial property	8
1.3.4 Brain responses of binocular rivalry	9
1.4 Psychophysics	11
1.5 Magnetoencephalography	12
1.5.1 Comparison with other brain imaging methods	12
1.5.2 MEG generation	13
1.5.3 MEG measurement	14
1.5.4 MEG analysis	16
2 Psychophysical property of binocular rivalry	17
2.1 Introduction	18
2.2 Methods	19
2.2.1 Subjects	19
2.2.2 Visual Stimuli	19
2.2.3 Instruments	19
2.2.4 Measurement of proportion of perceptual rivalry	20

2.2.5	Measurement of reaction time	21
2.2.6	Measurement of reaction time of conventional motion . . .	22
2.3	Results	23
2.3.1	Proportion of perceptual rivalry	23
2.3.2	Reaction time of rivalry motion	25
2.3.3	Reaction time of conventional motion	25
2.4	Discussion	28
2.4.1	Proportion of perceptual rivalry	28
2.4.2	Reaction times	30
2.4.3	Psychophysical models	31
2.4.4	Experimental design of MEG measurement	31
3	MEG responses of binocular rivalry	35
3.1	Introduction	35
3.2	Methods	38
3.2.1	Subjects	38
3.2.2	Instruments	38
3.2.3	Visual stimuli	39
3.2.4	MEG recordings	40
3.2.5	Analysis	41
3.3	Results	42
3.3.1	MEG responses for each angle	42
3.3.2	Perceptual rivalry for each angle	42
3.3.3	Relationship between the perceptual rivalry and MEG re- sponses	42
3.3.4	MEG responses for each perceptual condition	45
3.3.5	MEG responses of rivalry stimuli	46
3.4	Discussion	47
3.4.1	Non-monotone change of the perceptual rivalry	47
3.4.2	MEG responses	48
3.4.3	Comparison with previous studies	49
3.4.4	Influence of the other components	50
4	MEG responses of various types of rivalries	51
4.1	Introduction	52
4.2	Methods	53
4.2.1	Subject	53

4.2.2	Instruments	53
4.2.3	Visual stimuli	53
4.2.4	MEG recordings	55
4.2.5	Analysis	56
4.2.6	Dipole estimation	57
4.3	Results	57
4.3.1	MEG response of each stimuli	57
4.3.2	Dipole estimation	58
4.4	Discussion	63
4.4.1	Implications of dipole locations	63
4.4.2	Comparison with previous reports	63
4.4.3	Responses of perceptual switching	67
4.4.4	Wide spread sensor responses	68
5	Color motion and binocular rivalry	69
5.1	Introduction	70
5.2	Methods	72
5.2.1	Subjects	72
5.2.2	Visual stimuli	72
5.2.3	Instruments	72
5.2.4	Measurement of perceptual rivalry	73
5.2.5	MEG recordings	74
5.2.6	Analysis	75
5.3	Results	76
5.3.1	Angle dependency of perceptual rivalry	76
5.3.2	MEG responses	77
5.3.3	Comparison of the latency between luminance and color motions	80
5.3.4	Dipole estimation	82
5.4	Discussion	83
5.4.1	Angle dependency of perceptual rivalry	83
5.4.2	Responses of binocular rivalry	83
5.4.3	Latency of the late response	83
5.4.4	Physiological meaning of ECDs	86
6	Conclusions	89
6.1	Summary of the results	89

6.1.1	Two rivalries of motion rivalry stimuli	89
6.1.2	Brain responses of rivalry stimuli	90
6.1.3	Responses of various types of binocular rivalry	91
6.1.4	Application of binocular rivalry	91
6.2	General discussions	92
6.3	Future studies and engineering applications	93

Chapter 1

Introduction

This chapter presents the backgrounds of the present thesis, in which the relationship between binocular rivalry and neural activity recorded by magnetoencephalography (MEG) was studied. After an overview of binocular rivalry studies, the research questions and a strategy to tackle them are presented. Lastly, an introduction to MEG, which enables us to record human brain activities non-invasively with high temporal resolution, is given.

1.1 Binocular Rivalry

Binocular rivalry is a phenomenon created by presenting similar but slightly different images to each eye simultaneously. When such images were presented to two eyes, one of the images is perceived dominantly, and the other is suppressed. A perception of the dominant image stochastically alternates every few seconds. The spontaneous alternation of the perception is called as binocular rivalry. There are many patterns which cause binocular rivalry; orientation, motion direction, face, house, letter, color and etc. The examples of binocular rivalry stimuli are shown in Figure 1.1. Binocular rivalry is caused by observing these stimuli with such as mirror stereo-scope, freeviewing, liquid crystal shutter, anaglyph glasses, and etc.

Because the occurrence of binocular rivalry required very unnatural environment, it has been claimed that binocular rivalry is just a laboratory artifact [28]. However, there are some other representations of unstabilized perception as same as binocular rivalry, for example, ambiguous figures. Thus, the unstabilized perception is really natural for complex visual environment, and binocular rivalry is

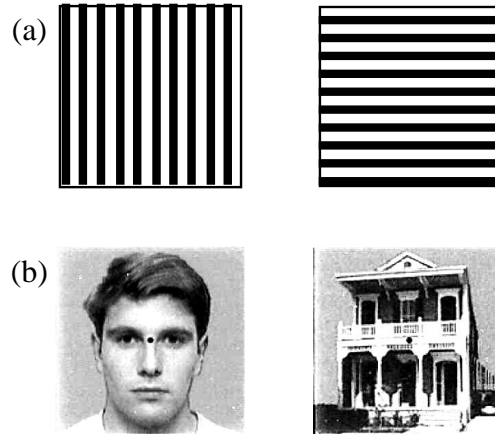


Figure 1.1: Examples of binocular rivalry stimuli. (a) orientation of gratings (b) face and house (Tong *et al*, 1998 [70])

just one of procedures to resolve such unstabilized perception. Asher has suggested that rivalry in fact reveals a fundamental aspect of human cognition, occurring all of the time for all of us [5].

Binocular rivalry has been reported by Porta in the sixteenth century for the first time, and the first scientific study has been performed by Wheatstone in 1838 using his newly invented mirror stereoscope [77]. The binocular rivalry has been investigated mainly by psychophysical methods for the long term [8]. Most of the studies investigated the relationship between stimulus property and its duration in which the perception was changed from one side to the other. The result suggested that the duration was influenced by stimulus properties; luminance, contrast and etc [47].

Recently, many non-invasive measurements have been performed in binocular rivalry. These studies used a psychophysical method in the measurement, and examined the modulation of neural response when the perception of the stimulus was changed between dominance and suppression. In EEG and MEG studies, binocular rivalry stimuli tagged with blinking frequency which mutually differed between right and left eyes were used. The result reported that the corresponding frequency component of the brain response for each stimulus was modulated by perceptual dominance, and many cortical regions from lower level to higher level were related with the process of binocular rivalry [13, 67]. Also in measurements using functional Magnetic Resonance Imaging (fMRI), like the result of EEG and MEG, a blood oxygenation level dependent (BOLD) signal corresponded with the

dominant stimulus was amplified, and the signal corresponded with the suppressed stimulus was attenuated [59, 70]. Moreover, in a electrophysiological experiment, the firing frequency of a neuron in the visual cortex is increased when the stimuli is dominance, or decreased when the stimuli is suppressed similarly [46].

Most of studies investigated about a steady state of dominance process where dominance or suppression to one stimulus were continued in binocular rivalry. However, the non-invasive measurement about the brain responses produced by perceptual transition in which a perception for one stimulus changes from dominance to suppressed during binocular rivalry is seldom performed.

The process where one stimulus dominated or the other suppressed in binocular rivalry condition would be related to a decision process. In fact, it has been reported that predominance of binocular rivalry were affected by 'top-down' attention [58]. Thus, the resolving process of binocular rivalry would be more spontaneous decision process than the others, the investigation about binocular rivalry will be contributed to clarify not only lower level, but also higher level brain processes.

1.2 Objectives of the study

Chapter 2 and 3, concerns how binocular rivalry of motion direction is processed in the brain. Chapter 4 extend the rivalry to various types of visual attributes, while Chapter 5 is about application of binocular rivalry to other psychophysical experiments.

1.2.1 Two rivalries for motion rivalry stimuli

Many previous studies investigated the property of binocular rivalry in steady state. Duration is one of the most general index to express the binocular rivalry. There are many reports about relationship between the visual property of stimulus and the duration for which the perception was changed from one side to the other. Those reports suggested that the duration was affected by the luminance, contrast, and other visual property, and stronger stimulus took longer duration [12, 23, 38, 54]. The duration of perceptual alternation have a gamma distribution [47].

A motion rivalry stimulus has motion directions which are mutually different by the right and left eyes, and has two perceptual interpretations, a pattern and a component motion [1]. These two perceptual interpretations are perceived

stochastically. This stochastic behavior appeared not only binocular motion, but also monocular motion which was composed of two superimposed different motions, plaid. The characteristic of this phenomena have been investigated using plaid stimuli, and reported that the stochastic process of perceptual alternation between pattern and component motions behaved as same as binocular rivalry between the right and left eyes [33]. Thus, The motion rivalry stimulus caused two rivalries at the same time; the rivalry between right and left eye, and between coherent motion and component motion. However, the relationship of these rivalries have not been clarified yet. Therefore as described in Chapter 2, we aim to investigate the relationship of these rivalries using psychophysical methods.

In order to clarify the neural basis of binocular rivalry, the understanding of the psychophysical basis was required. Most of previous studies of binocular rivalry focused on the duration of perceptual alternation. However, because two rivalries were mixed with each other, it is difficult to understand the character of the relationship by the duration. Thus, we focused on the transient behavior of both rivalries. We measured the reaction time of first perception of single direction.

1.2.2 Brain responses of rivalry stimuli

Most of measurements of binocular rivalry were only performed in steady state, and investigated the relationship between the dominance perception and the modulation of brain responses. Some EEG and MEG studies used binocular rivalry stimuli which blink at frequency which is different between the right and left eyes, and reported that the corresponding frequency component of the brain responses for each stimulus is modulated by whether the dominant eye is right or left [13, 67]. Also in measurements by functional Magnetic Resonance Imaging (fMRI), like the result of MEG, a blood oxygenation level dependent (BOLD) signal was amplified when the corresponding stimulus was dominant, and attenuated when the corresponding stimulus was suppressed [59, 70]. Moreover, in a electrophysiological experiment, the firing frequency of the neuron in the visual cortex was increased when the stimuli was dominance, or decreased when the stimuli was suppressed [46].

On the other hand, Only few non-invasive measurements have reported the brain responses produced by perceptual transition when a stimulus changes from dominance to suppressed during binocular rivalry. Lumer and colleagues have reported that there was a part to which the brain responses amplified by the perceptual transition of a binocular rivalry from the fMRI measurement which com-

pares the perceptual alternation of binocular rivalry and the physical alternation of visual stimuli [50]. Valle-Inclán and colleagues have reported that presenting a visual probe to the suppressed eye during rivalry accelerated the perceptual transition and evoked larger brain responses than a change of the dominant visual stimulus [73]. However, Polonsky and colleagues have suggested that there was no significant responses of the perceptual transition in a binocular rivalry from the time course of fMRI signals which synchronized with the perceptual transition [59].

As mentioned above, the brain responses of the perceptual transition during binocular rivalry has not been studied enough. In this study, we aimed to investigate the brain responses elicited by the perceptual transition during binocular rivalry. In the Chapter 2, we have measured the temporal property of binocular rivalry with psychophysical methods, and suggested that the transient response of binocular rivalry would be appeared in long latency after 400 ms. By these results, we also proposed the method of MEG measurements of binocular rivalry. In the Chapter 3, we aimed to measure the transient response of binocular rivalry using such a stimulus.

1.2.3 Various types of binocular rivalry

There are many visual attributes, and various types of binocular rivalry are also existed accordingly. In fact, various studies individually used various types of rivalry stimuli; grating orientation, motion direction, face vs. house, and face vs. grating, and so on. However, most of studies has not put emphasis on the rivalry type of the stimuli.

It is known that binocular rivalry modulated brain responses in many cortical regions from lower level to higher level [13, 67]. A few studies reported that binocular rivalry modulated especially in the region where the visual attributes corresponded to the rivalry was processed in the ordinary process. In fMRI study, Tong and colleagues used the rivalry stimulus of face vs house, and reported the rivalry depended modulation at fusiform face area (FFA) for face and parahippocampal place area (PPA) for house during binocular rivalry [70]. In physiological study, it was reported that a rivalry stimulus of motion direction modulated the responses in the middle temporal lobe where the motion information was processed, and same tendency was observed with rivalry of complex pattern modulated in inferotemporal lobe. [62, 63]

We investigated the transient responses of binocular rivalry using motion ri-

valry stimuli in Chapter 3. In 4, we aimed to investigate the response not only for motion but also for other visual attributes. We measured the transient MEG responses of binocular rivalry for three types of binocular rivalry and estimated equivalent current dipoles (ECD) for each rivalry stimuli. From the comparison of ECD locations, the relationship between brain responses of binocular rivalry and its visual attribute was speculated.

1.2.4 Application of binocular rivalry

We have investigated the transient behavior of binocular rivalry with psychophysical method and non-invasive measurement from Chapter 2 to 4. Those results suggested that the transient response of binocular rivalry was evoked in long latency at the cortices where the visual property which caused rivalry was processed. In Chapter 5, we try to apply these responses to a novel measurement.

Color motion is the motion which consisted of equal luminance red and green grating, and it has no luminance information. Although the motion was perceived in dependence upon luminance information generally, color motion which did not have the information could be also perceived. Previous physiological work suggested that the information pathway of color pattern differed much one of luminance pattern. The information of color and luminance patterns are separated by cone and rod cells on retina, magno-cells and parvo-cells on lateral geniculate nucleus (LGN). The separated informations are processed in two different pathways. They are called magnocellular pathway and parvocellular pathway, or dorsal pathway and ventral pathway [48]. The magnocellular pathway mainly process low frequency patterns and motions. The parvocellular pathway mainly process high frequency patterns and colors. Moreover many psychophysical studies showed the difference between luminance motion and color motion. Burr and colleagues have reported that there was a difference of the RT for a few hundreds milliseconds between luminance and color motion especially in very low speed condition (< 1 deg/s) [14].

These results suggested that color motion was processed differently with luminance motion. However, the non-invasive measurement could not explained the difference between luminance and color motion [52], and the neural basis of these difference has not been clarified yet.

In Chapter 5, we try to clarify the difference between luminance and color motion using the transient response of binocular rivalry. We performed both psychophysical and MEG measurements, and estimated the source location of MEG

responses. The results were compared between luminance and color motion, and speculated the visual process of both motions.

1.3 Previous studies on binocular rivalry

Binocular rivalry has been reported by Porta in the sixteenth century for the first time, and investigated by various methods for the long term. In this section, previous studies for binocular rivalry will be summarized.

1.3.1 Early studies

Binocular rivalry is a phenomenon created by presenting similar but different images for both eyes simultaneously. When two similar but different images were presented for two eyes, one of the images is perceived dominantly, and the other is suppressed. The perception of the dominant image stochastically alternates every few seconds. These spontaneous alternation of the perception is called as the binocular rivalry.

This interesting phenomena was first observed by Porta in the sixteenth century, and has been investigated for a long time [8]. The scientific study about binocular rivalry has been reported by Wheatstone in 1838 using a mirror stereoscope [77]. Around the early twentieth century, some scientist have investigated and reported the some property of binocular rivalry [36, 64, 75]. However, the more detailed experiment waited for the late twentieth century.

1.3.2 Duration of perceptual dominance

In psychophysical method, the behavior of binocular rivalry was evaluated by the duration of perceiving the dominance for one stimulus. It is empirically known that the duration varies stochastically and follows a gamma distribution (GD) [7, 47, 76]. Similar alternation is experienced with an ambiguous figure, such as the Necker cube or Rubin's face/vase and so on. Previous studies reported that the duration of ambiguous figure also varied stochastically as same as binocular rivalry, and followed GD [10, 21]. Murata and colleagues investigated the distribution of durations for both ambiguous figure and binocular rivalry more carefully. The result suggested that the shape-determining parameter α of the GDs took natural numbers [55]. It meant that the stochastic process of the duration was caused by the combination of several Poisson processes.

The duration is determined stochastically [43, 47]. However, the predominance of stimulus were affected by the stimulus property; luminance, contrast, contour density and so on. Stronger stimuli is more visible than weaker one. For example, brighter, higher contrast, and more dense stimuli have a longer dominance duration than the others. than a low contrast one [12, 38, 54] Moreover, the stimulus property mostly affect the duration of suppression rather than one of dominance [47]. Since the duration is related to the low-level property of the visual stimulus, it was suggested that rivalry is a relatively low-level process [47].

The changing the visual image in the suppressed stimulus induces The alternation of the dominance of rivalry [25, 43]. It is suggested that some bottom-up process is related with rivalry process. On the other hand, previous studies also reported the effect of top-down process, attention. Helmholtz has claimed to be able to hold one set of contours dominant for an extended period of time attending vigorously to some aspect of those contours [75]. Although this idea has been denied by another report [31], it is believed that the 'top-down' attention could modulate predominance of rivalry.

1.3.3 Spatial property

Mosaic dominance

When binocular rivalry stimulus were presented as sufficient large stimulus, a mosaic dominance is perceived, consisting of contiguous patches, each containing pattern of only one of the stimulus [9, 32]. Each patch of the dominance region and pattern is changed continuously, and a perceptual alternation is occurred in each patch. On the other hand, the rivalry which does not present mosaic dominance is called exclusive. Each patch of the mosaic dominance behave as exclusive dominance. Thus, the mosaic dominance consists of many patches with exclusive dominance. Blake *et al* determined the maximum size of exclusive dominance patch using two circular grating patches, and the result was 0.14 deg [9]. It was in good agreement with previous reports of physiology [61].

Traveling Wave

When the dominance is changed from one stimulus to the other during binocular rivalry, the transition does not switch instantaneously with a sufficient large stimulus, but the dominance emerges in a wave-like fashion, traveling wave. Wilson *et al* used a annular stimulus of which the part contrast abruptly increased in order to

elicit a transition of dominance, and measured the velocity of traveling dominance along the annulus [78]. The experiment was performed with both small (1.8 deg radius) and large (3.6 deg radius). As a result, the velocity of large radius on the stimulus was faster than one of small radius. However, if correct the difference between central vision and peripheral vision caused by the radius difference, it was shown that two stimulus has a same velocity on the cortices.

Lee *et al* measured fMRI signal correlated with traveling waves using the stimuli as same as Wilson's study [42]. They compared blood oxygenation level dependent (BOLD) signals between two cortical regions. One region positioned near the origin of the traveling wave, and the other positioned far from there. Because two stimuli had different contrast and caused different BOLD signals, the different latency of dominance transition cause the different BOLD signal intensity. Using this methods, they specified the response of traveling wave with fMRI.

1.3.4 Brain responses of binocular rivalry

There is many measurement studies about binocular rivalry with both invasive and non-invasive methods.

Electrophysiological studies

The neural behavior of binocular rivalry also investigated by electrophysiological methods. One of the problems of binocular rivalry is where binocular rivalry start from. Lehky and Sejnowski have measured the neural response during binocular rivalry in the lateral geniculate nuclei (LGN) of monkey [44]. The results showed that there was no evidence for rivalry modulation in the LGN.

Leopold and Logothetis examined the modulation of the brain responses in some visual areas of monkey using rivalry stimuli of face and star burst patterns [46]. From the psychophysical result which performed with the physiological measurement, the stochastic distribution of the perception of monkey was pretty similar to one of humans. Thus, it was suggested that monkey and human have a similar sensory property. From comparison measurement data with the psychophysical result, the proportion of modulating neurons was only 18 % in V1/V2, and 38 % in V4. Their previous study shows that 43 % neurons in middle temporal (MT) lobe were related to binocular rivalry [49], and another study shows the relation 90 % in inferotemporal (IT) lobe [62]. Therefore, binocular rivalry caused in higher level visual process rather than in lower level.

fMRI

Many fMRI studies have reported the steady state responses during binocular rivalry. Tong *et al*, reported that higher visual area, fusiform face area (FFA) and parahippocampal place area (PPA), could be modulated by the dominance transition during binocular rivalry between face and house. Polonsky *et al* used rival dichoptic images of two different contrasts; the contrast difference served as a 'tag' for the neural representations of the two monocular images. The rivalry-related fluctuations were observed in V1, and were roughly equal to those observed in other visual areas (V2, V3, V3a and V4). Although previous fMRI studies show no significant fluctuation in V1 during binocular rivalry, they suggested that the neural mechanisms responsible for binocular rivalry occur primarily in later visual areas. Lee & Blake also reported fluctuations in V1 by comparing the response of binocular rivalry stimuli with that of plaid stimuli [41]. Accordingly, the amplitude of V1 activity during rivalry fell midway between those in the two representing no suppression. This result suggested that neuronal events associated with binocular rivalry occur as early as V1.

Lumer *et al* examined not the steady state but the transient responses of binocular rivalry [50]. The transient response of binocular rivalry is the response evoked when the perceptual dominance is changed from one stimulus to the other. They used face and grating stimuli, and BOLD signals were compared between rivalry condition and "replay" condition which replay the perception during rivalry condition by physical alternation of stimuli. Cortical regions whose activity reflected perceptual transitions included extrastriate areas of the ventral visual pathway, and activity in the frontoparietal cortex was specifically associated with perceptual alternation only during rivalry.

EEG and MEG

Most of old EEG studies have reported reductions in the amplitude of the visual evoked potential (VEP) signal associated with the suppressed target [17, 40, 51, 66]. On the other hand, recent EEG and MEG studies of binocular rivalry employ a brilliant method, frequency tagging, which used a high temporal resolution of EEG and MEG effectively. The frequency tagging has been developed by Brown and Norcia [13]. Two flickering patterns which blinked different temporal frequency each other were used as rivalry stimuli, and tagged them by the flickering frequency. Measurement data were separated into some frequency component, and the component of the corresponding frequency were evaluated. In the result,

the transition of each stimulus components highly correlated with the perception of dominance and suppression. Thus, the transition of brain responses during binocular rivalry could be measured with the method.

The VEP measurement with frequency tagging performed a good temporal resolution. However, the spatial resolution is too low to understand the visual pathways. Srinivasan *et al* applied frequency tagging to MEG measurement [67]. The modulation of visual evoked field (VEF) were measured using frequency tagging during binocular rivalry, and analyzed the coherency among whole cortices based on the sensor position. The result demonstrated a direct correlation between the conscious perception of a visual stimulus and the synchronous activity of large populations of neocortical neurons. Moreover, Cosmelli *et al* expanded this method to use the position of equivalent current dipole (ECD), and analyzed the coherency based on the ECD position [19].

Others

There had been few non-invasive measurements except for methods described above. Only two studies with Positron emission topography (PET) were reported [24, 71]. It should be because the measurement of binocular rivalry requires a certain level of temporal resolution and PET does not have it. On the other hand, although near infrared spectroscopy (NIRS) have temporal resolution as same as fMRI, there are no study of binocular rivalry with it.

1.4 Psychophysics

In the present study, a psychophysical measurement was employed to record psychological values. Psychophysics is a one of quantitation method to measure a psychological value by a physical value. There are many types of perception and those psychological values: luminance, contrast, color and forms etc. However, the psychological values exist only in a brain, and we can not measure them directly. Since we can measure and quantify physical values of the stimulus which cause the perception, psychophysics bind the physical values to the psychological values in order to quantify the psychological values. Those values are binded on the basis of some perceptual landmark. A threshold value is the most general perceptual landmark, and point of subjective equality is a second one. Using these methods, psychological values were quantitatively measured by traditional physical measurements.

Moreover, psychophysical measurements are frequently combined with statistical analysis: for example t-test, Wilcoxon-test and analysis of variance (ANOVA) [34, 35]. The statistical analysis permit to discuss psychological values and its perception scientifically. In the present study, we examined the relationship between psychological values and MEG signals by MEG measurements at the same time as psychophysical measurements.

1.5 Magnetoencephalography

In the present study, MEG was employed to record neural responses that correlated with binocular rivalry. In this section, the basis of MEG will be summarized [18, 29, 65, 68].

1.5.1 Comparison with other brain imaging methods

Human brain imaging techniques are divided into two categories, structural and functional. The former, represented by computer tomography (CT) and magnetic resonance imaging (MRI), measures anatomical structures of the brain. MRI images, onto which dipoles of MEG sources are generally superimposed, are formed by measuring the orientation of hydrogen nuclei aligned in a strong magnetic field. MRI provides detailed images of brains with millimeter accuracy.

While structural imaging only gives a representation of static structure, functional imaging techniques are used to investigate which brain areas are involved in a particular function. In PET, a radioactive tracer introduced into the subject can indicate activated brain areas because gamma rays associated with positron emission from the areas can be detected [39]. Since the obtaining radioisotope is really difficult, and the measurement is invasive, PET has been replaced by fMRI, the most widely used technique for functional brain imaging [57]. fMRI has higher spatial resolution and is suitable for mapping brain areas involved in processing several kinds of stimuli and tasks. Local increase in metabolic rate results in increased delivery of blood to the activated region, which can be visualized in fMRI. Because both PET and fMRI do not directly measure electrical activity in the brain but measure an associated metabolic change which is thought to correlate well with cortical activity, they do not have high temporal resolution.

Such high temporal resolution can only be achieved by using a technique such as electroencephalography (EEG) or magnetoencephalography (MEG) which measures the electrical activity of the brain directly. EEG records volume current in-

duced by activation of a large population of neurons by using attached electrodes. Although EEG has a temporal resolution of about 1 ms, the spatial resolution is severely limited because the path from activated cortex to the electrodes is convoluted. On the other hand, MEG measures magnetic fields generated by electrical activities of neurons, and has the same temporal resolution as EEG. However MEG is less affected by the structure of the brain, skull and scalp, because those magnetic permeability are approximately equal [29, 65]. The spatial resolution of MEG is a few millimeters for the activities near the surface of the brain (1-3 cm), although the resolution is highly dependent on the number and depth of activated brain areas.

1.5.2 MEG generation

MEG is based on the principle that all electric currents generate magnetic fields [29]. Electric activities of neurons mainly consist of an action potential (AP) and postsynaptic potential (PSP). The latter can be classified into an excitatory postsynaptic potential (EPSP) and inhibitory postsynaptic potential (IPSP). MEG is generated mainly by EPSP rather than AP or IPSP. Although APs generate an electrical current of about 100 mV, they have a duration of only 1 ms. Therefore, spatial summation of APs is difficult, it could not making detection by MEG very difficult. PSPs, on the other hand, can be spatially summed and can produce detectable MEG signals, owing to their longer duration of tens of millisecond. Since EPSP generates strong electric currents compared with IPSP, MEG is generally thought to be generated by EPSP. However, the role of IPSP should be further investigated in the future.

Neurons are classified into two types, pyramidal and stellate, and it is the current flowing along apical dendrites of the former in the cortex that produces the extracranial magnetic fields detected by MEG. A distal excitatory synapse will induce a dipolar dendritic current that flows in one direction along the entire length of the dendrite towards the soma of the pyramidal cell. There are more than 100,000 pyramidal neurons per square millimeter of cortex, and they constitute nearly 70 % of neo-cortical neurons. The cells are oriented perpendicular to the cortex. As for stellate cells, their electric currents are canceled out and do not generate measurable MEG responses by their spatial symmetry.

It should be noted that only cells oriented parallel to the skull surface will produce magnetic fields that can be measured from outside of the brain. Considering that the sulcus is roughly tangential to the skull surface while the gyrus is roughly

parallel to the surface, we can deduce that MEG mainly measures neural activities of the sulcus rather than the gyrus. It is known that EEG, on the other hand, is sensitive to the activities in gyrus but is rather insensitive to the activities in the sulcus. Therefore MEG and EEG measure complementary signals in the brain.

1.5.3 MEG measurement

The intensity of magnetic fields generated by the brain is in the order of femto-tesla. Such weak magnetic fields could be only detected by superconducting quantum interference devices (SQUIDS). SQUIDS work on the principle that the quantum mechanical tunneling current passing through a weak link in a small superconducting loop is dependent on the magnetic flux through the loop. To overcome the problem of environmental noises such as terrestrial magnetism being much greater than the magnetic fields generated by the brain, a device known as a gradiometer has been developed. It is based on the assumption that distant noise sources are spatially uniform at the detector. The gradiometer responds only to spatial gradients of the field and are less susceptible to external noise. There are two types of gradiometers, axial and planar. Whereas axial gradiometers measure the gradient of the magnetic field perpendicularly to the sensor (e.g. $\partial B_z/\partial z$), planar gradiometers measure it tangential to the sensor (e.g. $\partial B_z/\partial x$, $\partial B_z/\partial y$ and $\partial B_x/\partial z$, $\partial B_y/\partial z$). A further solution to the noise problem is to use a magnetically shielded room.

MEG system used in this thesis

In the present study, we used a whole-head MEG system (PQ2440R, Yokogawa, Japan) with 230 axial-z sensors and 70x3 vector sensors in a magnetically shielded room [69] (1.2). The vector sensors consisted of one axial gradiometer ($\partial B_z/\partial z$) and two planar gradiometers ($\partial B_x/\partial z$, $\partial B_y/\partial z$), which measure signals independent of axial gradiometer. While $\partial B_z/\partial x$ and $\partial B_z/\partial y$, which are used in some MEG systems (ex. NeuroMag, Finland), only measure the z component of magnetic fields, $\partial B_x/\partial z$ and $\partial B_y/\partial z$ used in our system are completely independent of $\partial B_z/\partial z$. It has been demonstrated that dipole estimations can be made explicitly by using these vector sensors [56]. This method enables us to find the global minimum directly, without the need for repetitive calculations using several initial estimations necessary in many cases, since the solution often converges to a local minimum. Further studies are necessary to show the effectiveness of vector sensors.

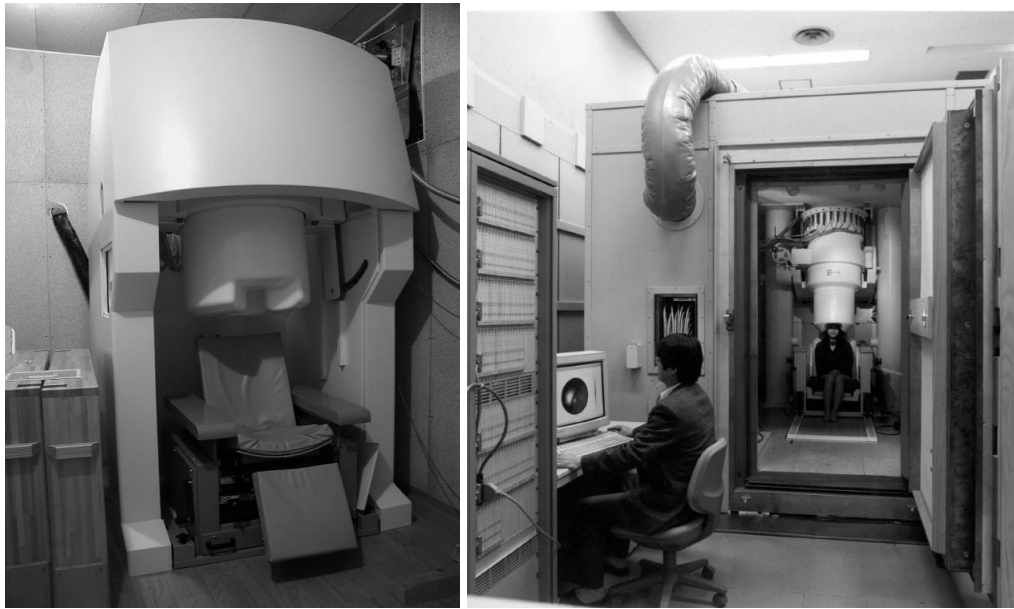


Figure 1.2: MEG systems used in this thesis. *left*: 440-channel whole-head MEG system (PQ2440R, Yokogawa, Japan) *right*: 64-channel whole-head MEG system (CTF, Canada)

1.5.4 MEG analysis

Dipole estimation

To specify the activated area in the cortex, it is necessary to solve the inverse problem, that is, the calculation of the distribution of the generated current within the brain from the measured magnetic field. The inverse problem is ill-posed, since there are many different current distributions within the brain that could produce the measured field. We can simplify the problem by assuming that the magnetic distribution was generated by a single localized source, in what is known as a single equivalent current dipole (ECD) model [29]. It is possible to increase the number of dipole, which is called multiple ECD model. The number of the dipoles must be decided prior to the calculations, which is very difficult in many cases.

Alternatively, to eliminate the ill-posed problem, spatial filtering technique or the beamformer approach, a filter that screens the signals originating from a particular course, can be used [60]. This is accomplished by simply multiplying the measurement matrix with a weighting matrix, which results in a zero output for input signals originating from other sources.

Methods that consider the time course of MEG have been also proposed. Multiple signal classification (MUSIC) is a signal subspace method, which uses the eigen structure of the measured data matrix [53]. The MUSIC algorithm finds the source locations whose corresponding array manifold vector is nearly orthogonal to the noise subspace.

Chapter 2

Psychophysical property of binocular rivalry

Drifting grating patterns with different motion directions independently presented to the two eyes induce two perceptual interpretations. One is “pattern motion” that forms a superimposed pattern moving with a single direction, equivalent to the vector sum of the two motion directions. The other is “component motion” that forms two independent motion directions followed by monocular dominance in which one eye’s motion is perceived alone. Although this perceptual process involves not only interocular rivalry (right or left eye’s image) but also motion-type rivalry (pattern or component motion), most of the previous studies discussed only one of those rivalries independently. Here we studied this double rivalry process during binocular rivalry of motion direction in terms of the temporal order of each rivalry. We measured reaction times (RTs) using a visual stimulus for which the probability of each perceptual interpretation was approximately equal. RTs to perceive a consistent motion direction in pattern and component motion conditions were 400 ms and 750 ms slower, respectively, than that in the condition when identical motion stimuli were presented to the two eyes. These results suggested that motion-type rivalry was resolved before interocular rivalry and these rivalries in motion perception were processed hierarchically. Moreover, it was also suggested that MEG responses of interocular rivalry could be specified by the comparison between pattern and component motion.

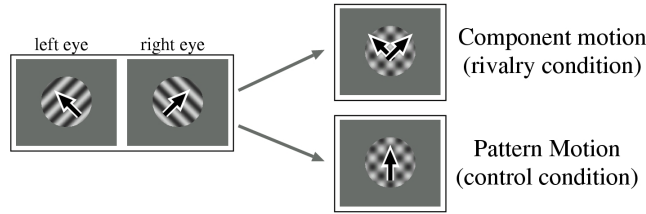


Figure 2.1: Schematic illustration of pattern and component motion. The arrows indicate the direction of the motion; they were not part of the stimulus. When the stimulus causing motion rivalry are presented, there are two perceptual interpretations. One is a pattern motion that does not cause them, and the other is a component motion that cause binocular rivalry and the perceptual alternation.

2.1 Introduction

When two similar but different images were presented for two eyes, one of the images is perceived dominantly, and the other is suppressed. The perception of the dominant image spontaneously alternates every few seconds. This spontaneous alternation of the perception is called binocular rivalry.

A motion rivalry stimulus is a set of drifting grating patterns with different motion directions independently presented to the two eyes, and induce two perceptual interpretations [1]. One is “pattern motion” that forms a superimposed pattern moving with a single direction, equivalent to the vector sum of the two motion directions. The other is “component motion” that forms two independent motion directions followed by monocular dominance in which one eye’s motion is perceived alone. Figure 2.1 shows an example of the perceptual interpretations. These perceptual interpretations alternates stochastically, and appeared not only binocular motion, but also monocular motion which was composed of two superimposed different motions, plaid. The characteristic of the stochastic behavior have been investigated about plaid stimuli, and it was demonstrated that the perceptual alternation between pattern and component motions behaved like binocular rivalry between right and left eyes [33]. Accordingly, this perceptual process involves not only interocular rivalry (right or left eye’s image) but also motion-type rivalry (pattern or component motion). However, most of the previous studies discussed only one of those rivalries independently. Here we studied this double rivalry process during binocular rivalry of motion direction in terms of the temporal order of each rivalry.

Most of previous studies of binocular rivalry mainly focused on the duration of perceptual dominance for one of stimuli, and it is difficult to discriminate among double rivalry only from durations. Thus no study investigated the relationship between these two rivalries, motion type rivalry and interocular rivalry. In this study, we investigated this relationship of double rivalry in terms of the temporal characteristic of each rivalry. We measured reaction times (RTs) using a visual stimulus for which the probability of each perceptual interpretation was approximately equal. RTs to perceive a consistent motion direction in pattern and component motion conditions were 400 ms and 750 ms slower, respectively, than that in the condition when identical motion stimuli were presented to the two eyes. These results suggested that motion-type rivalry was resolved before interocular rivalry and these rivalries in motion perception were processed hierarchically.

2.2 Methods

2.2.1 Subjects

The subjects were four healthy right-handed volunteers (22-29 years of age). All subjects had normal or corrected-to-normal acuity and normal color vision.

2.2.2 Visual Stimuli

A drifting sine-wave grating was displayed in a 2.0 x 2.0 deg circular window centered in the display (Figure 2.2). Two stimuli presented to the two eyes made an angle from 30 deg to 170 deg for every 20 deg. One stimulus tilted clockwise, the other tilted counter-clockwise based on the vertical upward direction. The luminance of stimuli and background were 4.0 cd/m², the spatial frequency of grating was 2.0 c/deg, and the motion speed was determined to be 0.8 deg/s. The contrast of gratings was larger than 95 %. A fixation point was a 0.2 deg cross-shape with black color, and displayed at the center of the screen through the observation. The stimulus was presented as a onset stimulus of the motion.

2.2.3 Instruments

Stimuli were generated on a PC with a VSG 2/3 (Cambridge Research Systems) graphics card and displayed on a 17 inch RGB monitor (Iiyama MT-8617ES). In order to present different images for each eye, a liquid crystal shutter (LCS) for

3D display was used. LCS was installed in front of the monitor, and synchronized with the monitor. Stimuli for right and left eyes were displayed alternatively for every frame, and the direction of circular polarization was synchronously alternated. By using polarizing glasses, subjects observed the visual stimuli that were independent between right and left eyes. The monitor frame rate was 120 Hz, and observed frame rate was 60 Hz for each eye. Viewing distance was 3.2m.

2.2.4 Measurement of proportion of perceptual rivalry

It is known that motion rivalry stimuli are perceived more as a component motion when the angle between two motion directions is large, and more as a pattern motion when the angle between two motion directions is small [4]. A component motion corresponds to the rivalry condition, and a pattern motion corresponds to the control condition. In this study, we aimed to measure RTs of rivalry and control conditions. To compare RTs between rivalry and control conditions, it is better to perform measurement by the same stimulus. The measurements of RTs with same stimulus is so efficient that the proportion of perceptual rivalry closed to 50 %. Thus, we examined the dependence of the angles on the proportion of perceptual rivalry.

The stimulus was presented as a onset stimulus of the motion pattern. First, the fixation point is only presented. Next, the drifting grating which evoked motion rivalry was presented at the center of the screen for 1.0 s. Last, the grating was dismissed, and the fixation point is only presented again. Figure 2.2 shows the sequence of stimuli. Eight stimuli which have angles from 30 deg to 170 deg every 20 deg were used, and presented random order. Subjects were instructed to press one of two buttons after dismissed the stimuli to answer their perception of motion type. Measurement was performed by 25 trials about each angle, and a total of 200 trials was carried out as one set. We assumed that subjects perceived rivalry when subjects perceive a component motion, and did not perceived rivalry when subjects perceive a pattern motion. The perceptual rivalry was calculated from results for each angle.

To obtain psychometric function from the result, the data were approximated to a sigmoid function by the least square method. A sigmoid function is described as follows:

$$f(t) = \frac{1}{1 + a \exp(-b\theta)} \quad (2.1)$$

Here, a and b were fitting parameter. By the result of approximation, the angle of which the proportion of perceptual rivalry was equal to 50 % was calculated

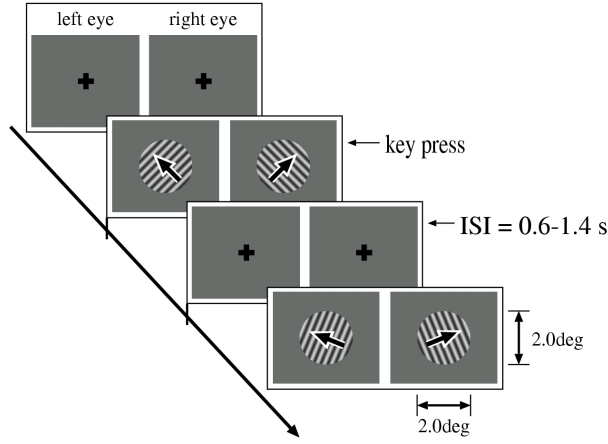


Figure 2.2: Schematic illustration of visual stimuli. First, the fixation point is only presented. Then, the drifting grating which evoked motion rivalry was presented. Eight stimuli which have angles from 30 deg to 170 deg every 20 deg were used, and presented random order. Each arrow indicates the direction of the motion; they were not part of the stimulus.

for each motions. Moreover, the stimulus which have most suitable angle in eight stimuli were obtained for each subject.

2.2.5 Measurement of reaction time

To clarify the difference between the inter-ocular rivalry and the motion type rivalry by the temporal property, we measured RT of each rivalry, and compared those results.

The stimulus was presented as a onset stimulus of a motion pattern as same as the previous experiment of perceptual rivalry. There were three perceptions about the stimulus: a single direction which made by the vector sum of two motion directions, single directions of left or right eye caused by a dominance of binocular rivalry, and nonuniform motion which was mixed with each motion. Because an RT measurement of nonuniform motion is difficult, we only measured RTs of single direction. Subjects were instructed to press one of three keys as soon as perceiving a single direction. The direction of each stimulus was based on the vertical upward direction. Three perceptions corresponded to a single upward direction which made by the vector sum of two motion directions, and single

diagonally upward right and left directions, respectively. We treated the upward direction as non-rivalry condition, and diagonally upward directions as rivalry condition.

The stimulus was presented as the following sequence. First, the fixation point is only presented. Next, the drifting grating which evoked motion rivalry was presented at the center of the screen. Last, the grating was dismissed, and the fixation point is only presented again. Figure 2.2 shows the sequence of stimuli.

The stimuli which had the angle obtained from previous experiment were mainly used. Although whether perceptual rivalry was caused is determined stochastically, it was suggested that a repetitive presentation of single ambiguous stimulus was caused a deviation of perception. Thus, in a part of trials, we did not use the stimuli with the angle obtained from previous experiment, but with random angles to avoid the deviation of perception. Measurement was performed 200 trials; 160 trials with the angle obtained from previous experiment, 40 trials with random angles. Results were classified by results of key press, and compared between them.

2.2.6 Measurement of reaction time of conventional motion

To compare with RTs of rivalry stimuli, RTs of stimuli which did not cause binocular rivalry were also measured. The stimulus was presented as a onset stimulus of the motion pattern. To avoid predicting the motion direction from the grating pattern, vertical upward and downward direction which have same grating patterns were used for stimuli. Because only one eye contributed to the motion perception when perceptual dominance were caused in a binocular rivalry condition, measurements were performed both binocular and monocular stimulus. The binocular stimulus was the stimulus presented to both eyes. The monocular stimulus was the stimulus presented to only one eye which selected randomly. Schematic illustration of conventional motion stimulus is shown in Figure 2.3. Subjects were instructed to discriminate the direction of stimulus, and press one of two keys as soon as perceiving a direction. Measurement was performed 100 trials for each stimulus, and results were compared with those of binocular rivalry stimuli.

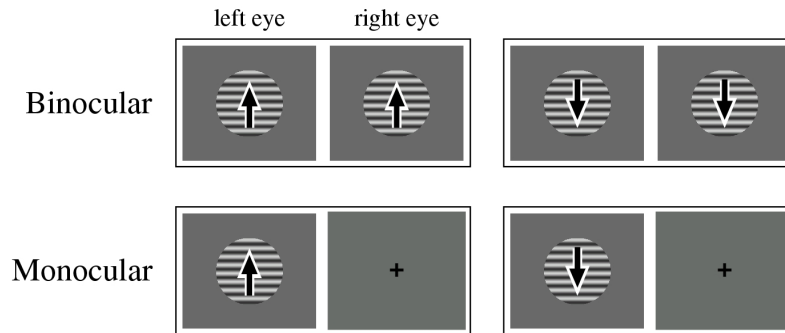


Figure 2.3: Schematic illustration of conventional motion. Each arrow indicates the direction of the motion; they were not part of the stimulus. The motion direction is vertical upward and downward to avoid predicting the motion direction from the grating pattern. Subjects were instructed to discriminate the direction of stimulus, and press one of two keys as soon as perceiving a direction.

Subject	KA	TH	YN	TS
preferred angle	84 deg	138 deg	129 deg	84 deg

Table 2.1: Angle of which the proportion of perceptual rivalry was equal to 50 %. The angle largely differed among each subject.

2.3 Results

2.3.1 Proportion of perceptual rivalry

The result of dependence of the angle between two motion directions on the proportion of perceptual rivalry was shown in Figure 2.4. Each curve shows the result of fitting with sigmoid function. The dependence largely differed among each subject, however, there was a tendency where increasing perceptual rivalry was related to increasing angles. The result very consistent with previous studies [4]. Table 2.1 shows the angle of which the proportion of perceptual rivalry was equal to 50 % calculated by the results of fitting. Because angles largely differed among subjects, the angle of stimuli of the RT measurement was selected for each subject from eight stimuli which has the angle from 30 deg to 170 deg every 20 deg.

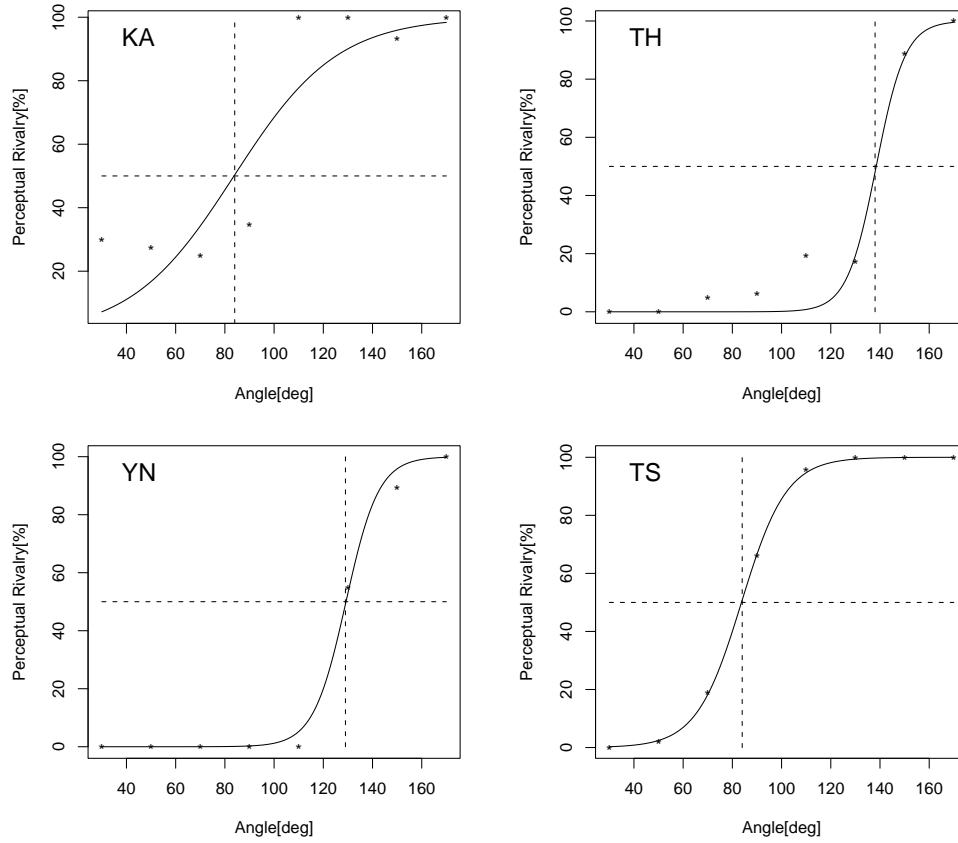


Figure 2.4: Dependence of the angle between the two motions on the proportion of perceptual rivalry. Each curves shows the results of fitting for sigmoid function. Horizontal and vertical axes indicate angles (degree) and proportions of perceptual rivalry. The dependence largely differed among subjects.

2.3.2 Reaction time of rivalry motion

Using the angle of which the proportion of perceptual rivalry was close to 50 % obtained by the previous results, RT measurements of single direction were performed. RTs were classified by the result of key-presses, and distribution of RTs for each condition was obtained. The result of RTs for each perceptual condition is shown in Figure 2.5. Four figures presented the result of each subjects, respectively. Depending on also the subject, however, distributions of RTs were differed between two perceptual conditions.

To compare distributions of RTs between two conditions quantitatively, those were averaged across all subjects. Figure 2.6 shows the grand averaged histogram of RTs for each condition. Non-parametric test was performed to examine the difference of their distributions, as a result, there was a statistically significant difference of RTs between two perceptual conditions.

To check the meaning of the difference between each perceptual condition, the data for rivalry condition were classified by two answers, upper right or upper left. Figure 2.7 shows distributions of RTs of both answers. Those distributions had quite similar distributions, and no statistically significant difference (Wilcoxon test, $p > 0.05$).

2.3.3 Reaction time of conventional motion

In order to compare the temporal property of perception of binocular rivalry stimuli with that of conventional motion, RTs of conventional motions were also obtained. Because only one eye contributed to the motion perception when perceptual dominance were caused in a binocular rivalry condition, measurements were performed both binocular and monocular stimulus. We measured RTs of conventional motions for both monocular and binocular stimulus, and averaged the results across all subjects. Figure 2.8 shows grand averaged distribution of RTs for binocular and monocular conditions. Two distributions had quite similar distributions, and no statistically significant difference (Wilcoxon test, $p > 0.05$). Thus, we treated these two as the same data, and next we compared between RTs for conventional motions and fusion conditions. Figure 2.9 shows distributions of RTs for conventional motion and fusion condition. Two distributions were differed completely from each other. There was statistically significant difference between them (Wilcoxon test, $p < 0.01$). Because the difference of RTs were reached about several hundreds ms, it is suggested that some rivalry process were performed in the term.

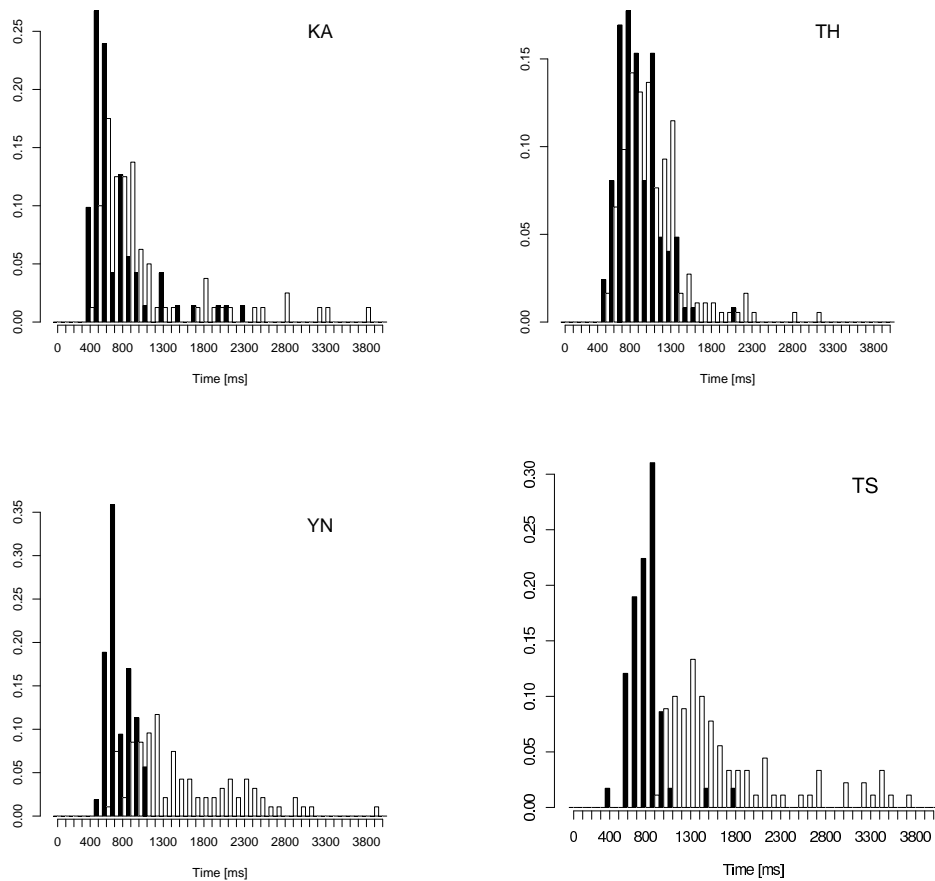


Figure 2.5: Distributions of RTs for each perceptual condition. Four figures presented each subject, respectively. Black bars indicate fusion conditions, and white bars indicate rivalry conditions. Distributions of RTs were differed between two perceptual conditions.

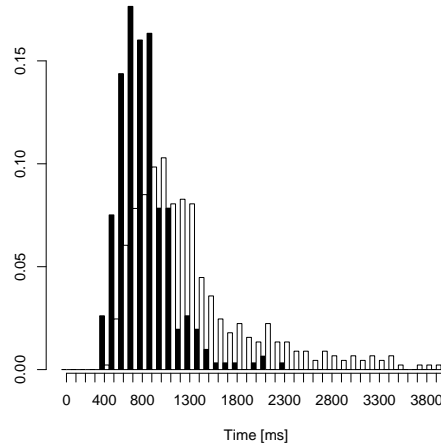


Figure 2.6: Grand averaged distributions of RTs for rivalry and fusion conditions. Black bars indicate fusion conditions, and white bars indicate rivalry conditions. Distributions of RTs for each condition were differed significantly (Wilcoxon test, $p < 0.01$).

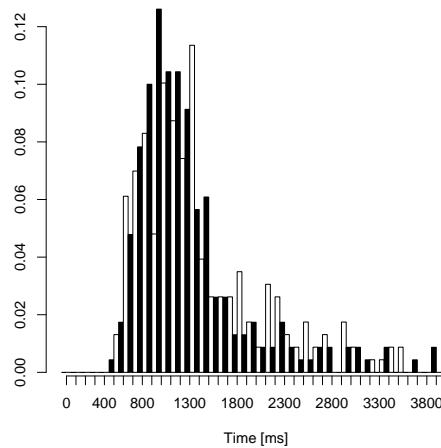


Figure 2.7: Grand averaged distributions of RTs for binocular and monocular conditions. Black bars indicate perception of upper right motion, and white bars indicate perception of upper left motion. Two distributions had quite similar distributions, and no statistically significant difference (Wilcoxon test, $p > 0.05$).

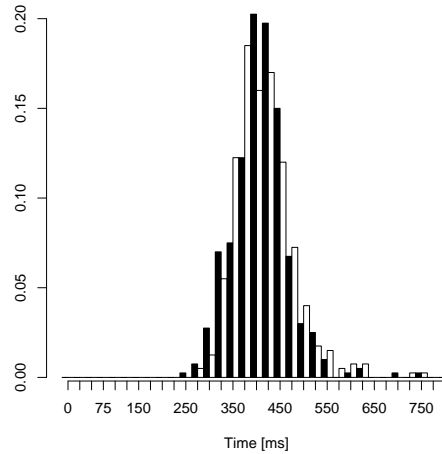


Figure 2.8: Grand averaged distributions of RTs for binocular and monocular conditions. Black bars indicate binocular condition, and white bars indicate monocular condition. Two distributions had quite similar distributions, and no statistically significant difference (Wilcoxon test, $p > 0.05$).

From the results, the median, interquartile range of RT, and the grand averaged value were calculated for each subject. Table 2.2 shows quantitative results of whole experiments. The difference of RTs between rivalry and fusion condition was about 300 ms, and the difference of RTs between conventional motion and fusion condition was about 400 ms. As a result, it was found that the RT increased in the order; control, fusion, and rivalry condition. On the other hand, the variance of each RT also increased in the same order.

2.4 Discussion

2.4.1 Proportion of perceptual rivalry

From the results, There was the trend that the proportion of perceptual rivalry which percept rivalry motion increased with angles between two motion directions. The trend was consistent with previous studies [4]. However, the angle of which the proportion of perceptual rivalry equal to 50 % differed largely between subjects.

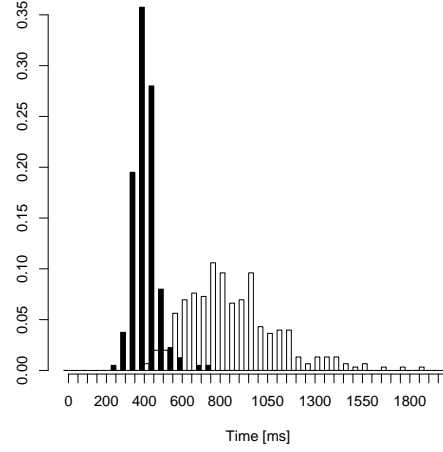


Figure 2.9: Grand averaged distributions of RTs for conventional motion and fusion condition. Black bars indicate conventional motion, and white bars indicate fusion condition. Two distributions were differed completely from each other. There was statistically significant difference between them (Wilcoxon test, $p < 0.01$).

Subject	KA	TH	YN	TS	All
rivalry	857	1039	1360	1484	1170
IQR	444	455	1010	778	636
fusion	651	931	776	889	836
IQR	292	354	246	194	300
monocular	382	438	416	446	418
IQR	48	85	43	85	63
binocular	364	426	444	442	424
IQR	66	59	47	42	68

Table 2.2: Results of measurement for each subject. The RT increased in the order; control, fusion, and rivalry condition. The variance of each RT also increased in the same order.

2.4.2 Reaction times

From comparison between RTs of monocular and binocular motion which did not cause binocular rivalry, there were no statistically significant difference (Figure 2.8). Binocular rivalry was caused when there were some inconsistency between two eyes, and not caused when the same visual information was presented in unilateral eye. Thus, it is suggested that the monocular stimulus used in this study does not cause motion rivalry. However, the luminance information was presented in both eyes, and had inconsistency. Thus, luminance rivalry should be caused, and subjects perceived a stimulus where contrast decreases partly. It is known that the luminance motion was not largely affected by the contrast of stimuli. Briefly, no RT difference between monocular and binocular motion was the result as a consequence of the robustness of perception for luminance motion. On the other hand, it is suggested that color motion of which perception was not robust to contrast was affected by monocular stimuli.

The RT for rivalry condition was significantly longer than that for fusion condition (Figure 2.6). The result of grand averaged RTs across all subjects showed the difference for about 300 ms. Although these conditions had same sequences at motion perception and key-press, it was only different whether subjects perceived binocular rivalry. Thus, it was suggested that the perception of binocular rivalry increased the RT for about 300 ms.

Moreover, the RT for fusion condition was also significantly longer than that for control condition in which stimulus was conventional motion (Figure 2.9). The result of grand averaged RTs across all subjects showed the difference for about 400 ms. These conditions differed on the existence of the motion type decision process between fusion and rivalry conditions. Thus, it was suggested that the existence of motion type decision process increased the RT for about 400 ms.

The decision process between pattern and component motions have been investigated using plaid stimuli, and reported that the stochastic process of perceptual alternation between pattern and component motions behaved as same as binocular rivalry between the right and left eyes [33]. Thus, it is suggested that the decision process is a kind of a rivalry process. In this study, both rivalries occurred at the same time, and caused increase of the RT for about several hundred milliseconds by those decision processes. Thus, the decision process which resolve rivalry information would take about several hundred milliseconds.

2.4.3 Psychophysical models

The stimulus of motion rivalry would cause two rivalries at the same time. One is motion type rivalry competed between rivalry and fusion conditions, and the other is inter-ocular rivalry competed between right and left eyes. There were two models for the relation between these rivalries. One is parallel processing model that all rivalrous property (ex. right eye motion, left eye motion, and pattern motion) competed simultaneously (Figure 2.10 *upper*). The other is sequential processing model that two rivalries were processed in sequentially. (Figure 2.10 *lower*). The occurrence of one rivalry depended on the results of the other rivalry in the model.

In order to clarify the relation between these rivalries, we performed a psychophysical experiment. From the result of RTs, both rivalries, motion-type rivalry and interocular rivalry, increased RTs. Interocular rivalry was only caused in rivalry condition which perceive transparent motion. If parallel processing model was approved, the RT of interocular rivalry must be equal to that of motion-type rivalry. However, interocular rivalry caused longer RTs for about 300 ms than motion-type rivalry. On the other hand, the RT and its variance were correspondingly increased. The increase of RT variance corresponded with that of RT suggested that some process which have time variance was added to the source process. To summarize, it was suggested that these rivalries were processed by sequential processing model (Figure 2.10 *lower*); First, a stimulus was distinguished between pattern motion and component motion. Then, when component motion was perceived, interocular rivalry was resolved. Therefore, the hierarchical structure of motion perception was clarified by psychophysical methods.

2.4.4 Experimental design of MEG measurement

From the result of perceptual rivalry measurements, it was suggested that the angle of which the proportion of perceptual rivalry closed to 50 % differed largely between subjects Table 2.1. From the result, it is found that perceptual rivalry did not have a common tendency in all subjects. On the other hand, all subjects perceive pattern motion with sufficiently small angle, 0 deg, and component motion with sufficiently large angle, 180 deg. This tendency agreed between all subjects. Thus, to produce the difference of perceptual rivalry without adjustment for each subject, we should use stimuli with sufficiently small or large angle.

From the result of RT measurements, the RT for rivalry condition was longer for about 300 ms than that for fusion condition. The difference between fusion and

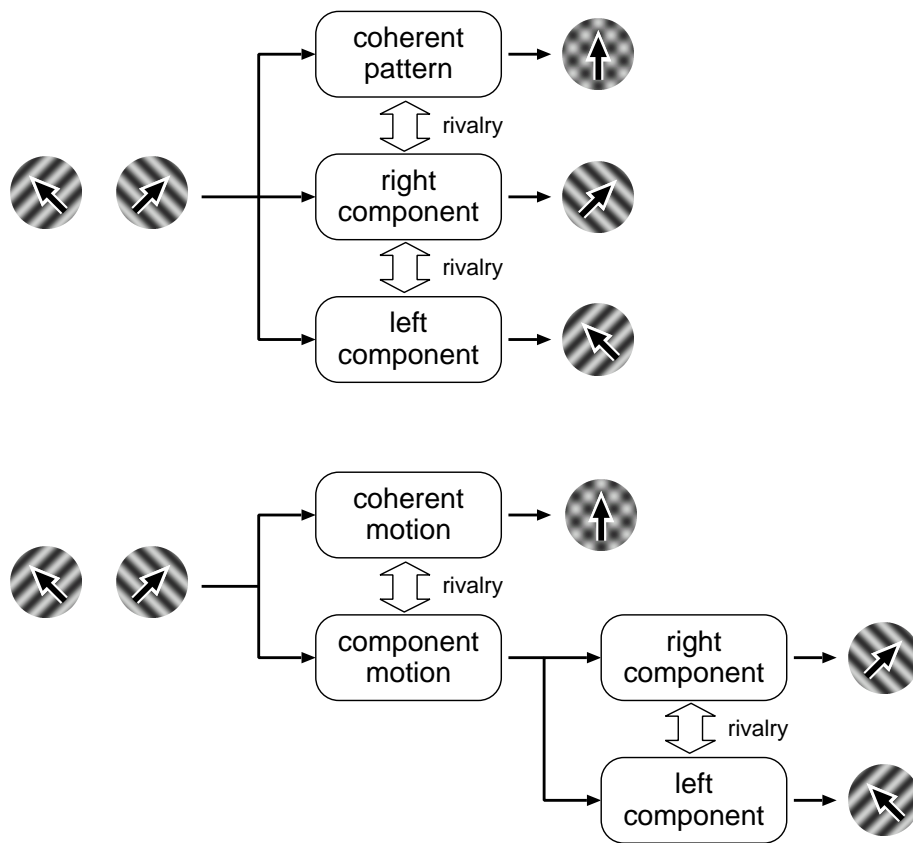


Figure 2.10: Psychophysical models.

rivalry conditions would be caused by interocular rivalry, and the rivalry was resolved through it. Because interocular rivalry was caused after the motion type rivalry which caused after perception of conventional motion. the difference would be caused in very long latency. It was suggested that interocular rivalry were resolved, and the transient response of binocular rivalry was caused in such a long latency. Thus, comparing the responses between fusion condition and rivalry condition would be able to measure the transient response of binocular rivalry.

Chapter 3

MEG responses of binocular rivalry

Binocular rivalry is a phenomenon created by presenting similar but different images for the two eyes simultaneously. Many previous studies have investigated various brain responses of binocular rivalry. However, a response of perceptual transition in binocular rivalry has not been clear yet. The present study aimed to measure the response of the perceptual transition in binocular rivalry using a motion rivalry stimuli with various motion angles. It is known that the perception of motion rivalry stimuli has two conditions depending on the angle between two motion directions. One is a rivalry condition that cause binocular rivalry and the perceptual transition, and the other is a fused condition that does not cause them. Visual evoked fields (VEFs) were recorded with five healthy subjects using a 440-channel whole-head magnetoencephalogram (MEG) system. We classified trials to rivalry or fused conditions, and calculated time averages of root mean square (RMS) values for every 100 ms in each condition. As a result, the time average of RMS values of the rivalry condition were significantly larger than those of the fused condition after 400 ms post-stimulus. These results suggested that the perceptual transition in binocular rivalry increased the late MEG component.

3.1 Introduction

When two similar but different images were presented for two eyes, one of the images is perceived dominantly, and the other is suppressed. The perception of the dominant image spontaneously alternates every few seconds. These spontaneous alternation of the perception is called as binocular rivalry. Binocular rivalry has been used as a tool in order to investigate a visual system for many years

[77]. There were many studies of binocular rivalry with various stimuli condition. Many studies were reported about the characteristics of the perceptual dominance or the alternation time with various visual stimuli by psychophysical methods [8]. However, most of these studies were studied about the steady state when the dominance or suppression to one stimulus were continued. On the other hand, the perceptual transition between the dominance and suppression does not process momentarily, but takes the time for about one second. While the perceptual transition, it is known that the stimulus with which the mixed image of two stimuli which presented for each eye will be perceived [50]. However, the brain responses of the perceptual transition has not been studied enough. In this study, we aimed to investigate the brain responses which caused at the perceptual transition in binocular rivalry condition.

Previous reports investigated the relationship between the brain activity evoked by binocular rivalry and the perceptual state when the dominance or suppression to one stimulus is continuing. Some EEG and MEG studies used binocular rivalry stimuli blinking at two frequencies which were different between the right and left eyes, and reported that the corresponding frequency component of the brain responses for each stimulus is modulated by whether the dominant eye is the right or left eyes [13, 67]. Also in measurements by functional Magnetic Resonance Imaging (fMRI), like the result of MEG, a blood oxygenation level dependent (BOLD) signal corresponded with the dominant stimulus is amplified, and the signal corresponded with the suppressed stimulus is attenuated [59, 70]. Moreover, in a electrophysiological experiment, firing frequency of a neuron in the visual cortex is increased when the stimuli is dominance, or decreased when the stimuli is suppressed [46].

However, there are only a few studies by the non-invasive measurement about the brain responses produced by perceptual transitions between dominance and suppressed. Lumer and colleagues have reported that there is a part to which the brain responses amplified by the perceptual transition of a binocular rivalry from the fMRI measurement which compares the perceptual alternation of binocular rivalry and the physical alternation of visual stimuli [50]. Valle-Inclán and colleagues have reported that the presenting a visual probe to the suppressed eye during rivalry caused a perceptual transition and evoked larger brain responses than that to the dominant visual stimulus [73]. They suggested that this responses were produced by the perceptual switching of binocular rivalry. However, in this report, it did not fully distinguished between the influence of a perceptual transition and a difference state of dominant or suppressed enough. Although the responses in

the long latency after 400 ms was amplified, the responses in the short latency before 240 ms was attenuated. Thus, the cause of each change was not fully explained. Moreover, Polonsky suggested that there were no significant responses of the perceptual transition in a binocular rivalry by the time course of fMRI signals which synchronized with the perceptual transition [59]. As mentioned above, the change of the brain activity evoked by perceptual transition in binocular rivalry is not clear enough.

In this study, we measure the MEG responses of a binocular rivalry in order to clarify the brain activity caused by the perceptual transition. Many previous studies about a binocular rivalry measured brain responses synchronized with the timing of button presses which showed a perceptual state. Although the timing appears the end of the perceptual transition, the random time for about 1 s is needed for the perceptual transition. Thus, it is difficult to measure the initial responses of the perceptual transition by the button presses synchronized with it.

In this study, a visual stimulus which caused binocular rivalry was used as a simple onset stimuli which was shown from the state which showed no stimulus to a certain timing. When a visual stimulus which caused a binocular rivalry were presented by such a method, one stimulus could not become a dominant stimulus immediately. Instead, it was known that the mixture of the two stimuli which presented to two eyes was perceived for about 1s after the presentation of stimuli, and is equivalent to the perceptual state when a perceptual transition were caused [16]. That is, by presenting the visual stimulus which causes a binocular rivalry as an onset stimulus, the perceptual transition is caused synchronized with the presentation of the stimulus, and it becomes possible to measure the brain responses corresponded to the perceptual transition.

This study used visual stimulus of motions that caused binocular rivalry, and we called them motion rivalry stimuli. A motion rivalry stimulus has motion directions which are mutually different by the right and left eyes, and has two perceptual interpretations [1]. One interpretation is a component motion. It is perceived as two independent movements on a same plane, and caused a binocular rivalry after few seconds. The other is a coherent motion. It is perceived as one lattice pattern which moves in the direction of the vector sum of two motions, and did not cause a binocular rivalry (Figure 3.1). These two perceptual interpretations are perceived stochastically. It is known that these motions are perceived more as a component motion when the angle of two motion directions is large, and more as a coherent motion when the angle of two motion directions is small [4]. Thus, by presenting the motion rivalry stimulus as an onset stimulus and varied the angle of

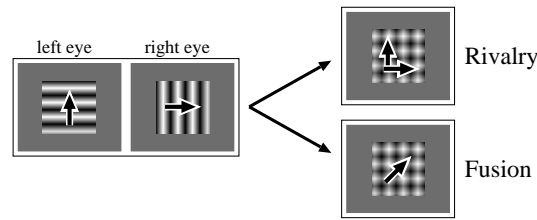


Figure 3.1: Schematic illustration of rivalry and fusion. The arrows indicate directions of motions; they were not part of the stimulus. When the stimulus causing motion rivalry are presented, there are two perceptual interpretations. One is a rivalry condition that cause binocular rivalry and the perceptual transition, and the other is a fused condition that does not cause them.

two motion directions which is presented to the right and left eyes, we can make both states which cause or does not cause a perceptual transition using same types of visual stimuli. In this study, we investigated the brain activity correlated with the perceptual transition of a binocular rivalry by measurement and comparison about these two perceptual conditions. Consequently, it was suggest that the peak response evoked by presenting visual stimuli was not affected by the perceptual transition, but the response at long latency after 400 ms was amplified by the perceptual transition.

3.2 Methods

3.2.1 Subjects

The subjects were five healthy right-handed volunteers (22-28 years of age). All subjects had normal or corrected-to-normal acuity.

3.2.2 Instruments

All visual stimuli were generated on a PC with a VSG 2/3 (Cambridge Research Systems, Cambridge, UK) graphics card and displayed on a 17-inch RGB monitor (Iiyama MT-8617ES, Japan). In order to present different images for each eye, a liquid crystal shutter (LCS) for 3D display was used (Figure. 3.2). The LCS was installed in front of the monitor. The stimuli for right and left eyes were displayed alternatively for every frame, and the direction of circular polarization

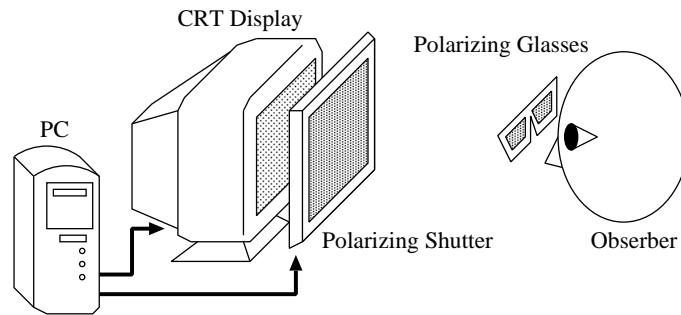


Figure 3.2: Schematic illustration of liquid crystal shutter (LCS) system. LCS was installed in front of the monitor, and synchronized with the monitor. The stimuli for right and left eyes were displayed alternatively for every frame, and the direction of circular polarization was synchronously changed. Subjects observed the visual stimuli by using polarizing glasses.

was synchronously changed. By polarizing glasses, subjects observed the visual stimuli that were independent between right and left eyes. The monitor frame rate was 120 Hz, and observed frame rate was 60 Hz for each eye. Viewing distance was 3.2 m.

3.2.3 Visual stimuli

A drifting sine-wave grating was displayed in a 2.0×2.0 deg square window centered in the display. Figure 3.3 shows a schematic illustration of visual stimuli. The mean luminance of the stimuli and the luminance of the background through the LCS and polarized glasses were equated at 4.0 cd/m^2 . The spatial frequency of grating was 2.0 c/deg, and the velocity of the motion was determined to be 1.6 deg/sec. The contrast of gratings was larger than 95 %. A fixation point was a 0.2 deg cross-shape, and displayed at the center of the screen during the experiment.

Motion directions of the stimuli were selected by the method as described below. First, the motion direction of the right eye was randomly selected from 8 directions of a unit 45 degrees. Then, the motion direction of the left eye was randomly selected from four directions which made an angle of 0, 45, 90, and 135 deg with that of right eye. Thus, to suppress the effect of brain responses depended on the motion direction, the direction of motion was selected randomly.

The stimulus was presented as a onset stimulus of the motion pattern. First, the fixation point is only presented. Next, the drifting grating which evoked motion

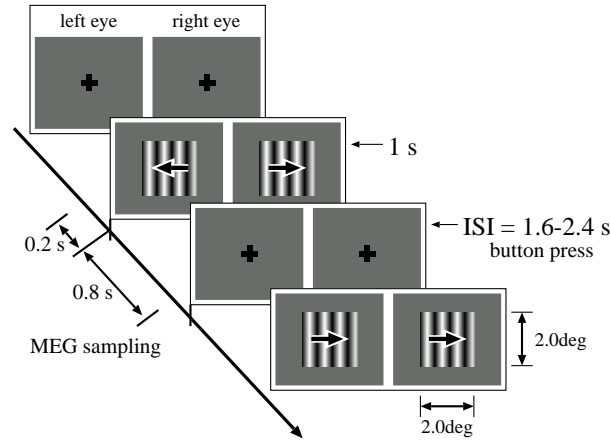


Figure 3.3: Schematic illustration of visual stimuli. First, the fixation point is only presented. Then, the drifting grating which evoked motion rivalry was presented for 1.0 s, and dismissed again. Four types of angles (0, 45, 90, 135 degree) between motion directions of the right and left eyes were presented randomly. The arrows indicate the direction of the motion; they were not part of the stimulus.

rivalry was presented at the center of the screen for 1.0 s. Last, the grating was dismissed, and only the fixation point was presented again. These stimuli with various angles of motion directions were presented random order. Measurement was performed by 100 trials about each angle, and a total of 400 trials was carried out as one set. Four subjects performed two sets of experiments, and one subject performed only one sets. The inter-stimulus interval (ISI) was randomly varied from 1.6 to 2.4 s.

In order to check the perceptual rivalry to motion stimuli, subjects were instructed to answer with two buttons whether the rivalry was perceived after a stimulus disappears. The proportion of perceptual rivalry for every angle were calculated from the result of the answer, and the relation between them was investigated.

3.2.4 MEG recordings

Visual Evoked Fields (VEF) beginning 200 ms before and ending 800 ms after the stimulus onset were recorded with a whole-head MEG system (PQ244OR, Yokogawa, Japan). Data were sampled at 1000 Hz with a 0.1 Hz high-pass filter

and a 200 Hz low-pass filter. Because some heads of subjects were very smaller than the helmet of the MEG instrument, subjects were instructed to attach their occiput to the helmet. In order to arrange conditions by all subjects, analysis was performed except for 128 channels of frontal area. The measurement data were averaged across each condition. In off-line averaging of MEG data, the trials that had maximum values of sensor outputs larger than 2.5 pT were assumed to be blinks or eye movements, and discarded. Moreover, it excepted similarly about the trial by which the button for a perception check was not pushed. The averaged responses were band-pass filtered at 1-40 Hz. All recordings were performed in a magnetically shielded room. The monitor was placed outside a magnetically shielded room, and subjects observed it through a small window of the room.

3.2.5 Analysis

In order to analyze the brain activity, the time course of Root Mean Square (RMS) values was calculated from the time course of the averaged measurement data. A RMS value is expressed with the squared average sum of each channel output at a latency, and described as follows,

$$RMS(t) = \sqrt{\frac{\sum_k^N \{s_k(t)\}^2}{N}} \quad (3.1)$$

Here $s_k(t)$ shows the sensor value of k th sensor at time t , and N shows the number of sensors of the MEG system. The RMS is thought as magnitude of brain activity. An RMS value is sharply changed with the noise level of the average of source data, and noise levels of averaged data are heavily dependent on the number of trials. Thus, when the number of trials used for averaging differed between every conditions, the noise levels also differed, and the calculated RMS values use inadequate to compare between them. In order to resolve this problem, it is necessary that a part of trials of which had more trials than the other was removed randomly, and the number of trials used for averaging was united with the other condition. Furthermore, the time average of RMS values before the stimulus onset was subtracted from whole RMS data in order to remove DC offset.

3.3 Results

3.3.1 MEG responses for each angle

First, the measurement data were classified according to the angle between two motion directions of visual stimuli and averaged during trials. Time course of stacked waveforms of averaged MEG responses between trial to four angles is shown in Figure 3.4. The most prominent peak was found at around 200 ms after the stimulus onset for each angle. Although a weak modulation of the peak amplitude according to angles was observed, no proportionality relation with the angle was observed. Time courses of RMS values between trials of four angles are shown in Figure 3.5. The peak response was observed near 200 ms after the stimulus onset for each angle. Although the RMS value of the peak response was changed between the various angles, the latency was not changed especially. The RMS values at a long latency after 300 ms showed no remarkable peak and a greatly different waveform for every stimulus conditions.

3.3.2 Perceptual rivalry for each angle

Figure 3.6 shows the relationship between the proportion of perceptual rivalry and the angle between the two motion directions presented for the right or left eyes. Each thin line shows the proportion of perceptual rivalry for each subject, The bold line shows the average across all subjects. The proportion of perceptual rivalry generally had the minimum value at around 0 deg, and the maximum value at around 135 deg. However, the proportion of perceptual rivalry in a middle angle greatly differed between subjects, and the increase of the proportion of perceptual rivalry did not necessarily correspond to the increase in the angle. As mentioned above, in order to investigate MEG responses correlated with binocular rivalry, it was suggested that it must be examined according not to the angle between the two motion directions but to perceptual rivalry.

3.3.3 Relationship between the perceptual rivalry and MEG responses

In order to investigate MEG responses correlated with binocular rivalry, we examined the relationship between the proportion of the perceptual rivalry and the RMS value of the first peak response. Figure 3.7 shows the relationship between

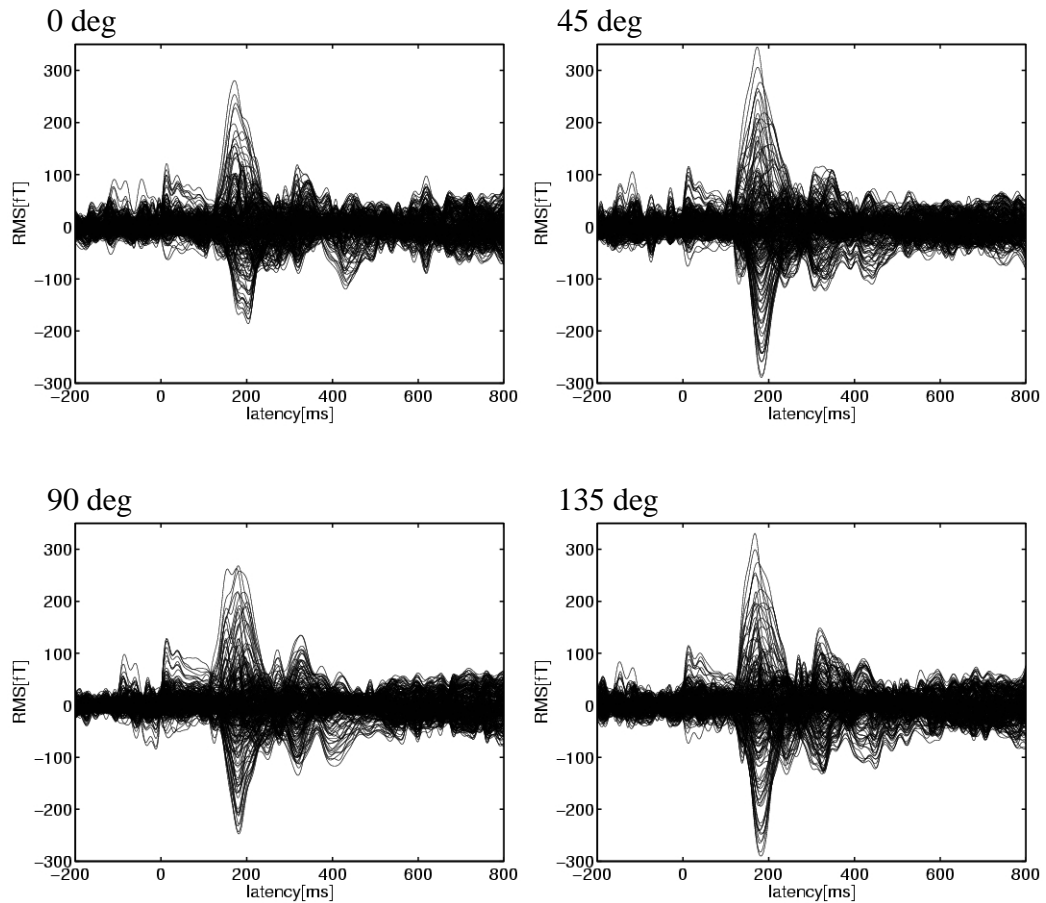


Figure 3.4: Typical stacked waveforms of MEG responses for each angle condition. Horizontal and vertical axes indicate latencies (ms) and amplitudes (fT). The most prominent peak was found at around 200 ms from the stimulus onset for each angle. Although there was a weak modulation of the peak amplitude according to angles, no proportionality relation with angles was observed.

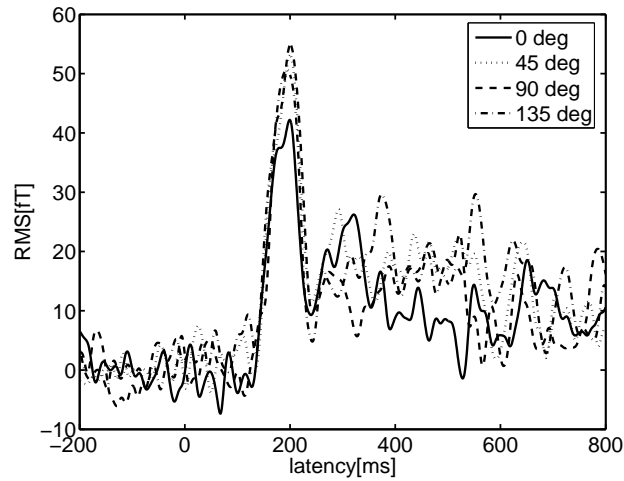


Figure 3.5: Typical example of RMS time course for each angle condition. Horizontal and vertical axes indicate latencies (ms) and amplitudes (fT), respectively. The difference of the latency in the first peak was not observed between various angles. The time course of RMS values at long latency after 300 ms did not have a remarkable peak, and showed a greatly different waveform between conditions.

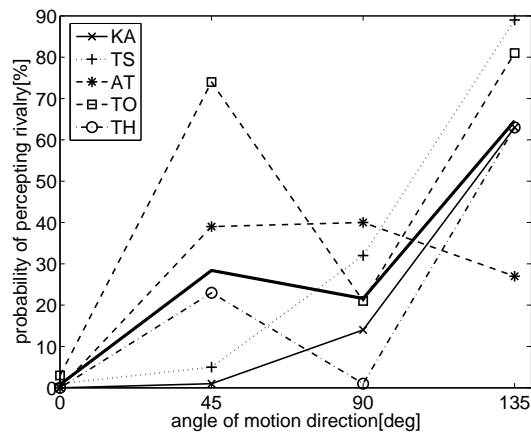


Figure 3.6: The proportion of perceptual rivalry which causes a binocular rivalry for each angle condition. Horizontal and vertical axes indicate angles (deg) and proportion of perceptual rivalry. Bold line shows grand average.

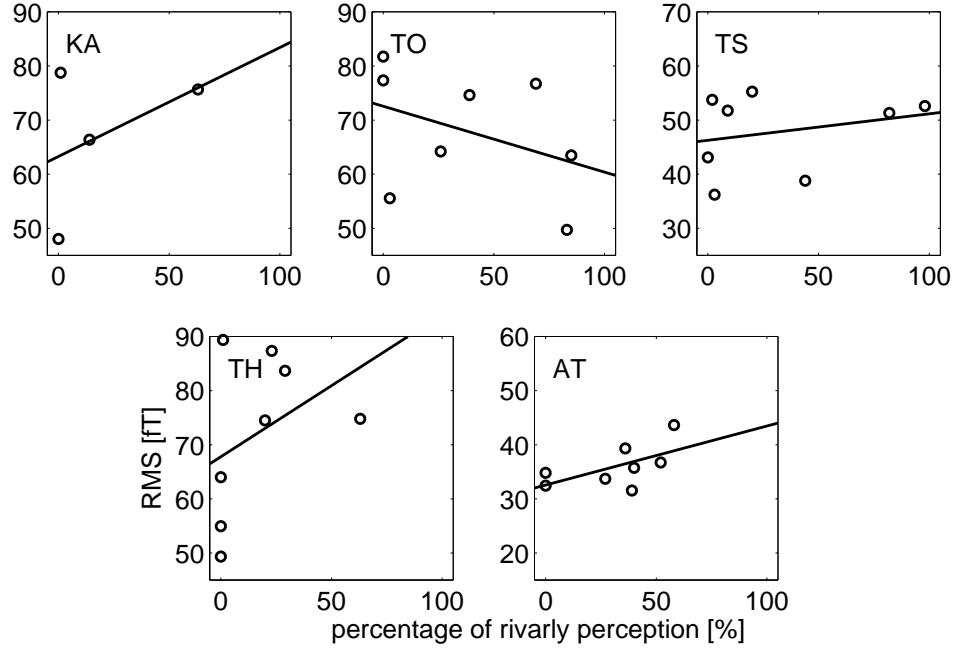


Figure 3.7: Relationship between percentage of perceptual rivalry and peak RMS values. The horizontal axis shows percentage of perceptual rivalry, and vertical axis shows peak RMS values.

the proportion of the perceptual rivalry and the RMS value of the peak response. Each regression line was calculated by the least squares methods. There were no clear trend with the RMS value of the peak response between subjects. Moreover, the correlation coefficient between the proportion of the perceptual rivalry and the RMS value of the peak response was calculated for each subject. The averaged value of correlation coefficient across all subjects was 0.21, and the standard deviation was 0.41. Thus it was suggested that there was no correlation between the proportion of the perceptual rivalry and the RMS value of the first peak response.

3.3.4 MEG responses for each perceptual condition

When the result classified according to the angle was analyzed, the response of binocular rivalry did not clarified. Thus, we analyzed the result not according to the angle, but the perceptual rivalry. We classified the MEG responses according to the perceptual rivalry, and averaged them. A time course of RMS values calculated for each perceptual state. Figure 3.8 shows typical example of the

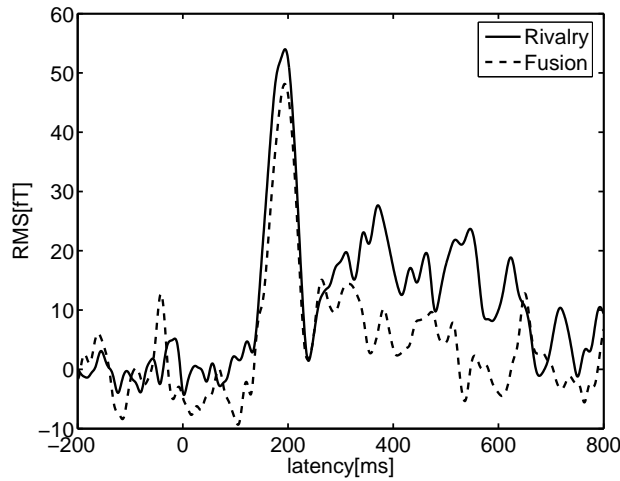


Figure 3.8: Typical example of RMS time course for rivalry (solid line) and fusion (dashed line) conditions. Horizontal and vertical axes indicate latencies (ms) and amplitudes (fT). The RMS values of the latency after 300 ms largely differed between two conditions. Although the most prominent peak was found at around 200 ms from the stimulus onset for each condition, no difference was observed about both its peak amplitude and latency.

time course of RMS values for each perceptual state. Although the most of the prominent peaks were found at around 200 ms, both intensity and latency had no significant difference between two perceptual state. On the other hand, at the latency after 300 ms, the response when subjects perceived rivalry is larger than when subjects did not perceive rivalry. Although the detailed time course differed among subjects, this tendency at long latency was observed in all subjects.

3.3.5 MEG responses of rivalry stimuli

In order to investigate the rough tendency of the response evoked by the perceptual transition without the detailed time course, time averages of RMS values for every 100 ms were calculated for each perceptual condition. These results were averaged across all subjects, and calculate the subtraction of the values between two conditions. Figure 3.9 shows the difference of time averaged RMS values between two conditions. A significant difference appeared at long latency after 400 ms (paired t-test, $p < 0.05$), especially after 500 ms (paired t-test, $p < 0.01$). On the other hand, the difference between two perceptual states was not so large

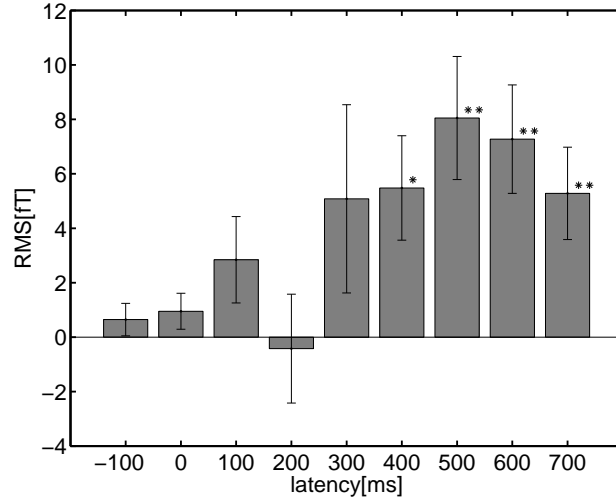


Figure 3.9: The subtraction of time averaged RMS values between rivalry and fused conditions. The results were averaged across all subjects. Horizontal and vertical axes indicate latencies (ms) and amplitudes (fT). The error bars show \pm SEM. A significant difference appeared at long latency after 400 ms (paired t-test, $p < 0.05$), especially after 500 ms (paired t-test, $p < 0.01$). On the other hand, the difference between two perceptual states was not so large at the short latency before 200ms. * $p < 0.05$, ** $p < 0.01$

at the short latency before 200ms. Although the small increase was observed at around 100 ms, it was not statistically significant ($p > 0.05$).

3.4 Discussion

3.4.1 Non-monotone change of the perceptual rivalry

Unlike previous studies, the increase of the angle between two motion direction did not always correspond to the increase of perceptual rivalry (Figure 3.6). The reason of this disagreement is thought that the previous studies have used angles between 70 to 150 deg [4], however, the present study used it between 45 to 135 deg. In fact, for almost all subjects, the tendency of monotone increase was observed in angles between 90 to 135 deg. On the other hand, the correlation between the angle and perceptual rivalry in lower angles differed from one in higher angle, so the increase of the angle did not always corresponded to the

increase of proportion of perceptual rivalry. Thus, we examined the relationship between the proportion for the perceptual rivalry and the RMS value of the peak response, however, there was no correlation between them (Figure 3.7).

3.4.2 MEG responses

In the time course of RMS values when the data were classified by the angle between two motion directions presented for the right and left eyes, clear MEG responses appeared only in the peak response at the short latency, and it is difficult to obtain a clear response at long latency (Figure 3.5).

When measurement data were classified and averaged by the perceptual rivalry, at the latency after 300 ms, the response when subjects perceived a rivalry was larger than when subjects did not perceive rivalry (Figure 3.8). Thus, time averages of RMS values for every 100 ms were calculated for each perceptual condition. A significant difference appeared at the long latency after 400ms (Figure 3.9). On the other hand, there was no significant difference at the short latency before 200ms where the maximum peak response appeared.

When two motions which directions were mutually different by the right and left eyes, two perceptual interpretations, a component motion and a coherent motion, were occurred stochastically. A component motion caused a binocular rivalry at the latency of few seconds after stimulus onset, and A coherent motion did not cause a binocular rivalry. It is known that the perception of the dominance or suppression of the stimulus needs time of about one second from stimulus onset [16], and it becomes a mixture state which is equivalent to the perceptual state where a perceptual transition were caused when time was shorter than few seconds.

Thus, it is thought that the specified response at the long latency was caused by the perceptual rivalry. It was suggested that the MEG response was not amplified at the latency of the peak response, but at the latency after 400 ms.

Although the mechanism of occurrence of MEG signals in the brain has not been not clarified yet, it is established that the occurrence of MEG signals needs a synchronous firing for many neuron groups. Thus, it is thought that the increase of MEG responses of binocular rivalry reflected the increase of a certain neuron activity. According to the previous studies of visual functions of human using MEG or EEG, the latency of the response of the visual cortices for visual stimulus is about 100 ms at V1 which is the lower visual area [26], and about 200 ms at middle temporal (MT) which is the higher visual area [2]. Thus, it was suggested that the MEG response at the very long latency after 400 ms was not a direct

response of the lower visual cortex to the visual stimulus, but was a response of the higher visual cortex or a indirect response caused by some kind of feedback signal from higher visual cortices.

3.4.3 Comparison with previous studies

The result of this study was that the brain activity was increased by the perceptual transition of binocular rivalry. It has a good agreement with an fMRI study of Lumer et al [50]. On the other hand, Valle-Inclán et al reported that a stimulus which caused binocular rivalry attenuated EEG responses at the short latency before 240 ms, and amplified them at the long latency after 400 ms [73]. The result obtained by this study showed the increase of MEG responses after 400 ms, and had well agreement with Valle-Inclán's report. However, the response at the short latency before 240 ms which they reported were not observed. They supposed that the response at the short latency was originated in a primary visual cortex, and was evoked by the perceptual state, dominance or suppressed, in binocular rivalry. However, their experiment did not distinguish between the initial state of the perception and existence of the perceptual transition. It was thought that the discrimination of causality between responses at the short and long latency was very difficult. In this study, we presented the stimulus which caused binocular rivalry from the state which a binocular rivalry did not caused, and measured the response which synchronized with the stimulus onset. Using these methods, we suppressed the difference of the initial state of the perception which they reported. The result showed only the responses which correlated with the perceptual rivalry at the long latency after 400 ms. It was suggested that we succeeded to specify the response correlated with the perceptual transition.

Polonsky et al measured the modulation of the fMRI signal correlated with the perception of binocular rivalry stimuli, and showed the result that there was no significant modulation correlated with the perceptual transition [59]. On the contrary, their results of the psychophysical experiments indicated the existence of the perceptual state where subjects could not perceive only one dominant stimulus. The state was risen between the transition of the dominance eye, and continued for about few second. Our result showed that the response correlated with the perceptual transition of binocular rivalry was observed at about 100 ms after the stimulus onset. When one of the stimuli was perceived as a dominant, it was thought that the brain response of the perceptual transition has been finished. It was very difficult to identify the brain response of the perceptual transition using

this methods, because the check of the perception by the button was still slower than the perceptual transition. Moreover, although Lumer et al used the stimuli which superimposed two images as a control stimuli in order to reproduce the state of the perceptual transition by a non rivalry stimulus, Polonsky et al omitted such methods especially. Thus, it was suggested that the difference between Lumer et al and Polonsky et al was caused by the difference of their methods, and the response could be measured only by Lumer et al since the methods was more suitable for the perceptual transition of binocular rivalry.

3.4.4 Influence of the other components

In this study, although the obtained response should be evoked by a binocular rivalry, it is also considered that the response was not evoked by a binocular rivalry, but by the difference of motion directions of various stimuli. Then, a part of stimuli of which the proportion of the perceptual rivalry was about 50 % was classified by the perceptual rivalry, and was compared in the same angle and same subject. This analysis obtained a same result as the case where the various angle was mixed. Therefore, it was suggested that the response obtained in this study was not caused by the difference of motion directions of visual stimuli, but by the perceptual rivalry, i.e., perceptual transition of binocular rivalry.

Although we used a grating image in order to present a motion stimulus in this study. It was thought that the grating image of which the motion direction mutually differed between the right and left eyes caused not only the motion rivalry but also the pattern rivalry. Therefore, it was necessary to consider not only the motion rivalry but also the pattern rivalry or the interaction between them. In order to clarify those questions whether the brain responses observed in this study was depended on the motion rivalry or the interaction of some rivalries, the further research about the relationship between the brain response and the interaction of various attributes of binocular rivalry (motion direction, orientation, color etc) was required.

Chapter 4

MEG responses of various types of rivalries

Binocular rivalry is a phenomenon created by presenting similar but different images for each eyes simultaneously. Some functional magnetic resonance imaging (fMRI) studies reported modulations of BOLD signal on the cortices where the corresponding visual attribute were processed in binocular rivalry. Electrophysiological measurements also reported similar results in which firing rate in middle temporal (MT) and inferior temporal (IT) lobes was modulated by the perceptual condition in binocular rivalry. However, both results were modulations of steady-state responses in binocular rivalry, and transient responses about various types of rivalry stimuli have not been clarified. In this chapter, we aimed to acquired source locations of transient responses of binocular rivalry for various types of stimuli, motion directions, grating orientations and colors. Visual evoked fields (VEFs) were recorded using a 440 channel whole-head magnetoencephalogram (MEG) system. In order to analyze the MEG data, we proposed to use two evaluation values. One is the ratio of the root mean squares (RMSs) of rivalry and non-rivalry conditions, and the other is the correlation coefficient between MEGs in the two conditions. Both values were calculated for entire recording time, and the latencies of rivalry specific responses were defined by them. Most of iso-contour maps of the selected latencies were identical or very similar among all subjects for each stimulus. Then, we estimated the source location of the response for each stimulus. As a result, source locations of motion direction, grating orientation and color were estimated at MT, parietal lobes and IT respectively. Those areas were corresponded to the cortices where the visual information was processed for non-rivalry condition. Thus, it was suggested that binocular rivalry activated the

cerebral cortex where the corresponding visual information was processed.

4.1 Introduction

When different images independently are presented to the two eyes, only one eye's image is perceived alone. This perceptual dominance of one eye alternates with one of the other eye spontaneously. The alternation is called binocular rivalry. Binocular rivalry has been investigated mainly by psychophysical methods for a long time. Recently, many non-invasive measurements investigated the brain response of binocular rivalry, but its transient response has not been clarified. In this chapter, our purpose is investigating the transient responses of binocular rivalry in terms of the spatial property.

Most of non-invasive measurements of binocular rivalry focused on responses of steady state, and only few studies investigated the transient response. Valle-Inclán *et al* recorded the transient response of binocular rivalry using electroencephalography (EEG) [20], but they could not specify the source location due to the low spatial resolution of EEG. On the other hand, Lumer *et al* studied the transient response of binocular rivalry with functional magnetic resonance imaging (fMRI). The result showed that frontoparietal area were activated by transient process of binocular rivalry. Both non-invasive and electrophysiological measurements suggested that the modulation of neural activity correlated to binocular rivalry was observed where the corresponded visual attribute was processed in conventional condition. However, Lumer *et al* use a rivalry stimulus between face and grating, and it was not clarified whether the location was depended upon visual attribute of rivalry stimuli. Then, we aimed to clarify the location of transient response of binocular rivalry and the visual attribute dependency of them.

In Chapter 3, we observed the transient response of binocular rivalry at long latency after 400 ms stimulus-onset. However, source locations of those responses were not clarified, because the responses had no drastic peak but very temporally broad. In this chapter, Visual evoked fields (VEFs) of three types of binocular rivalry were measured, and compared between rivalry and conventional condition for each stimuli. To analyze MEG data simpler than that in Chapter 3, we employed two evaluation values, root means square (RMS) ratio and correlation coefficient. Measurements were performed not only motion direction, but also grating orientation and color (Figure 4.1), and the source location of each stimulus were estimated. As a result, source locations of motion direction, grating

orientation and color were estimated at MT, parietal lobes and IT respectively.

4.2 Methods

4.2.1 Subject

The subjects were four healthy right-handed volunteers (22-26 years of age). All subjects had normal or corrected-to-normal acuity.

4.2.2 Instruments

All visual stimuli were generated on a PC with a VSG 2/3 (Cambridge Research Systems) graphics card and displayed on a 17 inch RGB monitor (Iiyama MT-8617ES, Japan). In order to present different images for each eye, a liquid crystal shutter (LCS) for 3D display was used. LCS was installed in front of the monitor, and synchronized with the monitor. The stimuli for right and left eyes were displayed alternatively for every frame, and the direction of circular polarization was synchronously changed. By using polarizing glasses, subjects observed the visual stimuli that were independent between right and left eyes. The monitor frame rate was 120 Hz, and observed frame rate was 60 Hz for each eye. Viewing distance was 3.2m. The monitor was placed outside a magnetically shielded room, and subjects observed it through a small window of the room.

4.2.3 Visual stimuli

Three types of visual stimuli which caused binocular rivalry were used. Figure 4.1 and 4.2 show schematic illustrations of visual stimuli. The stimulus was displayed in a 2.0 x 2.0 deg square window centered in the display. A fixation point was a yellow circle with a diameter of 0.1 deg and was displayed at the center of the screen through the observation. The sequence of stimuli was The stimulus was presented as a onset stimulus of the motion pattern. First, the fixation point is only presented. Next, the drifting grating which evoked motion rivalry was presented at the center of the screen for 1.2 s. Last, the grating was dismissed, a the fixation point is only presented again. These stimuli of rivalry and control conditions were presented random order. Measurement was performed by 100 trials about each condition, and a total of 200 trials was carried out as one set. The inter-stimulus interval (ISI) was randomly varied from 1.7 to 2.5 s.

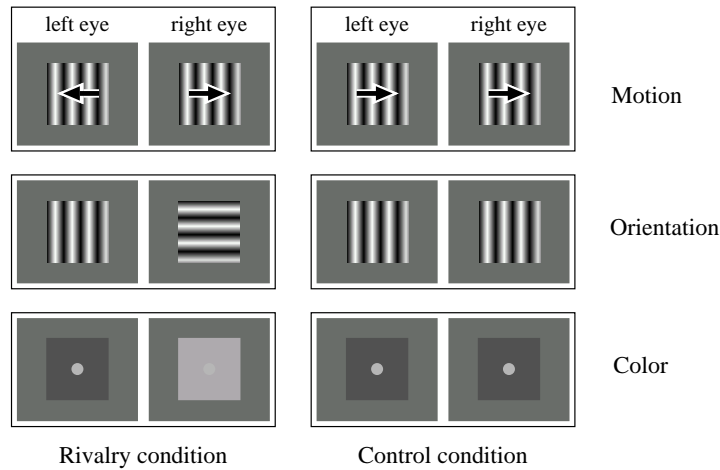


Figure 4.1: Schematic illustration of three types of rivalry stimuli. The arrows indicate the direction of the motion; they were not part of the stimulus. *top*: motion direction rivalry. *middle*: grating orientation rivalry. *bottom*: color rivalry.

Motion rivalry stimuli

A drifting sine-wave grating was used to cause motion rivalry (Figure 4.1 *top*). The spatial frequency of grating was 2.0 c/deg, and the velocity of the motion was determined to be 1.6 deg/sec. The contrast of gratings were larger than 95 %. A motion rivalry stimulus has two perceptual interpretations [1]. One interpretation is a component motion. It is perceived as two independent movements on a same plane, and caused a binocular rivalry after few seconds. The other is a pattern motion. It is perceived as one lattice pattern which moves in the direction of the vector sum of two motions, and did not cause a binocular rivalry. It is known that these motions are perceived more as a component motion when the angle of two motion directions is large, and more as a pattern motion when the angle of two motion directions is small [4]. In order to cause rivalry sufficiently, the angle of 180 degree between two motion directions was used for rivalry condition. Same motion directions for each eyes were used for the control condition.

Orientation rivalry stimuli

A static square-wave grating was used to cause orientation rivalry (Figure 4.1 *middle*). The spatial frequency of grating was 2.0 c/deg, and the contrast of gratings were larger than 95 %. The angle of 90 degree between two orientations was used

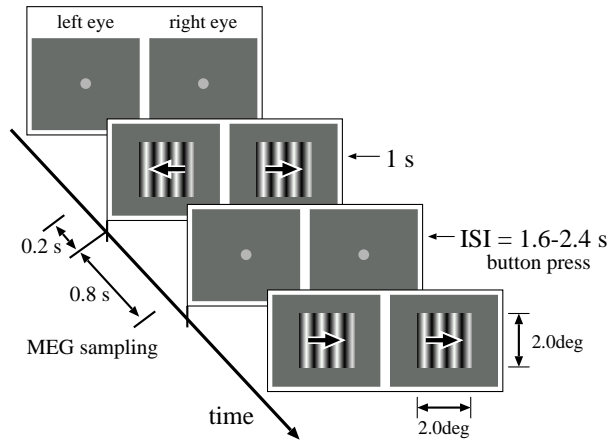


Figure 4.2: Schematic illustration of sequence of a stimulus. First, the fixation point is only presented. Then, the visual pattern which evoked some type of binocular rivalry (ex. motion rivalry) was presented for 1.0 s, and dismissed again. The arrows indicate the direction of the motion; they were not part of the stimulus. The inter-stimulus interval (ISI) was randomly varied from 1.7 to 2.7 s.

in order to cause rivalry sufficiently. Same orientation for each eye was used for the control condition.

Color rivalry stimuli

A simple filled pattern was used to cause color rivalry. (Figure 4.1 *bottom*). In order to make the rivalry which does not have luminance information, equal-luminance red and green were used to fill rectangles. Luminance of those colors were matched by a preliminary experiment using the minimum flicker method for each subject. Same color for each eyes was used for the control condition.

4.2.4 MEG recordings

Visual Evoked Fields (VEF) beginning 200 ms before and ending 800 ms after the stimulus onset were recorded with a whole-head MEG system (CTF, Canada). Data were sampled at 625 Hz with a 0.1 Hz high-pass filter and a 200 Hz low-pass filter. The measurement data were averaged across each condition. In off-line averaging of MEG data, the trials that had maximum values of sensor outputs larger than 2.5 pT were assumed to be blinks or eye movements, and discarded.

The averaged responses were band-pass filtered at 1-40 Hz. All recordings were performed in a magnetically shielded room. The monitor was placed outside a magnetically shielded room, and subjects observed it through a small window of the room.

4.2.5 Analysis

In order to analyze the brain activity, the time course of Root Mean Square (RMS) values was calculated by the time course of the averaged measurement data. A RMS value is expressed with the squared average sum of each channel output at a latency. Furthermore, to remove DC offset, the time average of RMS values before the stimulus onset was subtracted from whole RMS data.

We aimed to specify the source location of the binocular rivalry response, and source localization needs to specify the latency of the response. In Chapter 3, we demonstrated that transient responses of binocular rivalry were evoked at long latency after 400 ms. In order to specify such responses of binocular rivalry at long latency, we used two evaluation values, RMS ratio and correlation coefficient.

RMS ratio

The first value is RMS ratio that is defined by a division of the RMS in rivalry condition by that in non-rivalry condition. Each RMS value was normalized by the average of pre-trigger. The RMS ratio at time t was defined as

$$\frac{|a_t|}{\sum_k^{pre} |a_k|} \frac{\sum_k^{pre} |b_k|}{|b_t|}, \quad (4.1)$$

where a_t and b_t are the vectors formed by whole 64 channels MEG data at time t . a_t is in rivalry condition, and b_t is non-rivalry condition. Summation was conducted for -200 ms to 0 ms to normalize the data by the MEG strength during the pre-trigger period. The period that the ratio was 1.2 times larger than the maximum value during the pre-trigger period was selected for candidate time of visual rivalry, because it was supposed that the RMS ratio should increase by rivalry condition.

correlation coefficient

The second value is a correlation coefficient. It is a standardized inner product of whole 64 channels between two conditions in a time. The correlation coefficient

at time t was defined as

$$\frac{(a_t - \bar{a}_t) \cdot (b_t - \bar{b}_t)}{|a_t - \bar{a}_t| |b_t - \bar{b}_t|}, \quad (4.2)$$

where, \bar{a}_t is a mean vector of a_t . If specific brain activities might occur, they produce very different MEG patterns from the MEG in non-rivalry condition. Thus, it was supposed that the correlation coefficient decreases on rivalry condition. According to them, the period before and after 10 ms from the local minimum the value was selected for the other candidates of the visual rivalry.

Both values were calculated for entire recording time and periods to satisfy the both conditions were defined to be the rivalry specific periods.

4.2.6 Dipole estimation

To estimate the location of cortical activities, dipole estimations with the equivalent current dipole (ECD) model were conducted. 64 sensors were used for the analysis. The following criteria were adopted for the acceptance of the estimation; (1) the dipole should be in the cerebral cortex. (2) the goodness of fit (GOF) should be above 75 %. GOF was defined as

$$\left(1 - \frac{\sum_{i=1}^{64} (m_i - m_i^e)^2}{\sum_{i=1}^{64} m_i^2} \right) \times 100, \quad (4.3)$$

where m_i and m_i^e are measured and expected i th sensor values, respectively.

Because iso-contour maps of evoked MEG responses suggested the involvement of one or two dipoles, which differed depending on latency or subject, I selected one dipole model or two dipoles model on a case-by-case basis. Firstly, one dipole model was assumed, and the dipole was adopted if the above criteria were satisfied. When the criterion was not satisfied with one dipole model, two dipoles model was assumed. The dipoles were adopted if the above criteria were satisfied. The estimated dipoles were superimposed on three-dimensional MR images of each subject, and checked whether the dipole was in the cerebral cortex.

4.3 Results

4.3.1 MEG response of each stimuli

Time course of stacked waveforms of averaged MEG responses for each stimulus is shown in Figures 4.3 for motion direction rivalry, 4.4 for orientation rivalry, 4.5

for color rivalry. There was no significant difference at short latency, but difference at long latency for each stimulus. This tendency was consistent in all stimuli. Time courses of the RMS values between trials of both rivalry and non-rivalry condition are shown in Figure 4.6. The RMS value of rivalry condition was larger than one of non-rivalry condition after 200 ms. Time course of the RMS ratio is shown in Figure 4.7. There was the most prominent peak at 200 ms after stimulus onset, and continuous responses were appeared after 300 ms. Time course of the correlation coefficient is shown in Figure 4.8. The correlation coefficient had large continuous values from 100 ms to 300 ms and sporadic response synchronized with RMS ratios after 300 ms. Therefore, according to the definition of evaluate values, sporadic responses of binocular rivalry for each stimulus were specified after 300 ms. Although the precise latency was differed among each subject and stimuli, those latencies had same tendency for each stimuli. These results were in good agreement with results in Chapter 3.

4.3.2 Dipole estimation

Each response had a specific feature at long latency after 300 ms regardless of the type of stimulus. Most of iso-contour maps of specified responses were appeared to be similar patterns for each rivalry stimulus. Figure 4.9 shows a typical example of iso-contour map for each rivalry stimulus. For motion direction stimulus, the iso-contour map during the selected terms represented unambiguous two dipole pattern (Figure 4.9 (a)). The source localization resulted at the vicinity of middle temporal (MT) and front parietal (FP) lobes, (Figure 4.10). For orientation stimulus, the iso-contour map represented unambiguous one dipole pattern (Figure 4.9 (b)). The source localization resulted at the vicinity of posterior parietal (PP) lobe (Figure 4.11). For motion direction stimulus, the iso-contour map represented ambiguous bilateral pattern (Figure 4.9 (c)). However, the map of subject MY represented unambiguous two dipole pattern (Figure 4.9 (d)). It was suggested that the pattern shown in Figure 4.9 (c) was made by the flux cancellation. Thus, the source localization was performed by assuming two dipole in each case, and resulted at the vicinity of inferotemporal (IT) and FP lobes, (Figure 4.13). Because both dipoles for motion and color rivalry estimated at vicinity of right FP lobe, we also examined estimating by two dipoles for orientation rivalry. As a results, one of the dipoles was also estimated at vicinity of right FP lobe (Figure 4.12).

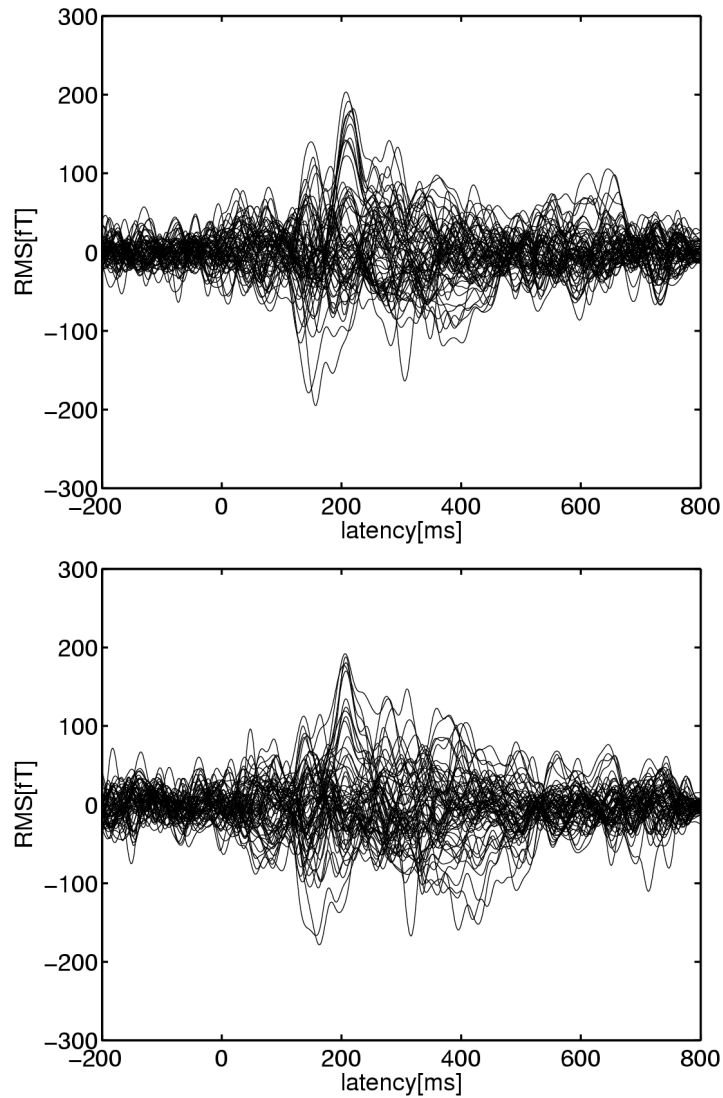


Figure 4.3: Typical stacked waveforms of averaged MEG responses of motion rivalry for rivalry (top) and control (bottom) conditions. The horizontal and vertical axes indicate latencies (ms) and amplitudes (fT). The most prominent peaks were found at around 200 ms from the stimulus onset for each condition.

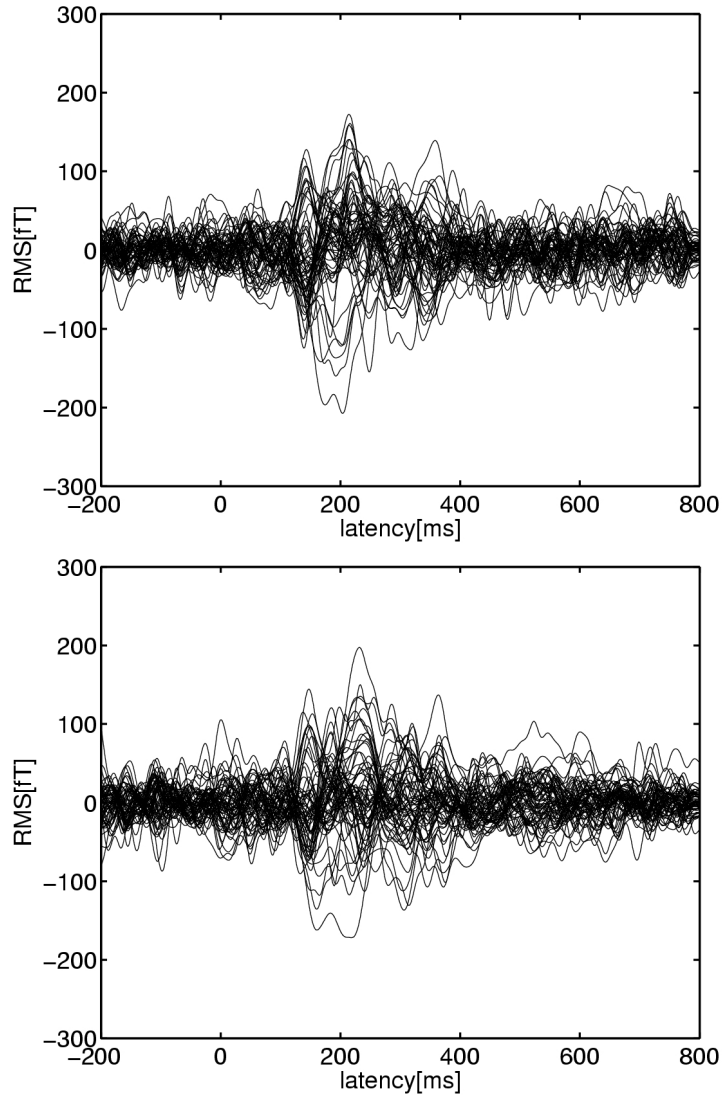


Figure 4.4: Typical stacked waveforms of averaged MEG responses of orientation rivalry for rivalry (top) and control (bottom) conditions. The horizontal and vertical axes indicate latencies (ms) and amplitudes (fT). The most prominent peaks were found at around 200 ms from the stimulus onset for each condition.

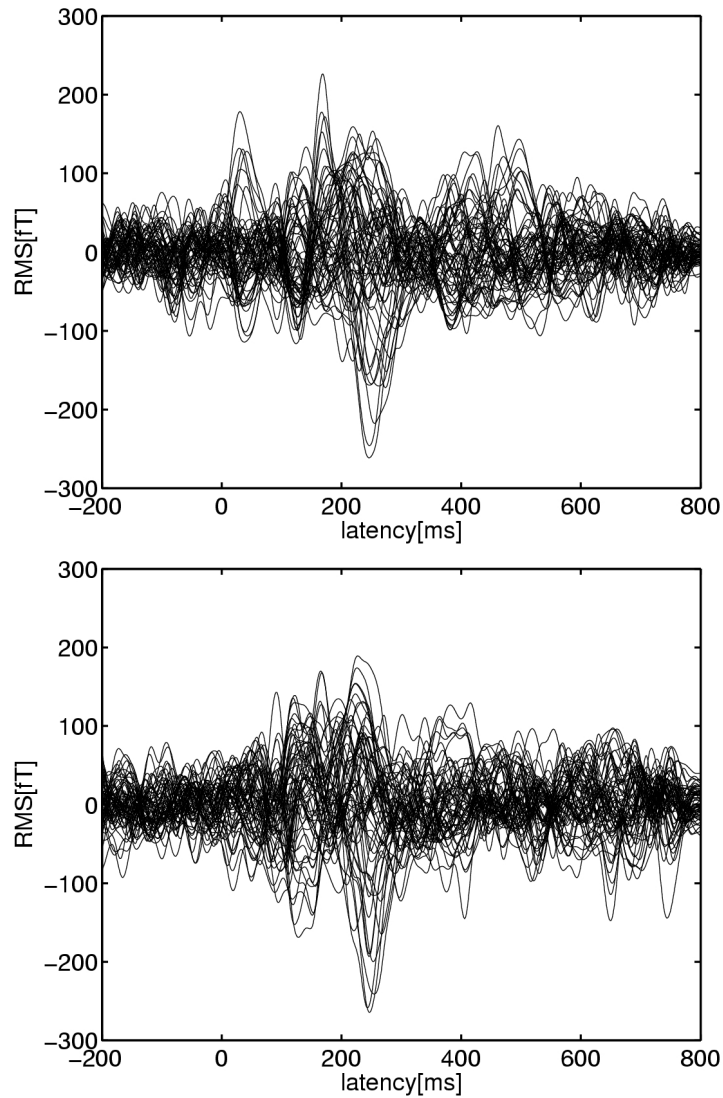


Figure 4.5: Typical stacked waveforms of averaged MEG responses of color rivalry for rivalry (top) and control (bottom) conditions. The horizontal and vertical axes indicate latencies (ms) and amplitudes (fT). The most prominent peaks were found at around 200 ms from the stimulus onset for each condition.

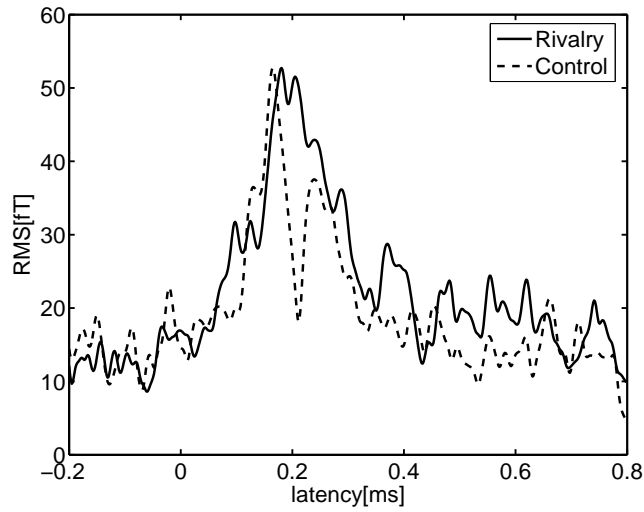


Figure 4.6: Typical time course of RMS for rivalry and non-rivalry condition. The horizontal and vertical axes indicate latencies (ms) and amplitudes (fT). The most prominent peaks were found at around 200 ms from the stimulus onset.

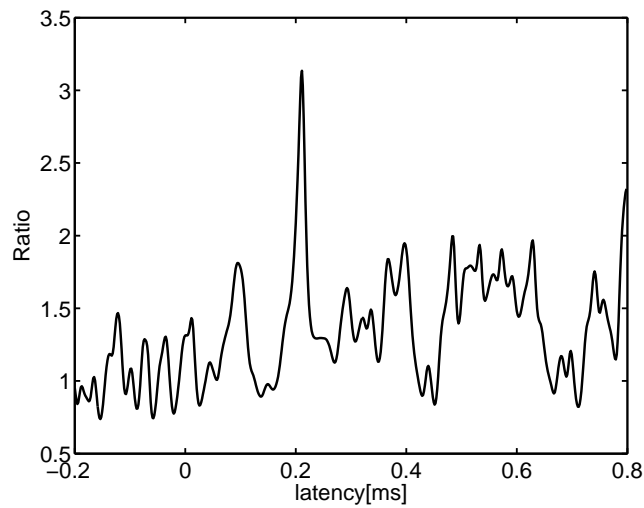


Figure 4.7: The time course of RMS ratio, the RMS of rivalry condition divided by the RMS of non-rivalry condition, for a typical subject. The horizontal and vertical axes indicate latencies (ms) and RMS ratio. The most prominent peaks were found at around 200 ms from the stimulus onset.

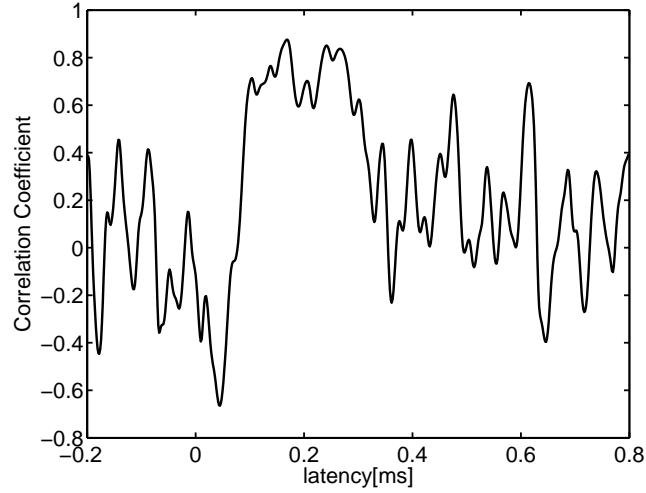


Figure 4.8: Time course of correlation coefficient calculated by rivalry and non-rivalry conditions. The horizontal and vertical axes indicate latencies (ms) and correlation coefficient. After the state where the correlation coefficient is high continues for about 200 ms, it has shifted to the state which has a large fluctuation.

4.4 Discussion

4.4.1 Implications of dipole locations

ECD specified by the two evaluation values were estimated at the vicinity of middle temporal (MT) lobe for motion direction rivalry (Figure 4.10), posterior parietal (PP) lobe for orientation rivalry (Figure 4.11) and bilateral inferotemporal(IT) lobes for color rivalry (Figure 4.13). The specified cortex was where the information of rivalrous attribute of each stimuli was mainly processed [74]. Thus, MEG responses of binocular rivalry was probably evoked at the cortex where the rivalrous attribute was processed. Moreover, the response of color rivalry was appeared at IT lobes. It is difficult to measure the response of color by non-invasive measurements. In this study, we succeeded to measure the response of color by amplifying MEG response with binocular rivalry.

4.4.2 Comparison with previous reports

In recent studies, contradicting reports of binocular rivalry have been presented for the invasive and non-invasive measurements. Most of electro-physiological stud-

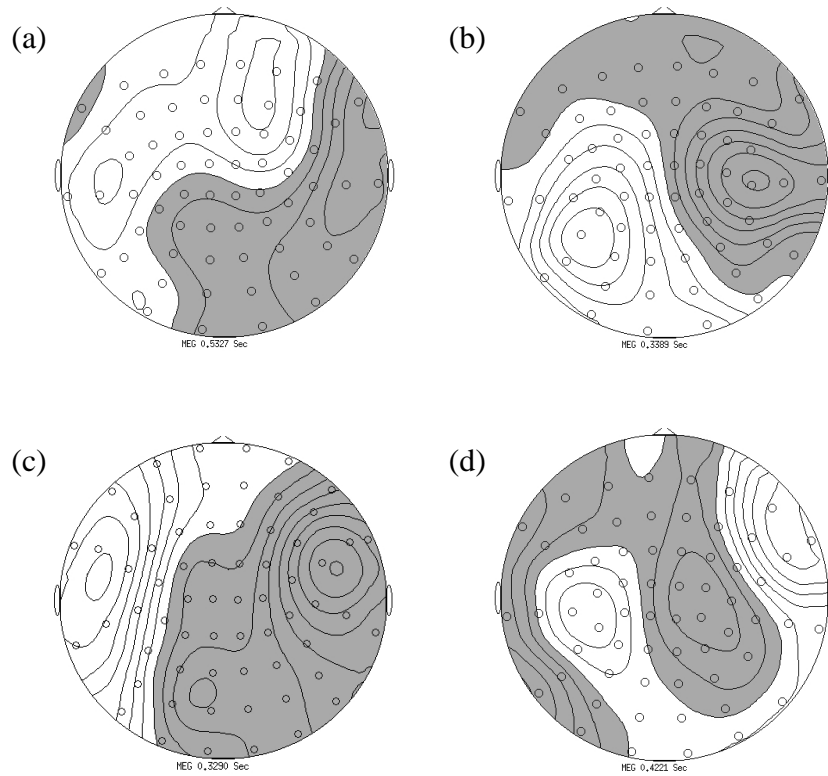


Figure 4.9: Typical iso-contour maps during binocular rivalry. Gray color showed inward flux, and white color showed outward flux. (a) the map of motion rivalry at around 532 ms. (b) the map of orientation rivalry at around 339 ms. (c) the map of color rivalry of a typical subject at around 329 ms. (d) the map of color rivalry of subject MY at around 422 ms.

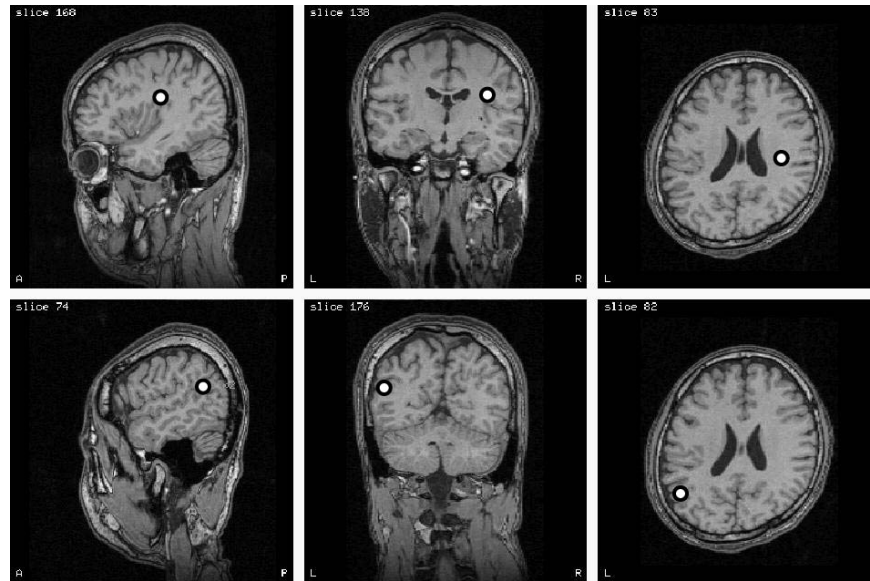


Figure 4.10: Typical example of estimated dipole locations for motion rivalry at around 532 ms (GOF 85.5 %). Each circle shows ECD existing in the slice, The dipoles were estimated in the vicinity of middle temporal (MT) area.

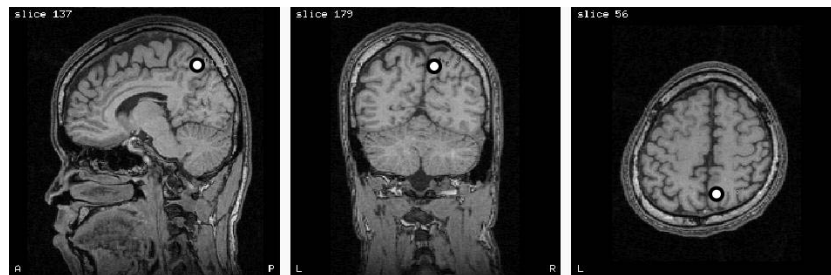


Figure 4.11: Typical example of estimated dipole location by one dipole for orientation rivalry. dipoles at around 339 ms (GOF 77.3 %). Each circle shows ECD existing in the slice, The dipoles was estimated in the vicinity of posterior parietal (PP) area.

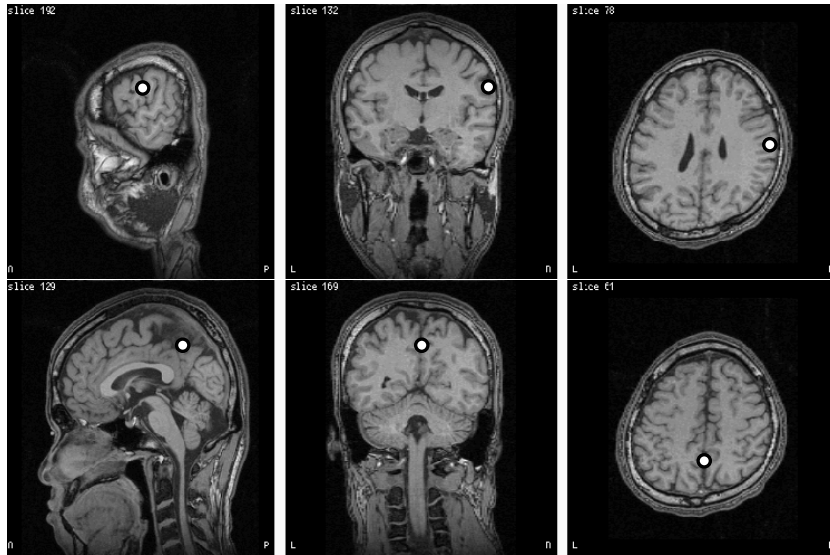


Figure 4.12: Typical example of estimated dipole locations by two dipoles for orientation rivalry at around 339 ms (GOF 83.9 %). Each circle shows ECD existing in the slice, The dipoles were estimated in the vicinity of posterior parietal (PP) area.

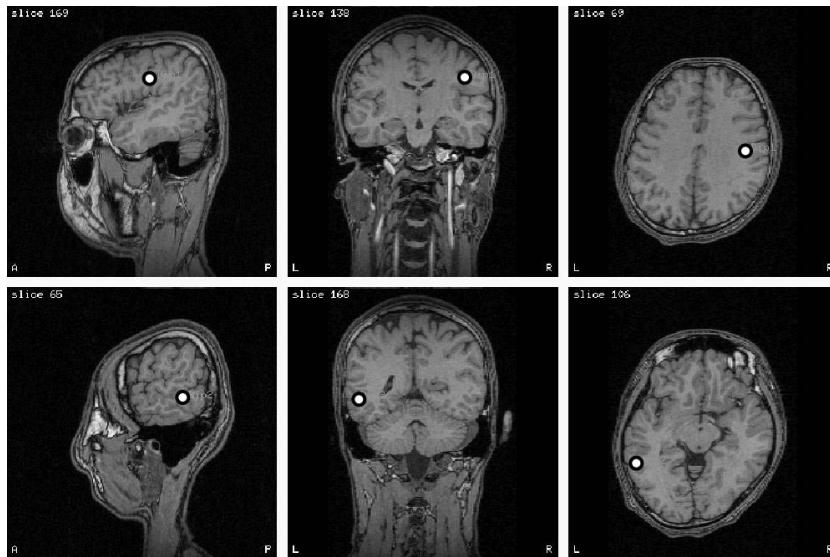


Figure 4.13: Typical example of estimated dipole locations for color rivalry at around 422 ms (GOF 76.8 %). Each circle shows ECD existing in the slice, The dipoles were estimated in the vicinity of inferotemporal (IT) area.

ies in alert monkeys showed the modulation in neural responses coincident with the monkeys perceptual reports at the higher level visual cortices, but the modulation was weak in lower level visual cortices. On the other hand several functional magnetic resonance imaging (fMRI) studies in human have mainly shown blood oxygen level dependent (BOLD) signal modulated in lower level visual cortices. This discrepancy has been an important issue to be resolved in binocular rivalry experiments, but has not been unresolved for a long time [8].

The result of the present study showed that the response of binocular rivalry appeared at higher level visual cortices. It was superficially consistent with only electro-physiological studies. However, previous MEG and EEG studies of binocular rivalry reported that the responses of binocular rivalry were existed at around occipital and temporal lobes, and indicated that from lower to higher level was related [13, 67, 72].

In the present study, MEG response at 100 ms after stimulus onset was amplified by binocular rivalry, but the correlation coefficient indicated high value which did not suited the assumed condition (Figure 4.7,4.8). This response would be evoked at V1, the lowest level visual cortex, and has not been interpreted to be the rivalry specific. If this response was also the rivalry specific, responses of binocular rivalry were differ between lower and higher visual cortices. Furthermore, it was suggested that there were two types of responses of binocular rivalry and electro-physiological and fMRI measurements specified mutually different responses.

4.4.3 Responses of perceptual switching

One of dipoles of each rivalry stimulus was estimated at the visual cortex where the attribute of rivalry was processed (Figure 4.10, 4.12, 4.13). On the other hand, the other dipole was estimated at right front parietal (FP) lobe at the same time. Lumer *et al* reported that the response of perceptual switching in binocular rivalry was evoked at the vicinity of right FP lobe [50]. The result of present study was in good agreement with this report. Because responses of FP lobe and the cortex where the attribute of rivalry was processed observed in same latency, it is suggested that perceptual switching induce neural synchronization between those cortices. Because Lumer *et al* used the rivalry stimuli between grating and face, the responses of these cortices probably attenuated. Thus, they could not specified the response depended on the attribute of rivalry stimuli.

4.4.4 Wide spread sensor responses

Srinivasan *et al* also argued that synchronous activities among whole cortices were appeared during binocular rivalry. However, they measured those responses with magneto sensor which did not have high spatial resolution. The present study demonstrated that binocular rivalry activated not only a visual cortex where the rivalrous attribute was processed, but also frontoparietal (FP) lobe at the same time. These sources formed wide spread responses 4.9, and most of sensors measured those responses. Thus it was suggested that the synchronous activities were not induced by neural synchronization of wide spread activities but by only few source activities.

Chapter 5

Color motion and binocular rivalry

Previous psychophysical studies reported the difference of a reaction time (RT) of a few hundreds milliseconds between luminance and color motion in low speed condition. Although electroencephalogram (EEG) studies reported a small difference between initial responses towards luminance and color motion also in low speed condition, a large difference reported by psychophysical studies of RTs has not been observed. The present study aimed to investigate late responses in order to clarify the difference of RTs between luminance and color motion in low speed condition. However, it is difficult to measure late responses which intensity is weaker than early responses. In Chapter 3, we reported that binocular rivalry stimuli evoked MEG responses at a long latency and the responses are greatly related to perceptions of stimuli. Thus, we used those responses as index of perception at a long latency, and investigated difference of perceptual processes between luminance and color motion using magnetoencephalogram (MEG). Before MEG measurements, we first measured the difference of perceptions for two types of stimuli by psychophysical methods. As a results, the perceptual rivalry of color motion was weaker than that of luminance of motion. Then, we recorded visual evoked fields (VEFs) of each stimulus with a whole-head MEG system. MEG responses of binocular rivalry were obtained from the subtraction between rivalry and control conditions, and those responses were shown between 400 to 550 ms after the stimulus onset for both stimuli. We also estimated source location of those responses, and presented that those responses originate at similar positions for both luminance and color motions. We also calculated the difference of latencies of those responses between the two stimuli. The latencies were obtained for each subject, and averaged across subjects for each stimulus. Consequently, the mean latency of the response of binocular rivalry for color motion was 5.7 ms

faster than that for luminance motion, but statistically significant difference were observed between them ($p > 0.05$).

5.1 Introduction

Many studies of visual motion perception used various types of motion stimuli, and most of them especially used luminance motion stimuli, such as gratings or random dot kinematogram [3, 11, 15, 37]. These motions defined by luminance is called first order motion. On the other hand, the motion defined by other visual properties (ex. color, texture and contrast) rather than by luminance is called second order motion [6, 45, 79]. Both first and second order motion are defined by luminance based information, and luminance has been assumed to be the principal factor of motion perception. However, there is other visual information which could define motion, color [22]. In this study, we aimed to investigate the MEG response of color motion using binocular rivalry stimuli.

Previous physiological work suggested that the information pathway of color pattern differed much one of luminance pattern. By physiological study, it is known that the information of color and luminance patterns are separated by cone and rod cells on retina, magno-cells and parvo-cells on lateral geniculate nucleus (LGN). The separated information is processed in two different pathways. They are called magnocellular pathway and parvocellular pathway, or dorsal pathway and ventral pathway [48]. The magnocellular pathway processes low frequency patterns and motions mainly using luminance information. The parvocellular pathway processes high frequency patterns and colors. However, because the motion which have no luminance information but have color information is also perceivable, it was suggested that color motion had a different information pathway from luminance motion [48].

There are some studies which compare color motion with luminance motion. Psychophysical studies have suggested that two separated streams process color motion and the separation of two motions depends on the speed of the motion [27]. In fast speed condition, color motion is processed as same as luminance motion. However, in low speed condition, color motion is processed differently from luminance motion. In addition, a difference of the reaction time (RT) for a few hundreds milliseconds between luminance and color motion were reported in very low speed condition (1 deg/s) [14]. As mentioned above, the information pathway differed much between luminance and color patterns. Electroencephalogram stud-

ies reported a small difference between initial responses towards luminance and color motion in low speed condition [52]. However, the large difference reported by psychophysical studies has not been observed.

To understand the process of color motion, a non-invasive measurement with high time resolution was needed. However, most of previous studies using EEG measured the response before 200 ms after stimulus onset which intensity was enough large to interpret. Responses after 400 ms stimulus onset were too weak to measure. In order to measure these weak responses, we used binocular rivalry motion stimuli. Binocular rivalry is a phenomenon created by presenting similar but different images for each eye independently [8]. In Chapter 3, we represented that brain responses of binocular rivalry were appeared at the long latency after 400 ms, and a previous study using EEG also reported such a response [73]. Since the perception of motion rivalry needs the perception of motion direction, the responses of motion rivalry would be heavily related to motion perception. Thus, we tried to measure the brain responses of color motion at the long latency using binocular rivalry stimuli.

Using two types of motion rivalry stimuli, we measured and compared MEG responses of binocular rivalry for luminance and color motions. To examine the perceptual rivalry for luminance and color motions, we also performed psychophysical experiments using same type of stimulus which used in MEG measurements. A motion stimulus which cause binocular rivalry has two directions which are mutually different by the right and left eyes, and has two perceptual interpretations [1]. One interpretation is a component motion. It is perceived as two independent movements on a same plane, and cause binocular rivalry after few seconds. The other is a pattern motion. It is perceived as one lattice pattern which moves in the direction of the vector sum of two motions, and does not cause a binocular rivalry. These two perceptual interpretations are perceived stochastically. It is known that these motions are perceived more as a component motion when the angle of two motion directions is large, and more as a pattern motion when the angle of two motion directions is small [4].

We measured the angle dependencies of perceptual rivalry for both motion, and verified whether the perception of luminance and color motion stimuli was differed. By the comparison of results between MEG and psychophysical measurements, It was suggested that the luminance motion and color motion were processed in a different pathway for lower level but in a same pathway for higher level. These results were very consistent with previous studies.

5.2 Methods

5.2.1 Subjects

The subjects were four healthy right-handed volunteers (22-27 years of age). All subjects had normal or corrected-to-normal acuity and normal color vision. All subjects participated in the MEG recordings, and two of them participated in the psychophysical measurement of perceptual rivalry.

5.2.2 Visual stimuli

A drifting horizontal sinusoidal grating was displayed in a 2.0 x 2.0 deg square window centered in the display (Figure 5.1). The luminance of stimuli and background were 4.0 cd/m^2 , and the spatial frequency of grating was 2.0 c/deg. Burr et al. have reported that the difference between RTs for luminance and color motion was remarkable at 1.0 deg/s or lower. Consequently, the motion speed was determined to be 0.8 deg/s. The gratings were black/white for luminance motion experiments, and red/green for color motion experiments. Red and green were set to isoluminance for each subject separately using the minimum flicker method. A fixation point was a yellow circle with a diameter of 0.1 deg and was displayed at the center of the screen through the experiment. In the control condition, the directions of the motions were identical to two eyes. In the rivalry condition, they differed 180 deg between the two eyes, and caused binocular rivalry sufficiently. These two conditions were presented in random order, and the number of trials was 100 for each condition. The inter-stimulus interval (ISI) was randomly varied from 1.6 to 2.4 s.

5.2.3 Instruments

Stimuli were generated on a PC with a VSG 2/3 (Cambridge Research Systems) graphics card and displayed on a 17 inch RGB monitor (Iiyama MT-8617ES). In order to present different images for each eye, a liquid crystal shutter (LCS), which was generally used to present 3D images, was used. The LCS was installed in front of the monitor, and its refresh rate synchronized with that of the monitor. The stimuli for right and left eyes were displayed alternatively for every frame, and the direction of circular polarization of LCS was synchronously changed. By using polarizing glasses, subjects observed the visual stimuli that were independent between right and left eyes. The monitor frame rate was 120

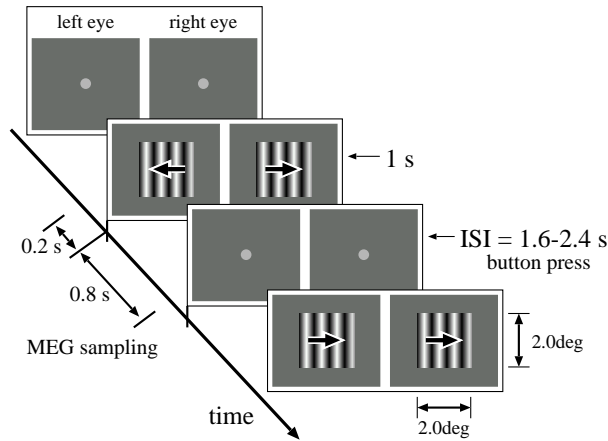


Figure 5.1: Schematic illustration of motion rivalry stimuli in luminance motion experiment. Drifting horizontal sinusoidal gratings were used. First, the fixation point is only presented. Then, the drifting grating which evoked motion rivalry was presented for 1.0 s, and dismissed again. The arrows indicate the direction of the motion; they were not part of the stimulus.

Hz, and observed frame rate was 60 Hz for each eye. Viewing distance was 3.2m. The monitor was placed outside of a magnetically shielded room, and subjects observed it through a small window of the room.

5.2.4 Measurement of perceptual rivalry

To verify whether the perception was differed between luminance and color motion stimuli, a psychophysical measurement of perceptual rivalry was performed. It is known that two motions are perceived more as a component motion when the angle between two motion directions is large, and more as a pattern motion when the angle between two motion directions is small [4]. A component motion corresponds to the rivalry condition, and a pattern motion corresponds to the control condition. In this study, we measured the angle dependencies of the proportion of perceptual rivalry for both luminance and color motions, and compared those results.

A drifting sinusoidal grating was displayed in 2.0 degree circular aperture centered in the display (Figure 5.2). The luminance of the stimulus and background were 4.0 cd/m², the spatial frequency of the grating was 2.0 c/deg, and the motion

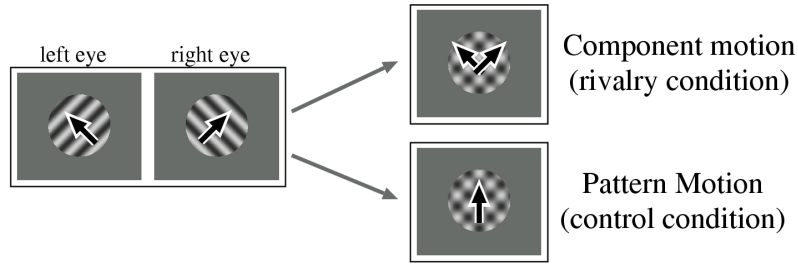


Figure 5.2: Schematic illustration of stimuli used in the psychophysical measurement. The arrows indicate the direction of the motion; they were not part of the stimulus. When the stimulus causing motion rivalry are presented, there are two perceptual interpretations. One is a component motion that cause binocular rivalry and the perceptual transition, and the other is a pattern motion that does not cause binocular rivalry.

speed was determined to be 0.8 deg/s. These parameters were as same as the parameters in MEG recordings. Two stimuli presented to right or left eye made an angle from 30 deg to 170 deg for every 20 deg. One stimulus tilted clockwise, the other tilted counter-clockwise based on the vertical upward direction.

The stimulus which had one of eight angles was randomly presented for 1 s. After the disappearance of the stimulus, subjects pressed one of two keys to indicate whether they perceived upward directions. Because the pattern motion corresponds to the control condition, the perception of the upward direction which were caused by hte pattern motion was considered as the control condition. When they did not perceive the upward directions, the perception of that trial was considered as the rivalry condition. They were instructed to attend only to the direction of stimuli, and not to attend to those grating patterns. Measurements were performed by 200 trials about each motion. A total of 400 trials was carried for each subject. The results of luminance and color motions were compared, and analyzed.

5.2.5 MEG recordings

Visual Evoked Fields (VEFs) beginning 200 ms before and ending 800 ms after the stimulus onset were recorded with a 440-channel whole-head MEG system (PQ2440R, Yokogawa, Japan). Data were sampled at 1000 Hz with a 0.1 Hz high-pass filter and a 200 Hz low-pass filter. All recordings were performed in a

magnetically shielded room.

The measurement data were averaged across each condition. In off-line averaging of MEG data, trials that had maximum values of sensor outputs larger than 2.5 pT were assumed to be blinks or eye movements, and discarded. The averaged responses were band-pass filtered at 1-40 Hz.

5.2.6 Analysis

RMS values

In order to analyze a brain activity, time courses of Root Mean Square (RMS) values were calculated from time courses of the averaged measurement data. A RMS value is expressed with the squared average sum of each channel output at a latency, and described as follows,

$$RMS(t) = \sqrt{\frac{\sum_k^N \{s_k(t)\}^2}{N}} \quad (5.1)$$

Here $s_k(t)$ shows the sensor value of k th sensor at time t , and N shows the number of sensors of the MEG system. The RMS is thought as magnitude of brain activity. In this study, the RMS was calculated with 300 ch sensor outputs excluded the channel of the frontal area in order to avoid the mixture of eye movement.

The RMS value is sharply changed with the noise level of the average of source data, and the noise levels of averaged data were heavily dependent on the number of trials. Thus, when the number of trials used for averaging differed between every conditions, the noise levels also differed and could not be compared between them. In order to compare RMS values between two conditions, it was necessary that a part of trials of which had more trials than the other was removed randomly, and the number of trials used for averaging was united across conditions. Furthermore, to remove DC offset, the time average of RMS values before the stimulus onset was subtracted from whole RMS data.

In order to analyze the brain activity, subtractions of root mean square between rivalry and control conditions were calculated. In Chapter 3, we have reported that the MEG response of binocular rivalry is evoked between 400 to 800 ms after stimulus onset and has low temporal frequency. Thus, we filtered the subtraction with 10 Hz low-pass filter, and determined the latencies of those responses by the latency of most prominent peak between 400 to 800 ms after stimulus onset.

Dipole estimation

To estimate the location of each cortical activity, a dipole estimation with the equivalent current dipole (ECD) model was conducted. 300 axial-z sensors, 70 of which were in vector sensors, were used for the analysis. The following criteria were adopted for the acceptance of the estimation; (1) the dipole should be in the cerebral cortex. (2) the goodness of fit (GOF) should be above 85 %. GOF was defined as

$$\left(1 - \frac{\sum_{i=1}^{300} (m_i - m_i^e)^2}{\sum_{i=1}^{300} m_i^2}\right) \times 100 \quad (5.2)$$

where m_i and m_i^e are measured and expected i th sensor values, respectively.

Because iso-contour maps of evoked MEG responses suggested the involvement of one or two dipoles, which differed depending on latency and subject, I selected one dipole model or two dipoles model on a case-by-case basis. Firstly, one dipole model was assumed, and the dipole was adopted if the above criteria were satisfied. When the criterion was not satisfied with one dipole model, two dipoles model was assumed. The dipoles were adopted if the above criteria were satisfied. The estimated dipoles were superimposed on three-dimensional MR images of each subject, and checked whether the dipole was in the cerebral cortex.

5.3 Results

5.3.1 Angle dependency of perceptual rivalry

The proportion of perceptual rivalry of the typical subject for luminance motion (solid line) and color motion (dashed line) are shown in Figure 5.3. The result shows the monotonic increase with increasing the angle of two motion directions. There was significant difference between the luminance and color motions. This difference suggested that the luminance motion was easier to cause perceptual rivalry.

To compare the data quantitatively, the data were approximated to a sigmoid function by the least square method. A sigmoid function is described as follows:

$$f(t) = \frac{1}{1 + \exp(-\theta)} \quad (5.3)$$

By the result of approximation, the angle of which the proportion of perceptual rivalry was equal to 50 % was calculated for each motion. The difference of angles

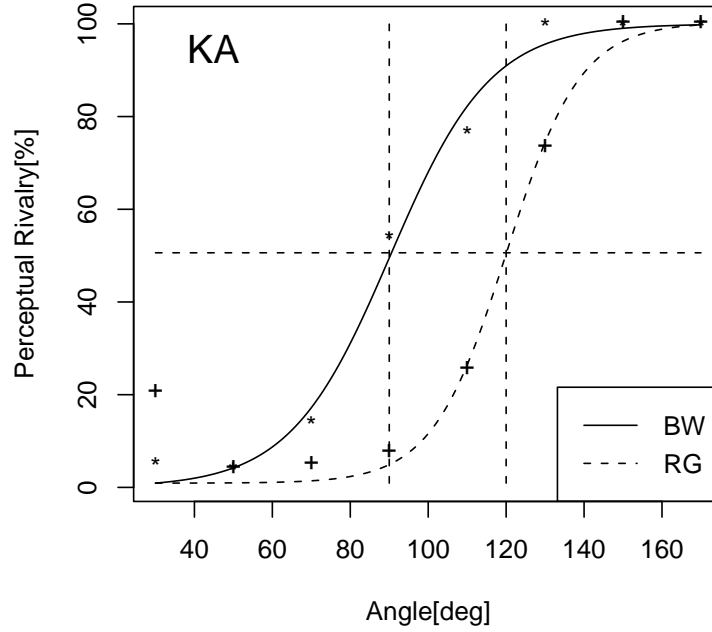


Figure 5.3: Typical example of the proportion of perceptual rivalry for luminance motion (solid line) and color motion (dashed line). The horizontal and vertical axes indicate angles (deg) and proportions of perceptual rivalry (%). Perceptions for two motions were distinctly different.

between the luminance and color motion was statistically significant (paired t-test, $p < 0.05$).

5.3.2 MEG responses

The time course of stacked waveforms of averaged MEG responses of luminance motion for both rivalry and control condition is shown in Figure 5.4. The most prominent peak was found at around 200 ms after the stimulus onset for each stimuli. At the latency after 300 ms, although there was no significant peak response, the response for rivalry condition was larger than for control condition.

Figure 5.5 shows the time course of stacked waveforms of averaged MEG responses of color motion for both rivalry and control condition. As well as luminance motion, the most prominent peaks were found at around 200 ms from the stimulus onset for each condition, and there was no significant peak response.

To analyze these MEG data, we calculated the time course of RMS values.

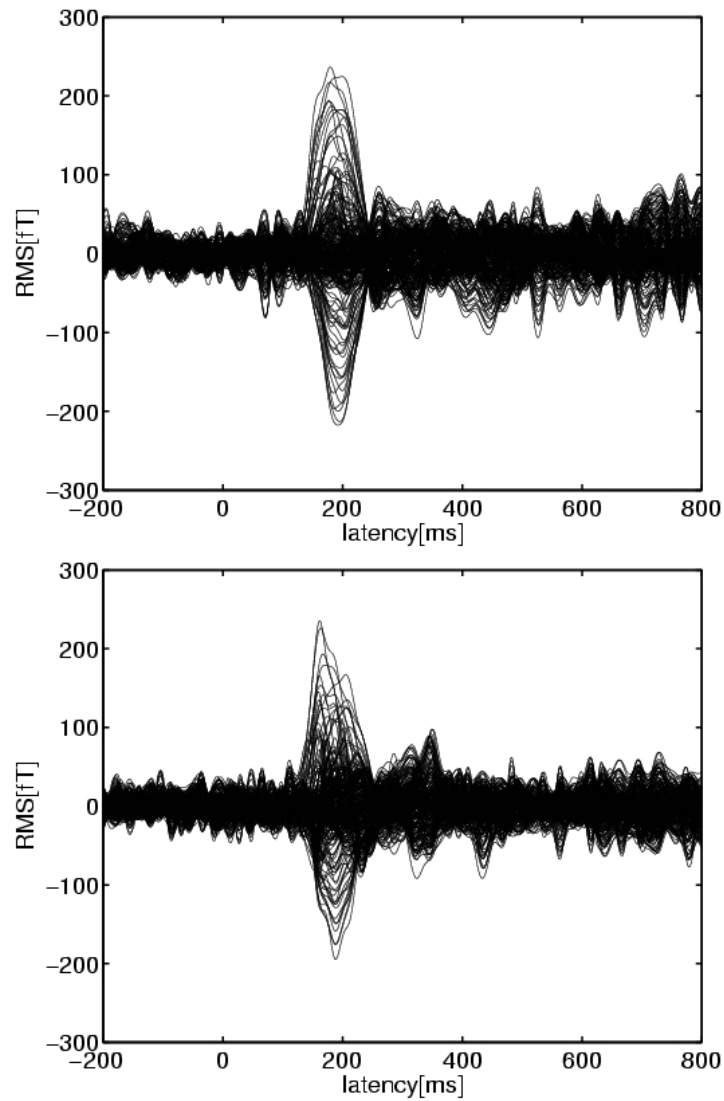


Figure 5.4: Typical stacked waveforms of averaged MEG responses of luminance motion under the rivalry (top) and control (bottom) condition. The horizontal and vertical axes indicate latencies (ms) and amplitudes (fT). The most prominent peaks were found at around 200 ms from the stimulus onset for each condition.

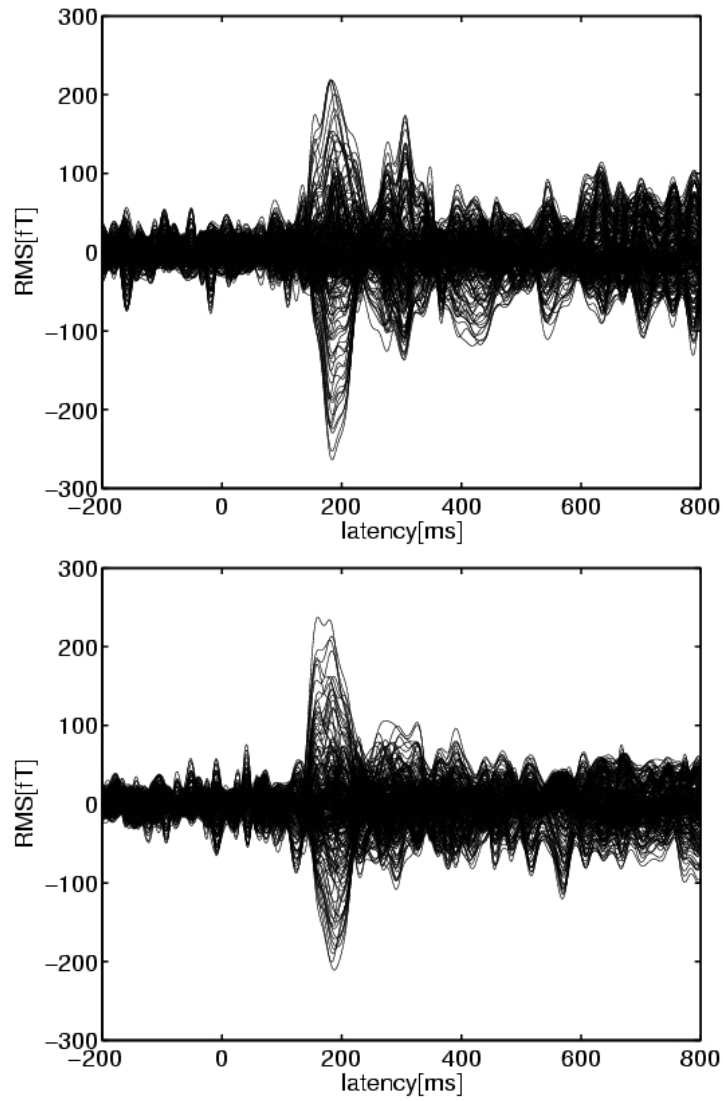


Figure 5.5: Typical stacked waveforms of averaged MEG responses of color motion under the rivalry (top) and control (bottom) condition. The horizontal and vertical axes indicate latencies (ms) and amplitudes (fT). The most prominent peaks were found at around 200 ms from the stimulus onset for each condition, as well as luminance motion

Figure 5.6 shows typical time courses of RMS values for each condition and each stimulus. As well as stacked waveforms, the most prominent peak (M1) was found at around 200 ms from the stimulus onset for all condition and stimulus. There are no significant difference about the latencies (paired t-test, $p > 0.05$) and intensities (paired t-test, $p > 0.05$) of M1. It was confirmed that the response of the rivalry condition at the long latency was larger than that of the control condition, and especially differed after 400 ms. These result consisted with the our previous study (Chapter 3). In Figure 5.6, there was large difference of the response for color motion between rivalry and control conditions. However, this difference was not observed for all subjects similarly. To resolve such a problem, the grand average of the responses for binocular rivalry averaged across all subjects was calculated.

To analyze MEG responses of binocular rivalry, we calculated the subtraction of RMS values of control condition from those of rivalry condition for each stimuli, and averaged across subjects. Figure 5.7 shows the time course of grand averages of RMS subtractions for luminance and color motion stimuli. There were large responses (M2) of binocular rivalry at around 400 ms for both motions. The early response which corresponded with M1 was appeared at around 200 ms only for luminance motion. These results were consisted with the result in Chapter 3. However, for color motion, no significant response was appeared at around 200 ms.

5.3.3 Comparison of the latency between luminance and color motions

It was reported that the RT of color motion was a few hundreds milliseconds later than the RT of luminance motion in very low speed condition (1 deg/s) [14]. It is conceivable that the latency of the late response of motion rivalry which is related to motion perception is closely related to the RT. Thus, the latency of the late response (M2) after 400 ms for each motion was acquired by the subtraction of RMS values of control condition from those of rivalry condition. Those latencies were compared between color and luminance motions. The difference of M2 latencies for luminance and color motion was calculated for each subject, and averaged across subjects. As a result, the latency of color motion was 5.7 ± 150.3 ms faster than luminance motion. However, there was no statistically significant difference between the peak latencies of the two motion perceptions (paired t-test, $p > 0.05$).

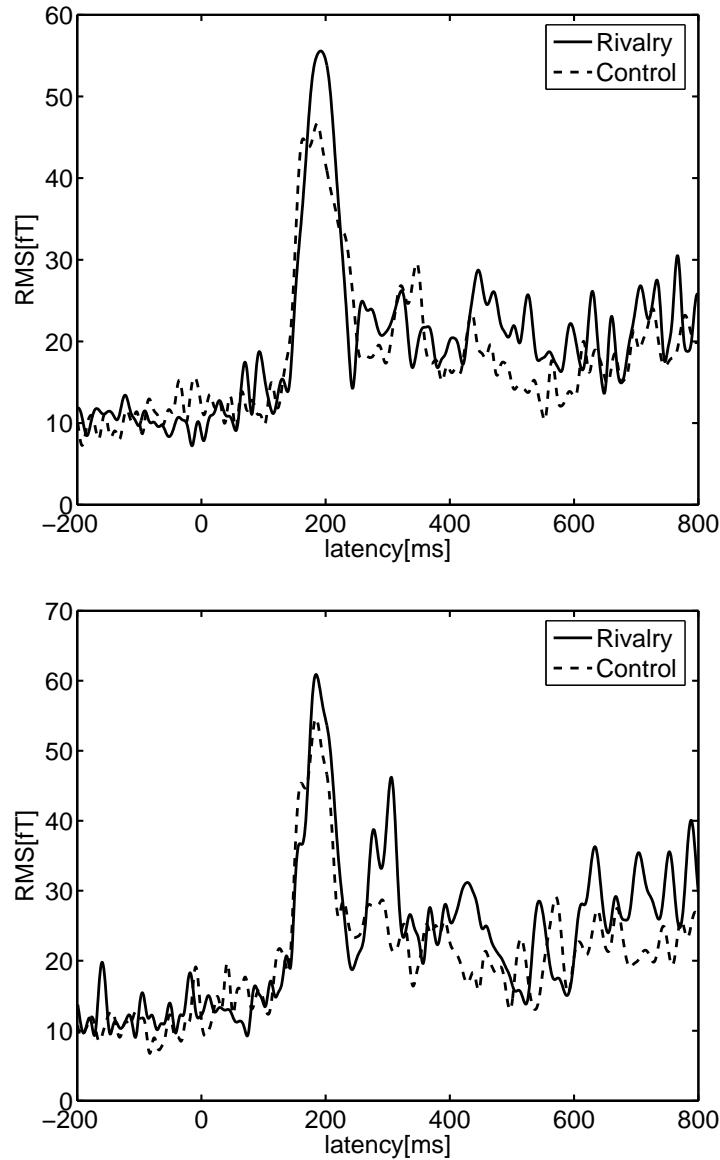


Figure 5.6: Typical example of the time course of RMS values for rivalry (solid line) and non-rivalry (dashed line) conditions. *top*: luminance motion rivalry. *bottom*: color motion rivalry. The horizontal and vertical axes indicate latencies (ms) and amplitudes (fT). The most prominent peaks were found at around 200 ms from the stimulus onset for each condition and each rivalry.

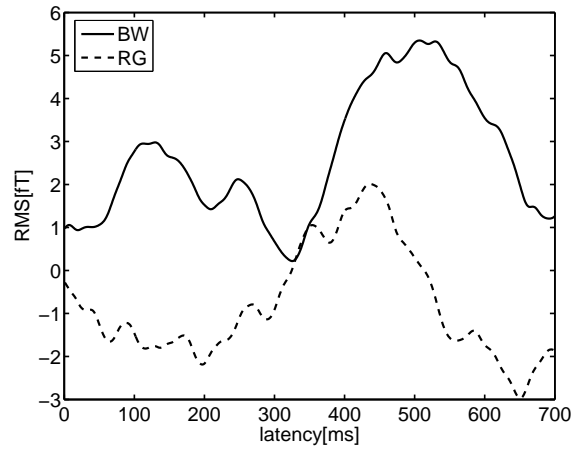


Figure 5.7: Time course of grand averages of RMS values for luminance (solid line) and color (dashed line) motion. The horizontal and vertical axes indicate latencies (ms) and amplitudes (fT). There were large responses (M2) of binocular rivalry at around 400 ms for both luminance and color motion. The early response which corresponded with M1 was also appeared at around 200 for luminance motion.

5.3.4 Dipole estimation

To interpret a physiological meaning of these responses, ECDs of the responses (M1 and M2) were estimated for each motion. The latency of M2 was used as described above. The iso-contour map of M2 clearly appeared the pattern which was evoked by two dipoles (Figure 5.8(d)). On the other hand, the map of M1 appeared the pattern which was evoked by one dipole. (Figure 5.8(c)). However, two dipoles model was performed each estimation in order to satisfy the criteria for the acceptance for the estimation.

Figure 5.8 shows the typical example of estimated dipole locations for luminance motion. The source localization for luminance motion was resulted at the vicinity of parietal area for M1, and at the vicinity of middle temporal (MT) and parietal area for M2 respectively. Figure 5.9 shows the typical example of estimated dipole locations for color motion. The source localization for color motion was resulted at similar positions to luminance motion for both M1 and M2 responses. Although, there was no significant response at the latency of M1 for color motion, the ECDs of color and luminance motions were similar very well. Thus, it was interpreted that responses for color and luminance motions were cor-

responded each other for both M1 and M2.

5.4 Discussion

5.4.1 Angle dependency of perceptual rivalry

The angle dependency of perceptual rivalry differed between the color and luminance motion. Previous physiological and psychophysical studies suggested that the information pathway of color pattern differed much that of luminance pattern. This result suggested that the process of the motion integration differed between color and luminance motions.

It is known that the information of color and luminance patterns are separated at early visual stage, and processed thorough different pathways [48]. Present study showed the stage by which the visual information was separated into color and luminance pathways.

5.4.2 Responses of binocular rivalry

The measurement of MEG responses of binocular rivalry were performed on color and luminance motions. The response of motion onset which was not exactly related to binocular rivalry was appeared at around 200 ms for each color and luminance motion. By the result of grand averages of RMS subtractions (Figure 5.7), responses related to binocular rivalry was appeared at around 400 ms for both conditions, and those latencies were consisted with our previous study in Chapter 3. Because responses were appeared for both conditions, it was suggested that the response about the color motion performed same response of binocular rivalry as luminance motion.

On the other hand, a weak response at around 200 ms was only appeared for luminance motion. Our previous study in Chapter 3 showed that the early response was not so strong response, however, tended to be amplified. The absence of this early response for color motion suggested that processes of the color and luminance motions were somewhat different at the early visual stage.

5.4.3 Latency of the late response

Although the motion speed was designed as 0.8 deg/s at which the responses to these motions were reported to differ largely [27], the difference of latencies of the

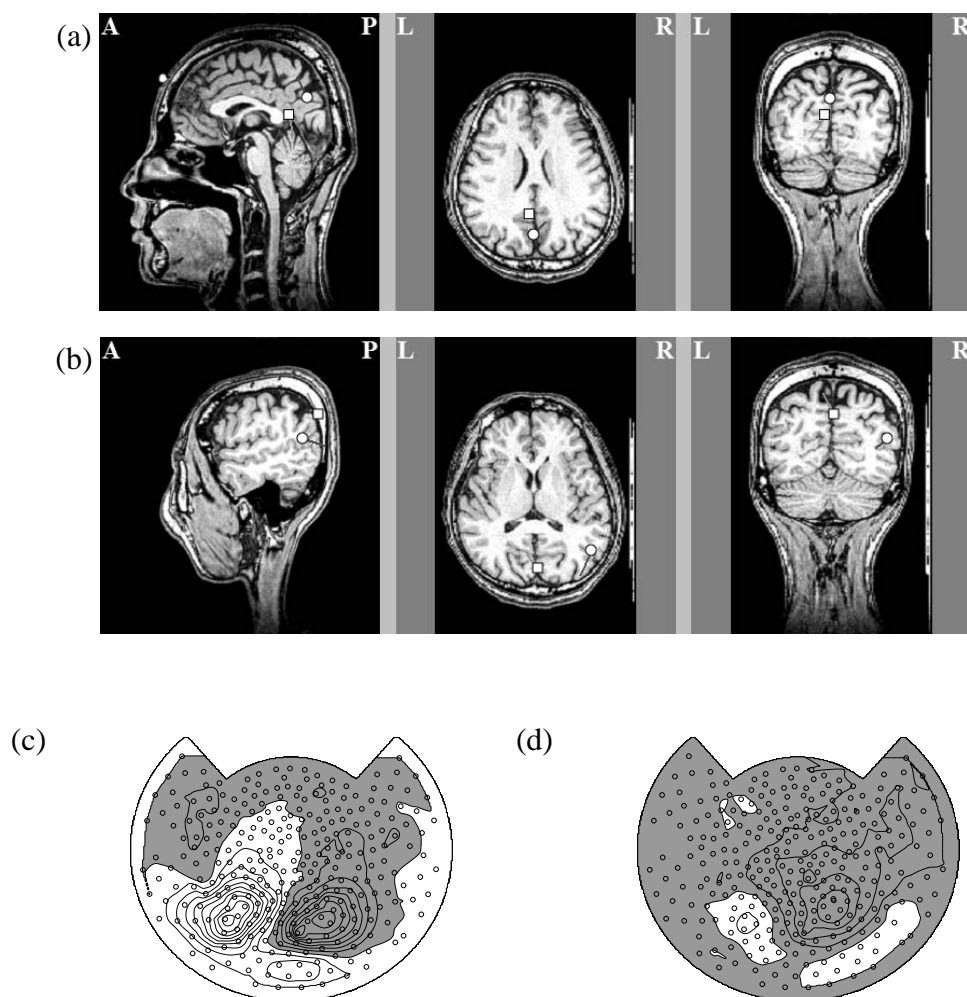


Figure 5.8: Typical example of estimated dipole locations for luminance motion. (a) dipoles for M1 response at around 178 ms (GOF 91.3 %). (b) dipoles for M2 response at around 438 ms (GOF 87.2 %). Each circle shows ECD existing in the slice, and each square shows one existing in another slice. The dipoles were estimated in the vicinity of parietal area for M1, and at the vicinity of middle temporal (MT) and parietal area for M2 respectively. (c,d) The iso-contour map of each response.

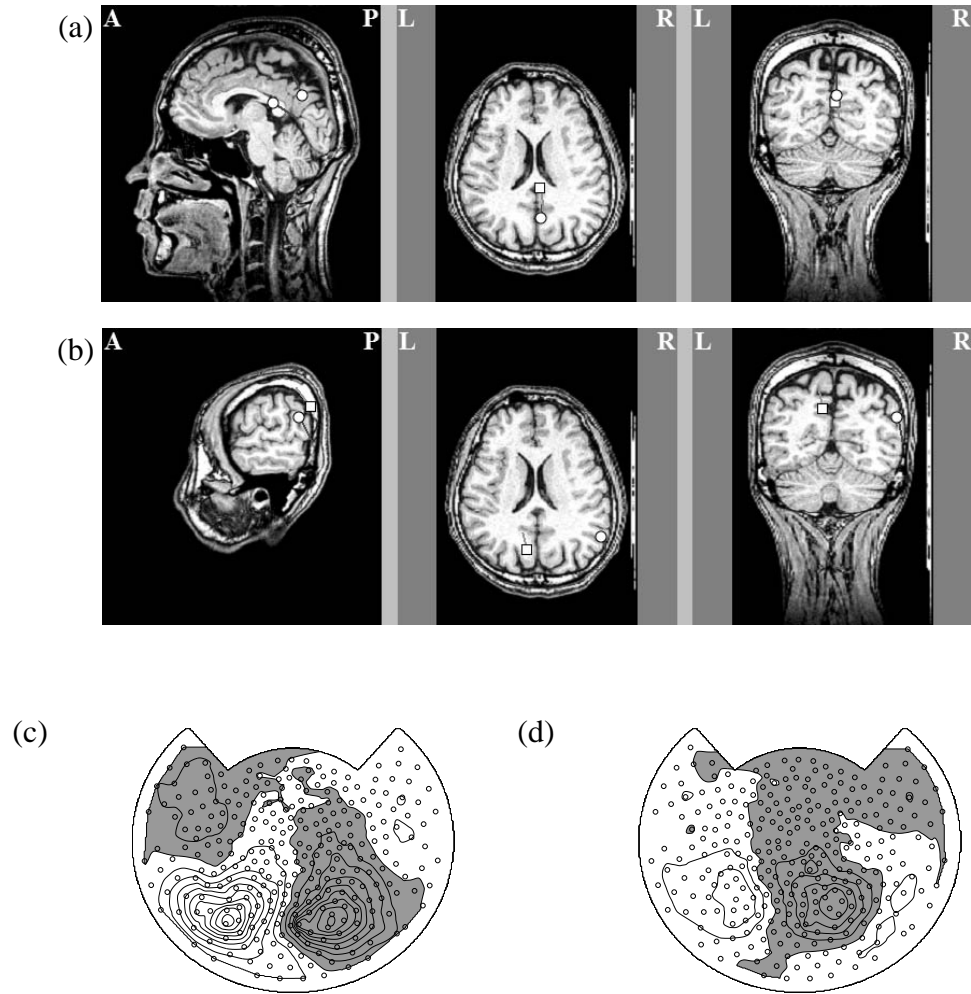


Figure 5.9: Typical example of estimated dipole locations for color motion. (a) dipoles for M2 response at around 180 ms (GOF 93.0 %). (b) dipoles for M1 response at around 421 ms (GOF 89.9 %). Each circle shows ECD existing in the slice, and each square shows one existing in another slice. The dipoles were estimated in similar positions to luminance motion. (c,d) The iso-contour map of each response.

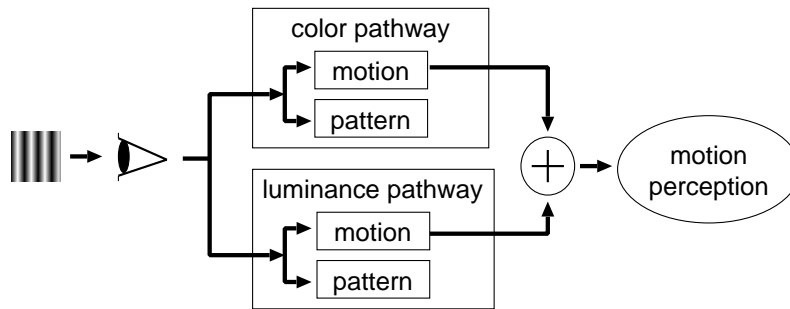


Figure 5.10: Schematic illustration of the process of motion perception.

late response between luminance and color motion had no statistically significant difference. On the other hand, previous psychophysical studies reported that the RT of color motion delayed for a few hundreds milliseconds. Reasons of the disagreement between present and previous studies were supposed to be as follows. One is that the difference of RT between the two motions was arisen in a process after the response of binocular rivalry, and could not be expressed at the latency when the response was evoked. Another is that the stimuli used in this study could not elicit perceptual difference enough. Burr et al. reported that the RT for color motion was sensitive to the contrast of stimuli, [14]. In this study, it was thought that RTs for luminance and color motion did not differ enough. The measurement of RT matched to the MEG measurement is necessary to clarify the suppositions.

5.4.4 Physiological meaning of ECDs

The ECDs of M1 were estimated at the vicinity of parietal area. There is the primary visual area, V1, where the visual information was processed first in cortices. Most studies of EEG and MEG generally reported that the first response of a visual stimulus evoked in the primary visual area. In this study, The first response, M1, was evoked at about 180 ms after the stimulus onset.

The ECDs of M2 were estimated at MT of right hemisphere for both luminance and color motions. Responses of M2 was evoked by binocular rivalry. Some fMRI studies have reported that binocular rivalry modulated the responses of the cortices concerning the attribute of stimuli [70]. On the other hand, electrophysiological experiments have indicated that the response of MT related to a motion [74]. The result suggested that M2 responses of both luminance and color motions were same response, and the binocular rivalry stimuli of color motion also evoked

rivalry responses as same as the luminance motion.

The result of ECDs also estimated the other dipole at V1. Thus, the rivalry response at MT could be synchronously with that of V1. Previous studies reported that whole visual areas from lower to higher levels were involved in binocular rivalry, and there were some interaction controlled dominance and suppression of lower visual area [67]. The result of this study suggested the existence of some interactions between higher and lower visual areas in binocular rivalry.

To summarize, it is suggested that the luminance and color motions were processes in different pathways at lower level of visual processing, but in same pathway at higher level. From the result of the psychophysical experiment, the luminance and color motions were integrated after integration of multiple motion information (Figure 5.10).

However, more detailed experimental research was required to confirm the difference between luminance and color motion processing.

Chapter 6

Conclusions

In this thesis, I studied characteristics of binocular rivalry which includes properties of perceptual rivalry, reaction times (RTs) towards motion rivalry stimuli, and MEG responses towards various types of rivalry stimuli. The first part of this chapter summarizes the results of all four experiments, in which several psychophysical measurements of binocular rivalry were compared with neural responses measured by MEG. Then, I discuss possible neural mechanisms of visual motion perception, putting together all experimental results. Lastly, future studies and engineering applications are presented.

6.1 Summary of the results

Four experiments presented in this thesis investigated neural mechanisms of binocular rivalry. They are summarized briefly in the followings.

6.1.1 Two rivalries of motion rivalry stimuli

Chapter 2 presented the first experiment, in which the transient property of binocular rivalry was studied by a psychophysical method. Firstly, we examined the relation between the proportion of perceptual rivalry and angles of rivalry stimuli between two motion directions which presented to two eyes. There was a tendency in the proportion of perceptual rivalry increasing with the angle. Then we fit those results with sigmoid curve, and those results differed among subjects. Secondly, using visual stimuli with nearly 50 % perceptual rivalry, we measured reaction times (RTs) in which only one direction was perceived for both pattern and component motion. The distribution of RTs for each motion perception was

differed among subjects. To compare distributions of RTs between all conditions quantitatively, the results were averaged across all subjects. Non-parametric test was performed to examine the difference of their distributions. As a result, there was a statistically significant difference of RTs between two perceptual conditions (Wilcoxon test, $p < 0.01$). Lastly, we compared RTs between conventional motion and pattern motion. Two distributions were differed completely from each other. Naturally, there was statistically significant difference between them (Wilcoxon test, $p < 0.01$). To summarize, RTs of conventional motion, pattern motion and component motion were about 400, 800 and 1100 ms, respectively. Moreover, the difference of RTs between pattern and component motions was about 300 ms, and the difference of RTs between conventional and pattern motions was about 400 ms. Therefore, the RT increased in the order; conventional, pattern, and component motions. It speculated that the RT also increased in the order; control, fusion, and rivalry condition. On the other hand, the variance of each RT also increased in the same order.

6.1.2 Brain responses of rivalry stimuli

Chapter 3 presented the second experiment studying neural activities involved in binocular rivalry. In order to examine the transient responses of binocular rivalry, we measured visual evoked fields (VEFs) using whole-head MEG system. Firstly, the measurement data were classified according to the angle between two motion directions presented for the right and left eyes. The peak response was observed at about 200 ms after the stimulus onset for each angle. On the other hand, the response at a long latency after 300 ms showed no remarkable peak and a greatly different waveform for each stimulus condition. Thus, we examined the relationship between the proportion of the perceptual rivalry and the RMS value of the first peak response. However, no correlation was observed between them. Then, we classified the MEG responses according to the perceptual rivalry, which was checked with MEG recording. However, in those results, both intensity and latency of the first peak response had no significant difference of between rivalry and control conditions. On the other hand, the response in rivalry condition at the latency after 300 ms was larger than that in control condition, and this tendency was observed among all subjects. Because the detailed time course of those responses differed among subjects, the time average of RMS values for every 100 ms was calculated for each perceptual condition in order to investigate the rough tendency of the response. These results were averaged across all subjects, and

compared between two conditions. Significant differences were appeared at long latency after 400 ms (paired t-test, $p < 0.05$), especially after 500 ms (paired t-test, $p < 0.01$). On the other hand, the difference between two perceptual states was not so large at the short latency before 200ms. Although the slight increase was observed at around 100 ms, it was not statistically significant ($p > 0.05$).

6.1.3 Responses of various types of binocular rivalry

Chapter 4 presented the third experiment studying transient responses of various types of binocular rivalry stimuli, orientation, motion direction and color. Averaged MEG responses of each stimuli showed same tendency that there were no significant difference at short latency, but large difference at long latency. To simplify the experimental analysis, two evaluate values were employed: the ratio of RMS values and correlation coefficient. These values efficiently specified the response of binocular rivalry. Each response had a specific feature at long latency after 300 ms regardless of the type of stimulus. Most of iso-contour maps of specified latencies were appeared to be similar patterns among all subjects for each rivalry. Source localizations resulted at separate places for each stimulus; the vicinity of middle temporal (MT) for motion direction, posterior parietal (PP) for direction, and inferotemporal (IT) for color rivalry, respectively.

6.1.4 Application of binocular rivalry

Chapter 5 presented the forth experiment, in which the difference between luminance and color motion was studied by the MEG response of binocular rivalry. Firstly, the proportion of perceptual rivalry for luminance motion and color motion were measured by psychophysical methods. The data was fit with a sigmoid function by the least square method. The angle of 50 % perceptual rivalry was calculated for each motion. By the result, the difference of angles between the luminance and color motion was statistically significant (paired t-test, $p < 0.05$). Next, MEG responses of motion onset stimuli were recorded for both luminance and color motion stimuli. To analyze MEG responses of binocular rivalry, we calculated the subtraction of RMS values from the values of rivalry condition by those of control condition for each stimuli, and averaged across all subjects. There were large responses (M2) of binocular rivalry at around 400 ms for both luminance and color motion. The early response which was named as M1 was appeared at around 200 ms only for luminance motion. Thus, the latency of the late

response (M2) after 400 ms was acquired for each motion, and the difference of latencies between luminance and color motions was calculated for each subject. As a result, the latency of color motion was 5.7 ms faster than that of luminance motion. However, there was no statistically significant difference between the peak latencies of the two motion perceptions (paired t-test, $p > 0.05$).

6.2 General discussions

From previous reports, it is known that the latency of primary visual processing takes about 100 ms, and the RT of motor system takes about 200ms. From our results, the RT for coherent motion was about 800 ms, and that for component motion was about 1100 ms. The difference of RTs for coherent and component motion from ordinary motion was 400 ms and 800 ms, respectively. Assuming that component motion elicited inter-ocular rivalry after resolve of motion type rivalry, the response of motion type rivalry is presented after primary visual processing and inter-ocular rivalry. Thus, the response would be presented at around 500 ms after stimulus-onset. Correspondingly, Chapter 3 resulted that the amplification of MEG response was elicited by motion type rivalry at around 500 ms and after. This result suggested that inter-ocular rivalry was resolved after the process of motion type rivalry.

From the results of Chapter 3 and 4, a transient response of binocular rivalry appeared as the amplification of MEG response at the cortex where the visual property of the rivalry stimulus are processed in natural condition. Results of both psychophysical and MEG measurements showed that the binocular rivalry was resolved when and where the visual property of the rivalry stimulus was processed.

Our results described above showed that the MEG response of binocular rivalry processed at the cortex where the visual property of the rivalry stimulus were processed in conventional condition. Some previous studies reported that the synchronous firing of tens of thousands of neurons is necessary in order to evoke a brain response which could be measured by MEG [30]. On the other hand, in a cerebral cortex, it is known that visual information is processed in some functional columns; For example, orientation columns in V1, motion direction columns in MT, or some characteristic columns in IT. Thus, the transient MEG response of binocular rivalry is probably elicited by population firing in functional columns.

The result in Chapter 2 indicated that existence of perceptual rivalry caused a delay of RT. Thus, binocular rivalry would be the process which resolve a com-

plex input to an acceptable certain image with some delay, and some neural circuit performed population firing in the task. It is known that the time constant of single neuron dynamics has less than 10 milliseconds. From the result of our psychophysical experiment, although the delay of perceptual rivalry was about 300 ms, the variance of the delay was also 300 ms. The result suggested that the fast response of binocular rivalry was near 0 ms, and there was not enough time which visual information passed through the loop of some cortical regions. Thus, the resolve of binocular rivalry may be processed with intra column loop rather than inter column loop. Because a resolving process within a column has been observed about a formation of tuning curve in primary visual cortex (V1), such an intra column loop may exist and perform a resolving process of binocular rivalry. Some previous studies investigated neural dynamics of binocular rivalry with mathematical or computational methods. However, the dynamics has not been clarified yet. Further studies are desirable to show the neural basis of binocular rivalry.

The response of binocular rivalry which measured in this thesis was the response caused by the visual stimulus which was hard to resolve. Previous studies reported same type of response, N400, about linguistic stimuli. N400 is a brain response presented non-verbal stimuli which formed some letters, and it was evoked at about 400 ms after stimulus-onset. Thus, it was suggested that the stimulus which was hard to resolve cause an amplification of brain response. In Chapter 5, we used binocular rivalry stimuli to measure the weak response of color motion. Therefore, conflicting stimuli probably enabled to measure a weak response of a higher level function and to make a functional mapping about them.

6.3 Future studies and engineering applications

In this thesis, we have measured some psychophysical properties of binocular rivalry. Nevertheless, many properties of binocular rivalry has not been clarified enough. For example, the RT measurement in Chapter 2 treated only the angle of which the proportion of perceptual rivalry was close to 50 %. However, the behavior of other angles which cause more or less rivalry is also necessary, because there is the possibility that RTs of binocular rivalry stimuli are affected by the rivalrous difficulty of an input stimulus. Moreover, although proportions of perceptual rivalry were compared between luminance and color motion in Chapter 5, the measurement of RTs also required for color motion. It will show the difference

of characteristics between luminance and color motion more clearly. For further studies, it will be necessary to investigate rivalry between color and luminance, which luminance motion and color motion have different directions each other, in order to speculate the neural mechanism of motion perception.

It is known that the predominance of binocular rivalry is affected by attention. In this thesis, we used a motion rivalry stimulus which caused two binocular rivalries, motion type rivalry and inter ocular rivalry, and obtained the brain responses of perceptual rivalry. In this case, whether motion type rivalry was occurred should be reasonably affected by attention. From our result, because the MEG response was varied by perceptual rivalry, it was suggested that the MEG response could be controlled by the perceptual rivalry which was controlled by attention. Therefore, the response of binocular rivalry with attention control would be applied to brain machine interface (BMI).

In addition, it has been difficult problem to measure the strength of attention quantitatively. In Chapter 2, we used the binocular stimulus with varied angle of motion directions between left and right eye, and obtained the angle of which the proportion of perceptual rivalry was close to 50 %. If attention affect the predominance of motion type rivalry and change the property of the perceptual rivalry, the strength of attention could be measured by comparison of the angle between attention and control condition. This measurement will be highly important for the investigation about attention.

Bibliography

- [1] Adelson, E. H. and Movshon, J. A. Phenomenal coherence of moving visual patterns. *Nature*, 300:523–525, Dec 1982.
- [2] Ahlfors, S. P., Simpson, G. V., Dale, A. M., Belliveau, J. W., Liu, A. K., Korvenoja, A., Virtanen, J., Huotilainen, M., Tootell, R. B., Aronen, H. J., and Ilmoniemi, R. J. Spatiotemporal activity of a cortical network for processing visual motion revealed by meg and fmri. *Neurophysiol.*, 82(5):2545–2555, Nov 1999.
- [3] Amano, K., Kuriki, I., and Takeda, T. Direction-specific adaptation of magnetic responses to motion onset. *Vision Res*, 45(19):2533–2548, Sep 2005.
- [4] Andrews, T. J. and Blakemore, C. Integration of motion information during binocular rivalry. *Vision Res.*, 42(3):301–309, Feb 2002.
- [5] ASHER, H. Suppression theory of binocular vision. *Br J Ophthalmol*, 37(1):37–49, Jan 1953.
- [6] Badcock, D. R. and Derrington, A. M. Detecting the displacement of periodic patterns. *Vision Res*, 25(9):1253–1258, 1985.
- [7] Blake, R., Fox, R., and McIntyre, C. Stochastic properties of stabilized-image binocular rivalry alternations. *J Exp Psychol*, 88(3):327–332, Jun 1971.
- [8] Blake, R. and Logothetis, N. K. Visual competition. *Nat Rev Neurosci.*, 3(1):13–23, Jan 2002.
- [9] Blake, R., O’Shea, R. P., and Mueller, T. J. Spatial zones of binocular rivalry in central and peripheral vision. *Vis Neurosci*, 8(5):469–478, May 1992.

- [10] Borsellino, A., De Marco, A., Allazetta, A., Rinesi, S., and Bartolini, B. Reversal time distribution in the perception of visual ambiguous stimuli. *Kybernetik*, 10(3):139–144, Mar 1972.
- [11] Braddick, O. A short-range process in apparent motion. *Vision Res*, 14(7):519–527, Jul 1974.
- [12] Breese, B. B. Binocular rivalry. *Psychol. Rev.*, 16:410–415, 1909.
- [13] Brown, R. J. and Norcia, A. M. A method for investigating binocular rivalry in real-time with the steady-state vep. *Vision Res.*, 37(17):2401–2408, Sep 1997.
- [14] Burr, D. C., Fiorentini, A., and Morrone, C. Reaction time to motion onset of luminance and chromatic gratings is determined by perceived speed. *Vision Res*, 38(23):3681–90, Dec 1998.
- [15] Castelo-Branco, M., Goebel, R., Neuenschwander, S., and Singer, W. Neural synchrony correlates with surface segregation rules. *Nature*, 405(6787):685–689, Jun 2000.
- [16] Chen, Y., Matthews, N., and Qian, N. Motion rivalry impairs motion repulsion. *Vision Res.*, 41(27):3639–3647, Dec 2001.
- [17] Cobb, W. A., Morton, H. B., and Ettlinger, G. Cerebral potentials evoked by pattern reversal and their suppression in visual rivalry. *Nature*, 216(120):1123–1125, Dec 1967.
- [18] Cohen, D. Magnetoencephalography: detection of the brain’s electrical activity with a superconducting magnetometer. *Science*, 175(22):664–666, Feb 1972.
- [19] Cosmelli, D., David, O., Lachaux, J. P., Martinerie, J., Garnero, L., Renault, B., and Varela, F. Waves of consciousness: ongoing cortical patterns during binocular rivalry. *Neuroimage*, 23(1):128–140, Sep 2004.
- [20] Labra, C.d and Valle-Inclán, F. Electrical activity in primary visual area due to interocular suppression. *Neuroreport*, 12(18):4099–4102, Dec 2001.
- [21] De Marco, A., Penengo, P., and Trabucco, A. Stochastic models and fluctuations in reversal time of ambiguous figures. *Perception*, 6(6):645–656, 1977.

- [22] De Valois, R. L. and De Valois, K. K. *Spatial Vision*. Oxford University Press, New York, 1988.
- [23] Fahle, M. Binocular rivalry: suppression depends on orientation and spatial frequency. *Vision Res*, 22(7):787–800, 1982.
- [24] Fortin, A., Faubert, J., Ptito, A., Gjedde, A., Kupers, R., and Ptito, M. Stereoscopic processing in the human brain as a function of binocular luminance rivalry. *Neuroreport*, 14(8):1163–1166, Jun 2003.
- [25] Fox, R. *Binocular Vision*. MacMillan, London, 1991.
- [26] Fylan, F., Holliday, I. E., Singh, K. D., Anderson, S. J., and Harding, G. F. Magnetoencephalographic investigation of human cortical area v1 using color stimuli. *Neuroimage*, 6(1):47–57, Jul 1997.
- [27] Gegenfurtner, K. R. and Hawken, M. J. Interaction of motion and color in the visual pathways. *Trends Neurosci*, 19(9):394–401, Sep 1996.
- [28] Gibson, J. J. The problem of temporal order in stimulation and perception. *J Psychol*, 62(2):141–149, Mar 1966.
- [29] Hämäläinen, M., Hari, R., Ilmoniemi, R. J., Knuutila, J., and Lounasmaa, O. V. Magnetoencephalography – theory, instrumentation, and applications to noninvasive studies of the working human brain. *Reviews of Modern Physics*, 65(2):413–505, 1993.
- [30] Hara, K. and Kuriki, S. *Brain Magnetics - SQUID measurements and medical applications (in Japanese)*. Ohm publishing, Tokyo, 1997.
- [31] Hering, W. *Outlines of a Theory of the Light Sense*. Harvard Univ. Press, Cambridge, Massachusetts, 1964.
- [32] Howard, I. P. and Rogers, B. J. *Binocular Vision and Stereopsis*. Oxford University Press, New York, 1995.
- [33] Hupe, J. M. and Rubin, N. The dynamics of bi-stable alternation in ambiguous motion displays: a fresh look at plaids. *Vision Res*, 43(5):531–548, Mar 2003.
- [34] Tokyo, S. C.i. U. o. *Introduction of statistics (in Japanese)*. Tokyo University publishing, Tokyo, 1991.

- [35] Tokyo, S. C.i. U. o. *Statistics for natural science (in Japanese)*. University of Tokyo publishing, Tokyo, 1992.
- [36] James, W. *The Principles of Psychology*. Macmillan, London, 1891.
- [37] Kaneoke, Y., Bundou, M., Koyama, S., Suzuki, H., and Kakigi, R. Human cortical area responding to stimuli in apparent motion. *Neuroreport*, 8(3):677–682, Feb 1997.
- [38] Kaplan, I. T. and Metlay, W. Light intensity and binocular rivalry. *J Exp Psychol*, 67:22–26, Jan 1964.
- [39] Kessler, R. M., Partain, C. L., Price, R. R., and James, A. E. J. Positron emission tomography. Prospects for clinical utility. *Invest Radiol*, 22(7):529–537, Jul 1987.
- [40] LANSING, R. W. ELECTROENCEPHALOGRAPHIC CORRELATES OF BINOCULAR RIVALRY IN MAN. *Science*, 146:1325–1327, Dec 1964.
- [41] Lee, S. H. and Blake, R. V1 activity is reduced during binocular rivalry. *J. Vis.*, 2(9):618–626, 2002.
- [42] Lee, S. H., Blake, R., and Heeger, D. J. Traveling waves of activity in primary visual cortex during binocular rivalry. *Nat Neurosci*, 8(1):22–23, Jan 2005.
- [43] Lehky, S. R. Binocular rivalry is not chaotic. *Proc Biol Sci*, 259(1354):71–76, Jan 1995.
- [44] Lehky, S. R. and Maunsell, J. H. No binocular rivalry in the LGN of alert macaque monkeys. *Vision Res*, 36(9):1225–1234, May 1996.
- [45] Lelkens, A. M. and Koenderink, J. J. Illusory motion in visual displays. *Vision Res*, 24(9):1083–1090, 1984.
- [46] Leopold, D. A. and Logothetis, N. K. Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature*, 379(6565):549–553, 1996.
- [47] Levelt, W. J. M. Note on the distribution of dominance times in binocular rivalry. *Br. J. Psychol.*, 58(1):143–145, May 1967.

- [48] Livingstone, M. and Hubel, D. Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science*, 240(4853):740–749, May 1988.
- [49] Logothetis, N. K. and Schall, J. D. Neuronal correlates of subjective visual perception. *Science*, 245(4919):761–763, Aug 1989.
- [50] Lumer, E. D., Friston, K. J., and Ree, G. Neural correlates of perceptual rivalry in the human brain. *Science*, 280(5371):1930–1934, Jun 1998.
- [51] MacKay, D. M. Evoked potentials reflecting interocular and monocular suppression. *Electroencephalogr Clin Neurophysiol*, 25(5):507–508, Nov 1968.
- [52] McKeefry, D. J. The influence of stimulus chromaticity on the isoluminant motion-onset vep. *Vision Res*, 42(7):909–922, Mar 2002.
- [53] Mosher, J. C., Lewis, P. S., and Leahy, R. M. Multiple dipole modeling and localization from spatio-temporal MEG data. *IEEE Trans Biomed Eng*, 39(6):541–557, Jun 1992.
- [54] Mueller, T. J. and Blake, R. A fresh look at the temporal dynamics of binocular rivalry. *Biol Cybern*, 61(3):223–232, 1989.
- [55] Murata, T., Matsui, N., Miyauchi, S., Kakita, Y., and Yanagida, T. Discrete stochastic process underlying perceptual rivalry. *Neuroreport*, 14(10):1347–1352, Jul 2003.
- [56] Nara, T., Oohama, J., and Ando, S. Direct reconstruction of current dipoles using the vector green formula. In *Mathematical engineering technical reports*, 2005.
- [57] Ogawa, S., Tank, D. W., Menon, R., Ellermann, J. M., Kim, S. G., Merkle, H., and Ugurbil, K. Intrinsic signal changes accompanying sensory stimulation: functional brain mapping with magnetic resonance imaging. *Proc Natl Acad Sci U S A*, 89(13):5951–5955, Jul 1992.
- [58] Ooi, T. L. and He, Z. J. Binocular rivalry and visual awareness: the role of attention. *Perception*, 28(5):551–574, 1999.
- [59] Polonsky, A., Blake, R., Braun, J., and Heeger, D. J. Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nat Neurosci.*, 3(11):1153–1159, Nov 2000.

- [60] Robinson, S. E. and Vrba, J. Functional neuroimaging by synthetic aperture magnetometry (sam). In *Recent Advances in Biomagnetism*, pages 302–305, 1998.
- [61] Schein, S. J. and Monasterio, F. M.d. Mapping of retinal and geniculate neurons onto striate cortex of macaque. *J Neurosci*, 7(4):996–1009, Apr 1987.
- [62] Sheinberg, D. L. and Logothetis, N. K. The role of temporal cortical areas in perceptual organization. *Proc Natl Acad Sci U S A*, 94(7):3408–3413, Apr 1997.
- [63] Sheinberg, D. L. and Logothetis, N. K. Noticing familiar objects in real world scenes: the role of temporal cortical neurons in natural vision. *J Neurosci*, 21(4):1340–1350, Feb 2001.
- [64] Sherrington, C. S. *Integrative Action of the Nervous System*. Yale Univ. Press, New Haven, Connecticut, 1906.
- [65] Singh, K. D. Functional imaging of the brain using superconducting magnetometry. *Endeavour*, 19(1):39–44, 1995.
- [66] Spekreijse, H., Tweel, L. H.v. d, and Regan, D. Interocular sustained suppression: correlations with evoked potential amplitude and distribution. *Vision Res*, 12(3):521–526, Mar 1972.
- [67] Srinivasan, R., Russell, D. P., Edelman, G. M., and Tononi, G. Increased synchronization of neuromagnetic responses during conscious perception. *J. Neurosci.*, 19(13):5435–5448, Jul 1999.
- [68] Takeda, T. *Brain Engineering (in Japanese)*. Corona publishing, 2003.
- [69] Takeda, T., Owaki, T., Haruta, Y., and Uehara, G. Characteristics of a 440ch meg system with vector sensors. In *Proceedings of Biomag2004*, pages 640–641, Aug 2004.
- [70] Tong, F., Nakayama, K., Vaughan, J. T., and Kanwisher, N. Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron*, 21(4):753–759, Oct. 1998.
- [71] Tononi, G. and Edelman, G. M. Schizophrenia and the mechanisms of conscious integration. *Brain Res Brain Res Rev*, 31(2-3):391–400, Mar 2000.

- [72] Tononi, G., Srinivasan, R., Russell, D. P., and Edelman, G. M. Investigating neural correlates of conscious perception by frequency-tagged neuromagnetic responses. *Proc Natl Acad Sci U S A*, 95(6):3198–3203, Mar 1998.
- [73] Valle-Inclán, F., Hackley, S. A., Labra, C.d, and Alvarez, A. Early visual processing during binocular rivalry studied with visual evoked potentials. *Neuroreport*, 10(1):21–25, Jan 1999.
- [74] Van Essen, D. C. and Gallant, J. L. Neural mechanisms of form and motion processing in the primate visual system. *Neuron*, 13(1):1–10, Jul. 1994.
- [75] Von Helmholtz, H. *Treatise on Physiological Optics*. Dover, New York, 1866/1925.
- [76] Walker, P. The subliminal perception of movement and the 'suppression' in binocular rivalry. *Br J Psychol*, 66(3):347–356, Aug 1975.
- [77] Wheatstone, C. On some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philosophical Transactions on Royal Society of London*, 128:371–394, 1838.
- [78] Wilson, H. R., Blake, R., and Lee, S. H. Dynamics of travelling waves in visual perception. *Nature*, 412(6850):907–910, Aug 2001.
- [79] Zanker, J. M. Theta motion: a paradoxical stimulus to explore higher order motion extraction. *Vision Res*, 33(4):553–569, Mar 1993.