SPATIOTEMPORAL DYNAMICS OF BINOCULAR RIVALRY

By

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Dissertation
Submitted to the Faculty of the
Graduate School of Vanderbilt University
in partial fulfillment of requirements
for the degree of
DOCTOR OF PHILOSOPHY
in
Psychology
May, 2009
Nashville, Tennessee

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To my parents,

for their support, patience and sacrifice for the last 35 years

ACKNOWLEDGEMENTS

The completion of this thesis would have been impossible without the help and support of other people. It is therefore my greatest pleasure to thank all these people. As I write this acknowledgement, I enjoy remembering the unforgettable days spent struggling for the advancement of science and life.

I am greatly indebted to my academic advisor Randolph Blake. He has continuously encouraged me to develop myself in a number of areas. First, I cannot imagine how much my understanding of science, its implication and practice, has improved over the years. Without his help, my understanding of science would have remained within the area where science and folk psychology are mixed. Second, Randolph has shown enormous patience when teaching me how to communicate scientific material. Without his help, my communication skills including scientific writing, would remain disorganized and incoherent. Third, I have learned a lot from him about how maintain integrity not only as a scientist but also as a responsible human being.

I thank my Ph.D. committee members – Jeffrey Schall, Thomas Palmeri and Vivien Casagrade – for their invaluable criticism, discussion and encouragement. In addition, I extend my thanks to AB Bonds who gave me the most critical advice. I still keep those pieces of advice in mind and will remember them.

I thank Sang-hun Lee and his lab members, and David Heeger. They have developed several crucial ideas that are the bases of this dissertation. Without their continual input, a number of interesting observations would have been impossible.

For the past 7 years, I have truly enjoyed the life in Blake Lab and am proud to have been part of it. I thank David Bloom and Daniel Shima for their technical support. I also thank Sang-chul Chong, Lee Gilroy, Emily Grossman, Sharon Gutterman, Stuart Jackson, Sammy Hong, Chai-youn Kim, Sam Ling, Kazushi Maruya, Joel Pearson, Ken Sobel, Tony Rassian, Duje Tadin and Eunice Yang. I believe all graduate students agree that no graduate student can finish his/her thesis without close collaboration, discussion and, most of all, kegs of beer with his/her lab members. This is especially true for those graduate students like me who have failed their qualifying examinations. They pulled me whenever I was in despair and pushed me whenever I stood still.

I offer thanks to my friends in Nashville and Vanderbilt University. I am grateful to Geoff Woodman and Pierre Pouget. I really enjoyed the enthusiasm they created during my years in animal research facilities: they brought new ideas and challenges every day to the lab. I would like to mention Leanne Boucher and Corrie Camalier who helped me in a number of ways in my graduate school life. I will also remember Olivia Cheung and Julia High who shared the office with me. I also thank Alan Wong, Jay Todd, Erik Emeric and Jejoong Kim. We have spent years in this building with me. We always encourage each other that someday we will leave this building with a smile. Deserving of special mentions are several Korean friends at Vanderbilt – Young-jin Cho, Sungho Choi, Hakyu Jeong, Geung-young Kim, Young-tae Lee, Ki-tae Nam, Jaeyong Suh, Jae-youn Yi and Do-joon Yi. Without their help, life in this foreign country would have been too difficult to stay for the last seven years. In particular, I express my sincere gratitude to Jeong-oh Kim and Bo. Choi. They have changed my life such that now I view the world with a totally different perspective, which I could not have imagine a few years ago. I would like to acknowledge my friends in Nashville Korean United Methodists Church for their prayers. I thank Sejin Kim, Sunghoon Cho and Yoonsuk Kam for sharing many delightful moments. In addition, I especially thank my girlfriend Min-Young Kim for her support and encouragement. She endures all the troubles that a boyfriend preparing dissertation defense has produced.

Some friendships last 10, 20 and 30 years. I show my earnest thanks to those friends. Jung-keun, Heejae, Howon, Jiwon and Jieun have always been willing to entertain me despite their busy schedules. I also thank my college friends, the "gangsang" brethren: Jong-hyuk, Jae-eun, Narae, Bo-won, Jongwhan, Yeonsang, Jonghyun, Jeong-duk, Sang-won, Chang-hoon, Tesu, Dongwook, Ungseup, Daehee, Sungho and Changhee. In particular, I will not forget those refreshing and deflightful travels with some "gangsang" brethren studying in the States, Yujin, Jaeyul, Eunjoo, Geumbong and Jihoon. We traveled to the Grand Canyon, Yellow Stone, Olympic, Acadia, and Glacier National Parks. I also thank Kyung-rok, a buddy since our military service together and now a buddy for playing golf. I thank Sungho and Hyunae for their encouragement and inspiring questions. I truly thank all of them.

Finally, I express my best thanks to my family for their patience, sacrifice, love and prayers. I thank my sister and her husband. I have been studying with less burden because they have taken care of family business. I also thank my uncle and aunt in Indiana. Most of all, to my parents, I express my best and earnest thanks. Dad and Mom, I love you. And I thank God for everything.

This research was supported by the Vanderbilt University's College of Arts and Science, Vanderbilt University Psychology Department and grants from the U. S. National Institute of Health EY13385 and EY16752.

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CHAPTER I

INTRODUCTION

1.1 Perceptual experiences of binocular rivalry

Binocular rivalry refers to the perceptual alternations that occur when two dissimilar images are presented to the two eyes: while one image is perceptually dominant, the other image is suppressed from visual awareness; but shortly thereafter the dominant image disappears and the suppressed image becomes dominant. This description of rivalry, however, is not entirely correct. Perception tends to alternate distinctly between two entire rival stimuli if the stimuli are small; but, periods of mixed dominance consisting of intermingled portions of both eyes' views often appear when the rival targets subtend several degrees in visual angle. In the latter situation, overall rivalry seems to appear as if binocular rivalry occurs simultaneously within several 'zone's distributed over the visual field (Blake, O'Shea, & Muller, 1992), and the state of this mixed dominance is dynamically changing over space and time (Wilson, Blake, & Lee, 2001). It means that the perceptual experiences of binocular rivalry are spatiotemporal in nature.

Historically, the spatiotemporal nature of binocular rivalry dynamics was documented by the pioneering study of Sir Charles Wheatstone (1838), in which he described the perceptual experiences of rivalry when two different letters were viewed by the two eyes: "At the moment of change the letter which has just been seen breaks into fragments, while fragments of the letter which is about to appear mingle with them, and are immediately after replaced by the entire letter” (p. 386). You can also experience what the spatiotemporal nature of rivalry dynamics means without difficulty. Spend some time to see the two rival patterns in Figure 1.1a by free fusing the two eyes, or see the series of images mimicking a perceptual experience of binocular rivalry transition over time in Figure 1.1b.

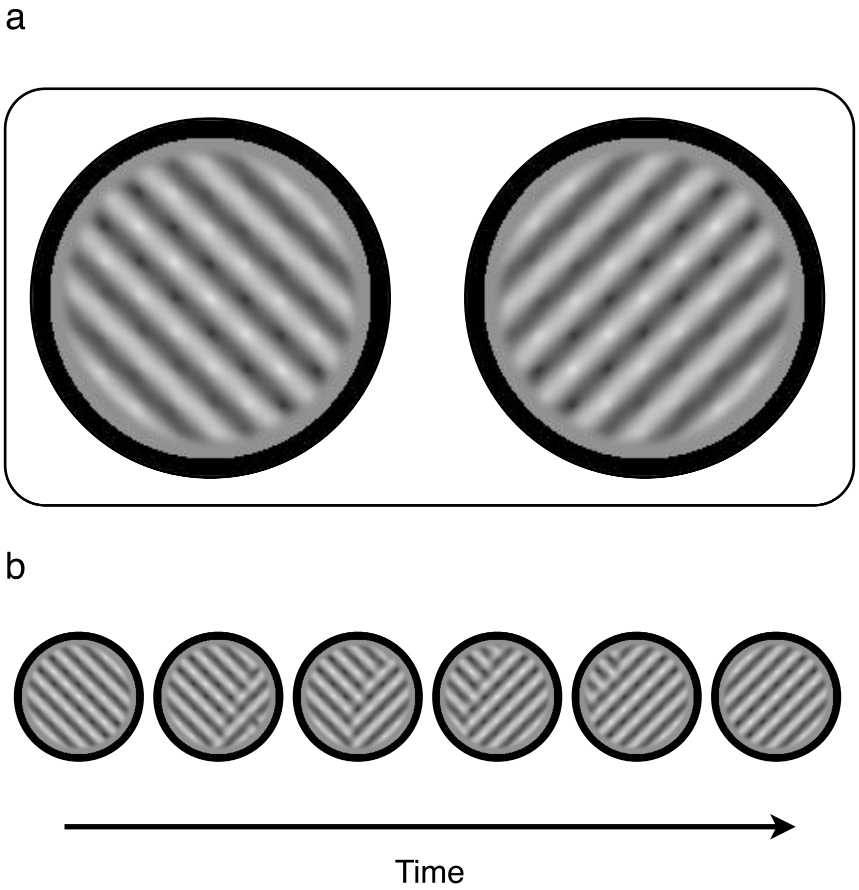

Figure 1.1 Perceptual experiences of binocular rivalry. a) These two rival stimuli – designed to be viewed by crossing the eyes to superimpose the two half-images binocularly – illustrate the hallmark characteristics of binocular rivalry: periods of mixed dominance and propagation of perceptual dominance. b) Illustration of a transition period during binocular rivalry in which the right-tilted grating propagates to the left-upward direction.

Despite the frequent incidence of mixed dominance and the dynamic changes of dominance over space and time, the spatiotemporal dynamics of binocular rivalry have until recently remained largely unexplored for two reasons: the complexity of the perceptual experiences and the lack of theoretical framework. First, it is difficult to characterize rivalry dynamics over space and time. The difficulty of characterizing spatiotemporal dynamics of binocular rivalry becomes evident if we consider the conventional technique for studying rivalry dynamics: observers report the perceptual alternations over time with (usually) three response categories: two responses for the perceptual dominances of the two entire stimuli respectively but a single response for all the subjective perceptual experiences during periods of mixed dominance. Second, the central theoretical framework leading binocular rivalry researches for the last century views binocular rivalry as competition between two pools of neurons, representing the two entire views presented to the two eyes respectively or two coherent stimulus interpretations (see section 1.2 for details regarding this framework). Within this context, the spatial mixtures comprising the two eyes' view are difficult to explain.

Recently, however, a number of studies have pointed out the importance of studying the spatiotemporal dynamics of binocular rivalry for the following reasons. First, periods of mixed dominance can contribute to our understanding of the nature of competing representations through interocular grouping phenomenon (Diaz-Caneja, 1928; translated by Alais, O'Shea, Mesana-Alais, & Wilson, 2000; Lee & Blake, 2004; Kovács, Papathomas, Yang, & Fehér 1996). As illustrated in Figure 1.2, even though the two rival stimuli are the scrambled patchworks of the two pictures (monkey face and the scene), these non-coherent images are sometimes reorganized by the brain to form a coherent percept of either the monkey or the scene. Kovács et al. (1996) thought that the high-level object interpretation such as a face of monkey is a main driving force for producing this interocular-grouping. Second, Wilson, Blake & Lee (2001) and Alais, Loreanceau, Arrighi and Cass (2006) showed that perceptual experiences of binocular rivalry reflected the perceptual organization associated with contour integration, proposing that binocular rivalry can be a useful psychophysical tool for studying perceptual organization. Third, the spatiotemporal dynamics are important to achieve a comprehensive understanding of rivalry dynamics. For example, until recently the contrast dependent rivalry dynamics, called Levelt's 2nd proposition, have been controversial. However, combined experimental and modeling work presented in Chapter 3 of this dissertation reconciles this controversy, suggesting that spatiotemporal dynamics are important for understanding the overall dynamics of binocular rivalry (Kang, in press).

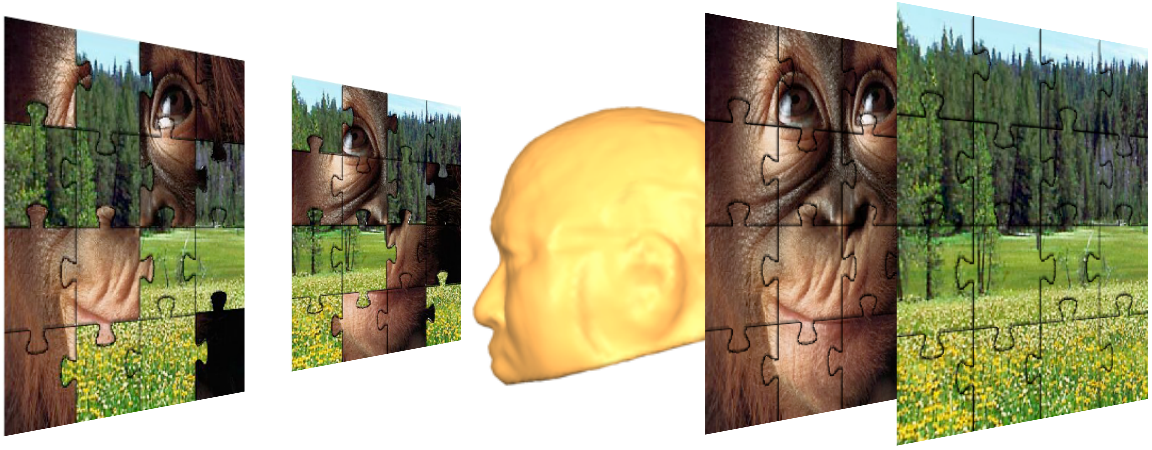

Figure 1.2 Illustration of interocular grouping paradigm. Two rival stimuli are the spatial mixture of a picture of monkey face and a picture of a natural scene. When these two images are presented to the two eyes, perception of the monkey face and the natural scene alternately emerges over the course of binocular rivalry (redrawn based on Kovács et al. 1996).

The spatiotemporal dynamics of binocular rivalry is nowadays considered to arise from cooperative and competitive spatial interactions among retinotopically organized, discrete neural events, with binocular rivalry transpiring within local regions (Blake, O'Shea & Mueller, 1992; Paffen, Naber, & Verstraten, 2008). Recent computational models have systematized this consideration and proposed several factors associated with those spatial interactions (Stollenwerk & Bode, 2003; Wilson et al., 2001). Studying spatiotemporal dynamics of binocular rivalry by focusing on identifying and characterizing those spatial interactions is the purpose of this dissertation.

In Chapter I, I will briefly review the theoretical debates regarding the nature of visual competition during binocular rivalry (section 1.2) and discuss general perceptual characteristics of binocular rivalry (section 1.3). These two sections cover a broad range of previous studies, providing an overview about binocular rivalry. In section 1.4, I discuss the perceptual characteristics and the theoretical framework of spatiotemporal dynamics of binocular rivalry, the subject of this dissertation. Outlines of this dissertation and the specific issues are given in section 1.5.

1.2 Neural bases of binocular rivalry

It has been debated at which processing stage the visual competition of binocular rivalry occurs. Helmholtz (1866) thought that inputs from the two eyes remain potentially available until the last stages of attentional selection and that perceptual alternations of binocular rivalry resulted from instantaneous attentional fluctuations. This view, endorsed by prominent scientists including William James (1891) and Sir Charles Sherrington (1909), had predominated without notable competition until the 1960s. In contrast, Levelt (1965) described rivalry as a consequence of reciprocal inhibition between the two eyes and, thus, claimed that visual competition of binocular rivalry occurs in the early processing stage.

These two classes of theories are distinguished with respect to the stage of visual processing involved with rivalry alternations. From the perspective of cortical organization, this distinction is consistent with the hierarchically organized visual system, in which local image features are analyzed in lower visual areas (V1 and V2), and higher visual areas (V4, MT and IT) are implicated in processing integrated forms (Felleman & Van Essen, 1991; Hubel & Wiesel, 1962). In this regard, the ‘early theory’ situates the locus of competition in the primary visual cortex V1 where the output of two monocular neurons are integrated to binocular neurons (Blake, 1989), but the ‘late theory’ places this locus in higher brain areas than V1 (Leopold & Logothetis, 1999). In a related vein, different types of representations competing at these brain areas have been emphasized: eye (interocular) competition (Blake, 1989) and stimulus (pattern) competition (Logothetis, Leopold, & Sheinberg, 1996).

Over the decades, these two theories have inspired other theoretical frameworks and experimental paradigms, and nowadays it is considered that both high and low level processes are implicated in perceptual alternations of binocular rivalry (Blake & Logothetis, 2002; Tong, Meng, & Blake, 2006). In this section, I briefly review the variations of these two theories and relevant empirical findings, and then summarize the current view.

1.2.1 Psychophysical studies

Four psychophysical procedures, which are commonly found in the previous literature, are discussed: the eye swapping procedure, visual sensitivity to probe stimuli, adaptation aftereffects with the suppressed stimulus, and information processing in the suppression phase (dynamics of rivalry are also informative to the neural bases of binocular rivalry; but, they are discussed in the section 1.3).

First, the eye swapping procedure, in which a stimulus in the left-eye is subsequently presented to the right-eye and vice versa, has been used to test whether the types of representations competing for perceptual dominance contain eye-of-origin information (i.e. whether the currently dominant stimulus is neurally associated with a given eye). This procedure is relevant because if binocular rivalry does not have the eye-of-origin information to which the stimulus is presented, then, perceptual experiences should be indistinguishable from binocular rivalry even after swapping stimuli between eyes. Blake, Westendorf, and Overton (1980) showed that after swapping the stimuli the dominant image became immediately suppressed and the suppressed image abruptly achieved perceptual dominance. This result indicates that the dominant eye remains dominant after the swapping procedure: it is the eye that competes for perceptual dominance. In contrast, Logothetis, Leopold, and Sheinberg (1996) applied the same logic but changed the sequence of stimuli: two images were rapidly flickered and swapped faster than the normal rivalry alternation rate. In this experiment, they found that perceptual dominance survived over several swaps and alternated slowly like binocular rivalry. This clearly demonstrates that representations do not require eye-of-origin information and this type of rivalry is termed stimulus rivalry. However, stimulus rivalry is easily disrupted by visual transients (Kang & Blake, 2008) and, thus, occurs under limited conditions, specifically, at low contrast and high spatial frequency levels (Lee & Blake, 1999). These results suggest that at least eye-of-origin information competes for perceptual dominance for a wide range of stimulus conditions (Lee & Blake, 1999).

Turning to the second technique, the relative fate of a test stimulus presented to an eye during phases of suppression and phases of dominance provides an indirect measure of the effect of suppression. In general, if a probe is presented onto the suppressed image, sensitivity to the visual probe decreases compared to a probe being presented onto the dominant image. This is true for probes of diverse visual attributes (Blake & Fox, 1974a; Fox & Check, 1968; Smith, Levi, Harwerth, & White, 1982). This non-selective suppression falling within the suppressed eye is taken as evidence for the interocular inhibition of binocular rivalry, because it is not specific to visual attributes that are suppressed. However, there is empirical evidence showing that the probe sensitivity gradually decreases as the involvement of visual attributes processed in higher visual areas increases (Alais & Melcher, 2007; Li, Freeman, & Alais, 2005). For example, Li et al. (2005) presented phase shifting patterns for the two rival stimuli and, thus, motion perception was induced during binocular rivalry. Over the different tracking sessions, the rival stimuli were parametrically changed from the grating pattern to the spiral pattern, in which the grating pattern produced up or downward motion and the spiral pattern produced clockwise or counterclockwise motion. Li et al. then briefly changed the speed of one rival stimulus either in dominance or in suppression phase and observers had to discriminate whether the speed was increased or decreased for that brief period. When relative sensitivity was obtained by measuring threshold level speed change in dominance and in suppression phase, the relative sensitivity was higher for the up or downward motion associated with the grating pattern compared to sensitivity for the clockwise and counterclockwise motion associated with the spiral pattern. Li et al. interpreted that the magnitude of suppression was higher for the spiral motion because it is processed in higher brain areas like MT/MST (Graziano, Anderson, & Snowden, 1994, Huk, Dougherty, & Heeger, 2002) compared to the linear motion pattern, which is processed in lower visual area V1 (Hubel & Wiesel, 1962, 1968).

The third procedure pairs binocular rivalry with visual adaptation. Aftereffects can still occur even though the stimulus is invisible during binocular rivalry. By measuring the magnitude of adaptation aftereffect during binocular rivalry, it is possible to determine whether suppression is equivalent to turning the adaptation process off completely or, alternatively, simply turning it down. If the suppression occurs before the site of adaptation, the magnitude of aftereffect should decrease. However, if the suppression occurs after the site of adaptation, the aftereffect magnitude during the suppression phase should be equal to the aftereffect magnitude during the dominant phase. During binocular rivalry, one rival target adapts during both the dominant and suppression phases. In order to match the adaptation occurring during the dominant phases, a control condition was created by presenting stimuli alternatively to the dominant eyes according to the time course of rivalry. Called the mimic condition, it appears like binocular rivalry without suppressed stimulus. In early studies, diverse aftereffects induced during binocular rivalry were found to be greater than those induced during the mimic condition such as aftereffects adaptation to spatial frequency (Blake & Fox, 1974b), tilt (O'Shea & Crassini, 1981, Wade & Wenderoth, 1978) and linear motion (Lehmkuhle & Fox, 1975). These studies provide converging evidence that aftereffect magnitude is not reduced during the suppression phases of binocular rivalry, implying that the adaptation stimulus is fully processed even when perceptually suppressed. A recent study, however, has raised the possibility that the aftereffect magnitude saturates when a strong inducing stimulus (i.e. high contrast stimulus) is used (Blake, Tadin, Sobel, Chong, & Raissian, 2006; Gilroy & Blake, 2005). In this case, attenuation caused by suppression is too small to decrease the magnitude of the aftereffect. Blake et al. (2006) used a wider range of adaptation contrast values and found substantial attenuation of the aftereffect when the inducing stimulus' contrast was low. This finding indicates that neural events underlying binocular rivalry begin at an early stage of visual processing.

The fourth procedure, lastly, was inspired by the theoretical view of Helmholtz (1866) in which the two inputs are available at the last selection stage and, thus, the contents of suppressed stimulus should be available. However, it remains controversial as to whether the meaningful contents of a stimulus are processed during suppression phases of rivalry. Somekh and Wilding (1973) showed that when a neutral face was perceptually dominant while a word expressing facial expression (e.g. "cheerful") was presented to the suppressed eye, observers' judgments of the facial expression were biased toward the invisible word. Jiang et al. (2006) showed that a suppressed visual cue could apparently guide spatial attention if the cue was an erotic stimulus. Recently, Almeida and colleagues (2008) showed that a tool image presented in the suppression phase of rivalry speeded up the response time to a subsequently presented tool image. This result is consistent with a recent brain imaging study in which brain activity within dorsal cortical brain areas sensitive to objects was activated to the tool images even when they were rendered invisible owing to rivalry suppression (Fang & He, 2005). In addition, the amygdala can be activated in response to a fearful face presented during suppression phases of rivalry (Williams, Morris, McGlone, Abbott & Mattingley, 2004). All these results imply that some contents, especially those that are ecologically relevant like facial expression, are processed despite being suppressed from visual awareness. However, rival targets in these studies are presented too briefly (from 200msec to 800msec) to result in binocular rivalry suppression (Wolfe, 1983). In addition, when letter strings (or symbolic cues) were completely suppressed during the course of rivalry alternations, this condition was not different from when the stimulus was physically removed (Blake, 1988; Cave, Blake, & McNamara, 1998; Schall, Narwot, Blake & Yu, 1993; Zimba & Blake, 1983). Regarding these incompatible results, it remains to be seen whether particular contents are processed in suppression phase of rivalry or whether a wide range of stimulus contents are processed depending on the physical codition of suppression (e.g. suppression time).

1.2.2 Neurophysiology and neuroimaging studies

For the last three decades, neurophysiology and neuroimaging studies have provided exciting empirical results regarding the early and late theory debate, by directly examining the neural correlate of binocular rivalry. The rationale of the studies is that the underlying physiological states must be different for the two perceptual states, one image being perceptually dominant and the other being suppressed during binocular rivalry (Teller, 1984). Despite the original promise that the neural correlate of perceptual dominance would provide the conclusive answer to this debate, the evidence from neurophysiology, specifically spiking rate obtained from single cell recordings, disagrees in some critical respects with the evidence from neuroimaging studies.

I first discuss the evidence that both the spike rate and BOLD (Blood Oxygen Level Dependent) response agree. These two neural responses agree that several higher brain areas reflect the perceptual experiences of binocular rivalry: the Inferior Temporal cortex (IT) of monkey (Sheinberg & Logothetis, 1997) and its human homologue fusiform gyrus (Tong, Nakayama, Vaughan & Kanwisher, 1998); Middle Temporal (MT)/Superior Temporal Sulcus (STS) of monkey (Logothetis & Schall, 1989) and human (Moutoussis, Keliris, Kourtzi, & Logothetis, 2005). The modulation in neural response reflecting the perceptual state of binocular rivalry generally increased over the ventral pathways (Leopold & Logothetis, 1996; Sheinberg & Logothetis, 1997). This has led to the view that the ventral pathway is involved with conscious perceptual experiences (Fang & He, 2005).

However, spike rate and BOLD response disagree about whether neural activity in early visual area V1 or subcortical area LGN (Lateral Geniculate Nucleus) reflects perceptual states of binocular rivalry. Leopold and Logothetis (1996) found that modulations in the neural activity within a large proportion of neurons in V1/V2 in monkeys were unrelated to perceptual alternations of binocular rivalry, and Fries and colleagues also confirmed this observation in visual areas 17/18 in strabismic cats (1997; 2002). In LGN, Varela and Singer (1987) originally reported neural correlates of binocular rivalry, but later studies failed to confirm this result (Lehky & Maunsell, 1996; Sengpiel, Blakemore, & Harrad, 1995). In contrast, several brain imaging studies have reported that BOLD response in V1 (Lee, Blake, & Heeger, 2005, 2007; Haynes, & Rees, 2005; Polonsky, Blake, Braun & Heeger, 2000; Tong & Engel, 2001) and in LGN (Haynes, Deichman, & Rees, 2006, Wunderlich, Schneider, & Kastner, 2005) were modulated according to the perceptual alternations of binocular rivalry.

Why, then, have neurophysiological studies measuring spike activity failed to observe modulation reflecting perceptual state during binocular rivalry in early visual area V1, or in the subcortical area LGN? Growing evidence indicates that the two neural responses, spike rate and BOLD, carry different information. Recent studies indicate that the LFP (Local Field Potential) is more strongly correlated with the BOLD response compared to spike rates (Belitski et al., 2008; Logothetis, Pauls, Augath, Triath, & Oeltermann, 2001; Mukamel et al., 2005; Niessing et al., 2005; Rauch, Rainer, & Logothetis, 2008; Thompson, Peterson, & Freeman, 2003). These results are consistent with previous studies demonstrating that LFPs are modulated by binocular rivalry but spike rate is not (Fries et al., 1997; 2001).

With these incompatible results, it has been speculated that BOLD modulation during binocular rivalry reflects feedback signals, possibly driven by attention from higher visual areas (Logothetis, Pauls, Augath, Triath & Oeltermann, 2001; Logothetis & Wandell, 2004; Kamitani & Tong, 2005). Even if this is true, strong modulation of LGN, where all neurons are driven by monocular input, indicates that eye-of-origin information should be retained to guide feedback signals to the corresponding monocular representations in LGN. In this regard, advocates of interocular suppression consider V1 as a reasonable candidate for feedback signaling (Tong, Meng & Blake, 2006) based on the following two pieces of evidence: 1) cortico-geniculate projections from V1 to LGN in monkeys are topographically organized, suggesting that the cortex can influence the activity of LGN representing the left and the right eyes independently (Ichida, & Casagrade, 2002) and 2) binocular interaction, predominantly inhibitory, has been reported in the LGN (Marrocco, & McClurkin, 1979; Singer, 1970).

1.2.3 Conclusion: converging view

I have discussed mainly incompatible empirical evidence bearing on both the early and late theories of binocular rivalry. All these pieces of evidence make it clear that neither a single brain area nor a single process is involved with the binocular rivalry. Instead, binocular rivalry is considered as an outcome of multiple neuronal operations distributed across several brain areas (Blake & Logothetis, 2002; Tong et al., 2006). For example, one particular view, called the multiple stage hypothesis, proposes that rivalry suppression increases in strength across visual areas: specifically, neural representations of the suppressed stimulus are weakened in early visual areas including LGN and V1 where local image features are processed, and continue to decrease over visual area V4. The representation of the suppressed stimulus is nearly inactive in area IT where the representation of objects is fully constructed. However, the specific interactions between different brain areas and their processes remain to be clarified in the future studies.

1.3 Temporal dynamics of binocular rivalry

1.3.1 Introduction: What triggers binocular rivalry?

What key stimulus conditions must be considered when characterizing the dynamics of binocular rivalry? In order to answer this question, I discuss two factors affecting temporal dynamics of rivalry along with its perceptual characteristics: cognitive processes such as attention and visual attributes of the rival stimuli. But first, I will address the conditions that produce binocular rivalry. Specifically, how dissimilar should the two visual inputs be?

Binocular rivalry occurs if the two rival targets are sufficiently different in any one of the following stimulus dimensions: contrast, luminance, contrast polarity, spatial frequency, orientation, or direction of motion. Rivalry can be observed even when both rival targets are not simultaneously presented but are alternately presented to the two eyes (O'Shea & Crassini, 1984). Note, however, that dissimilar dichoptic visual stimulation does not inevitably yield binocular rivalry. In this subsection, I highlight five stimulus conditions that do not yield binocular rivalry because, otherwise, it is easy to instigate binocular rivalry with any pair of two dissimilar stimuli presented to the two eyes.

First, binocular rivalry is susceptible to transient stimuli such as moving patterns, flickering patterns and a brief stimulation like a flash. For example, dichoptic stimulation lasting less than 150 milliseconds precipitates an incomplete suppression of one rival target (Wolfe, 1983); if two random dot patterns move in opposite directions with a large speed difference, observers see both targets as transparently superimposed (van de Grind, van Hof, van der Smagt, & Verstraten, 2001); two stimuli flickering with different temporal frequencies rarely result in binocular rivalry. In this last case, observers tend to describe "visual beats" which resemble a single flicker percept whose temporal frequency is the difference of flicker frequencies of the two rival targets (Baitch & Levi, 1989; Carlson & He, 2000; O'Shea & Blake, 1986). Second, large differences in spatial frequency often fail to produce binocular rivalry (Yang, Rose and Blake, 1992). Third, Liu and colleagues (1992; 1995) have reported 'binocular combination' in which, at near-detection threshold contrast, both orthogonal rival stimuli are simultaneously visible as if they are superimposed. Fourth, if dissimilar monocular stimulation is compatible with the pattern of stimulation one would experience while viewing a partially occluded surface, the occluded surface remains suppressed (see Figure 1.3 for illustration; Shimojo & Nakakyama, 1990; 1994). Fifth, Carlson and He (2004) have developed a novel stimulus condition in which cells in two meshes are filled with different colors creating two images which are globally different but similar at corresponding local regions. Binocular rivalry does not occur with these stimulus conditions.

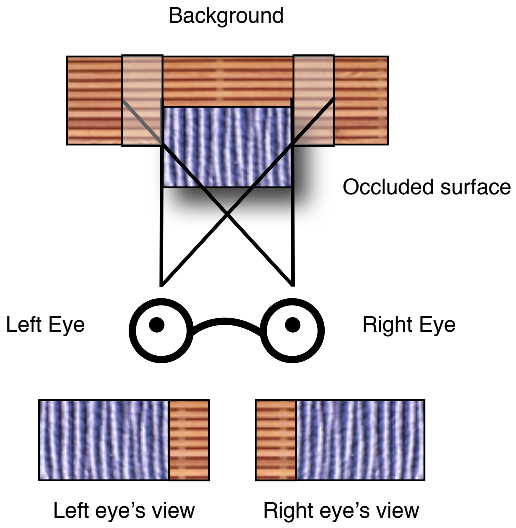

Figure 1.3 Illustration of how interocularly-unpaired regions can occur during viewing in a natural 3-D environment. The horizontal texture is occluded by a vertical texture. The two views of the left- and the right-eyes are different as shown at the bottom of the figure. The shaded areas within the background texture represent the interocularly-unpaired regions.

1.3.2 Initial dominance of binocular rivalry

What will happen immediately after the presentation of two rival targets? If the two rival stimuli of equal contrast are presented simultaneously, it is impossible to predict which one is initially dominant. However, it is possible to bias the initial dominance of one stimulus. Three techniques are discussed in this subsection. I emphasize the technical aspects because it is controversial whether these techniques affect the same neural circuits instigating perceptual alternations of binocular rivalry.

First, Wolfe (1984) has shown that if an observer views a monocular stimulus (1-2 sec) before the simultaneous presentation of a rival target, the monocular stimulus is invisible at the beginning. This finding has been replicated under diverse stimulus conditions for human observers (Holmes, Hancock & Andrews, 2006) and animals (Fries, Schröder, Singer & Engel, 2001, Sheinberg & Logothetis, 1997). Furthermore, it is possible to completely suppress one rival target for an extended period of time by continuously presenting visual transients (Tsuchiya & Koch, 2005). These techniques, collectively called flash suppression, prove to be also useful in suppressing a conspicuous visual stimulus in one eye even when visual input to the corresponding region of the other eye is absent (Wilke, Logothetis & Leopold, 2003).

Second, the initial dominance of binocular rivalry is susceptible to attention. Mitchell, Stoner, and Reynolds (2004) dioptically presented two transparent dot patterns rotating in opposite directions and cued one surface. Subsequently, when these two rotating dot patterns were separately presented to the two eyes, the cued surface was more likely to be dominant. In another study, explicit instruction (endogenous attention) to one rival stimulus or a brief contrast increment (exogenous attention) of one stimulus also facilitated the initial dominance of the attended target (Chong & Blake, 2006). Considering that both rival targets occupy the same spatial location, these results are interpreted in the context of object-based/feature-based attention (Mitchell et al. 2004).

Third, although perception alternates stochastically with prolonged viewing of binocular rivalry, these alternations are slowed or halted if the stimuli are presented intermittently (Leopold, Wilke, Maier & Logothetis, 2003) and, thus, it is possible to bias the initial dominance of subsequently presented rival targets. Memory of the recent perceptual experience has been proposed to account for this stabilization (Chen & He, 2003, Pearson & Clifford, 2004, Pearson & Clifford, 2005) and Pearson and Brascamp (2008) proposed that the nature of this perceptual memory is similar to the memory system associated with priming.

1.3.3 Ongoing perceptual alternations

A hallmark property of binocular rivalry is the stochastic nature of perceptual alternations. This stochastic nature is well described by 1) a unimodal but skewed distribution of dominance durations, 2) low autocorrelation coefficients at varying time lags except the zero lag (Fox & Herrmann, 1967, Branscamp, van Ee, Pestman & van den Berg, 2005, Lehky, 1995). We cannot change this aspect of rivalry alternations (but see a single exception, Carter & Pettigrew, 2003); however, it is possible to change some statistical properties of rivalry alternations such as mean dominance duration and alternation rate. I discuss three means to bias rivalry dynamics.

Firstly, some cognitive processes such as voluntary attention bias rivalry dynamics. Dominance durations of one rival stimulus increase on average by deploying attention to that particular stimulus (Breese, 1899; Chong, Tadin & Blake, 2006; Helmholtz, 1866; Lack, 1978; Neisser & Becker, 1975; van Dam & van Ee, 2005). When deploying of attention is manipulated by a concurrent task, the dominance durations increase with decreasing task difficulty (Paffen, Alais & Verstraten, 2006). In addition, practice over days can increase the alternation rate only for the rival stimulus to which attention is given (Breese, 1899; Meredith & Meredith, 1962; Lack, 1969): this speeding of alternations over days has been characterized as a form of attention-dependent cortical plasticity (Suzuki & Grabowecky, 2007). However, all of these studies have pointed out that the influence of attention is modest and it is impossible to maintain dominance of one percept indefinitely.

The influence of attention on the perceptual dominance still occurs even when eye-movements are controlled. There has been a concern that the effect of voluntary attention to the perceptual dominance originates with peripheral signals such as eye movements, blinking and tension of muscles controlling the eye movements (Breese, 1899, Hering, 1964, Meredith & Meredith, 1962). This concern is reasonable considering that attention tends to be deployed toward the gaze direction (Kowler, Anderson, Dosher & Blaser, 1995, Kustov & Robinson, 1996, but see Juan, Shorter-Jacobi & Schall, 2004). In addition, there is also evidence showing that eye-movements, specifically retinal image shift accompanied by eye movements, modulate the incidence of perceptual switches during binocular rivalry (van Dam & van Ee, 2006). However, when Lack (1978) eliminated any influence of eye movements by stabilizing retinal inputs using afterimages or by temporarily paralyzing the eye muscles, observers could still exert mental effort to control the rivalry dynamics.

On the other hand, secondly, visual attributes associated with low level sensory processing also affect dominance durations. The dynamics of rivalry systematically change with variations in stimulus properties such as luminance (Kaplan & Metlay, 1964, Fox & Rasche, 1969), contrast (Whittle, 1965, Hollins, 1980, Levelt, 1965), spatial frequency (Hollins, 1980, Fahle, 1982), size (O'Shea, Sims & Govan, 1997), orientation difference between the two gratings (Thomas, 1978), visual field location (Chen & He, 2003) and retinal eccentricity (Fahle, 1987). In general, a stronger stimulus (e.g. a high contrast grating) predominates during binocular rivalry. However, there are reasons to believe that this stimulus "strength" does not reflect the physical strength; rather, it is likely to be related to the level of sensory stimulation. Blake (1977) measured the threshold contrast of binocular rivalry by adjusting the contrast of the one eye's view to the minimum value that would allow it to be "temporarily visible", while an orthogonal grating was presented to the other eye. The pattern of contrast threshold of binocular rivalry is very similar to the pattern of detection contrast sensitivity at varying contrast levels (Kulikowski & Tolhurst, 1973) and at varying retinal eccentricities (Rovamo, Virsu & Näsänen, 1978).

In general, stronger stimuli predominate by staying suppressed for shorter periods of time, but they do not necessarily remain longer in perceptual dominance (Levelt, 1965, Fox & Rasche, 1969). This rather counterintuitive behavior is called Levelt's 2nd proposition. According to this proposition, a stimulus remains perceptually dominant for more or less the same periods of time, even though the strength of that stimulus increases. However, there is also evidence to suggest longer dominance for various "stronger" stimuli in terms of contrast, luminance and motion speed (Bossink, Stalmeier

& De Weert, 1993, Brascamp, van Ee, Noest, Jacobs & van den Berg, 2006, Mueller & Blake, 1989). I discuss this controversy regarding Levelt's 2nd proposition more closely in Chapter 3 of this dissertation.

Lastly, binocular rivalry is also influenced by non-rivaling stimuli presented in the surround called context. Fukuda and Blake (1992) found that a monocular annulus-shaped context increases the perceptual dominance of the rival stimulus presented in the same eye; but the predominance gradually decreases as the distance increases between the rival target and the surrounding annulus context. In addition, the perceptual dominance of the right-tilted grating presented to one eye (presented along with the left-tilted grating to the other eye) was lower when that right-tilted grating was accompanied by dioptic stimulation with an annulus-shaped context filled with the same right-tilted grating. However, this suppression that accompanies by the surround context changes depending on the contrast level (Paffen, Tadin, te Pas, Blake, & Verstraten ,2006). Whereas Fukuda and Blake (1992) conducted experiments with full contrast (100%) stimuli, Paffen et al. (2006) used two contrast levels. When a high contrast grating context was presented dioptically, the rival target of matching orientation remained suppressed longer during the viewing period, consistent with Fukuda and Blake (1992). In contrast, the same rival target matching orientation to the context stimulus predominated when a low contrast level context was used.

1.3.4 Summary and conclusions

I have discussed the temporal dynamics of binocular rivalry over three parts. First, I discussed the conditions producing binocular rivalry, and then discussed the initial perceptual experiences, occurring for the first approximately 500msec after the presentation of rival stimuli. In the last part, I described a number of factors affecting the dynamics regarding ongoing perceptual alternations during binocular rivalry. During the periods of perceptual alternations, however, periods of mixed dominance occur between the alternations of the entire rival stimuli, suggesting that the temporal dynamics are spatiotemporal in nature. In the next section, I summarize the perceptual characteristics of spatiotemporal dynamics of binocular rivalry and their theoretical implications, and then provide a formal theoretical framework.

1.4 Spatiotemporal dynamics of binocular rivalry

Considering that retinal input stimulates a discrete population of neurons whose receptive fields are retinotopically organized, these patchwork-like perceptual experiences are not surprising. Yet, the ways in which the interactions of binocular rivalry occur within local regions are largely uncharacterized. In this section, I discuss the spatiotemporal dynamics of binocular rivalry, focusing on three topics. Firstly, perceptual organization and its possible neural representation are considered to provide a relevant theoretical framework for the spatial interactions of binocular rivalry. Secondly, I discuss perceptual characteristics of the spatiotemporal dynamics of binocular rivalry and their implications. Specifically, I organize these studies into three parts: first, psychophysical characterization of local rivalries; second, the cooperative/competitive interactions among spatially distributed rivalries; and, third, wave-like perceptual switches over space. These three topics refer to qualitatively different aspects of the spatiotemporal dynamics of binocular rivalry and therefore different methodologies are also considered. Lastly, a formal theoretical framework inspired by recent computational models (Stollenwerk & Bode, 2003; Wilson et al., 2001) is presented, which provides guiding principles for this dissertation.

1.4.1 Perceptual organization

One fundamental question in visual perception is how local image features are integrated to form a global configuration and eventually perceived as an object. Gestalt psychologists proposed that perceptual organization in the brain orchestrate integrating these local image features by studying several grouping phenomena. Since the pioneering work of Hubel and Wiesel (1962), this integration process was thought to occur through a hierarchically organized visual system, such that local image features are analyzed in lower visual areas (V1 and V2) and the higher visual areas (V4, MT and IT) are implicated in processing integrated forms (Felleman & Van Essen, 1991; Hubel & Wiesel, 1962). Recently, however, growing evidence has suggested that the integration also occurs within the lower visual areas.

In particular, contour integration, which has been extensively studied for the last 15 years, is considered a synonym for the Gestalt rule of good continuation. This rule of good continuation states that discrete objects, which are arranged in either a straight line or a smooth curve, tend to be seen as a single unit. Psychophysically, the rule of good continuation has been characterized by the two representative paradigms: ‘path paradigm’ and ‘lateral interaction paradigm’. First, in the path paradigm as shown in Figure 1.4a, a path is defined by a set of similarly-oriented gratings within a two-dimensional array of oriented gratings, appearing continuous with increasing correlation of their orientations and, thus, distinguishing themselves against the background in which the orientation of the gratings are random. (Field, Hayes & Hess, 1993; Kovács & Juleze, 1993). Second, in the lateral interaction paradigm, three vertical gratings were presented vertically and observers had to detect the target stimulus at the center (Figure 1.4b). The detection contrast threshold was reduced when the two high contrast flankers were presented collinearly compared to when the target grating was presented in isolation (Polat & Sagi, 1993; 1994). This enhanced apparent contrast, termed collinear facilitation, was also demonstrated electrophysiologically using a similar experimental procedure (Polat & Norcia, 1996).

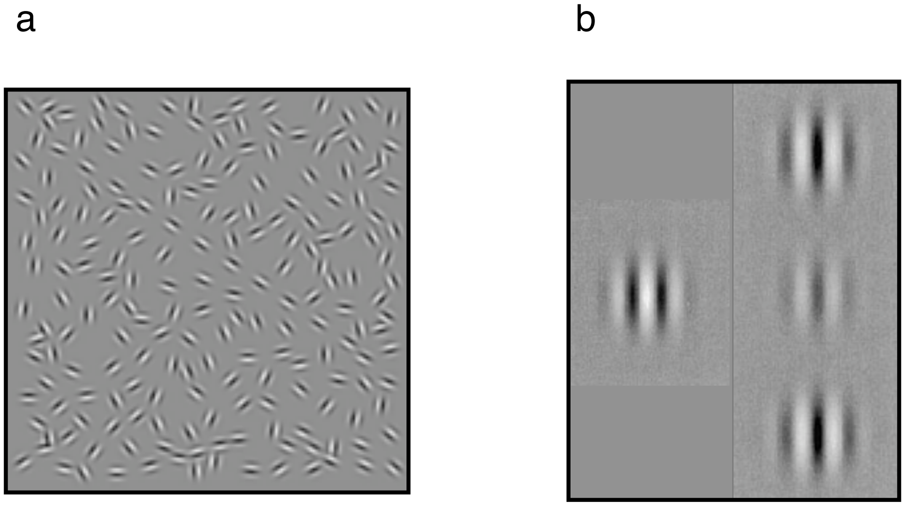

Figure 1.4 Stimuli used for 'path paradigm' and 'lateral interaction paradigm'. a) a path was defined by a set of similarly-oriented gratings (this figure is adapted from Hess & Field, 1999). b) the left column shows a condition in which a target stimulus is presented in isolation whereas the right column shows a condition in which a target stimulus is presented with two collinear flanker stimuli (this figure is adapted from Chen, Kasamatsu, Polat & Norcia, 2001).

However, the underlying mechanisms producing this contour integration and collinear facilitation have been debated. In order to account for the cooperative contour integration revealed by the path paradigm, Field and his colleagues (1993) proposed a hypothetical region, termed “association field,” in which each oriented grating can link its response to the responses of its neighboring gratings. Yet this contour integration mechanism is not sufficient to explain how the collinearly distributed gratings distinguish themselves from background. Polat and Sagi (1993; 1994) claimed that the continuous contour is distinguished from background because the apparent contrast of the target grating is enhanced. However, Hess and colleagues (1998) pointed out that this apparent contrast enhancement occurs at near detection threshold level, being unable to explain the contour integration occurring at suprathreshold level as shown by path paradigm. Recently, Petrov, Verghese and McKee (2006) additionally showed that spatial attention can explain this collinear facilitation effect of the lateral interaction paradigm, consistent with the view that the perceptual grouping occurs because of an inability to distribute attention over individual objects (Li, Piëch, & Gilbert, 2008; Kahneman, Treisman, & Gibbs, 1992; Scholl, 2001). Although debated, it has been thought that the interactions of spatially arranged neurons in lower brain areas are involved in contour integration (Angelucci & Bullier, 2003).

Consistent with the psychophysical characterizations, neural responses from cats and monkeys reflect human perceptual experiences associated with this contour integration. Neurons in primary visual cortex respond to specifically oriented line segments falling within a restricted region of the visual field, called receptive field (De Valois, Albrecht & Thorell, 1982; Hubel & Wiesel, 1962; 1968). Yet, the concurrent presentation of stimuli outside the receptive field modulates the firing rate of these neurons (Allman, Meizin & McGuinness, 1985; Maffei & Fiorentini, 1976). In particular, consistent with the contour integration studies in humans, similar patterns outside the receptive field increase the neural response to the stimulus within the receptive field (Crook, Engelmann & Löwel, 2002; Kapadia, Ito, Gilbert & Westheimer, 1995; Polat, Mizobe, Pettet, Kasamatsu & Norcia, 1998). In addition, alert monkeys could easily find a straight path consisting of small line segments embedded in noise line segments, and their neural response to that segment increased accordingly (Li, Piëch & Gilbert, 2006; 2008).

What then is the neural substrate subserving this physiological facilitation? Gilbert and Wiesel (1979) characterized the functional property of a cell by examining its response to the stimulus and, then, identified the anatomical connection by intracellular injection. They found that a neuron in layer 2/3 projected to a distant column of cells representing similar orientations. This observation was corroborated by number of subsequent studies using simultaneous recordings (Ts'o, Gilbert & Wiesel, 1986), optical imaging (Das & Gilbert, 1995; Malach, Amir, Harel & Grinvald, 1993) and an inactivation study (Crook et al., 2002). Taken together, it is generally considered that the long-range lateral connections are involved with this facilitation (Angelucci & Bullier, 2003; Stemmler, Usher & Niebur, 1995).

Besides these psychophysical, physiological and anatomical studies, there is reason to believe in the existence of the neural substrate subserving Gestalt rule of "good continuation" from an evolutionary perspective. The statistical properties of natural images show strong correlation among edges of similar orientation in proximity (Geisler, Perry, Super, & Gallogly 2001, Sigman, Cecchi, Gilbert & Magnasco, 2001). With these findings in mind, I return to the spatiotemporal dynamics of binocular rivalry.

1.4.2 Spatial interaction during binocular rivalry

Under the consideration that binocular rivalry is the outcome of cooperative and competitive interactions among discrete population of neural events, three related aspects have been examined: 1) what are the characteristics of local rivalry, the binocular rivalry occurring within a local region?; 2) to what extent do the two local rivalries interact?; 3) what are the dynamics of this interaction? In the following paragraphs, I discuss previous studies and the results relevant to these three questions.

Firstly, what are the characteristics of binocular rivalry occurring within a local region? In order to answer this question, the size of local rivalry in which a spatial mixture does not occur should be estimated. The rationale of this strategy is that a spatial mixture cannot occur within a single, spatially localized discrete neuronal population. I term this hypothetical cluster of neurons a local rivalry zone. Accordingly, by decreasing the size of rival stimuli, the incidence of mixed dominance decreases so that the size of rival stimuli producing a criterion level of spatial mixture could be estimated as a measure of the size of local rivalry. Using this technique, three organizing principles has been identified. First, the size of a local rivalry increases in the visual periphery according to the cortical magnification factor of human primary visual cortex (Blake et al., 1992). Second, this size of local rivalry changes depending on figural components such as the number of contours, i.e. the size of local rivalry decreases as the spatial frequency increases (Liu & Schor, 1994; O'Shea, Sims & Govan, 1997), reflecting the sampling theory in early visual cortex (Geisler & Hamilton, 1986). Third, the size of local rivalry increases abruptly when the luminance of a stimulus decreases to around the level at which humans cannot see colors (O'Shea, Blake & Wolfe, 1994), reflecting receptive field size differences for different pathways (Shapley, 1990). All of these results show that the sizes of local rivalry zones change dynamically according to cortical organizations and their functional characteristics.

Secondly, the extent of spatial interaction between the two local rivalries has been studied by measuring the total periods of concurrent perceptual dominance of spatially distributed rival stimuli. Alais and Blake (1999) presented two horizontally separated gratings to one eye and two noise patterns in the corresponding retinal locations of the other eye. They found that concurrent perceptual dominance of the two gratings was greater when the orientations of the two gratings were both horizontal (collinearly aligned) compared to two other combinations (horizontal/vertical and vertical/vertical). This result along with others (Wade, 1973; Alais et al., 2006) suggests that binocular rivalry is sensitive to the perceptual organization associated with contour integration. However, the total periods of concurrent perceptual dominance cannot show how the perceptual experience changes over time because concurrent dominance can occur in either of ways: 1) two gratings become perceptually dominant simultaneously or 2) the second grating becomes dominant while the first grating has already been perceptually dominant.

Thirdly, therefore, the dynamics associated with spatial interactions require special treatment. About 40 years ago, Whittle, Bloor and Pocock (1968) observed that contour-segments belonging to the same line tend to achieve perceptual dominances simultaneously. Recently, Alais et al. (2006) investigated the simultaneous perceptual changes more systematically in which observers had to independently track the perceptual alternations of two sets of rival stimuli. Similar to the experiment mentioned above (Alais & Blake 1999), two rival stimuli were presented in one eye and two noise patterns were presented to the other eye. Consistent with collinear facilitation, simultaneous perceptual alternations increased with increasing collinearity and with decreasing separation of the two rival stimuli in one eye.

One striking phenomenon during binocular rivalry is the wave-like propagations of perceptual dominance: the perceptual dominance of a suppressed pattern emerges locally and expands progressively as it renders the other pattern invisible (see Figure 1.5 for illustration of this wave phenomenon). Characterizing this wave-like propagation of perceptual dominance, however, is challenging because the following two aspects are unpredictable: which part of the figure changes its phase first and in what direction the dominance wave propagates. Wilson et al. (2001) devised a novel stimulus condition that maintained these unpredictable factors under control. First, they controlled the direction of wave propagation by creating annulus shape rival stimuli in which a perceptual switch at any region of the figure produced traveling waves spreading either in a clockwise or counterclockwise direction. Second, they controlled the time and location of the onset of traveling waves using a trigger, a brief increment of contrast at a specified location of the suppressed stimulus. On each trial, observers waited until one designated image became completely dominant and then depressed a button to initiate the trigger. For each trial, a traveling time of a wave was obtained when it reached a designated location. The traveling waves were characterized by using the traveling distance and time and, in general, the traveling time increased linearly with increasing travel distance.

Using this technique, Wilson et al. (2001) found that the measured traveling waves of binocular rivalry reflected several organization principles of the human primary visual cortex V1. First, the waves propagate faster when they propagate around a concentric ring pattern (high collinearity) compared to a radial grating as carrier (low collinearity), consistent with collinear facilitation. Second, the traveling waves also reflected the cortical magnification of human primary visual cortex. When the traveling waves were measured at different eccentricities, the waves tended to be faster at the larger eccentricity compared to those at the smaller eccentricity. However, when the distance around the annulus was converted into centimeters across the cortex using cortical magnification, resulting travel speeds at those two cortical regions were similar.

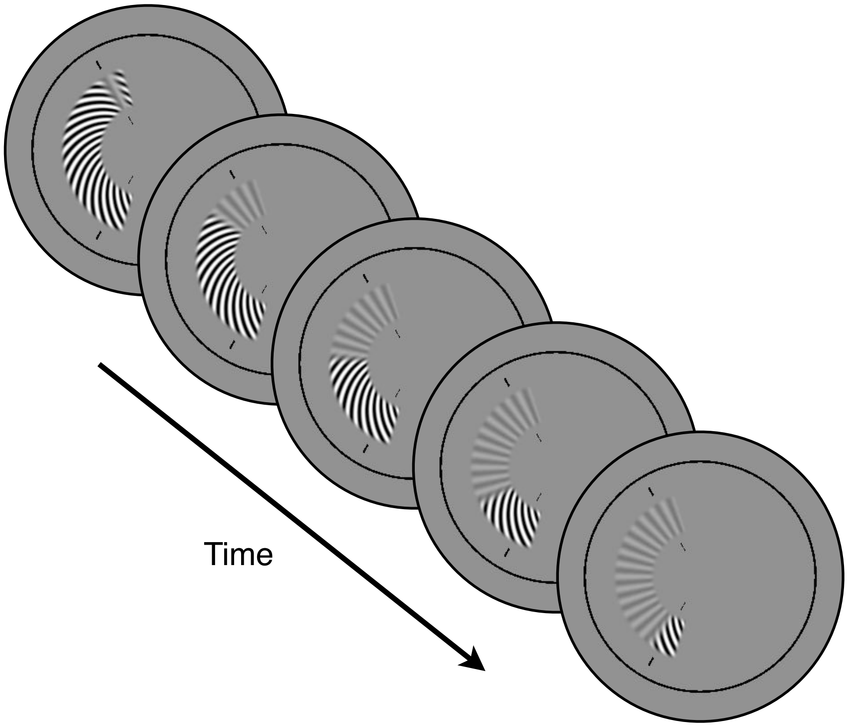

Figure 1.5 Illustration of a traveling wave during binocular rivalry. Spiral pattern is initially dominant and a trigger is given to the upper corner of the radial grating, the suppressed pattern. A dominance wave emerging from the radial grating propagates in a counterclockwise direction.

All these results show that the dynamics associated with periods of mixed dominance during binocular rivalry are not random, by which I mean that the perceptual alternations within one region of a rival figure depend upon the perceptual alternations within another region. In addition, the characterized spatial interactions during binocular rivalry reflect several organizing principles of the primary visual cortex. This implies that the neural circuitry associated with perceptual organization is involved with producing the spatiotemporal dynamics of binocular rivalry.

1.4.3 Multi-zone network model of binocular rivalry

In order to achieve a comprehensive understanding of the spatiotemporal dynamics of binocular rivalry, it is necessary to consider binocular rivalry in the context of the outcome of cooperative/competitive spatial interactions of spatially distributed local rivalry zones, i.e. spatially localized discrete neuronal populations. Recently, Stollenwerk and Bode (2003) and Wilson et al. (2001) formalized this hypothetical context as a network of neurons in which two sets of neurons represent the two rival stimuli respectively, and these two sets of neurons are connected by reciprocal inhibition, producing organized perceptual alternations over space and time. In this dissertation, I use the term Multi-Zone Network Model (MZNM) of binocular rivalry to indicate any model in which binocular rivalry occurs over spatially interacting multiple local rivalry zones.

Figure 1.6a illustrates how a MZNM represents the two rival stimuli and their interactions. In this model (at the center), the black open circles represent the neurons associated with the two rival stimuli: the neurons in the left column represent the vertical grating presented to the left eye and the neurons in the right column represent right-tilted grating presented to the right eye. The green circles drawn on top of the rival stimuli show the receptive fields or the regions of local rivalry zones in which the two competing neurons represent the same retinal location. Note that the grating patterns within all local regions are identical except for their orientations. If these neurons selectively respond to the vertical and right-tilted gratings respectively, the stimulus presented within the receptive field should produce similar neural responses. The blue lines and the red lines represent the connections associated with the recurrent excitations and reciprocal inhibitions respectively. As shown in this figure, the extent of recurrent excitation is larger for neurons representing the vertical grating compared to those representing the right-tilted grating. The extent of recurrent excitation reflects the collinear bias in the arrangement of horizontal connections in layer 2/3 of the primary visual cortex, in which the density of connection is higher for the preferred direction compared to non-preferred direction (Bosking, Zhang, Schofield, & Fitzpatrick, 1997; Chisum, Mooser, & Fitzpatrick, 2003). Based on this neural circuitry, therefore, the strength of interaction and the extent of interaction should be distinguished in the MZNM.

Nevertheless, I also acknowledge that increasing the interaction strength can produce similar MZNM model behaviors as increasing the extent of interaction. I explain how these two factors can produce similar model behavior. In order to illustrate how the strength of interaction and the extent of interaction produce similar model behavior, consider a very simple condition in which the firing rate of a neuron B, $F(B)_{,}$ is a constant multiple of the firing rate of the connected neuron A, satisfying $F(B) = cF(A)$. Now, imagine a simple case with three neurons A, B, and C. In one case (Figure 1.6b), neuron A drives neurons B and C, and neuron B drives neuron C (I term this long-range excitation model in this section). The resulting firing rate of neuron C in this long-range model is represented by the interaction constant of the individual connection c and the firing rate of neuron A as follows, $F(C) = cF(A) + cF(B) = (c + c^2)F(A)$. In another case (Figure 1.6c), neuron A drives only neuron B and neuron B drives only neuron C (I term this short-range excitation model in this section), resulting in $F(C) = cF(B) = c^2F(A)$. Figure 1.6d shows the two curves representing the sum of interaction constants associated with the long- and short-range models respectively.

Note that these two curves increase monotonically, suggesting that the strength of interaction and the extent of interaction produce similar behavior. In particular, these two models produce the same sum of interaction constant by adjusting each interaction constant as illustrated in Figure 1.6d: the interaction constant of the long-range model should be always smaller than the interaction strength of the short-range model. In this regard, manipulating the strength of interaction, rather than the extent of interaction, could produce speed difference in propagating traveling waves in the original implementation of MZNM by Wilson et al. (2001).

MZNM is important because it provides a formal theoretical framework. Previously, I mentioned that the spatiotemporal dynamics are largely unexplored despite their frequent incidence during the course of binocular rivalry. One reason was the lack of a theoretical framework; this network model provides a general but formal theoretical framework for studying the overall dynamics of binocular rivalry. Specifically, as will be seen in Chapters 4 through 6, the hypothetical but biologically plausible structure of

MZNM of binocular rivalry provides testable hypotheses and a useful framework for interpreting the results of experiments.

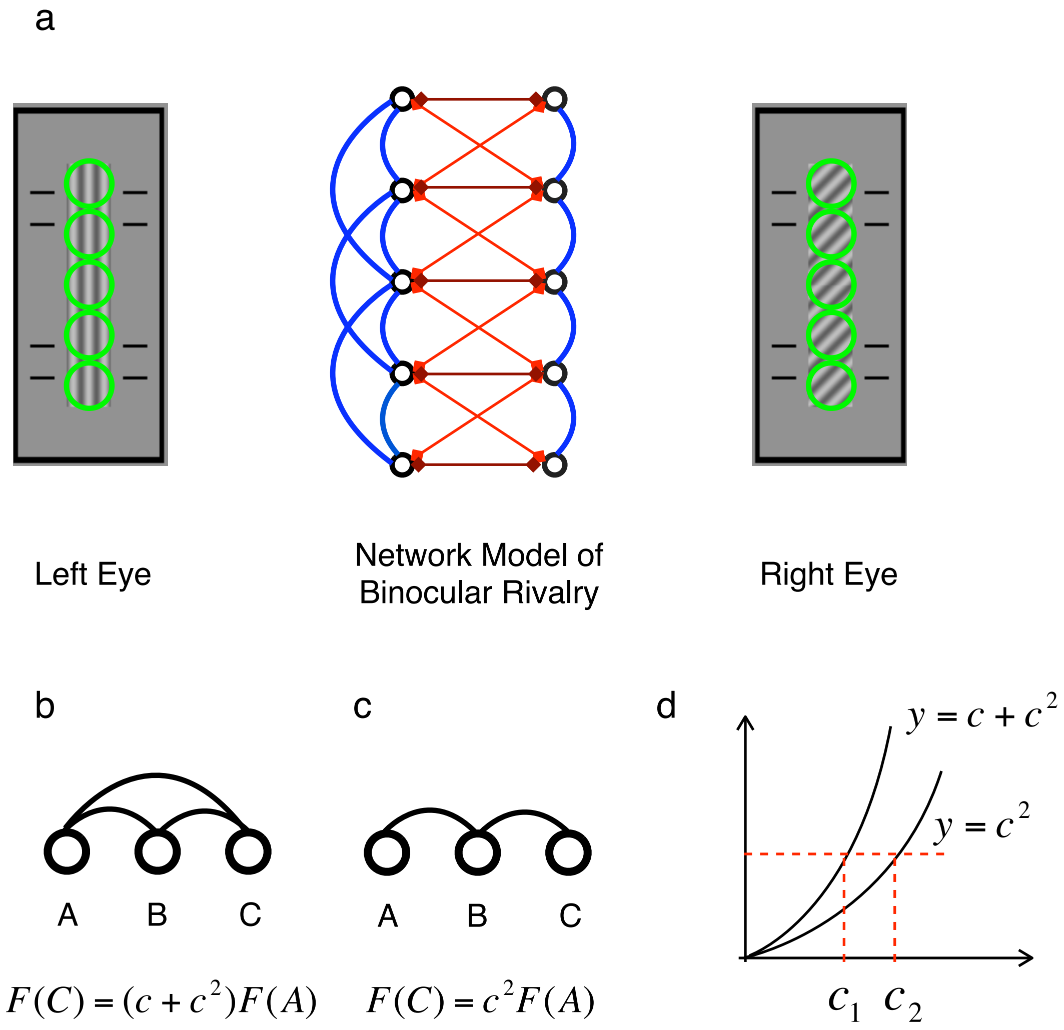

Figure 1.6 Illustration of a Multi-Zone Network Model (MZNM) of binocular rivalry. a) In this model (at the center), the black open circles represent the neurons: the neurons in the left column are associated with the left eye and the neurons in the right column are associated with the right eye. The green circles drawn on top of the rival stimuli show the receptive fields of these neurons. The blue lines and the red lines represent the recurrent excitations and reciprocal inhibitions respectively. b) Illustration of the long-range excitation model. c) Illustration of the short-range excitation model. d) Each curve represents the sum of interaction constants of the long- and short-range excitation models.

1.5 Specific issues and outlines

The goal of this dissertation is to characterize the spatiotemporal dynamics of binocular rivalry in the context of the MZNM of binocular rivalry. Specifically, I examined the following four aspects of rivalry's spatiotemporal dynamics. First, I asked what are the mechanisms producing perceptual alternations of local rivalry or binocular rivalry within a small region (Chapter 2). Although this question is not directly related to the spatiotemporal dynamics, this question is important considering the spatiotemporal dynamics of binocular rivalry as the organized behavior of local rivalries. With this understanding, it is then possible to examine any spatial interactions promoting or suppressing perceptual alternations in neighboring regions. In Chapter 3, I examine the influence of stimulus strength on the alternation behavior of binocular rivalry, including the implications of spatial interactions on this behavior, and then I investigate the relation between dominance duration and the speed of traveling waves in Chapter 4. The role of recurrent excitation in the spatiotemporal dynamics of binocular rivalry is examined in Chapter 5. I summarize the dissertation in Chapter 6.

CHAPTER II

CAUSES OF PERCEPTUAL ALTERNATIONS OF BINOCULAR RIVALRY

2.1 Introduction

In the framework of multi-zone network model (MZNM) of binocular rivalry, perceptual alternations during binocular rivalry are governed by alternations within the individual local rivalry zones, comprising the extended multi-zone network. It is, therefore, important to consider the mechanisms producing perceptual alternations of individual local rivalry in order to achieve a comprehensive understanding of binocular rivalry's spatiotemporal dynamics. In this chapter, I provide the strongest evidence to date that (neural) adaptation is involved in rivalry alternations, and discuss other related mechanisms.

Adaptation, in general, means diminishing neural response due to some prior experience. It is well known that exposure to a high contrast grating reduces the contrast sensitivity at threshold level (Blakemore & Campbell, 1969; Blakemore, Nachmias & Sutton, 1970; Pantle & Sekuler, 1968) and perceived contrast at suprathreshold level (Blakemore, Muncey & Ridley, 1971; 1973). Both the elevation of contrast threshold and the perceived contrast reduction are specific to the spatial frequency (Blakemore & Campbell, 1969; Pantle & Sekuler, 1968; Blakemore, et al., 1973) and the orientation (Blakemore & Nachmias, 1971; Blakemore, et al., 1973) of the adaptation pattern. For that matter, the perceived contrast of a pattern progressively weakens during the prolonged viewing of that pattern (Georgeson, 1985).

Psychophysical studies have shown that adaptation operates over a wide range of time scales. Contrast detection threshold is elevated even after adaptation periods as brief as one second (Greenlee, et al., 1991), and the magnitude of adaptation continues to rise up to 30-60min of adaptation (Anstis, 1996; Blakemore & Campbell, 1969; Magnussen & Greenlee, 1985; Rose & Evans, 1983). However, the magnitude of adaptation saturates quickly (within approximately 10sec to 100sec) when perceived contrast is measured relative to the detection threshold (Hammett, Snowden & Smith, 1994; Blakemore et al., 1971). Nevertheless, all these results have shown that brief contrast adaptation affects the neural representation of a subsequently presented stimulus.

Binocular rivalry dynamics reflect the influence of the adaptation associated with this perceived contrast reduction. It is well established that stimulus strength (e.g. contrast or luminance) of rival stimuli produces systematic changes in mean dominance duration such that dominance durations tend to increase with decreasing stimulus strength of both rival stimuli (Levelt, 1965). In addition, as mentioned above, perceived contrast of a pattern decreases during prolonged viewing of that pattern (Georgeson, 1985). Consistent with these two facts, over the tracking periods of rivalry alternations, the dominance durations tend to increase (Lehky, 1995; Suzuki & Grabowecky, 2007). However, the adaptation associated with binocular rivalry alternations should be distinguished from adaptation associated with perceived contrast reduction.

One widely discussed mechanism operating for rivalry alternations involves (neural) adaptation (Köhler, 1940; McDougall, 1906). In this adaptation hypothesis, the neural response of the perceptually dominant stimulus decreases over time due to adaptation. This decreased response simultaneously reduces the inhibition to the suppressed stimulus and thus, the neural response of that suppressed stimulus increases accordingly. A perceptual switch occurs when these two neural responses associated with the two rival stimuli reach in equilibrium. Therefore, the neural adaptation occurring within the circuitry producing rivalry alternations decreases dominance durations. However, the same neural adaptation occurring outside of this circuitry reduces the perceived contrast and thus increases the dominance durations. For this matter, the adaptation involved in rivalry alternation should be distinguished from the general adaptation producing perceived contrast reduction (Lehky, 1995; Suzuki & Grabowecky, 2007).

There is evidence that adaptation is indeed involved with alternations of binocular rivalry. Blake, Sobel and Gilroy (2003) found that the alternation rate was reduced when two rival stimuli were moved slowly and smoothly around an imaginary circle. This manipulation presumably reduces neural adaptation by recruiting unaffected pools of neurons along of the motion path. The adaptation hypothesis also predicts that durations of perceptual dominance should be reduced when they are preceded by particularly long dominance durations, producing some correlation between the successive dominance durations. Recently, Gao et al. (2006) showed a significant correlation between the successive dominance durations, pointing out the lack of statistical power for failing to see meaningful correlations in the previous studies (Fox & Herrmann, 1967; Lehky, 1995; Leopold, Logothetis, & Sheinberg, 1996).

Additionally, prior monocular adaptation of a grating viewed in one eye reduced perceptual dominance of that stimulus within the same eye when two rival stimuli were presented immediately after this adaptation period (Blake, Overton, 1979; van Boxtel, Alais, & van Ee, 2008; Wade & de Weert, 1986). Similarly, Blake, Westendorf, & Fox, (1990) manipulated the magnitude of adaptation when the two rival stimuli were presented. They perturbed the perceptual dominance by briefly increasing the contrast of one rival stimulus whenever the other rival stimulus became dominant. These perturbations caused the temporarily suppressed stimulus immediately regained perceptual dominance. By forcing one stimulus to remain dominant during a prolonged period, the perturbations were presumably increasing the duration of adaptation of the perturbed eye's view. Consistent with the previous monocular adaptation studies, when dominance durations of the view within the perturbed eye were measured after the perturbation period, they were briefer compared to a control condition in which dominance durations were measured without the prior perturbation period.

However, in all these monocular adaptation experiments, the duration of monocular adaptation is considerably longer (from 10sec to 60sec) than the average dominance durations (2-3 sec). In order to explain the alternations in perception during binocular rivalry, adaptation should operate in short periods of time comparable to the dominance durations.

Motivated by this consideration, I examined the influence of monocular adaptation by parametrically manipulating the adaption duration within a range of values comparable to the dominance durations of binocular rivalry. If adaptation is involved with rivalry alternations, the dominance durations after monocular adaptation should decrease systematically as adaptation duration increases. I tested this prediction in the experiment described in this chapter.

2.2 Experiment

Figure 2.1 illustrates the stimulus sequence consisting of a period of binocular rivalry followed by a period of monocular adaptation. To examine the influence of monocular adaptation on alternations of binocular rivalry, I physically removed the suppressed pattern and then reintroduced that pattern after a given period of time, which I refer to as the adaptation duration, while observers were tracking ongoing perceptual alternations during binocular rivalry. If neural adaptation of the dominant stimulus causes perceptual switches, the dominance durations should decrease systematically with increasing adaptation duration after reintroducing the previously suppressed stimulus.

We need to consider one technical issue associated with this experiment. It is well established that binocular rivalry is easily disrupted when the suppressed pattern changes abruptly, probably because of visual transients (Blake et al., 1990; Walker & Powell, 1979). This is particularly true when presentation of rival stimuli is followed by prior monocular adaptation (Wolfe, 1984). To reduce visual transients introduced during the reintroduction of the rival stimulus, two stimulus sequences were created: the flicker sequence and the composite sequence. In the flicker sequence, the rival stimuli were flickered "on" and "off" at 15Hz, a stimulus manipulation that should mask any transients associated with reintroduction of the rival stimulus (Logothetis, Leopold & Sheinberg, 1996). In the composite sequence the composite configuration created by superimposing both stimuli was presented dioptically during the "off" period of the flicker sequence (Kang & Blake, 2008).

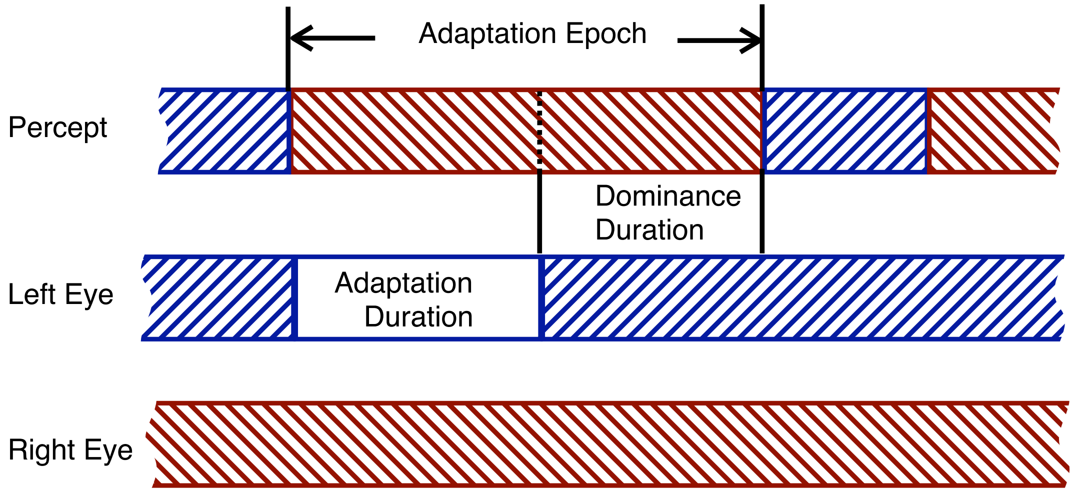

Figure 2.1 Illustration of stimulus sequence. The top figure illustrates the perceptual experiences whereas the lower two figures illustrate the physical stimuli presented to the two eyes. The sequence consists of a series of epochs. For the adaptation epoch, stimulus is removed for the adaptation duration. The dominance duration is determined from the reintroduction of the suppressed stimulus to the perceptual switch.

2.2.1 Method

All aspects of this study were approved by the Vanderbilt University Institutional Review Board. Seven observers, including the author of this dissertation participated in this experiment (5 male, 2 female; mean age 28). Except for the author, all other observers were naïve to the purpose of the study. All had normal or corrected-to-normal vision and all gave informed consent after thorough explanation of the procedures.

A Macintosh G4 computer running OS 9.2.2 (Apple, CA) was used to control the experiment. Stimuli were generated using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) in conjunction with Matlab (Mathworks, MA). Stimuli were presented on the screen of a Sony E540 21-inch monitor (1024H x 768V resolution; 120Hz frame-rate) in a dimly illuminated room. The luminance level of the monitor was linearized using a gamma corrected look-up-table. In all experiments, the stimuli were viewed on a gray background (21.67cd/m2) through a mirror stereoscope placed 90 cm from the monitor.

Rival stimuli were circularly windowed right- and left-tilted gratings whose diameter was 1.8° in visual angle. The boundary of the stimuli was smoothed using a Gaussian filter whose σ equaled three pixels. The contrast of the rival stimuli was 20% and their spatial frequency was 3 cycle/deg. In order to promote alignment of the two eyes, a black circular boundary was presented for both eyes, and its diameter was 1.9° and width was 0.2°. In addition, a circular fixation was presented at the center of rival stimuli whose diameter was approximately 0.2°. The composite configuration was created by adding the two rival gratings, and the contrast of each component was set at 10% so that the contrast of the composite stimulus equaled 20%.

Before conducting the experiment, the average dominance duration was estimated for each observer to determine the range of adaptation durations to be used for that observer. By using the same stimulus sequence, three adaptation durations were determined by 33%, 66% and 100% of this base dominance duration. The stimulus sequence of the adaptation experiment is described by a series of epochs (Figure 2.1). An adaptation epoch is defined from a period of monocular adaptation followed by a period of binocular rivalry until perception switches. It is important to remember that the dominance duration of an adaptation epoch was defined from the reintroduction of the suppressed pattern until perception switches. Within each tracking session, each adaptation epoch (33%, 66% and 100%) was randomly repeated three times. Note also that both rival stimuli were presented for one or two perceptual alternation(s) between any two adaptation epochs. This epoch is refereed to as the no adaptation epoch or 0%

adaptation epoch. With the no adaptation epoch, I could also randomize the adapted eyes over time in addition to obtaining dominance durations associated with 0% adaptation epoch. The experiment was conducted over two days. For each day, the two stimulus sequences (flicker/composite) were repeated four times in a pseudo-randomized order.

Despite the complexity of the experiment, the task of observers was simple: they were instructed to track the alternations in perception by pressing and holding one of two keys each of which corresponded to the left- and right-tilted gratings respectively. When perceptual dominance became indistinct, they were instructed to press neither key.

2.2.2 Result

Figure 2.2 shows the results from the adaptation experiment. In this dissertation, I only describe the results obtained from the flicker sequence because both the flicker and composite sequences provided very similar results. Figure 2.2a shows the mean dominance duration as a function of adaptation duration. Notice that for all observers the dominance durations tended to decrease with increasing adaptation duration. In addition, notice that for all observers the dominance duration decreased in similar rate with increasing adaptation duration. These two observations were confirmed by two-way ANOVA with factors of observer and adaptation duration, yielding a significant main effect of adaptation duration [$F(1,14)=17.87$, $p<0.0001$] but a non-significant interaction of these two factors [$F(6,14)=0.19$, $p>0.5$].

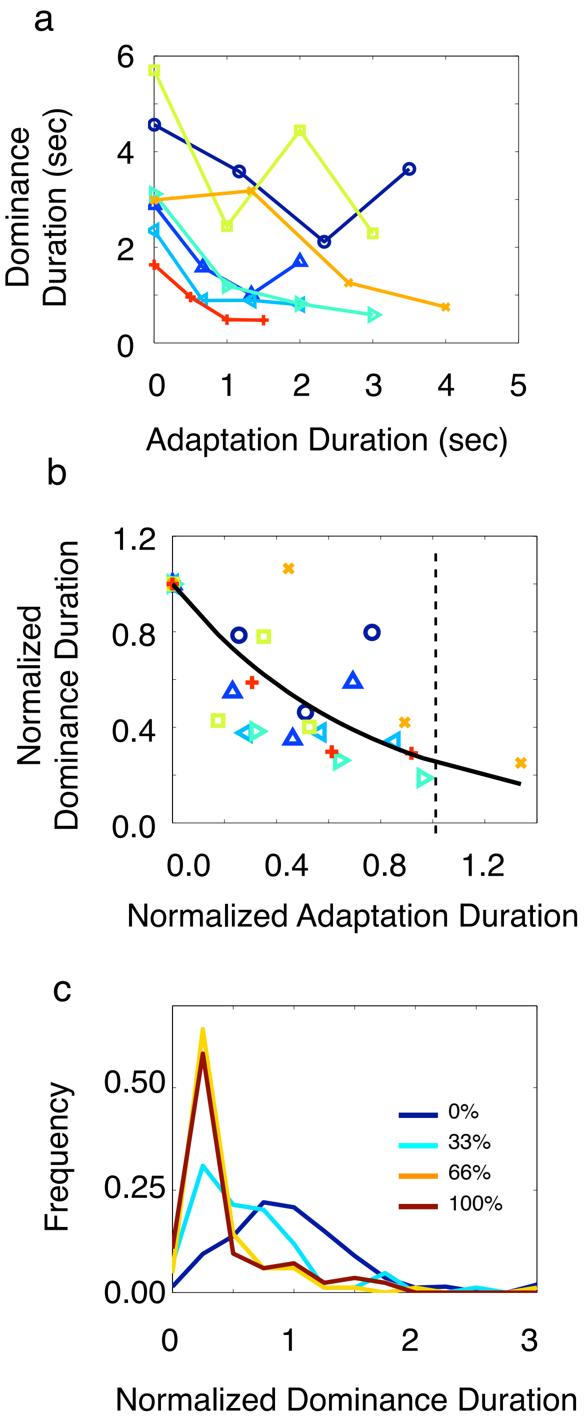

Figure 2.2 Results of the adaptation experiment. a) Mean dominance durations are plotted as a function of adaptation duration. Seven colors represent the data points from seven observers respectively. b) Normalized dominance durations are plotted as a function of normalized adaptation duration. The solid line is the fitted exponential function. c) Distribution of dominance durations for four adaptation epochs and four colors indicate the four adaptation conditions respectively.

Figure 2.2b shows the normalized dominance duration as a function of normalized adaptation duration using the same data creating Figure 2.2a. Both dominance durations and adaptation durations were normalized individually by dividing them by the mean dominance duration obtained from the 0% adaptation epoch. The seven markers with different colors indicate the data points obtained from seven observers respectively. I fitted the exponential model $T_D = T_0 \exp(-t/\tau_A)$ in which T_D is the normalized dominance duration; T_0 is the normalized dominance duration with no adaptation, and τ_A is an adaptation time constant. The estimated adaptation time constant τ_A equaled 0.74sec and its Pearson's correlation r equaled 0.81, meaning that the dominance duration on average reduces by approximately 75% for the first one second.

One thing to note in Figure 2.2b is that, except for one orange cross marker, all data points reside to the left of the dashed vertical line representing values of the normalized adaptation duration. This implies that dominance durations tended to increase over time for the following reasons. First, adaptation durations were normalized by the mean dominance duration associated with 0% adaptation epoch. Second, the 100% adaptation duration equaled the base mean dominance duration measured prior to the adaptation experiment. Therefore, the normalized adaptation duration less than 1 indicates that mean dominance duration of rivalry during the adaptation experiment is longer than the mean dominance duration before the adaptation experiment. This increase in dominance durations during the adaptation experiment is likely related to neural adaptation associated with perceived contrast reduction (Lehky, 1995; Suzuki & Grabowecky, 2007).

In addition to the decreased dominance durations with increasing adaptation duration, the distribution of dominance durations is consistent with the prediction of adaptation hypothesis. A recent model predicted that the variance in the dominance durations decreases with increasing adaptation so that the distribution of dominance durations is narrower with strong adaptation compared to distribution of dominance durations with weak adaptation (Moreno-Bote, Rinzel, & Rubin, 2007). Consistent with this prediction, the normalized dominance durations are narrowly distributed with increasing adaptation duration (Figure 2.2c).

2.3 Discussion

The present result provides the strongest evidence to date for the involvement of adaptation in producing rivalry alternations. Clearly, dominance durations decrease systematically with increasing adaptation duration and, moreover, the duration of monocular adaptation is comparable to the dominance durations of binocular rivalry. In the next section, I first consider the site of neural adaptation associated with binocular rivalry alterations and then discuss mechanisms producing alternations during binocular rivalry.

2.3.1 Adaptation during binocular rivalry

Neural adaptation occurs throughout the visual hierarchy, from peripheral neural events within the retina (Boynton & Whitten, 1970) to the high level visual areas in dorsal (Tootell, et al., 1995) and ventral streams (Grill-Spector & Malach, 2001). However, not all these sites of neuronal adaptations are necessarily involved with rivalry alternations, and there is a strategy to identify neural sites not associated with rivalry alternations. According to the adaptation hypothesis, neuronal response associated with the suppressed stimulus should be greatly reduced because activity evoked by that stimulus should be attenuated or even abolished owing to interocular inhibition exerted by the dominant stimulus. This means that if neural adaptation associated with the suppressed stimulus produces an aftereffect of magnitude similar to the neural adaptation associated with the stimulus when it is dominant, those neurons are not part of the neural circuitry producing binocular rivalry.

Several studies have shown that neurons associated with the suppressed stimulus produce adaptation aftereffects (Blake & Fox, 1974a; Blake & Overton, 1979; Blake, Tadin, Sobel, Rassian, & Chong, 2006; Lehmkuhle & Fox, 1976; Wade & Wenderoth, 1978). In particular, a recent aftereffect study suggested that the neurons in primary visual cortex V1 are involved with binocular rivalry alternations (Blake et al., 2006). In this study, an orientation specific aftereffect, which is assumed to occur in V1, was measured for both the dominance and suppression phases of binocular rivalry. This aftereffect was attenuated when it was induced by a suppressed rival stimulus, suggesting that the neurons in V1 are plausibly involved with rivalry alternations.

However, another recent psychophysical study suggested that the neurons associated with contrast gain-control are not involved with rivalry alternations. Watanabe and colleagues (2004) measured the contrast increment threshold for the visual probe in dominance and suppression phase of binocular rivalry. Consistent with previous studies, the contrast increment threshold was elevated during suppression phase of binocular rivalry (Blake & Camisa; 1978; Fox & Check, 1972; Nguyen, Freeman, & Wenderoth, 2001). However, the pattern of the increment threshold contrast was similar between the dominance and the suppression phase of binocular rivalry across a wide range of pedestal contrast. Based on this result, Watanabe et al. (2004) concluded that the contrast gain control precedes neural site(s) of suppression.

These two psychophysical results suggest that it is reasonable to separate the early visual processing associated with binocular rivalry into a gain-control stage and binocular rivalry stage. In the gain-control stage, the aftereffect associated with the suppressed stimulus occur so that neurons in this stage remain active regardless whether they are associated with the suppressed stimulus or with the dominant stimulus, producing similar aftereffects for both phases of binocular rivalry. Based on previous physiological studies, layer 4 in V1 is a potential candidate for this first stage because activity in the monocular neurons rarely fluctuates according to the perceptual state during binocular rivalry (Leopold & Logothetis, 1996; Sengpiel & Blakemore, 1994) and the contrast gain-control occurred largely within the monocular level (Truchard, Ohzawa, & Freeman, 2000). On the other hand, neurons in the binocular rivalry stage reflect the perceptual state of binocular rivalry and their adaptation is involved with rivalry alternations. I expect that some neurons in the layer 2/3 of V1 may be involved with rivalry alternations because the majority of neurons reflecting perceptual state of rivalry are binocular neurons (Leopold et al., 1996) and several studies have shown that binocular rivalry reflects the perceptual organization associated with long-range horizontal connection in layer 2/3 of V1 (Alais & Blake, 1999; Alais, Loreanceau, Arrighi & Cass, 2006; Wilson, Blake & Lee, 2001).

2.3.2 Mechanisms producing perceptual alternations

Besides neural adaptation, several other mechanisms have been proposed to explain the perceptual alternations during binocular rivalry. Logothetis and Leopold (1999) hypothesized that goal directed behavior in perceptual decision processing is involved with rival alternations, stating that "continually steered and modified by central brain structures involved in planning and generating behavioral actions" (p. 254). Consistent with this view, mental effort such as attention can modulate the alternation rate of binocular rivalry (Breese, 1899; Chong, Tadin, & Blake, 2006; Helmholtz, 1866; Lack, 1974, 1978; Neisser and Becker, 1975; Paffen, Alais, & Verstraten, 2006). In addition to attention, a recent study showed that hand movements could modulate the perceptual dominance during binocular rivalry when those movements are congruent with the direction of a stimulus' motion in suppression phases (Maruya, Yang & Blake, 2008).

Pettigrew (2001) believes that a central oscillator governs perceptual alternations during binocular rivalry. Consistent with this proposal, the alternation rate of binocular rivalry is highly correlated with the alternation rate of other forms of bistable perception such as motion-induced blindness (Carter & Pettigrew, 2003; Sheppard & Pettigrew, 2006). Alternation rate is also influenced by mood (Pettigrew, 2005; Carter et al., 2005), suggesting some psychopharmacological substances in the brain play a central role in driving this putative oscillator (Carter et al., 2007). However, it is unknown how these two proposed mechanisms explain a wide range of temporal dynamics of binocular rivalry; a high contrast stimulus remains longer in perceptual dominance compared to a low contrast stimulus (Levelt, 1965).

A number of computational models have shown that (neural) adaptation during binocular rivalry can produce systematic changes in dominance durations depending on the contrast level. Within these models, the adaptation produces periodic perceptual switches and noise produces the irregularity in dominance durations (Kalarickal & Marshall, 2000; Laing & Chow, 2002; Lehky, 1988; Stollenwerk & Bode, 2003; Wilson, 2003; Wilson, 2007). However, another category of models, called noise-driven attractor models, produce similar dynamics of binocular rivalry without adaptation. In these models, noise is an essential factor for producing both perceptual alternations and the stochastic nature of the resulting durations (Lankheet, 2006; Moreno-Bote et al., 2007; Noest, van Ee, Nijs, & van Wezel, 2007). Both the adaptation- and noise-driven models agree that adaptation and noise are necessary for producing stochastic perceptual alternations during binocular rivalry, but they disagree regarding what factor is essential for producing perceptual alternations.

The double-well energy description shown in Figure 2.3 can illustrate the distinction between these two classes of models. Within the energy landscape, perceptual bistability is represented by the two local energy minima, which represent the two perceptual states respectively, and the ball denotes the current perceptual state (Brascamp et al., 2006; Kelso, 1995; Kim, Suzuki & Grabowecky 2005; Moreno-Bote et al., 2007). According to the adaptation model, the energy minimum of the dominant eye changes over time, and the ball's motion is governed by this changing energy landscape alone. Therefore, perception changes only when the adaptation deforms the energy landscape until there is a single energy minimum (Figure 2.3a). On the noise model, however, the dynamics of the ball are governed by noise arising within a fixed energy landscape; perception changes when the noise provides enough perturbation so that the ball climbs over the energy barrier. This random process results in perceptual alternations (Figure 2.3b).

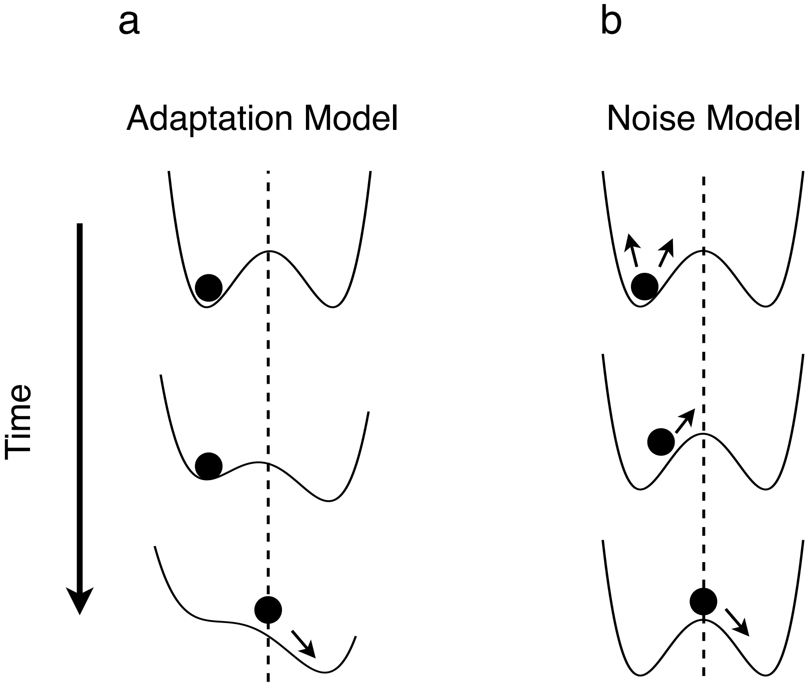

Figure 2.3 Energy description of two models of rivalry alternation. Perception switches at the same time despite the fact that specifications of the models are different. a) Adaptation model in which the energy landscape changes over time due to adaptation and the ball moves according to the changes of this energy landscape. b) Noise model in which the energy landscape remains unchanged but the motion of the ball is governed by both energy landscape and the random noise.

There is empirical evidence supporting the noise driven perceptual alternations. Kim et al. (2006) periodically modulated the contrast of two rival stimuli in anti-phase, such that when the contrast of one stimulus dropped from high to low, the contrast of the other rival stimulus rose from low to high and vice versa. They found the periodicity in distribution of dominance durations; the distribution histogram appears multiple peaks at dominance durations corresponding to those odd-harmonics of the contrast modulation frequency (1/2, 3/2, 5/2 and so on). Based on this result and computer simulations, Kim et al. (2006) concluded that noise is important for producing perceptual alternations during binocular rivalry. Brascamp and colleagues (2006) examined the incidence of return transitions, which means the occasions when an eye loses and regains dominance without intervening dominance of the other eye. They claimed that noise is important for alternation dynamics of binocular rivalry because the existing models based on adaptation hypothesis failed to produce the systematic dynamics associated with return transitions. Lanhkeet (2006) provided more direct evidence for the involvement of noise using reverse correlation technique. He presented two random dot motion displays one to each eye in which dots were moving in opposite directions in those two displays. Over the course of rivalry, the coherence levels of the two rival stimuli were changed independently. When the coherence level was averaged with respect to the perceptual switches, perceptual switches were highly correlated with the incidence of high coherence levels of moving dots in the suppression phase occurring immediately before the perceptual switch. This is consistent with the simulation results of Moreno-Bote et al. (2007).

One may then ask whether the noise model can produce systematic decreases in dominance durations with increasing monocular adaptation, for example, the results from the experiment detailed earlier in this chapter. The noise model cannot reproduce the result of this experiment. There may be chances that a perception switches immediately after the reintroduction of the suppressed pattern because high amplitude noise occurring immediately before the reintroduction of the suppressed pattern.

However, importantly, except some chance driven alternations, the periods of monocular adaptation does not affect the perceptual switches of rivalry after reintroducing the suppressed pattern because the level of noise is independent from adaptation duration and occasional large amplitude noise can cause the perceptual switch at any time (Lankheet, 2006; Moreno-Bote et al., 2007).

2.3.3 Final thought

Do the results of this study then rule out the noise-driven model? One critical distinction of the adaption model from the noise model is that the perceptual switches occur by (neural) adaptation. In the context of energy description in Figure 2.3a, adaptation should deform the energy landscape until it has a single energy minimum to produce a perceptual switch. Otherwise, the ball should remain in the same perceptual dominance indefinitely. With the presence of noise, however, it is impossible to show that the adaptation eventually deforms the energy landscape to have a single energy minimum.

Instead, it is possible that the two mechanisms operate simultaneously within the complementary phases of binocular rivalry. The present results have shown that monocular adaptation operates mainly within the perceptually dominant stimulus. In contrast, noise may operate mainly within the suppression phase of rivalry: both empirical and simulation studies have shown that high amplitude noise within the suppression phase increases the probability of perceptual alternations (Lankheet, 2007; Moreno-Bote et al., 2007). These two mechanisms therefore are not mutually exclusive but are instead complementary, with both operating simultaneously.

CHAPTER III

SIZE MATTERS: CONTRAST DEPENDENT SPATIOTEMPORAL DYNAMICS

Adapted from Kang M.-K. (in press). Size matters: A study of binocular rivalry dynamics. *Journal of Vision.*

3.1 Introduction

It is well established that dynamics of binocular rivalry are systematically influenced by the stimulus strength such that strong stimulus (e.g. high contrast stimulus) stay in perceptual dominance longer than weak stimulus (e.g. low contrast stimulus). In the framework of multi-zone network model (MZNM) of binocular rivalry, however, binocular rivalry dynamics are also the outcome of cooperative and competitive spatial interactions of local rivalries. In this chapter, I examined one controversy regarding the influence of the stimulus strength to the rivalry dynamics in the context of MZNM of binocular rivalry. Implications of cooperative and competitive spatial interactions to the rivalry dynamics are discussed.

To understand the underlying mechanisms of rivalry alternations, two aspects of rivalry dynamics have been studied: the unpredictability of individual dominance phases and the dependence of the durations of those phases on stimulus variables. It is well established that perceptual alternations during binocular rivalry are stochastic, meaning that successive dominance durations are uncorrelated (Fox & Herrmann, 1967; Lehky, 1995; Logothetis, Leopold & Sheinberg, 1996). In general, the distribution of those dominance durations is unimodal and skewed toward longer values (Brascamp, van Ee, Pestman, & van den Berg, 2005; Lehky, 1995). Despite the inherent variability of dominance durations, those durations behave lawfully, on average, when aspects of the rival stimuli are varied over trials. Most notably, dominance durations vary systematically depending on the contrast of rival stimuli, and this dependence was formalized by W.J.M. Levelt in his influential monograph on binocular rivalry (Levelt, 1965).

Referred to as Levelt's 2nd proposition, the contrast-dependent behavior of rivalry can be divided into two complementary parts: 1) as the contrast level of the other eye's stimulus increases, dominance durations of one eye's stimulus decrease on average, and 2) as the contrast level of that stimulus increases, dominance durations of a given eye's stimulus do not vary on average. For several decades, Levelt's 2nd proposition has been construed as a hallmark property of binocular rivalry that any successful model of rivalry must reproduce (Laing & Chow, 2002; Kalarickal & Marshall, 2000; Mueller & Blake, 1989; Stollenwrek & Bode, 2003; Wilson, 2003). There is widespread agreement that the first part of Levelt's proposition is correct (Blake, 1977; Fox & Rasche, 1969; Logothetis, et al., 1996), but concerning the second part – called the contrast invariant property of Levelt's 2nd proposition – there is conflicting evidence. Specifically, a number of studies have found that increasing the contrast of one eye's stimulus tends to increase the dominance durations of that stimulus (Bossink, Stalmeier, & De Weert, 1993; Brascamp, van Ee, Noest, Jacobs & van den Berg, 2006; Mueller & Blake, 1989). Thus, the generality of Levelt's 2nd proposition may be overemphasized, and the emphasis on simulating the contrast-invariant part of the proposition may have obscured other, important characteristics of rivalry's mechanisms.

Several reasons have been offered to explain violations of the contrast invariant property of Levelt's 2nd proposition. For one, Brascamp et al. (2006) pointed out that the range of contrast values used in most previous studies was limited: Levelt (1965) presented a high contrast stimulus to one eye and a variable contrast stimulus in the other eye, but he did not test the condition in which the stimulus presented to one eye was fixed at a low contrast level and the other eye's stimulus was varied over higher contrast levels. Second, Blake and Mueller (1989) reckoned that periods of mixed perceptual dominance might undermine the generality of Levelt's 2nd proposition by distorting measures of predominance. The consideration of mixed dominance is particularly important when rival stimuli are large because periods of exclusive dominance decrease with larger-sized rival stimuli (Blake, O'Shea & Mueller, 1992; O'Shea, Sims & Govan, 1997). It is noteworthy, therefore, that violations of Levelt's 2nd proposition have been found with relatively small rival stimuli (Table 3.1).

Table 3.1 Summary of previous literature. In the Result column, O indicates the result of the study supporting Levelt 2nd proposition and X indicates the violation of Levelt 2nd proposition.

Study	Stimulus	Size	Result
Levelt (1965)	reversed luminance contrast	6.00°	O
Fox & Rasche (1969)		3.24°	O
Bossink et al. (1993)		1.32°	X
Meng & Tong (2004)	sine wave grating	6°x2°	O
Logothetis et al., (1996)		3°	O
Blake (1977)		1.25°	O
Muller & Blake (1989)		0.80°	X
Brascamp et al. (2006)		0.62°	X

In Chapter 3, I identify what turns out to be a key stimulus variable governing the effect of contrast on dominance durations and, hence, on the conditions under which Levelt's 2nd proposition is valid. Table 3.1 summarizes the size of rival stimuli used in eight widely-cited studies, together with their conclusions regarding the contrast-invariant property of the Levelt's 2nd proposition. As evident in this Table, violations of Levelt's 2nd proposition arise when the size of the rival stimuli is relatively small, suggesting that stimulus size is critical in governing the temporal dynamics of binocular rivalry. This suggests that the dynamics of binocular rivalry are inherently spatio-temporal in nature, an idea that is supported by both empirical and theoretical studies: specifically, perceptual experiences during binocular rivalry are the outcome of cooperative and competitive interactions of spatially distributed local rivalries (Alais, Lorenceau, Arrighi, & Cass, 2006; Knapen, van Ee, & Blake, 2007; Stollenwrek & Bode, 2003; Wilson et al. 2001). Yet, previous studies of contrast's effect on dominance and suppression durations have ignored this spatiotemporal nature of rivalry dynamics. In this chapter, I have reexamined the contrast dependence of rivalry.

3.2 Experiment

To examine the implication of the results summarized in Table 3.1, I measured the effect of rival stimulus contrast as the function of the size of those stimuli. Over trials I used three different contrast values for the right-eye and the left-eye rival stimuli, and factorially combined those values to yield a total of nine different contrast pairings for the two eyes' stimuli. This way of pairing rival target contrast values follows the strategy used by Brascamp et al. (2006), which does not limit measurements to one high contrast value for one stimulus paired with lower values for the other stimulus. Additionally, I also investigated the spatial interactions of binocular rivalry by employing two tracking strategies. In a partial-tracking condition, observers were asked to track rivalry dominance for local regions of a spatially extended rival target; in a whole tracking condition, they tracked dominance for the entire, spatially extended pattern. By comparing these two tracking strategies, I examined the degree to which the rivalry dynamics within a local region reflect the rivalry dynamics over the entire extent of the rival stimuli. In this way I could evaluate the influence of mixed dominance on Levelt's 2nd proposition.

3.2.1 Method

All aspects of this study were approved by the Vanderbilt University Institutional Review Board. Eight observers including the author of this dissertation participated in this experiment (4 male, 4 female; mean age 25). Except for the author, all other observers were naïve to the purpose of the study, and four of those observers had no experience whatsoever in observing and tracking binocular rivalry. All had normal or corrected-to-normal vision, and all gave informed consent after thorough explanation of the procedures.

All trials and their related events were controlled by a Macintosh G4 computer running OS 9.2.2 (Apple, CA). Stimuli were generated using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) in conjunction with Matlab (Mathworks©, MA). Stimuli were presented on the screen of a Sony E540 21 inch monitor (1024H x 768V resolution; 120Hz frame-rate) in a dimly illuminated room. The luminance level of the monitor was linearized using a gamma corrected look-up-table. In all experiments, the stimuli were viewed on a gray background (21.67cd/m2) through a mirror stereoscope placed 90 cm from the monitor.

Two different-sized pairs of rival stimuli were created ("large" and "small"): the large pair comprised vertically elongated rectangles whose horizontal and vertical dimensions were 0.8° by 3.2° visual angle, and the small pair comprised 0.8° x 0.8° squares. Rival stimuli were left- and right-tilted sinusoidal gratings whose spatial frequency was 4.5cyc/deg. Three contrast levels were used, whose values are separated by multiple of two, and all combinations of the contrasts were presented. For five observers, the stimuli were 7.5%, 15% and 30% in contrast; for the other three observers contrast values were 10%, 20% and 40% in contrast (these three observers had trouble reliably seeing rivalry alternations at 7.5% contrast). Small side markers (0.2° x 0.8°) were presented 0.7° to the left and the right of the center of the rival stimuli to indicate the center of rival stimuli. To ensure stable binocular alignment of the two rival stimuli, both stimuli were framed by identical black rectangular borders 3.2° X 5°.

Observers reported fluctuations in perceptual dominance by pressing one of two keys corresponding to the two rival orientations. Tracking records were obtained during test periods lasting approximately one minute (each period was terminated coincident with the release of a key, so as not to truncate the dominance duration recorded at the end of the period).

In different blocks of trials, one of two tracking instructions was followed: whole tracking and partial tracking. In the whole tracking condition, observers reported perceptual dominance of a rival stimulus only when the stimulus was visible exclusively, with no hint of the other rival stimulus. In the partial tracking condition, observers reported alternations in dominance within a small central region of the rival stimuli (approximately 0.8° x 0.8°), termed the monitoring region. On partial tracking trials, observers pressed one of two keys only when either of the two stimuli was exclusively visible within the monitoring region. It should be noted that the monitoring region's size is equivalent to the small-size rival stimuli. In addition, the height of the two side markers was identical to that of the small rival stimuli, thus clearly indicating the tracking region of interest within the large rival stimuli during the partial tracking condition. Observers reported no trouble associated with the partial tracking procedure when asked after the experiment.

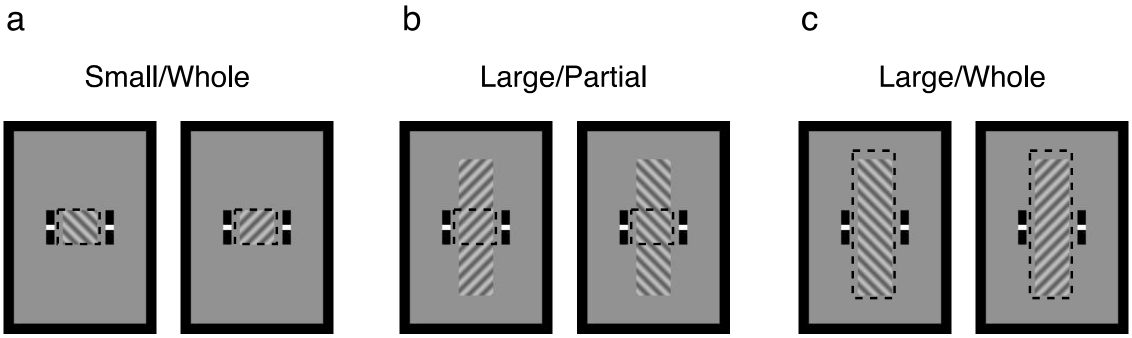

Figure 3.1 Illustration of three experimental conditions (SW, LP & LW). Dashed boxes indicate the monitoring regions which were not shown during the experiment.

The three experimental conditions are illustrated in Figure 3.1 (SW: small stimulus/whole tracking instruction; LP: large stimulus/partial tracking instruction; LW: large stimulus/whole tracking instruction). The monitoring region is represented by the dotted box (which was not shown during the experiment). Note that the size of the monitoring region is identical to the size of rival stimuli in the whole tracking condition. For each experimental condition, a total of 18 tracking records were obtained (i.e., the three contrast levels of the left- and right-tilted gratings were combinatorially presented between the two eyes, yielding 3x3x2 tracking sessions). The experiment was conducted for three days, with observers completing three experimenal conditions per day. The order of conditions was pseudo-randomized.

3.2.2 Result

Figure 3.2 summarizes the average mean dominance durations obtained from the nine combinations of left-eye and right-eye contrasts tested in each of the three conditions. In each panel, the y-axis plots the mean dominance duration of the rival stimulus I shall term the ipsilateral stimulus, the x-axis designates the contrast of that ipsilateral stimulus, and the three separate lines in each panel refer to the contrast values of the other, contralateral rival stimulus. The contrast values of the ipsilateral and contralateral stimuli are specified in terms of multiples of the lowest contrast level tested for those stimuli. The following results are based on analyses of actual dominance durations collected over an entire tracking period. However, I also analyzed these data in two other ways: by transforming all dominance durations to their log (Hupé & Rubin, 2003) and by eliminating perceptual dominance durations during the first 10 sec the tracking period (Logothetis, et al., 1996). These alternative ways of treating the data did not change the pattern of results described below.

Comparing the dominance durations among the three panels, it is apparent that the average dominance durations for given contrast pairs decrease across the three experimental conditions (from Figure 3.2a to 3.2c). A repeated measures, 3-factor ANOVA (experimental condition, ipsi-contrast and contra-contrast) shows significant decreases in dominance duration across the three experimental conditions [F(2,14)=18.12, p<0.001]. This is not surprising considering that increases in the size of rival stimuli increase the incidence and duration of mixed dominance (Blake, et al., 1992; O'Shea et al., 1997), thereby reducing the durations of exclusive dominance. In addition, a perceptual switch within a local region of a rival figure tends to propagate to neighboring regions (Wilson et al., 2001). Combining these two facts about rivalry, the probability of a spontaneous perceptual switch within a local region of a rival target should increase with larger-sized rival stimuli, and thus a perceptual switch within any local region can spread to produce perceptual switches over the entire figure. This can account for the dominance durations measured in the LP condition being shorter than those measured in the SW condition.

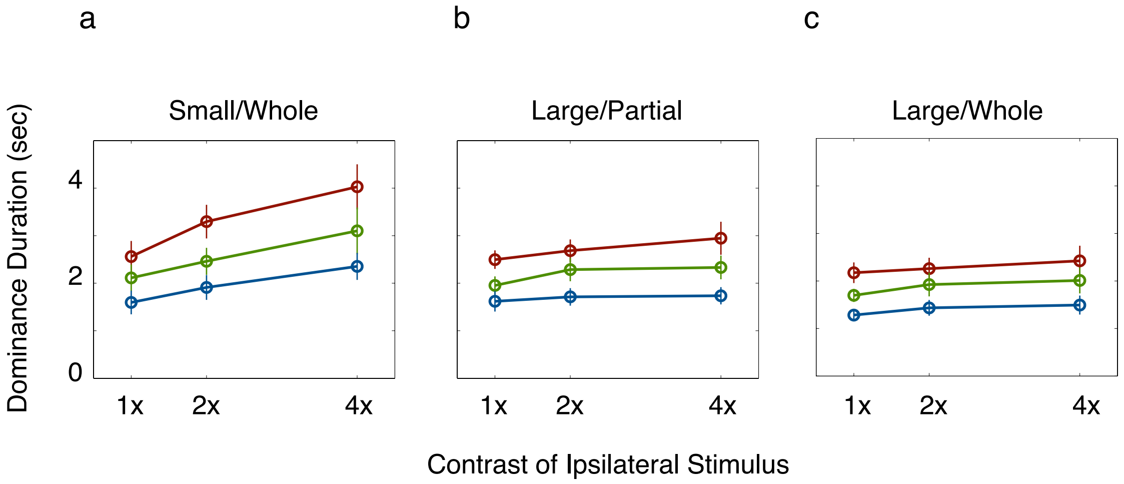

Figure 3.2 Mean dominance durations averaged across eight observers for the three experimental conditions (SW, LP & LW). The y-axis represents the mean dominance duration of the ipsilateral stimulus. The contrasts are represented as multiples of the lowest contrast level. In each panel, the x-axis represents the contrast of the ipsilateral stimulus, and the separate lines represent the contrast of the contralateral stimulus (red line — for 1x; green line — for 2x; blue line — for 4x). Error bar equals ±1 S.E.

But what about the contrast dependence of rivalry dynamics in these data? Just as a reminder, Levelt's 2nd proposition states the mean dominance duration of a given rival stimulus should vary as the contrast of the other rival stimulus is varied, but its mean dominance duration should remain constant as its own contrast is varied. In Figure 3.2, results consistent with these predictions would appear as three lines separated vertically in the order blue, green and red (going from shorter to longer dominance durations). How do these predictions stand up to the results?

It is indeed the case that decreases in the contrast of the contralateral stimulus increased the average dominance durations of the other, ipsilateral rival stimulus. In all three panels of Figure 3.2, the three lines are separated in the predicted order (blue, green and red being ordered from shorter to longer mean dominance durations). These differences in average dominance duration are statistically significant for each experimental condition as revealed by a two-way repeated measure of ANOVA with factors of ipsi-contrast and contra-contrast [$F(1,7)=24.76$, $p<0.01$ for the SW condition; $F(1,7)=25.82$, $p<0.01$ for LP condition; $F(1,7)=37.79$, $p<0.001$ for the LW condition]. This result is consistent with the first part of Levelt's 2nd proposition.

The second prediction from Levelt's proposition, however, is only true under limited conditions, owing to the effect of stimulus size on rivalry dynamics. I compared dominance durations for the SW and LW conditions, for which observers tracked durations of exclusive visibility of the entire rival stimulus. Considering the average dominance durations for the SW condition, we see that increasing ipsi-contrast values paired with a given, fixed contra-contrast produced an increase in average dominance durations for the ipsilateral stimulus [Figure 3.2a; $F(1,7)=19.96$, $p<0.01$], consistent with the findings of Brascamp et al. (2006). This pattern of results is particularly conspicuous when the contra-contrast is low [interaction; $F(1,7)=8.46$, $p<0.05$]. This outcome is incompatible with the contrast invariant property of Levelt's 2nd proposition. But for the LW condition the dominance durations remain invariant irrespective of the ipsi-contrast [$F(1,7)=2.08$, $p=0.19$]. The interaction between the ipsi-contrast and contra-contrast was not statistically significant either [$F(1,7)<1$, $p>0.5$]. This result for the LW condition is consistent with the contrast-invariant property of Levelt's 2nd proposition, suggesting that this property emerges in consequence of spatial interactions associated with large rival stimuli.

Next compare the average dominance durations for the LP and LW conditions, which used identical stimuli but different tracking instructions (exclusive dominance within the central region of the large stimuli vs exclusive dominance over the entire region of the large stimuli). Aside from the previously mentioned difference in average dominance durations, we find no meaningful difference in the influence of ipsi-contrast on mean dominance durations: for neither condition did an increase in the ipsi-contrast affect dominance durations [Figure 3.2b; $F(1,7)=3.48$, $p=0.10$ for LP condition] and the interaction between the ipsi-contrast and contra-contrast was not statistically significant either [$F(1,7)=3.33$, $p=0.11$ for LP condition]. Other than the expected differences in the incidence of mixed dominance in LP and LW conditions, the behavior of the dynamics of rivalry within a limited region of a large rival stimulus are comparable to the behavior of the dynamics of that entire stimulus. This comparability leads me to conclude that the size of rival stimuli is the major factor determining the dynamics of binocular rivalry in terms of their dominance durations -- periods of mixed dominance are not critical in producing the contrast-invariant property of Levelt’s 2nd proposition for large rival stimuli.

3.3 Simulation

The current results, together with earlier work, imply that the perceptual experiences of binocular rivalry are the outcome of interactions among spatially distributed local rivalry zones in the context of MZNM of binocular rivalry (Alais et al., 2006; Blake et al., 1992; Knapen, et al., 2007; O’Shea et al., 1997; Wilson et al., 2001). Accordingly, these results cannot be explained by models that treat rivalry as a winner-take-all competition between competing neural representations of the two rival stimuli, or between competing pools of monocular neurons activated by left or right eyes (Blake, 1989; Logothetis, Leopold & Sheinberg, 1996; Laing & Chow, 2002; Lehky, 1988; Kalarickal & Marshall, 2000; Mueller & Blake, 1989). These models, while perhaps appropriate at a local level, do not incorporate the spatial interactions among neighboring regions of rivalry and the consequent occurrence of mixed states of dominance in which complementary states are represented across those regions. In recognition of this limitation, several recent models have incorporated the notion of MZNM of binocular rivalry (Stollenwrek & Bode, 2003; Wilson, 2001).

Inspired by these network models, I conducted a set of simulations to determine whether a MZNM of binocular rivalry can simulate the pattern of results found in this study. In this simulation, I expanded the double-well potential model proposed by Moreno-Bote and colleagues (2007) as a model of binocular rivalry within a local region, local rivalry zone. In particular, I spatially interconnected multiple local rivalry zones to produce a multi-zone network representing two entire rival stimuli. I chose this energy model for several reasons. First, this energy model produces a wide range of contrast-dependent dominance durations of binocular rivalry despite its simple structure (Moreno-Bote, Rinzel, & Rubin, 2007). Second, the double-well potential model has provided a general description of the dynamics of binocular rivalry (see also Chapter 2.3.2). Previous studies of perceptual alternations during rivalry have employed the concept of the double-well potential, even though the energy model itself was not implemented for simulations (Brascamp et al., 2006; Kim, Grabowecky, & Suzuki, 2006). Third, coupled bistable systems have been studied in the context of other forms of spatiotemporal dynamics in which wave-like behavior is observed (Lindner et al., 1998; Zhang, Hu, & Gammaitoni, 1998).

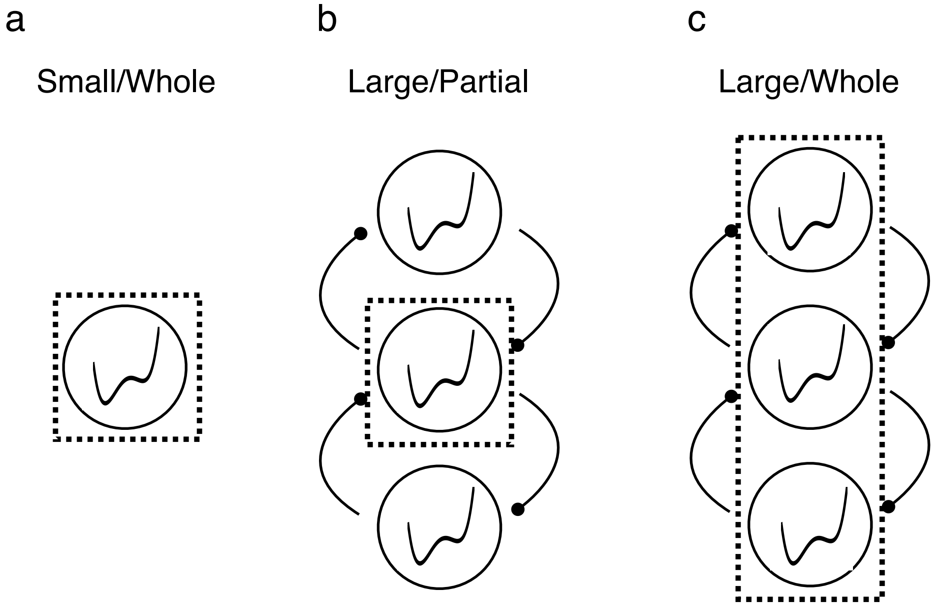

Figure 3.3 Illustration of the three models corresponding to the three experimental conditions (SW, LP & LW). A single local rivalry zone indicates the binocular rivalry of the two small size rival stimuli (a) whereas three local rivalry zones with the interaction term comprise the binocular rivalry of the vertically-elongated large rival stimuli (b and c). Dotted boxes indicate the hypothetical monitoring regions.

Figure 3.3 illustrates the three configurations of the simulation corresponding to the three experimental conditions studied in this chapter. Figure 3.3a illustrates a single local rivalry zone whose dynamics are set to produce a pattern of dominance durations similar to those of the SW condition of this experiment (termed SW model in this simulation). To simulate the large stimulus size condition (termed LP model and LW model respectively), I used three local rivalry zones, each of which has the same parameters as the single local rivalry zone of the SW model; those component zones interact through coupling. For the LW model, the dominance durations were measured when the perceptual states of all three local rivalry zones were the same, but for the LP model, only the perceptual state of the middle local rivalry zone was used to obtain the dominance durations within the monitoring region (the dotted boxes indicate the monitoring region of the models). The dynamics of these models are governed by the following three equations.

$$E_i(r) = r^2(r^2 - 2) + g_A(r-1)^2 + g_B(r+1)^2 \qquad [3\text{-}1]$$

$$\tau \frac{dr}{dt} = -\frac{dE_i(r)}{dr} + \eta X(E_j, E_i) + \omega n_i(t) \qquad [3\text{-}2]$$

$$X(E_j, E_i) = \frac{1}{K_i} \sum_{j \in NB_i} ([E_j] - [E_i]) \qquad [3\text{-}3]$$

Equation [3.1] represents the energy function, where r represents the difference in firing rates of the two competing populations. This energy function has two local minima and each local maximum determined by the input strength parameters g_A and g_B respectively. In the context of this energy-based formalism, it is more difficult for a system to escape from a state with increasing depth of that state or increasing energy barrier between the two states. This increased difficulty produces, in average, longer dominance durations during binocular rivalry [see Brascamp et al., (2006), Kim et al., (2005) and Moreno-Bote et al. (2007) for a detailed discussion of the dynamics of local rivalry with the energy model]. The dynamics of local rivalry satisfy $\tau \frac{dr}{dt} = -\frac{dE_i(r)}{dr}$.

To create a MZNM of binocular rivalry from this energy model, the coupling term $\eta X(E_j, E_i)$ and the noise term $\omega n_i(t)$ are added as shown in equation [3-2]. As defined in equation [3-3], $X(E_j, E_i)$ governs the interaction between the perceptual states of the two local rivalry zones such that local rivalry zone i only interacts with the nearest other local rivalry zones j (NB_i indicates the set of the nearest neighbors of the local rivalry zone i). K_i is the normalization factor which corresponds to the number of neighboring local rivalry zones connected to the local rivalry zone i (but additional simulation without this normalization factor produced qualitatively similar results). $[E_i]$ represents the perceptual state of the given local rivalry zone i, which is either +1 or -1. This ±1 value is used because the energy function has a local minima at $r \tilde{} \pm 1$. Therefore, if the perceptual states of the two adjacent local rivalry zones are the same, this interaction does not influence the equation [3-2]. The coupling strength of the network model is determined by η in equation [3-2] and this η equals 0 for SW model (details about the model parameters and the simulation procedures are described in Appendix A).

The three (SW, LP and LW) models were investigated by changing the key parameters of the simulation (g_A, g_B and η). In Figure 3.4, line style (width and solid/dashed) indicates the dominance durations at a given contra-contrast g_A whereas color indicates the coupling strength η as shown at right of Figure 3.4c. First, g_A and g_B were varied among 0.1, 0.2 and 0.4 for the SW model. In the model, they correspond to the contrasts of the two rival stimuli. The mean dominance durations produced by the simulation of the single local rivalry zone were very similar to the experimental results (Figure 3.4a). This is consistent with the simulation of Moreno-Bote et al. (2007), confirming that the SW model produces dominance durations whose variation violates the contrast invariant property of Levelt's 2nd proposition: increasing ipsi-contrast g_B increases the mean dominance duration.

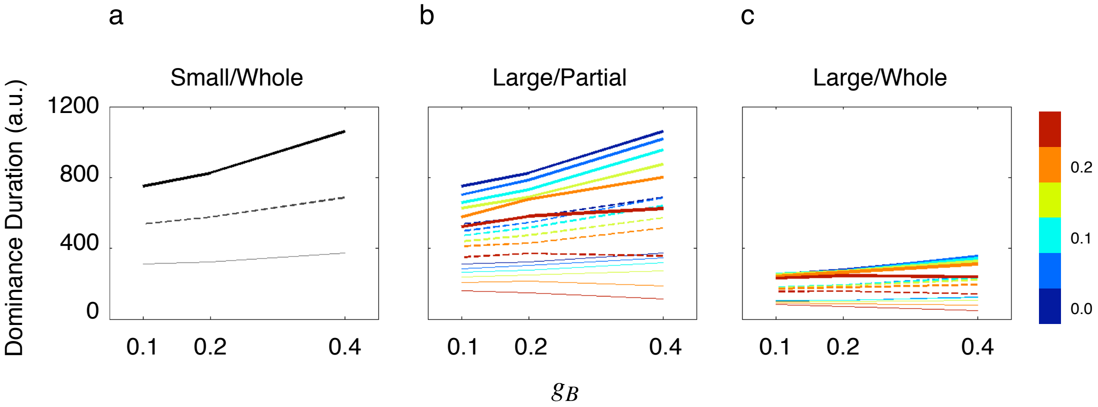

Figure 3.4 Simulation results of dominance durations. Line style indicates the dominance durations at a given (thick line for=0.1; dotted line for =0.2; thin gray line for =0.4) as a function of . The color of each line indicates the coupling strength from 0 to 0.25 by step size 0.05 as shown in the color bar at the right side of (c).

Now, the critical test of this simulation is to see whether the coupling strength η parameter inherent in the LP and LW models produces patterns of results mirroring those obtained from the experiments, especially the contrast-invariant property of Levelt's 2nd proposition. Figures 3.4b and Figure 3.4c summarize the dominance durations of the LP and LW model, respectively. When η equals 0, the LP model's dominance durations are identical to the dominance durations of SW model, as they should be. Consistent with experimental results, dominance durations decrease with increasing g_A at the same coupling strength η for all three models. In addition, as the coupling strength η increases, overall dominance durations decrease for LP and LW models compared to the SW model. Most importantly, with the properly selected coupling strength η, the mean dominance durations remain relatively unchanged at increasing ipsi-contrast g_B and this pattern of result is particularly conspicuous for LW model. Thus, this simulated behavior of the LW model captures the contrast-invariant property of Levelt's 2nd proposition.

3.4 Discussion

In this chapter, I examined contrast-dependent dynamics of binocular rivalry for different sized rival targets. The most important empirical finding of the study showed that the contrast invariant property of Levelt's 2nd proposition depends on the size of the rival stimuli, reconciling conflicting claims in the literature. In addition, a simple energy model with spatial coupling could reproduce the empirical findings of this study, suggesting that rivalry dynamics are the outcome of cooperative/competitive interactions among spatially distributed local rivalry zones (Alais et al., 2006; Blake et al., 1992; Knapen, et al., 2007; O'Shea et al., 1997; Wilson et al., 2001).

Why do large sized rival stimuli produce the contrast invariant property consistent with Levelt's 2nd proposition while small sized rival stimuli violate this proposition? For purposes of answering this question, I will focus on the SW and LW conditions, for it is the results from those two conditions that highlight this seemingly contradictory behavior. One possible explanation for this size-dependent behavior emerges from consideration of two characteristics of binocular rivalry. First, we know that large sized rival stimuli often produce mixed dominance states, whereas small sized rival stimuli are less likely to produce mixed dominance. Mixed dominance states introduce the possibility of return transitions (RTs): state changes in which an exclusively dominant rival pattern temporarily enters a state of mixed dominance but then becomes exclusively dominant again. It stands to reason, then, that large rival targets are more likely to yield RTs than are small rival targets. Second, we know that the fraction of RTs systematically changes dependent on the contrast of rival stimuli (Brascamp et al., 2006). So it is reasonable to wonder whether the dependence of Levelt's 2nd proposition on size might be attributable to the differential incidence of RTs associated with SW and LW. The analyses in the following section evaluate this possibility,

3.4.1 Dynamics of return transitions

I analyzed the fraction of return transitions (FRTs: proportion of RTs out of all transitions) for the SW and LW conditions. To evaluate the dependence of RTs on contrast, I borrowed the concept of "departure" contrast as used by Brascamp et al. (2007): "departure" contrast refers to the contrast of the dominant pattern before a RT. I will refer to the contrast of the other stimulus, i.e., the one that did not achieve complete dominance following the mixed dominance state, as "companion contrast." In Figure 3.5, the departure contrast is represented along the x-axis and companion contrast is represented by the color of three lines. Consistent with Brascamp et al. (2007), the FRTs increased with departure contrast and decreased with increasing companion contrast [three way ANOVA with factor of two experimental conditions (SW & LW) X departure contrast X companion contrast showed significant effect of the departure contrast F(1,7)=8.45, p<0.5 and companion contrast F(1,7)=14.86, p<0.01]. This observation is most pronounced at the highest departure contrast and the lowest companion contrast. Importantly, the RTs occur in similar proportions for both SW and LW conditions [F(1,7)=2.75, p=0.14], suggesting that the incidence of RTs cannot explain the contrast-invariant property of Levelt's 2nd proposition. To provide converging evidence for this tentative conclusion, I performed additional analyses of the dynamics of RTs for these two conditions.

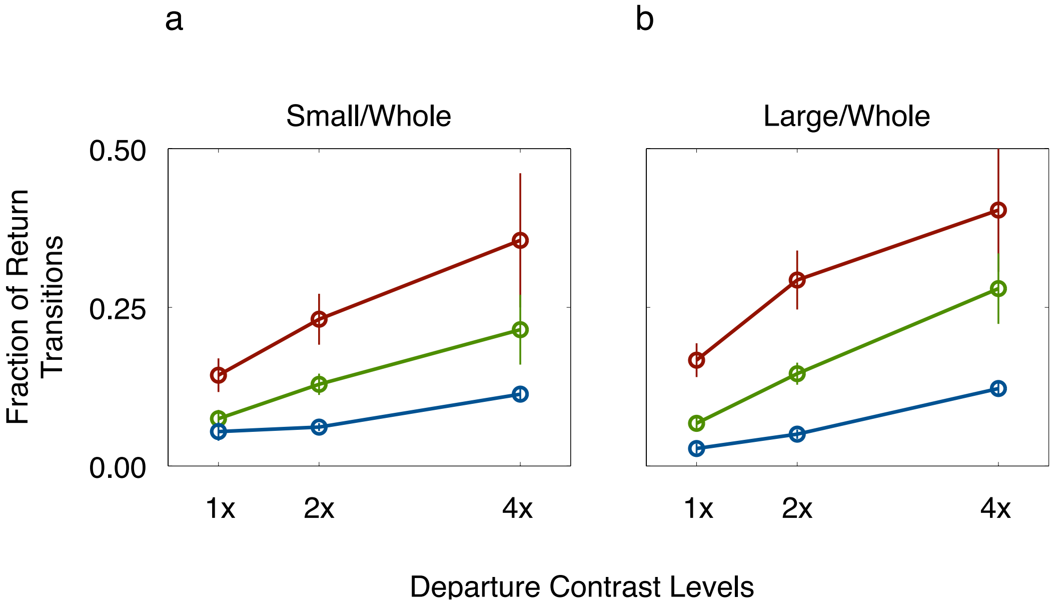

Figure 3.5 FRTs (Fraction of Return Transitions) of the two experimental conditions (SW & LW). The x-axis represents the departure contrast and the three lines represent the companion contrast (red line – for 1x; green line – for 2x; blue line – for 4x). Error bar equals ±S.E.

To begin, I computed predominance for each of the contrast pairings in both tracking conditions (SW and LW); predominance is defined as the sum of all dominance durations associated with the ipsilateral stimulus divided by total duration of a tracking period. Those predominance values are shown in Figure 3.6, and here it can be seen that predominance of the ipsilateral stimulus increased with ipsilateral contrast for both conditions. This means, in other words, that predominance does not mirror the effect of ipsilateral contrast on average dominance durations (Figure 3.2), for those average durations increased only for the SW condition. Is it possible that RTs are responsible for this difference in behavior between predominance and average dominance durations?

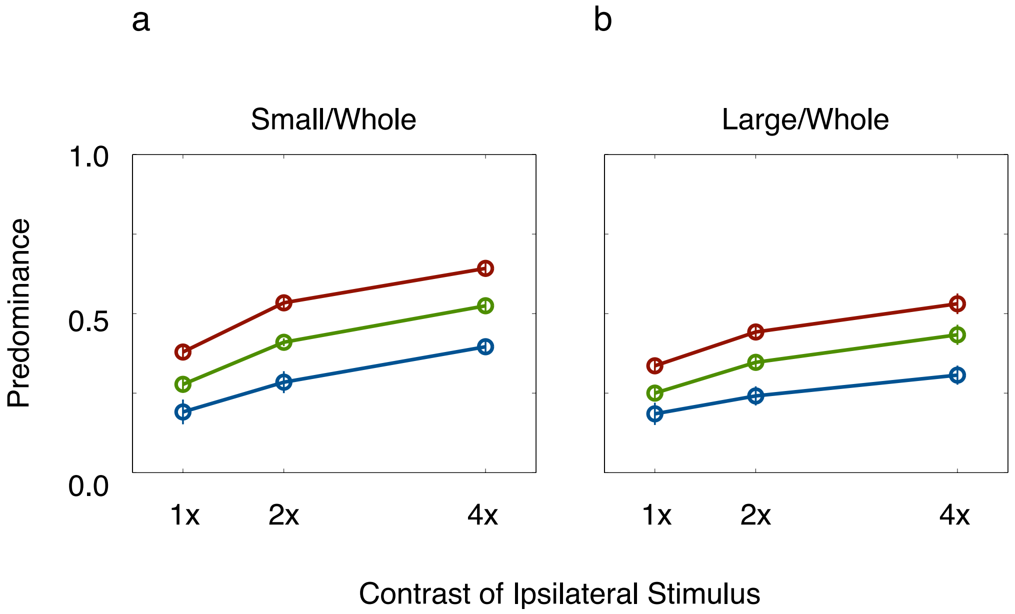

Figure 3.6 Predominance of the two experimental conditions (SW & LW). The x-axis represents the contrast of the ipsilateral stimulus and the three lines represent the contrast of the contralateral stimulus whose colors are the same as Figure 3.2. Error bar equals ±S.E.

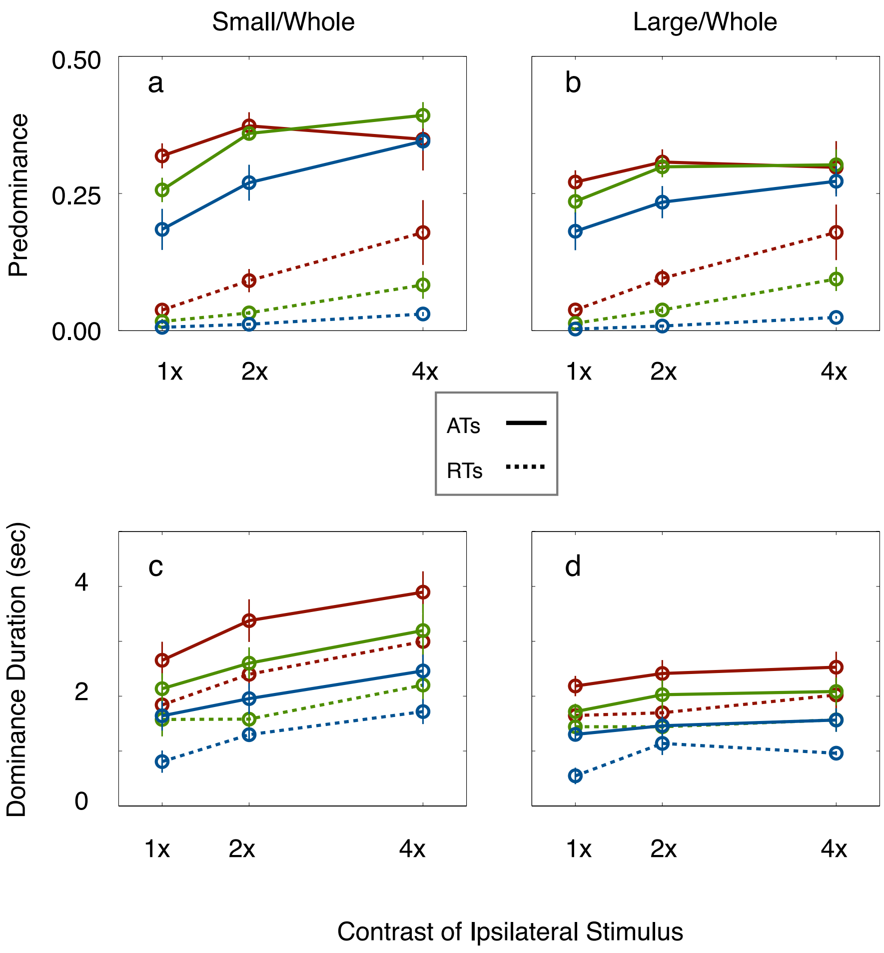

Figure 3.7 Dynamics of ATs (alternation transitions) and RTs (return transitions) of the two experimental conditions (SW & LW). a) and b) show the predominance and c) and d) show the mean dominance durations. The solid lines present the measures obtained from ATs and the dotted lines represent the measures obtained from the RTs. The x-axis represents the contrast of the ipsilateral stimulus and the three lines represent the contrast of the contralateral stimulus whose colors are the same as Figure 3.2. Error bar equals ±S.E.

To answer this question, I compared the predominance and the average dominance durations for two categories of dominance states: 1) those associated with RTs, and 2) those associated with alternation transitions (ATs), i.e., episodes in which dominance switched from one stimulus to the other. The first category, then, consists of dominance durations associated with episodes where a stimulus was dominant, it transitioned to the mixed state and it then transitioned back to dominance – the durations associated with that second, return state constitute RT durations. The second category, ATs, consists of dominance durations associated with episodes where one stimulus was dominant followed by dominance of the other stimulus (irrespective of whether a mixture occurred in between) – the durations associated with that second dominance state constitute AT durations. With these two categories of dominance durations established, I computed mean dominance duration and predominance for all contrast pairs for both of the tracking conditions. Those results are shown in Figure 3.7, with the dynamics of RTs shown by the dotted lines and the dynamics of ATs shown by the solid lines.

Figure 3.7a and 3.7b show the dynamics associated with the predominance of the SW and LW conditions, respectively. Considering first the RTs (dotted lines), as ipsi-contrast level increased, the predominance associated with these RTs increased [with two-way ANOVA with factors of ipsi- and contra- contrasts, $F(1,7)=58.10$, $p<0.001$ for the SW condition; $F(1,7)=9.20$, $p<0.05$ for the LW condition]. This pattern of results is particularly conspicuous at low contra-contrast and high ipsi-contrast levels, accounting for much of the increased predominance shown in Figure 3.6. However, the mean dominance durations of ATs and RTs, shown in Figure 3.7c and 3.7d, change similarly as a function of ipsi-contrast level: when the ipsi-contrast level increases, the mean dominance durations associated with both the ATs and RTs increase for the SW condition but remain unchanged for the LW condition. An ANOVA with three factors (transition type, ipsi-contrast and contra-contrast) shows no significant interactions between the transition type and ipsi-contrast [$F(1,7)=0.71$, $p=0.43$ for the SW condition; $F(1,7)=0.08$, $p>0.5$ for the LW condition]. Thus, the contrast-invariant property of

Levelt's 2nd proposition observed with large rival stimuli is not accounted for by mean dominance durations associated with RTs.

3.4.2 Spatiotemporal dynamics during binocular rivalry

The empirical results in this paper confirm that rival stimulus size is an important factor determining rival dynamics (Figure 3.2). Moreover, the simulations in this paper demonstrate that a MZNM of binocular rivalry can reproduce these empirical results (Figure 3.4). Those models work because of coupling among neighboring zones of rivalry that entrain equivalent states within those zones: couplings embody the size-dependent behavior measured perceptually. The model I implemented, however, is undoubtedly oversimplified. For example, the sizes of the zones were arbitrary and were not scaled for retinal eccentricity, which they should be to conform with known properties of early visual mechanisms. A more refined version of this model needs to take into account other factors, as well. These include connection topology (e.g. longer connection for the collinear pattern; Wilson et al., 2001) and noise statistics (Lindner et al., 1998; Stollenwrek & Bode, 2003; Zhang, et al., 1998).

Finally, a successful model must accommodate the influence of stimulus complexity on rivalry dynamics, including the dynamics specified by Levelt's 2nd proposition. Very little is known about these kinds of influences, although there is some hint in the literature that they matter. Specifically, Meng and Tong (2004) measured rivalry alternations using large dichoptic stimuli comprising pictures of a house and a face. They varied the contrast levels of these stimuli and found that increasing the ipsi-contrast increased mean dominance durations, a violation of the contrast-invariant part of

Levelt's 2nd proposition. As shown in my experiments (Figure 3.2) and in the other studies listed in Table 3.1, however, large rival stimuli comprising simple figures do obey Levelt's 2nd proposition. It may be, then, that the sizes of the local rivalry zone forming a multi-zone network and the strength of the coupling among those zones vary with stimulus complexity. This possibility is not far-fetched, based on the notion that rivalry transpires at multiple levels within the visual hierarachy (Blake & Logothetis, 2002; Freeman, 2005; Logothetis, et al., 1996; Nguyen, Freeman, & Alais, 2003; van Boxtel, Alais, & van Ee, 2008).

3.5 Conclusion

The present chapter shows that the contrast-invariant property of Levelt's 2nd proposition appears by increasing the size of stimuli. This result reconciles the conflicting claims of previous literature. The present empirical and modeling studies shed light on how to consider dynamics of binocular rivalry.

CHAPTER IV

ALTERNATION DYNAMICS AND PROPAGATION DYNAMICS OF BINOCULAR RIVALRY

Adapted from Kang M.-K., Heeger, D., & Blake, R. (in press). Periodic perturbations producing phase-locked fluctuations in visual perception. *Journal of Vision.*

4.1 Introduction

The traveling waves accompanying transition phases of binocular rivalry provide an adequate way to study the relation between the perceptual switches and their spatial interactions within local regions of binocular rivalry. This is because the traveling waves during binocular rivalry have been considered as a series of perceptual switches over space and time. However, it is unknown how these spatial interactions influence the dynamics associated with spontaneous perceptual alternations. In this chapter, I describe a novel technique termed periodic perturbation in which it is possible to characterize both the traveling waves and spontaneous alternations using the same task. Using this technique, I have investigated the relations between the spontaneous perceptual alternations and traveling waves during binocular rivalry, and consider the results in the context of multi-zone network model (MZNM) of binocular rivalry.

In the original implementation of characterizing traveling waves during binocular rivalry (Wilson, Blake & Lee, 2001), observers attempted to initiate transitions on discrete trials dependent on the subjective perceptual state. With that procedure, a large fraction of trials had to be discarded because the traveling waves were disrupted by spontaneous perceptual alternations or because the triggers were ineffective. Moreover, it required observers to distribute their attention over different regions of the visual field when initiating triggers and, then, when monitoring rivalry.

However, this procedure is not adequate for the question of this chapter for two reasons. First, the goal of the study is to examine the relations between spontaneous perceptual alternations and perceptual alternations associated with traveling waves. To do this, observer's task should be identical to ensure that similar processes are applied when characterizing both aspects of binocular rivalry. Second, in some cases, it is impossible to categorize whether a perceptual switch within a region of rival figure is associated with a spontaneous alternation or with alternations associated with the traveling waves, because any timely perceptual switch over space and time provides the impression of traveling waves. This ambiguity undermines the categorization procedure previously used. Therefore, I modified the procedure as described below.

4.2 Experiments

To circumvent the above mentioned inefficiencies and challenging task demands, I have developed novel psychophysical and analytical techniques for creating and characterizing perceptual waves associated with transitions in rivalry dominance.

This novel technique, which differs in several important respects from the one developed by Wilson et al. (2001), is illustrated in Figure 4.1. This technique – termed periodic perturbation – entails remotely triggering switches in perceptual dominance and indexing the spatio-temporal properties of those switches based on simple, binary categorizations performed by observers viewing binocular rivalry between two dissimilar monocular patterns. The technique exploits the potency of a localized increment in contrast to promote local dominance of a small part of a previously suppressed pattern and, moreover, for that local region of dominance to spread over neighboring areas of the visual field (Wilson et al, 2001).

The observer views two rival patterns, one presented to each eye via a mirror stereoscope, and simply indicates by key presses which one of the two patterns is currently dominant within a restricted, central region of the display (the “monitoring region”). Because this region is small, the state of rivalry tends to be unitary and unambiguous throughout the viewing period. Within two small regions of the rival patterns, one above and the other below the monitoring region, local contrast increments are periodically presented in antiphase (i.e., one increment delivered to the top of one eye’s pattern and then, some time later, the other increment delivered to the bottom of the other eye’s pattern, and so on). With appropriately timed triggers, the dominance state within monitoring region switches repetitively between the two rival patterns, with these switches delayed but time-locked to the triggers.

4.2.1 Method

Stimuli and trial-related events were controlled by a Macintosh G4 computer (Apple, CA) running Matlab (Mathworks, MA) in conjunction with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Stimuli were presented on the screen of a Sony E540 21 inch monitor (1024H x 768V resolution; 120 Hz frame-rate; 21.67 cd/m2 mean luminance) in a dimly illuminated room. In this experiment, stimuli were presented against a gray background (21.67 cd/m2) through a mirror stereoscope placed 90 cm from the monitor.

Vertically elongated rival stimuli (0.8° X 5° visual angle) were presented to the left and right eyes. To promote stable binocular alignment, each rival stimulus was bordered with a black rectangular frame (3.6° X 8°) the width of which was 0.25°. Observers carefully adjusted the mirrors of the stereoscope until the two half-images were accurately aligned. The rival stimuli comprised left- and right-tilted sinusoidal gratings of spatial frequency 4.5 cyc/deg. The contrast of the two rival stimuli was identical. In Experiment 4.1 (traveling waves and trigger period), contrast was either 22.5% or 40.0% and for Experiment 4.2 (traveling waves and trigger distance) only one contrast level 22.5% was used. A small region at the center of each rival stimulus was demarcated by the presence of dotted indicating markers located to the left and the right of this central monitoring region. At locations symmetrically spaced above or below this monitoring region could appear brief (200 msec), localized (˜ 0.8° X 0.2°) contrast increments to each of the rival gratings. For any given observation period, these increments occurred in the upper part of one eye's rival grating and in the lower part of the other eye's rival grating.

Observers were instructed to fixate the center of the monitoring region and to track fluctuations in perceptual dominance within that region by pressing and holding either of two keys associated with left/right-titled gratings. Observers declared dominance only when one or the other of the rival gratings within the monitoring region was exclusively dominant, with neither key being pressed when mixtures are experienced. Each tracking episode lasted 80 sec, and all test conditions were repeated four times with the order of conditions randomized within a block of trials. Enforced rest periods were interleaved between all trials.

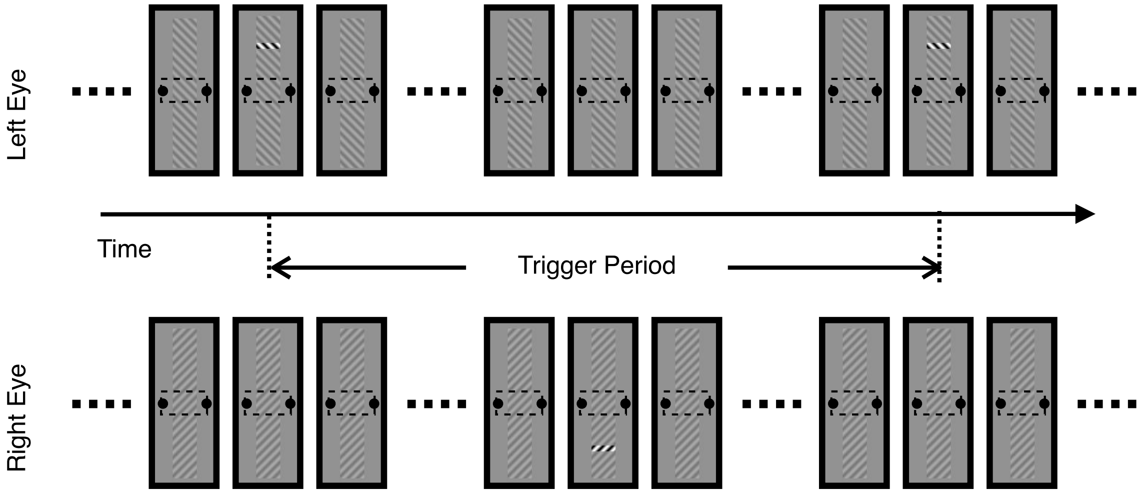

Figure 4.1 Schematic diagram illustrating the periodic perturbation technique. Triggers are presented repetitively in anti-phase within the upper region of one pattern and within the lower region of the other rival pattern, with this sequence lasting throughout an extended period of binocular rivalry. (The dots denote extended periods during which the rival targets are presented without triggers.) Trigger period is defined as the interval of time elapsing between two successive trigger presentations to the same eye. The observer simply reports perceptual alternations in rival dominance within the central region of rival stimulation, called the monitoring region and indicated here by a dashed box (which was not presented during the experiment). Also shown in this figure are the indicating markers that were present on either side of the central monitoring regions.

Trigger period is defined as the time elapsing between successive trigger presentations within the same eye (Figure 4.1). The initial pilot observations suggested that the optimal trigger period for a given observer was dependent on that observer's average rate of rivalry alternations (a point verified in the Results section). Thus in Experiment 4.1, the effect of periodic triggers on rivalry dynamics within the monitoring region was assessed for trigger periods ranging from 2–6 sec. I also included conditions in which the contrast of the trigger increment was zero, meaning that the alternations in rivalry at the monitoring region are governed entirely by intrinsic neural events; these data provided for each observer an estimate of mean dominance duration associated with the spontaneous perceptual alternations unaffected by external triggers. In Experiment 4.1 the trigger distance (center of trigger to center of monitoring region) was always 1.5°, and in Experiment 4.2 three trigger distances (1.0°, 1.5° and 2.0°) were used to determine whether perceptual switches at the monitoring region were systematically delayed dependent on trigger distance.

A total of nine observers (8 males, 1 female) including the author participated in Experiment 4.1. Both 22.5% and 40.0% contrast stimuli were examined for four observers and, for the other five observers, one of these two contrast levels was used. Seven of these observers, all male, participated in Experiment 4.2. Except for the author and the advisor of this dissertation, all other observers were naïve to the purpose of the study. All had normal or corrected-to-normal visual acuity and normal stereopsis; all gave informed consent after thorough explanation of the procedures. All aspects of this study were approved by the Vanderbilt University Institutional Review Board.

4.2.2 Experiment 4.1: Traveling waves and trigger period

The perceptual consequence of appropriately timed, repetitive triggers was obvious to all observers: the dominant pattern switched periodically between the two alternatives, and this periodicity was conspicuous in the observers’ tracking records. Rather than comprising a series of unpredictable dominance durations (Fox & Herrmann, 1967) the periodic perturbation technique yielded a highly ordered series of dominance states (Figure 4.2). This outcome resembles what happens when the rival targets themselves are flickered in anti-phase (Kim, Grabowecky, & Suzuki, 2006). The important difference is that here entrainment is being produced by stimulus events occurring elsewhere within the visual field and is preceding the perceptual transitions within the monitoring region by many hundreds of milliseconds.

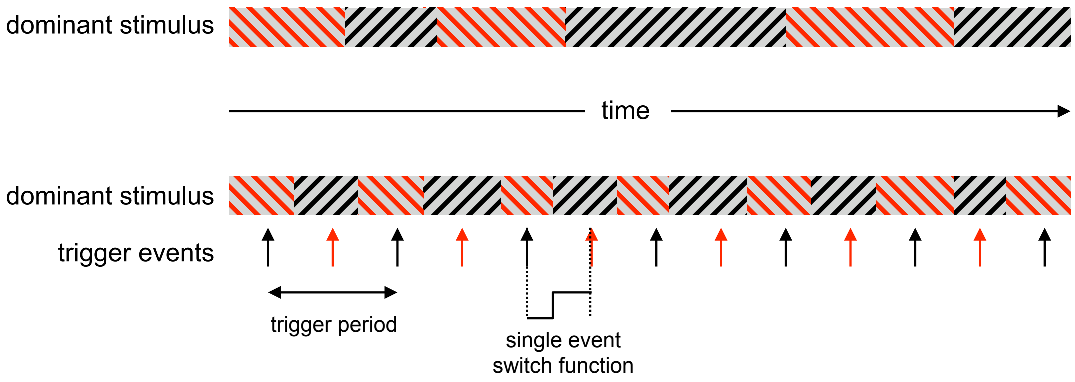

Figure 4.2 Perceptual alternations for rivalry and periodic perturbation. The upper time series represents perceptual alternations measured without periodic trigger presentations. Excerpt (~ 40 sec) from an 80-sec time series of fluctuations in rivalry dominance (denoted here as gray and red gratings) within the central "monitoring" region of a pair of rival targets like those shown in Figure 4.1. Not shown are the very brief periods of mixed dominance between successive periods of exclusive dominance. The lower time series shows successive durations associated with presentation of periodic triggers at locations above and below the monitoring region. Triggers at these two locations are presented in anti-phase, i.e., to one stimulus and then to the other (red arrows indicate triggers delivered to the rival target whose contours are oriented diagonally right; black arrows indicate triggers delivered to the diagonal left grating). Triggers are delivered independently of rival state, but at an optimal trigger period rival states become entrained (with a phase lag) with the triggers. From each extended period of rivalry tracking, the states of rivalry following each trigger (including mixtures) are recorded as a string of binary data (with mixed states equaling 0.5) that spans the period from one trigger to the next. All of those individual records are averaged to produce the switch function for that tracking sequence (see Figure 4.3).

To quantify the salience of periodicity in perceptual switches in the time domain, I created an index termed the probability switch function that provides a succinct but comprehensive representation of the trigger's propensity to entrain dominance durations. As illustrated in Figure 4.2, I derived for each periodic trigger event a record of the rivalry state time-locked to that trigger and extended until the next trigger was presented to the other eye. I then averaged all of those records to obtain the switch function for that observer tested on a given stimulus condition. Figures 4.3a-c show representative, average switch functions for different trigger periods.

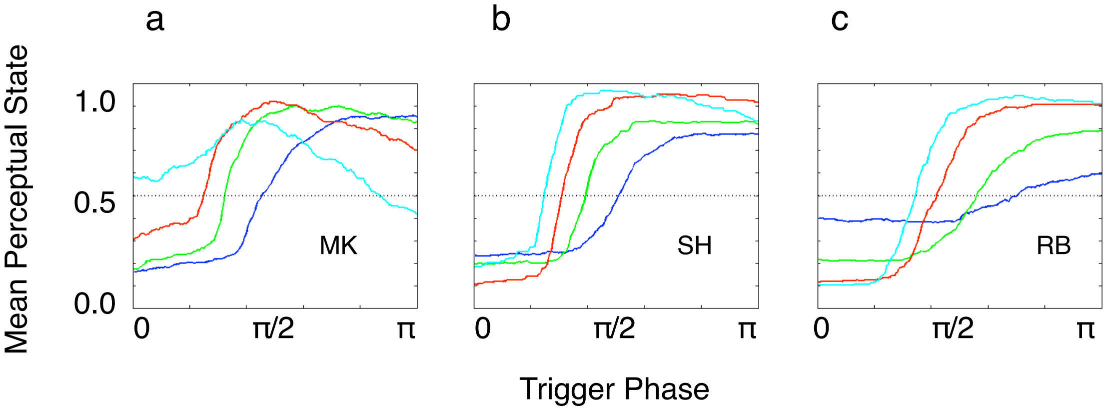

Figure 4.3 Switch functions for three representative observers. (a –c) Four different trigger periods indicated by four colors (blue: 3 sec, green: 4 sec; red: 5 sec; cyan: 6 sec). A switch function expresses the probability (y-axis) that a given rival target is dominant at different times relative to trigger presentations (x-axis). Each switch function was created by averaging the sequences of tracking records time locked to the onsets of the triggers. Optimal trigger periods identified from these switch functions are 4 sec (MK), 5 sec (SH), and 6 sec (RB) sec respectively

Three key characteristics of rivalry can be deduced from the switch function. First, the index specifies the likelihood of a change in perceptual state at given times following presentation of a trigger. When the timing of the local contrast increments is grossly out of synchrony with the observer's average rate of spontaneous rivalry alternations, the values defining the switch function fluctuate irregularly around a value of 0.5 – switches in perceptual dominance occur irregularly relative to the periodic triggers. In contrast, for trigger periods more closely matching a given observer's alternation rate, the switch function more nearly resembles a step function – switches in perceptual dominance are closely time-locked to the trigger period. Second, the mean perceptual state of the switch function at the onset of trigger reveals the probability that a trigger was delivered during a suppression phase of rivalry, and the difference in amplitude across the perceptual switches reveals the effectiveness of triggers. Third, the switch function reflects the delayed perceptual switches in response to the triggers; an index of this latency can be derived by estimating the delay time where the switch function crosses the mean perceptual state equaling 0.5.

For any given observer, the optimal trigger period is defined as the value yielding a switch function most closely resembling a step function; this property is readily defined by the amplitude between the minima and maxima of the switch function. Large amplitude values mean that most triggers were being delivered during suppression phases of rivalry, with the triggers reliably inducing perceptual switches and with the incidence of spontaneous perceptual alternations being minimal.

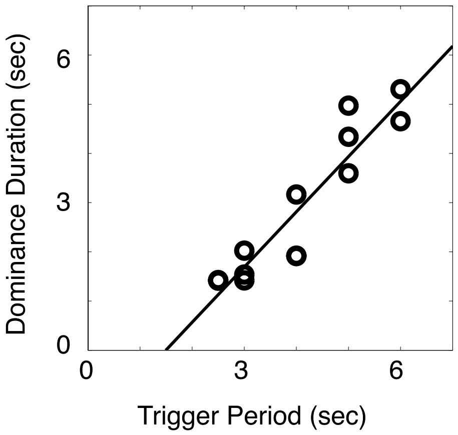

Figure 4.4 Correlation between the optimal trigger period and the mean dominance duration. Correlation between the optimal trigger periods derived from the switch function and mean dominance durations obtained when triggers are not presented. To avoid overlapping data points, three data points (at trigger periods of 2.5, 3 and 4 sec) are jittered horizontally. The regression line is approximately unity in slope.

Results from these measurements confirm what my pilot observations suggested: the optimal trigger period for a given observer is strongly related to that individual's mean dominance durations obtained from rivalry tracking records without trigger presentations (Figure 4.4). This is true regardless of the contrast of the rival stimuli, so all contrast conditions are combined for analysis [Pearson's correlation r=0.92, t(11)=8.33, p<10-3]. Thus, the optimal trigger period must be specified individually, and with this particular data set a valid estimate for the optimal trigger period is a value approximately 1 sec less than the mean dominance duration for a given observer.

4.2.3 Experiment 4.2: Traveling waves and trigger distance

Using the trigger period optimized for a given observer, I next collected tracking data under conditions where the distance between the triggers and the monitoring region was varied over trials. Figure 4.5a shows the averaged switch function from seven observers at three different trigger distances. Notice that switch functions are shifted rightward as the trigger distance increases, as expected if the consequence of the trigger propagates from trigger location to monitoring region – this is the perceptual signature of a traveling wave. Figure 4.5b, summarizing the latencies at three trigger distances, shows that the latency increases linearly as a function of trigger distance. This pattern of results was seen in the results of each of the seven observers tested, and it was statistically significant as revealed by one-way repeated measure of ANOVA with three levels of trigger distance [F(1,6)=15.04, p<0.01]. I interpret this monotonic variation in latency as the signature of a perceptual wave originating at the trigger site and traveling to the monitoring region.

One might suspect that it is necessary to use different trigger periods for the different trigger distances, since for trigger positions closer to the monitoring region the current state of the monitoring region will get perturbed a little earlier in time (relative to the time at which the state changed) than it will when the trigger positions are located farther away. But this time difference (Figure 4.5b, latency differences between the largest and smallest trigger distances are about 0.2-0.5 sec) is an order of magnitude shorter than the trigger period used to evoke perceptual waves (Figure 4.4, trigger periods are about 3-6 sec)and, therefore, inconsequential to the estimates.

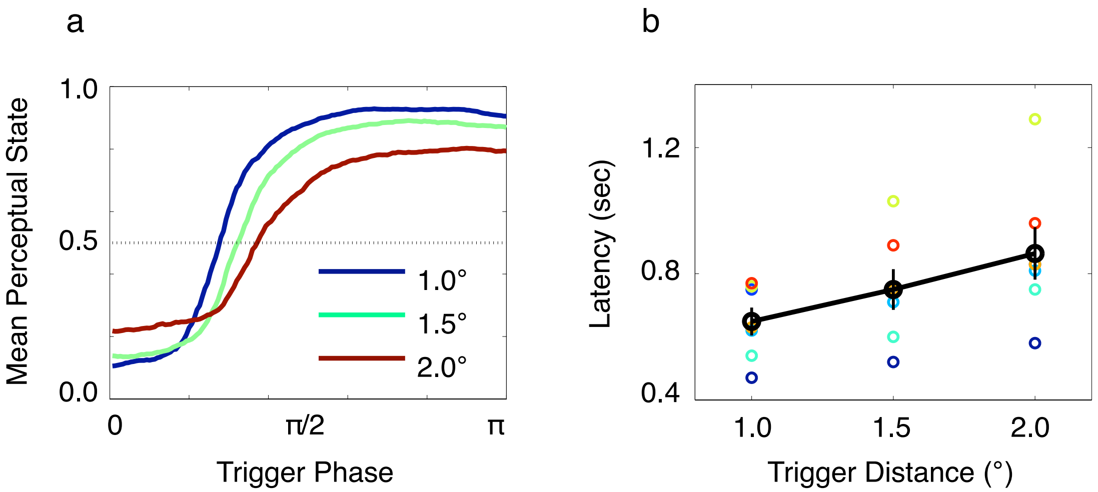

Figure 4.5 Traveling waves and trigger distance. Perceptual switches within the monitoring region for three trigger distances. a) Averaged switch function from seven observers. The three curves are switch functions obtained from three trigger distances (1°, 1.5°, and 2°). Switch functions are shifted rightward as trigger distance increases. b) Averaged latencies at three trigger distances. Latency is derived from individual switch functions by estimating the time value at which the switch function crosses the 0.5 line. The average latency increases linearly as the trigger distance increases, evidencing perceptual waves during binocular rivalry. Small symbols indicate latencies of seven observers.

In addition to the rightward shift in switch functions, the mean perceptual state of the switch function becomes closer to 0.5 as the trigger distance increases, implying that the repetitive triggers closer to the monitoring region more reliably promote perceptual switches. This second observation is not surprising because several sources of variability are introduced by increasing the trigger distance, including the increased likelihood of spontaneous perceptual switches.

This result also implies that the speed of the traveling waves is different across observers. To confirm this, I conducted a two-way ANOVA with trigger distance and observer as factors; there was a significant interaction between these two factors, suggesting that speed of the traveling waves actually differ among observers [$F(6,7)=24.07$, $p<0.001$]. Is this individual difference in propagation speed then related to the alternation rate of binocular rivalry?

4.2.4 Traveling waves and spontaneous perceptual alternations

Do observers whose alternation is relatively slow (slow alternators) see slow traveling waves compared to observers whose alternation is fast (fast alternators)? To answer this question, I examined the relation between the speed of traveling waves and the mean dominance durations associated with spontaneous perceptual alternations.

In Figure 4.6a, the estimated speed of traveling wave was plotted as a function of mean dominance duration. I estimated the speed of traveling waves using the same data set used to create Figure 4.5b by regressing the latency as a function of trigger distance. The inverse of the slope is the estimated speed of traveling waves. The mean dominance duration associated with the spontaneous perceptual alternations was obtained from Experiment 4.1 for a given observer. With increasing dominance duration, the speed of traveling waves tended to decrease [$r=-0.81$, $t(5)=2.50$, $p<0.05$]. One prediction of this negative correlation between the speeds of traveling waves and the mean dominance durations is that the latency of the traveling waves should monotonically increase with increasing dominance duration. As shown in Figure 4.6b, I confirmed this prediction by plotting the latencies of the traveling waves as a function of mean dominance durations using the same data set for creating Figure 4.4 [r=0.79, t(11)=3.82, p<0.01]. These two analyses imply that the slow alternators indeed experience slower traveling waves during binocular rivalry compared to the fast alternators.

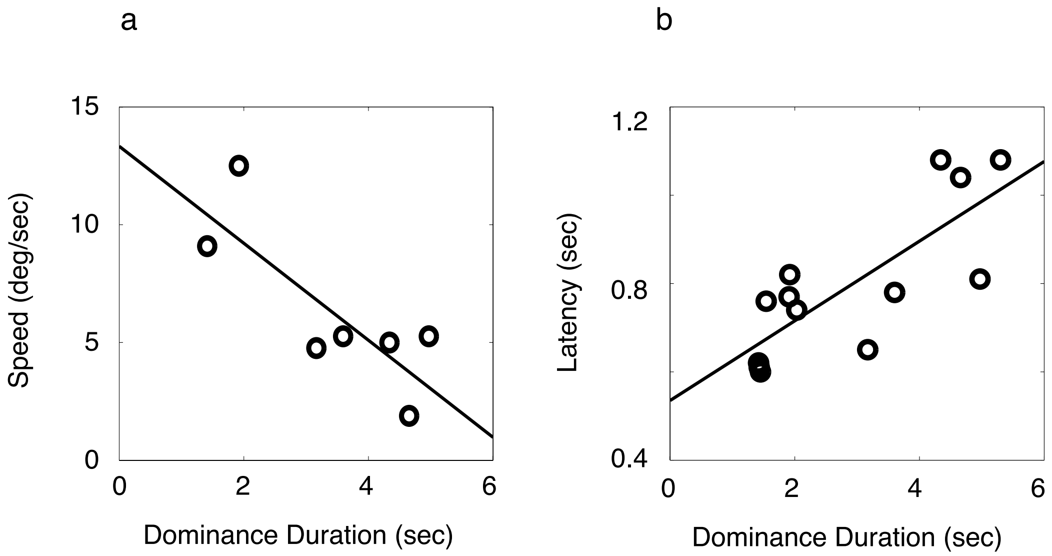

Figure 4.6 Speed of traveling wave as a function of dominance duration. a) Using the same data for creating Figure 4.5b, the speed of traveling waves was estimated and plotted as a function of mean dominance duration using the data set for creating Figure 4.4. The regression line means that the speed of traveling waves decreased by approximately 2°/sec by increasing dominance duration by 1sec. b) Using the same data for creating Figure 4.4, the latency was estimated and plotted as a function of mean dominance duration. The regression line means that the traveling waves slowed down by approximately 0.1sec by increasing dominance duration by 1sec.

4.3 Discussion

The study discussed in this chapter introduces and validates a novel technique for producing and characterizing the propagation of perceptual dominance over space and time. From an observer's standpoint, the task is quite simple: tracking alternations in perceptual dominance within a limited region of the visual field. Unlike other techniques developed to study rivalry waves, this one does not require observers to wait for a designated rival state to arise before manually triggering a local perturbation, and it is not necessary to discard trials because of failure to generate transitions in dominance. It is straightforward to characterize the perceptual waves emerging from either of the two rival stimuli simultaneously. It is possible to consider stochastic dynamics of binocular rivalry together with the perceptual waves simply by omitting or presenting periodic perturbations while the observer performs the same task. This last characteristic now makes it possible directly to interrelate multiple factors governing spatio-temporal behavior of binocular rivalry.

4.3.1 Mechanism producing traveling waves during binocular rivalry

What is the mechanism responsible for the influence of a contrast increment delivered in one part of the visual field on the delayed change in perceptual dominance in another region of the visual field? It is natural to wonder whether shifts in attention caused by triggers might be the source of these periodic perceptual changes (Baylis & Driver, 1992; Egly, Driver, & Rafal, 1994). According to this hypothesis, attention is ordinarily focused on the dominant stimulus at the monitoring area, but the brief contrast increment above or below that stimulus provides an exogenous cue that draws attention to the location of the increment. This temporary removal of attention from the currently dominant stimulus, in turn, causes a switch in dominance. For several reasons, however, I am disinclined to attribute perceptual entrainment to putative switches in attention. For one thing, triggers occur repetitively throughout the extended tracking period and should, therefore, lose their novelty and, presumably, some of their power to commandeer exogenous attention (Yantis & Jonides, 1990; Theeuwes, 1991). In fact, entrainment does not dissipate throughout an observation period. More importantly, a recent study showed that diverted attention toward a secondary take while tracking perceptual alternations of binocular rivalry decreased the alternation rate of binocular rivalry (Paffen, Alais, & Verstraten, 2006). This evidence cannot explain how temporary removal of attention from the monitoring region causes a switch in dominance by increasing the alternation rate.

This is not to say, however, that attention plays no role in the instigation of traveling waves. Perhaps observers need to see the trigger for it to generate a dominance wave, in which case failure to see the trigger because of inattentional blindness would weaken or abolish its effectiveness. In the experiments, I did not explicitly instruct observers to attend to trigger events, but that does not mean they ignored them. Attention's influence on a trigger's effectiveness remains to be determined, and with the addition of a distracting task the periodic perturbation technique should be suitable for this question.

Rather than shifts in attention, I believe that the triggers' influence on rival stimuli is carried by a wave of excitatory activity propagating from the trigger point to the monitoring region. This kind of propagation has been invoked by Grossberg and

Mingolla (1985) to account for traveling waves during perceptual filling-in, neon color spreading and illusory contour formation, and it is the mechanism posited by Wilson et al (2001) to explain traveling waves in binocular rivalry (see also Lee et al, 2005, 2007). In general, propagation within interconnected neurons is broadly consistent with the neural diffusion process proposed by Ermentrout and Kleinfeld (2001), resonating with MZNM of binocular rivalry.

4.3.2 Alternation dynamics and propagation dynamics

In this chapter, I reported that the speed of traveling waves decreased monotonically with increasing dominance durations (Figure 4.6a), thereby implying that the fast alternators tend to see fast traveling waves compared to the slow alternators. This correlation between the dominance duration and the traveling wave speed suggests that the perceptual experiences of the traveling waves are more vivid for slow alternators. The vivid perceptual experiences mean that the traveling waves are slow enough to be traceable. If the traveling waves are considerably fast and the incidence of spontaneous perceptual alternation is also frequent as identified above, the perceptual experiences of traveling waves become similar to the perceptual experiences of spontaneous perceptual alternations. This is the reason why the perceptual experiences of traveling waves are less vivid for fast alternators than for slow alternators. This is consistent with my experiences as an experimenter: slow alternators tended to report perceptual experiences of traveling waves without any difficulties compared to fast alternators.

What is then the theoretical implication of this correlation? Specifically, what factor produces this correlation across observers? I examine the implication of the relation between the traveling wave speed and the mean dominance duration in the context of the cooperative and competitive spatial interaction of MZNM of binocular rivalry.

Previous studies have suggested that the increased propagation speed of traveling waves is associated with the increased extent of spatial interaction. Alais et al. (2006) showed that the increased extent of spatial correlation promoted simultaneous perceptual alternations among the spatially separated rival stimuli. If we consider simultaneous perceptual alternations over several local rivalries as involving extremely fast traveling waves, these results suggest that an enlarged extent of spatial interaction should increase the speed of propagation. Consistent with this consideration, Wilson et al. (2001) directly showed that traveling waves propagated faster with the increased extent of spatial interaction (the relation between the stimulus pattern and the extent of interaction is discussed in Chpater 1.4.3). However, it is unknown how the extent of spatial interaction influences the perceptual dominance associated with spontaneous perceptual alternations.

On the other hand, the simulation study in Chapter 3 suggests that the increased strength of spatial interactions between any two local rivalry zones decreases the dominance durations; the work in this chapter shows the propagation speed of traveling waves increase. The relation between the dominance duration and interaction strength is obvious in that simulation: when the three adjacent local rivalry zones were connected to produce binocular rivalry over an extended rival figure, the mean dominance duration of the local rivalry at the center decreased with increasing coupling strength (Figure 3.4b). Additionally, increasing the coupling strength also increased the simultaneous perceptual alternations across those three local rivalry zones in that simulation. If Figure 3.4b and Figure 3.4c are compared, the mean dominance duration of the local rivalry at the center became gradually similar with increasing coupling strength to the mean dominance duration measured when all three local rivalry zones are in the same perceptual state. Similar to the relation between the incidences of simultaneous perceptual alternations and the traveling wave speed discussed above (Alais et al., 2006; Wilson et al., 2001), the increased simultaneous perceptual alternations suggest that the increased coupling strength also increases the traveling wave speed.

Based on these results, I speculatively conclude that that the strength of spatial interaction plays an important role for producing systematic spatiotemporal dynamics across observers as shown in the correlation between the traveling wave speeds and the dominance durations. However, it remains to be seen how to directly manipulate the strength of spatial interaction between any two local rivalries and thus empirically test this hypothesis. One may wonder whether we can test this prediction by changing the stimulus strength of rivalry stimuli by assuming that changing stimulus strength also affects the strength of spatial interaction in addition to modulating the dominance durations during binocular rivalry. I consider this problem next.

4.3.3 Contrast dependent traveling waves dynamics

I have discussed the relation between traveling wave dynamics and the alternation dynamics among observers. Does this mean, then, that traveling waves propagate faster for a given observer when the mean dominance duration is decreased by increasing the contrast of both rival stimuli? This question may be difficult to examine for both technical and theoretical reasons.

It is well established that dominance durations on average decrease when the contrast of both rival stimuli is increased (Levelt, 1965). However, technically, it is difficult to experience vivid traveling waves during binocular rivalry when the alternation rate increases as discussed in the previous section. In addition, the potency of the contrast increment trigger decreases for the high contrast rival stimuli (for example, it is impossible to produce a contrast increment trigger for a 100% contrast rival stimuli). It is also unknown whether the propagation dynamics of the traveling waves interact with the trigger period if we need to optimize the trigger period for different contrast levels.

More importantly, from a theoretical perspective, contrast dependent spatial summation may interact with the extent of interaction and the strength of interaction between two local rivalries. Both psychophysical and neurophysiological studies have shown that the area of spatial summation increases as the contrast of the stimulus decreases. Neurophysiological studies have shown that the neural response remained active outside this receptive field with a low contrast stimulus when that receptive field was identified using a high contrast rival stimulus (Kapadia, Westheimer & Gilbert, 1999; Sceniak, Ringach, Hawken & Shapley, 1999). Psychophysical studies have shown that the area of spatial interaction increases with decreasing contrast (Cannon & Fullenkamp, 1993; Ejima & Takahashi, 1985; Tadin, Lappin, Blake & Gilroy, 2003). This contrast dependent spatial interaction is also observed during binocular rivalry: perceptual dominance of a rival stimulus increases when it is surrounded by a low contrast stimulus compared to when it is surrounded by a high contrast stimulus (Paffen, Tadin, te Pas, Blake & Verstraten, 2006).

The theoretical concern regarding this contrast dependent extent of spatial interaction is that the strength of spatial interaction operates in an opposite direction to the extent of spatial interaction in modulating the propagating speed of traveling waves during binocular rivalry. It means that the high contrast rivalry stimuli should speed up the propagation of traveling waves because of strong spatial interaction compared to low contrast rivalry stimuli. Simultaneously, however, the same high contrast stimuli should slow down the propagation of traveling waves because the extent of spatial interaction is smaller compared to the low contrast rival stimuli. A recent study conducted by Alais et al. (2006) provided results consistent with contrast dependent spatial interaction although their result was not statistically significant: reducing contrast of rival stimuli tended to decrease the strength of spatial interaction but to increase the extent of spatial interaction.

4.3.4 Conclusion

Using this novel stimulus technique called periodic perturbation, I showed that the traveling wave speed tends to increase with decreasing mean dominance durations associated with spontaneous perceptual alternations. This correlation suggests that the same neural circuitry is involved with diverse perceptual experiences of binocular rivalry. In the context of MZNM of binocular rivalry, this correlation is likely to originate from individual differences in the strength of spatial interaction.

CHAPTER V

HOW DOES THE COLLINEAR FACILITATION OPERATE DURING BINOCULAR RIVALRY

5.1 Introduction

I have considered several factors (e.g. adaptation, noise, strength of rival stimuli and strength of spatial interactions) associated with rivalry dynamics in the context of the multi-zone network model (MZNM) of binocular rivalry. In this chapter, I examine the influence of the extent of spatial interactions on the traveling wave dynamics that are experienced during transitions in perceptual states during binocular rivalry.

A fundamental question in visual perception is how local image features are integrated to form a global configuration (e.g. an object). Gestalt psychologists proposed that self-organizing forces in the brain orchestrate integration of local image features, a conclusion they reached based on diverse grouping phenomena. During the latter part of the 20th century, feature integration was thought to occur within hierarchically organized visual stages, with local image features being analyzed in lower visual areas (V1 and V2) and then integrated within higher visual areas (V4, MT and IT) where neurons have large receptive fields responsive to configurations of features (Felleman & Van Essen, 1991; Hubel & Wiesel, 1962). Recently, however, growing evidence has suggested that feature integration also occurs within the lower visual areas.

Neurons in primary visual cortex (V1) respond to specifically oriented line segments falling within their receptive fields (De Valois, Albrecht & Thorell, 1982; Hubel & Wiesel, 1962; 1968). Yet, the concurrent presentation of stimuli outside of the conventional receptive field can modulate the firing rate of these neurons (Allman, Meizin & McGuinness, 1985; Maffei & Fiorentini, 1976). In addition, the spatial extent of receptive fields change depending on the contrast of stimuli activating those neurons (Kapadia, Westheimer & Gilbert, 1999; Sceniak, Ringach, Hawken & Shapley, 1999). These dynamic properties of cortical receptive fields in V1 neurons imply that neural signal are being integrated beyond the boundaries of the conventionally defined receptive field, and it is now thought that the long-range lateral connections within layers 2/3 of the primary visual cortex mediate this integration (Angelucci et al., 2002; Cavanagh, Bair & Movshon, 2002; Chisum, Mooser & Fitzpatrick, 2001; Crook et al., 2002; Das & Gilbert, 1995; Gilbert & Wiesel, 1979; Ts'o, Gilbert & Wiesel, 1986). One particular form of integration mediated by these lateral connections is collinear facilitation, in which similar patterns outside the receptive field increase the neural response to a stimulus within the receptive field (Chisum et al., 2001; Crook et al., 2002; Kapadia, Ito, Gilbert & Westheimer, 1995; Li, Piëch, & Gilbert, 2006; Polat, Mizobe, Pettet, Kasamatsu & Norcia, 1998). In addition, several models have produced results consistent with this physiological facilitation in which the recurrent excitation mediated by this long-range lateral connection is implicated in processing the contour integration (Grossberg, Mingolla, & Ross, 1997; Stemmler, Usher, & Niebur, 1995).

Psychophysically, the mechanisms associated with this integration process have been identified using two experimental paradigms. One is called the 'path paradigm' (see Figure 1.4a) in which oriented gratings are presented 2-dimensionally and a small number of gratings whose orientations are correlated. These gratings are perceived to form a continuous, extended contour relative to the background in which orientations of the gratings are uncorrelated (Field, Hayes, & Hess, 1993; Kovács, & Juleze, 1993). The other is called ‘lateral interaction paradigm’ (see Figure 1.4b) in which two oriented gratings (flanker stimuli) are concurrently presented above and below a foveally viewed target grating. In this paradigm, thresholds for detecting the target stimulus are lower when flanking gratings are collinear with the target grating compared to when the flankers are orthogonal or the target grating appears in isolation (Cass & Spehar, 2005; Cass & Alais, 2006; Polat & Sagi, 1993; 1994).

There is also evidence that long-range lateral connections operate during binocular rivalry. Alais and colleagues (1999; 2006) examined this interaction by presenting two target patterns (oriented gratings) to one eye and two noise patterns to the other eye. Consistent with collinear facilitation, the concurrent perceptual dominance of the two patterns increased with increasing collinearity of the orientations of the two gratings.

In another study, Wilson, Blake and Lee (2001) showed that collinear facilitation operates during binocular rivalry by capitalizing on a compelling aspect of rivalry: during transitions in perceptual state, one typically sees traveling waves in which the perceptual dominance of a suppressed pattern emerges locally and expands progressively as it renders the other pattern invisible (Lee, Heeger, & Blake, 2005; 2007). Wilson et al. prepared three annulus rival stimuli varying in extent of collinearity: a radial grating, a spiral and a concentric ring. In this experiment, waves transpiring within the concentric ring pattern (high collinearity) propagated faster than those transpiring within the radial grating (low collinearity) when the spiral pattern was a rival stimulus for both. Similarly, the propagation speed of the traveling waves between the two rival gratings whose contours moved in opposite directions provided converging evidence for collinear facilitation (Knapen, van Ee, & Blake, 2007). In recent neural models, this collinear facilitation revealed by traveling waves of binocular rivalry was instantiated by long-range lateral connections in V1 (Knapen et al., 2007; Wilson et al., 2001). In this chapter, I examine how this long-range lateral interaction operates during binocular rivalry based on predictions of recent computation models (Knapen et al., 2007; Wilson et al., 2001). By way of preview, my results show that the long-range lateral interactions alone cannot explain the empirical results. Instead, I introduce the idea that context dependent gain-control, in addition to long-range lateral interactions, is also involved in spatiotemporal dynamics governing traveling waves.

5.2 Experiment 5.1: traveling waves during binocular rivalry

Wilson et al (2001) developed a neural model explaining the traveling waves accompanying transitions from suppression to dominance. This model consists of excitatory and inhibitory connections between two layers of neurons representing the two eyes' views, respectively. Inspired by the model developed by Wilson, I create MZNM of binocular rivalry in which the extent of recurrent excitation increased with the stimulus' collinearity within a given eye's view, whereas the pattern of inhibitory connections remains unchanged and independent of the collinearity of the rival stimuli (see Chapter 1.4).

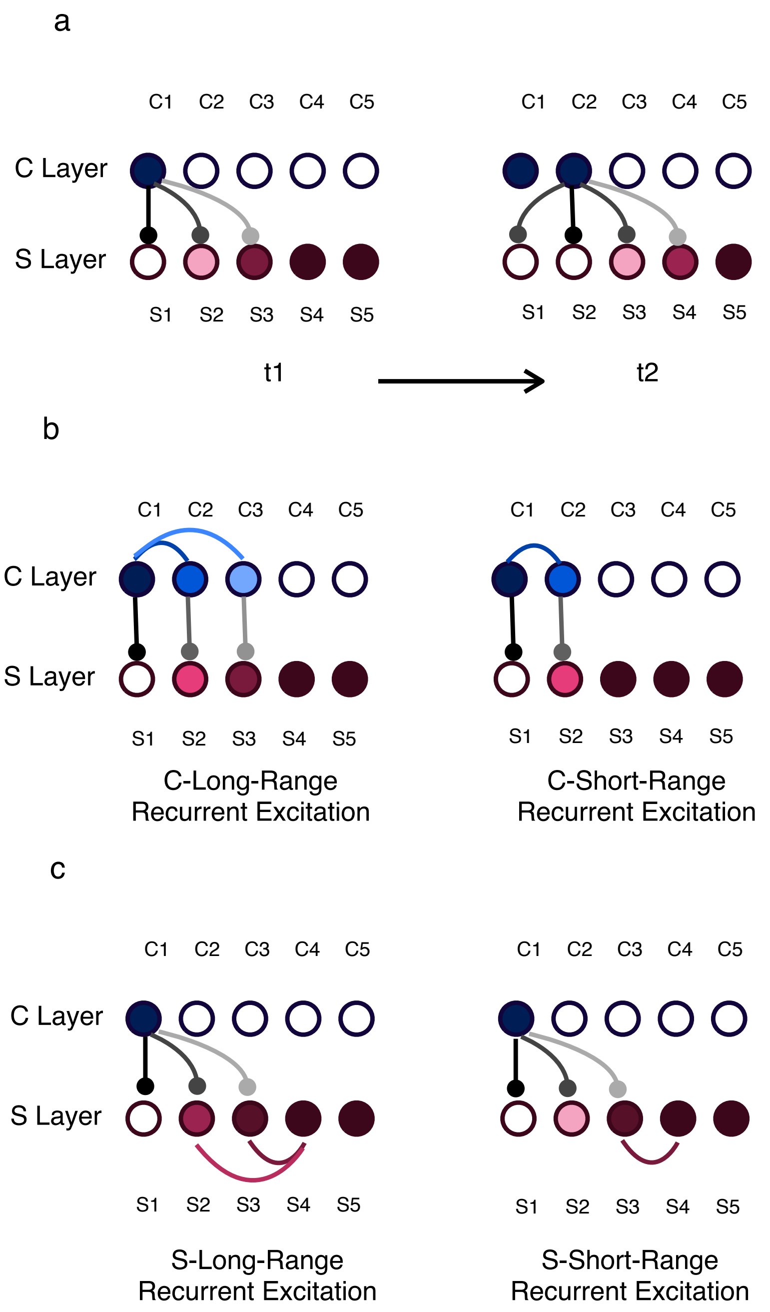

Figure 5.1 Illustration how MZNM of binocular rivalry produces traveling waves. The two layers are indicated as C and S respectively. The C (blue) refers to the carrier of the waves in which rival stimulus initially suppressed so that the traveling waves emerge from that stimulus and spread over the entire figure. The S (red) refers to the suppressor of the waves, which is the rival stimulus initially dominant. Each circle represents neurons and the color gradient inside that circle represents the neural response with darker colors indicating the stronger responses compared to the light colors. a) Illustration of how reciprocal inhibition produces traveling waves. b) Illustration regarding how the extent of recurrent excitation in C layer modulates the traveling wave speed. c) Illustration regarding how the extent of recurrent excitation in S layer modulates the traveling wave speed.

Figure 5.1 illustrates how this model produces the traveling waves. The two layers are indicated as C and S respectively. The C (blue) refers to the carrier of the waves, i.e., the initially suppressed rival stimulus within which traveling waves are experienced as that stimulus emerges from suppression, its dominance spreading over the entire figure. The S (red) refers to the suppressor of the waves, the rival stimulus initially dominant. Each circle represents the neurons and the color gradient inside that circle represents the neural response, with darker colors indicating the stronger responses compared to the light colors.

Figure 5.1a illustrates how reciprocal inhibition within the network produces traveling waves. Neuron C1 within Layer C becomes dominant at time t1, inhibiting not only a neuron in the same retinal location S1 but also neurons S2 and S3 within neighboring regions. The strength of inhibition exerted by C1 decreases with increasing distance, as shown in gray. Next, the weakened response S2 decreases its inhibitory connection to C2 and C2 becomes dominant. This process entrains perceptual switches over the entire rival figure, producing a traveling wave emerging from the carrier associated with the layer C.

Figure 5.1b illustrates how the extent of recurrent excitation in the C layer modulates the traveling wave speed. For simplicity, I only draw the inhibitory connection from the C to S layer between the two neurons in the same retinal locations. When perception switches so that the C1 becomes dominant and S1 becomes suppressed, the neural response in the neighboring region (C2 and C3 for long-range excitation; C2 for short-range excitation) increases with input from the recurrent excitation originating from C1. With increased extent of recurrent excitation, there is an increase in the number of neurons in the S layer being inhibited by the neurons in the C layer. Therefore, the traveling waves associated with the longer recurrent excitation (high collinearity) are faster than those associated with the shorter recurrent excitation (low collinearity).

However, this model predicts the opposite for the extent of recurrent excitation in the S layer (Figure 5.1c). For the same C layer, a perceptual switch occurs so that C1 becomes dominant and S1 becomes suppressed. In both S layers (short- and long-range recurrent excitations), inhibitory connections and their strength from C1 are identical for both S layers. However, the neural response of S2 is higher for the S layer of long-range recurrent excitation compared to the S layer of short-range recurrent excitation. This is because the S3 and S4 neurons provide more input to the S2 neuron in the S layer due to the longer range of recurrent excitation (left) compared to the short-range recurrent excitation (right). Therefore, with the increased extent of recurrent excitation, the S-layer increases its resistance to being suppressed and, thus, the traveling waves should slowed down. In other words, the traveling waves should be slower for the suppressor of high collinearity compared to the suppressor of low collinearity. Remember that according to the model the traveling waves should be faster for the carrier of high collinearity compared to the carrier of low collinearity

Here, I investigated the mechanisms producing the traveling waves by testing these predictions shown in Figure 5.1b and 5.1c. To do this, I examined the traveling waves during binocular rivalry produced using the periodic perturbation technique whose efficacy was validated in Chapter 4. Figure 5.2a illustrates this periodic perturbation technique. The technique exploits the potency of a localized increment in contrast to promote local dominance of a small part of a previously suppressed pattern and, moreover, for that local region of dominance to spread over neighboring areas of the visual field (Wilson et al, 2001). The traveling wave dynamics are inferred based on the observer's binary categorization of the perceptual experiences within a restricted region of the rival figure termed the monitoring region. Perceptual switches at the monitoring region are delayed but time-locked to the triggers, suggesting the existence of wave-like signals that propagate from the trigger site to the monitoring region.

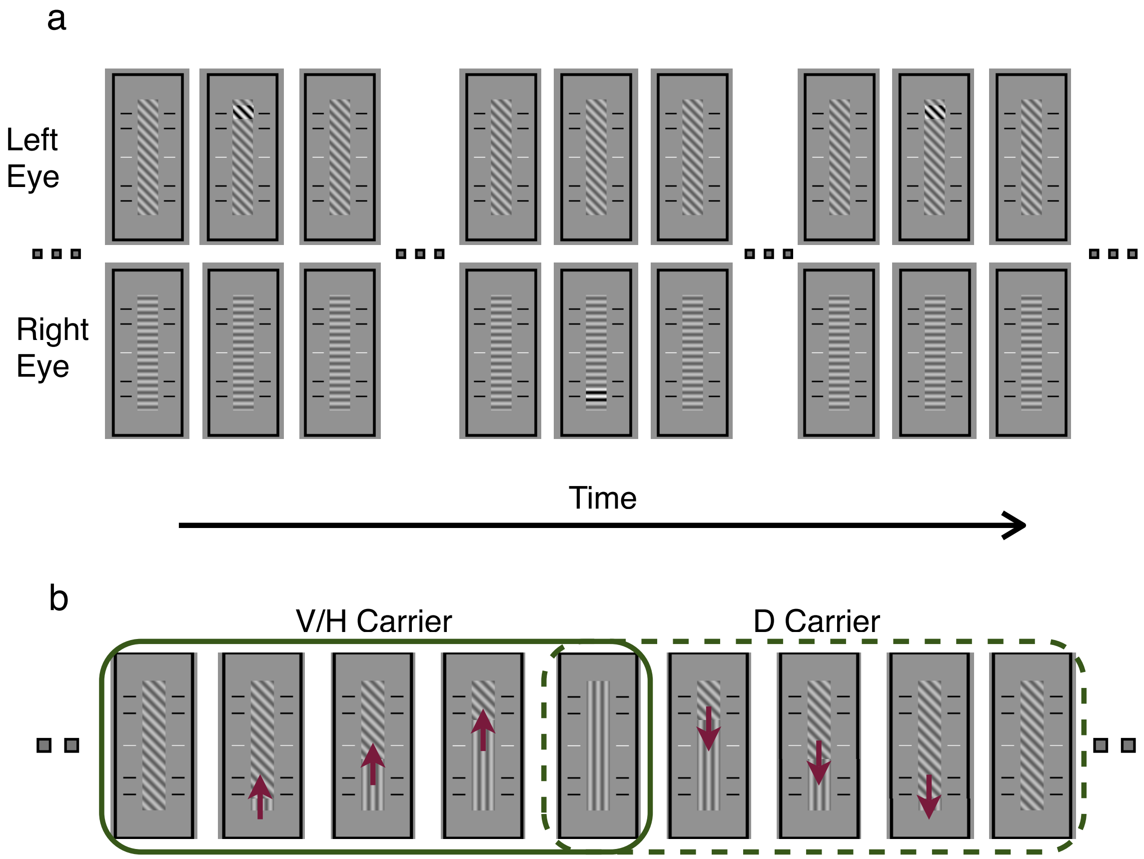

Figure 5.2 Illustration of Experiment 5.1. a) Illustration of the periodic perturbation technique (see Chapter 5). The diagonal pattern is always presented to one eye and either a vertical or a horizontal grating is presented to the other eye. b) In the periodic perturbation technique, the traveling waves emerge successively from the two different carriers. A wave emerging from either the vertical or horizontal grating is illustrated within the solid box whereas a wave emerging from the diagonal carrier is illustrated within the dotted box.

Figure 5.2b illustrates the perceptual experience produced by the periodic perturbation technique: a trigger given to a lower region of the vertical grating produces an upward traveling wave that emerges from the vertical grating, whereas a trigger given to an upper region of the diagonal pattern produces a downward traveling wave. As shown in this figure, this periodic perturbation technique is particularly useful for this experiment because both rival stimuli can be the carriers of the waves over the different phases of the trigger presentations.

To test how the collinearity of the rival pattern operates for the traveling wave dynamics, the diagonal (D) pattern was always presented in one eye and either a vertical (V) or a horizontal (H) grating was presented in the other eye. In all experiments including Experiment 5.1 of this chapter, the collinearity was operationally maximized by the vertical grating but minimized by the horizontal grating. Therefore, this experiment provides the traveling wave dynamics for the four conditions consisting of two carrier conditions (D vs V/H) with two types of collinearity (V vs H). By doing this, I planned to replicate the previous studies (Knapen, et al, 2007; Wilson et al., 2001), showing whether the traveling waves were faster from the vertical grating carrier compared to the horizontal one. Simultaneously, I could see whether the traveling waves emerging from the diagnoal carrier were slower when that carrier was viewed with a vertical grating compared to a horizontal grating.

5.2.1 Methods

All aspects of this study were approved by the Vanderbilt University Institutional Review Board. Five observers participated in this experiment. Except the author of this dissertation, all other observers were naïve to the purpose of the study. In order to obtain reliable traveling waves, it is important that perceptual alternations are relatively slow (reasons are given in Chapter 4) and, thus, I screened slow alternators (whose mean dominance duration is relatively long ~ 5sec). All had normal or corrected-to-normal vision, and all gave informed consent after thorough explanation of the procedures.

Stimuli and trial-related events were controlled by a Macintosh G4 computer (Apple, CA) running Matlab (Mathworks, MA) in conjunction with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Stimuli were presented on the screen of a Sony E540 21 inch monitor (1024H x 768V resolution; 120 Hz frame-rate; 21.67 cd/m2 mean luminance) in a dimly illuminated room. In this and the following experiments, stimuli were viewed against a gray background (21.67 cd/m2) through a mirror stereoscope placed 90 cm from the monitor.

Vertically elongated rival stimuli (0.8° X 5° visual angle) were presented to the left and right eyes, and to promote stable binocular alignment each rival stimulus was bordered with a black rectangular frame (3.6° X 8°) the width of which was 0.25°. Five pairs of horizontal line segments were presented at both sides of rival stimuli whose length equals 0.5°. Two pairs of them indicated the trigger locations (at ±1.5° with respect to the center of the stimuli) and one of the other three pairs (±1.0° and 0°) served for the monitoring region, indicated by the white color. The monitoring region of Experiment 5.1 was at the center of stimuli. Stimuli were vertical, diagonal (either left- or right-tilted) and horizontal gratings. Remember that the vertical grating was assumed to maximize the collinearity whereas the horizontal grating was assumed to minimize it. The spatial frequency of all these gratings was 4cyc/deg. Before the experiment, the contrast of the rival stimuli was adjusted individually (15%~30%) so that mean dominance durations of the three rival patterns were not largely different.

Triggers were periodically presented at the upper and lower region of each stimulus respectively. Observers were instructed to fixate at the center of the stimuli (it is also the middle of the two side markers at the center) and to track fluctuations in perceptual dominance by pressing and holding either of two keys within the monitoring region. Observers declared dominance only when one or the other of the rival gratings within the monitoring region was exclusively dominant, with neither key being pressed when mixtures were experienced. Each tracking session lasted 60sec and each condition repeated eight times. For each condition, trigger positions, the eye receiving the diagonal grating and its pattern (left- or right-tilted) were counterbalanced over two blocks. Within each block, both vertical and horizontal gratings were randomly presented with the diagonal patterns.

5.2.2 Result

The switch function was obtained from the tracking record of the periodic perturbation technique, which represents the mean perceptual states as a function of trigger phase, $M(\theta)$ (M is the mean perceptual state and θ is the trigger phase). The procedure for obtaining this switch function is discussed in Chapter 4. As shown in Figure 5.3a, the switch function representing the traveling waves emerging from the vertical grating (blue solid line) is shifted leftward compared to the switch function representing the waves emerging from the horizontal grating (red solid line). This means that the increased collinearity of the vertical carrier produced faster traveling waves, consistent with previous studies (Knapen et al., 2007; Wilson et al., 2001). However, contrary to the prediction associated with the collinearity within the suppressor, the traveling waves emerging within the diagonal carrier were faster when that carrier was paired in rivalry with the vertical grating (blue dotted line) compared to when the horizontal grating was the other rival stimulus (red dotted line).

For the statistical analysis, I estimated the latency of the waves from the switch function. The latency reflects the time at which both perceptual states of both rival stimuli are equally likely. If traveling waves occur in response to all triggers, the latency would correspond to the time at which the mean perceptual state $M(t)$ equals 0.5. However, if the periods of perceptual dominance differ for the two rival stimuli and, thus, one rival stimulus remains dominant for longer periods of time, the mean perceptual state will increase or decrease over the entire trigger phase, implying that the latency identified based on the mean perceptual state $M(t) = 0.5$ is not adequate. For this reason, a general procedure was devised in which the switch function was modeled by a sigmoid function, $\alpha + \beta / (1 + \exp(-(\theta - \theta_T)/\sigma)$ in which α equals $M(0)$, the mean perceptual state at trigger phase equals 0; β equals $M(\pi) - M(0)$, the difference between the mean perceptual states between the two trigger onsets; θ_T is the threshold level of the trigger phase in the sigmoid function and σ is the growth rate. Latencies of the traveling waves were identified individually by obtaining values of the threshold trigger phase θ_T and transforming those values to the latency values in msec by using the trigger period.

Figure 5.3b shows latency values associated with the four conditions. Consistent with visual inspection of the switch functions (Figure 5.3a), the latency values obtained for those four conditions show that the traveling waves emerging from the vertical grating were faster than those emerging from the horizontal grating carrier, as expected (Knapen et al., 2007; Wilson et al., 2001). However, contrary to the model prediction, traveling waves emerging from the diagonal carrier were not slower than the horizontal grating when paired in rivalry with the vertical grating. A two way ANOVA with the factors of carrier pattern (V/H or D) and collinearity (V or H) revealed that the effect of collinearity was statistically significant [F(1,4)=16.97, $p<0.05$] but the effect of carrier pattern was not [F(1,4)=0.16, $p>0.5$]. The latency obtained at the switch function $M(t)=0.5$ provided similar results.

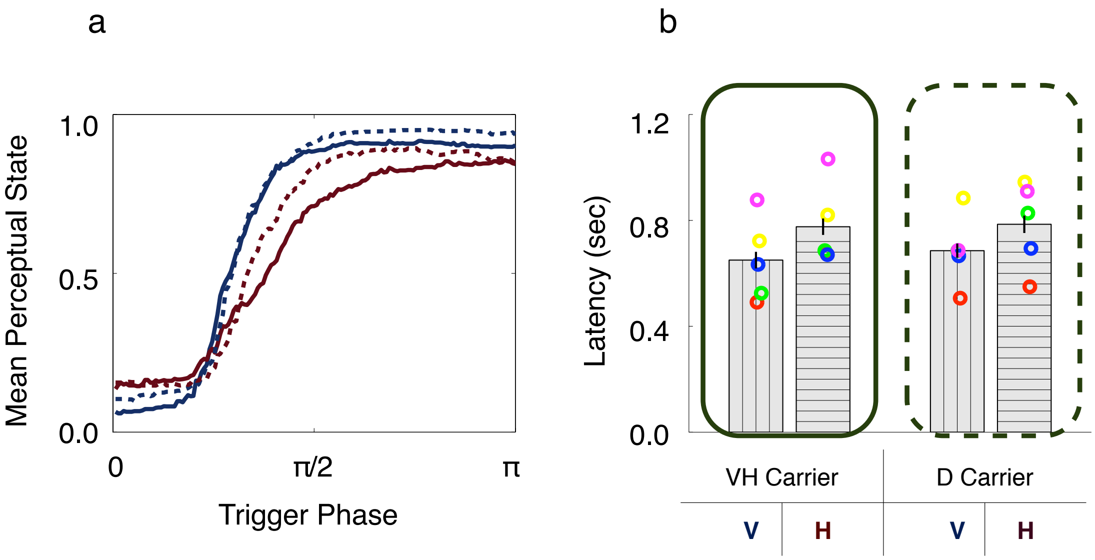

Figure 5.3 Results of Experiment 5.1. a) The averaged switch functions associated with two carrier conditions (V/H carrier for solid line and D carrier for dotted line) and two collinearity conditions (V pattern for blue and H pattern for red). b) The averaged latencies associated with two carrier conditions (V/H within the solid box and D carrier within the dotted box) and two collinearity (V pattern for vertical pattern filled bar and H pattern for horizontal pattern filled bar). The colored circles indicate the latencies for individual observers (N=5). The error bars indicate ±1 S.E.

This result challenges the rivalry model based on extended recurrent excitation and reciprocal inhibition discussed previously. Before considering how the underlying neural network, especially the long-range recurrent excitation, operates in producing traveling waves during binocular rivalry, I examined other aspects of the spatiotemporal dynamics of binocular rivalry in the next two experiments to evaluate the generality of the results from Experiment 5.1.

5.3 Experiment 5.2: perceptual dominance within the region of a physical gap

Kaufman (1963) investigated the spread of rivalry suppression by presenting two vertical lines in the one eye and one horizontal line to the other eye. Even though there was no competing stimulus pattern between the two vertical lines, a portion of the horizontal line between the vertical lines was occasionally suppressed from awareness over the course of binocular rivalry. This incidence of suppression increased as the separation of the two vertical lines decreased, suggesting that the suppression of the horizontal line spreads from the regions of intersection with the two vertical lines to the interior region where no explicit conflict existed between the two monocular figures.

Extending Kaufman's study, I examined to what extent the collinearity of the rival pattern affects the spread of suppression during binocular rivalry by introducing a physical gap to one of the two rival stimuli. Figure 5.4 illustrates the stimulus conditions. As in Experiment 5.1, a diagonal grating was presented to one eye and either a vertical or a horizontal grating was presented to the other eye. The collinearity was operationally maximized by the vertical grating but minimized by the horizontal one. In addition to the two types of collinearity (V vs H), two gap conditions were prepared: the gap was present within the diagonal stimulus (GwD condition) or within the vertical/horizontal stimulus (GwVH condition). Based on Kaufman's study (1963), the perceptual dominance of the stimulus without gap, termed no-gap-stimulus in this dissertation (e.g. diagonal stimulus is considered no-gap-stimulus when the gap is present within either the vertical or horizontal grating), should increase with increasing gap size.

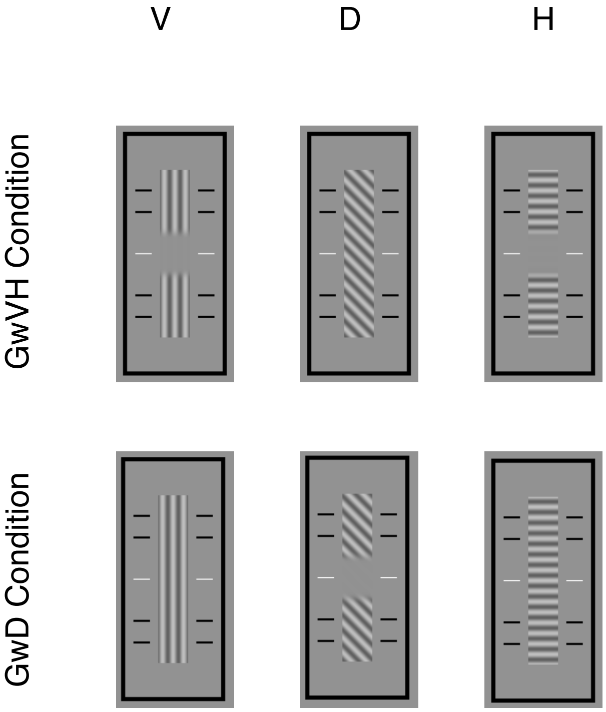

Figure 5.4 Illustration of stimulus condition of Experiment 5.2. Similar to Experiment 5.1, the diagonal grating was always presented to one eye and the other eye received either the vertical or horizontal grating. The physical gap was presented one of the rival stimuli at the central region. GwVH condition indicates the stimulus condition in which the physical gap was introduced to V/H grating and the GwD condition indicates the stimulus condition in which the physical gap was introduced to D grating.

However, the long-range recurrent excitation provides the opposite prediction for the GwD and GwVH conditions regarding the perceptual dominance of the no-gap-stimulus. For the GwVH condition, the vertical grating in the suppression phase provides stronger input to the physical gap via recurrent excitation than does the horizontal grating. Therefore, perceptual dominance of the diagonal stimulus within the region of the gap should be reduced when paired with the vertical grating compared to the horizontal grating for a given gap size. In contrast, for the GwD condition, the recurrent excitation in the dominant phase provides stronger suppression within the gap region so that perceptual dominance of the vertical grating should increase compared to the perceptual dominance of the horizontal grating at a given gap size.

5.3.1 Method

The same stimuli were used except that a physical gap was introduced at the central region of one rival stimulus. The size of the gap was either 0°, 0.5° or 1.0°. These three gap sizes equaled 0, 2, and 4 cycles of the horizontal grating and from now on I will use the number of cycles to indicate the gap size. The boundaries of the gap were smoothed using a Gaussian kernel. The same observers who participated in Experiment 5.1 also participated in this Experiment 5.2. The task was identical such that observers tracked the perceptual dominance within the monitoring region of the stimuli over a 60sec tracking session. Note that when the gap was present, the tracking record comprises exclusive dominance of the no-gap stimulus, exclusive dominance of the gap and the partial dominance of the grating; only the periods of exclusive dominance of the no-gap-stimulus within the monitoring region were considered for the analysis. The same conditions were repeated four times, and the eye receiving the diagonal stimulus was counterbalanced. Observers received the GwD and the GwVH conditions in separate blocks. Within each block, both vertical and horizontal gratings were randomly presented for each tracking session.

5.3.2 Result

Figure 5.5 summarizes the result of Experiment 5.2 in which the perceptual dominance of the no-gap-stimulus was plotted as a function of gap size for four different conditions: two gap conditions (GwVH and GwD) and two collinearity conditions (V and H). These four conditions are shown within the table above the plot. The x-axis represents the gap size for all four conditions and the y-axis represents predominance, which is measured by summing all dominance durations of the continuous stimulus divided by the total tracking periods.

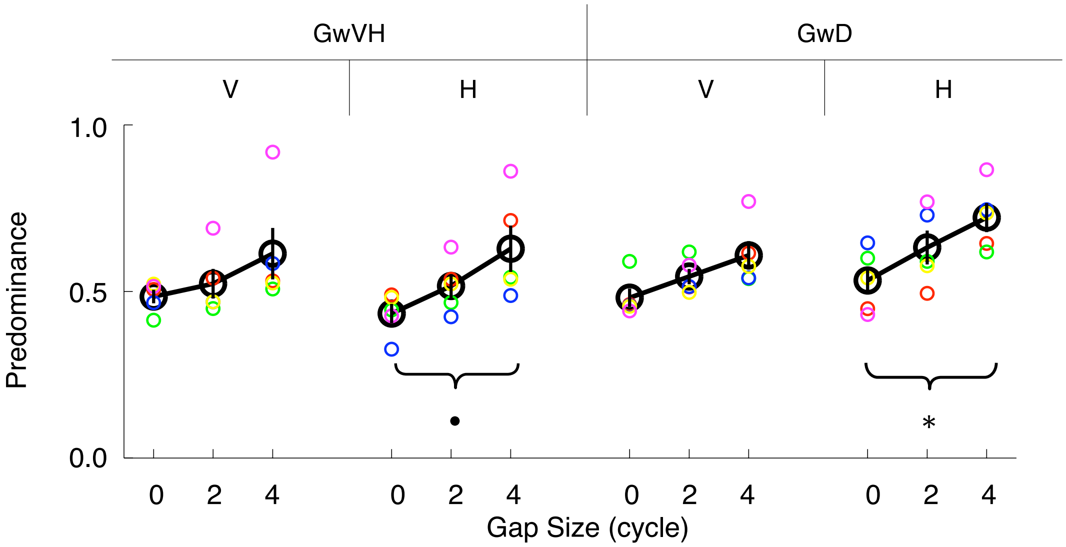

Figure 5.5 Results of Experiment 5.2. For four conditions (two gap conditions and two collinearity conditions), predominance of the continuous stimulus is plotted as a function of gap size. The large black circles indicate the averaged predominance of the five observers and the colored small circles indicate the predominance of individual observers. The error bar indicates ±1 S.E. The statistical significance of the effect of gap size is indicated • for 0.1 and * for 0.05.

Perceptual dominance tends to increase with increasing gap size, but this pattern of result was more conspicuous when the horizontal grating was presented, compared to when the vertical grating was presented (Figure 5.4). However, overall results are similar for both GwD and GwVH conditions. A three-way ANOVA with factors of the two gap conditions (GwVH and GwD), collinearity (V and H) and gap size confirmed this observation by showing a significant interaction between the collinearity and gap size [F(1,4)=17.00, p<0.05]. However, there is no significant difference between the GwVH and GwD conditions [F(1,4)=2.07, p=0.22], contrary to the prediction based on long-range recurrent excitation.

5.4 Experiment 5.3: when traveling waves are interrupted by the physical gap

To confirm the previous two observations, I investigated a third aspect of spatiotemporal dynamics of binocular rivalry by capitalizing on the fact that the propagation of dominance waves tends to be disrupted when a relatively large physical gap is introduced (Wilson et al., 2001; Kim, Blake, & Lee, 2005). In these studies, the probability of a successful wave was measured by having observers initiate a wave when the rival stimulus with a gap was completely suppressed. Thus, when a wave was successfully propagated, the entire carrier stimulus, including the physical gap, became perceptually dominant over time. This constituted a successful wave, and the probability of successful waves was obtained by dividing the total incidence of successful waves by the total number of trials.

This propagation of waves over a gap is particularly interesting within the context of recurrent excitation in binocular rivalry. The gap can be construed as a localized, temporary lesion within the neural circuitry involved in propagation of the traveling waves. Specifically, in the context of recurrent excitation, the propagation dynamics should be less disrupted when the lesion is placed within the vertical grating carrier compared to the horizontal grating carrier, because the extent of facilitation mediated by the recurrent excitation is larger for the vertical grating carrier than it is for the horizontal grating carrier. In contrast, when the gap is introduced within the diagonal carrier, the traveling waves should be more disrupted with the vertical grating compared to the horizontal one, because the longer recurrent excitation associated with the vertical grating promotes stronger suppression within the region of the gap. In this experiment I examined the propagation dynamics using different sized gaps with an eye toward learning whether those unexpected rivalry dynamics found in the two previous experiments would arise in this context.

To measure the vulnerability of wave propagation to the presence of a gap, the periodic perturbation technique was used. The periodic perturbation technique has advantages compared to the technique in which waves are categorized on discrete trials (Kim, Blake, & Lee, 2005; Wilson et al., 2001). Specifically, with discrete trials, one cannot distinguish whether a wave arriving at one side of the gap triggers and continues on the opposite side of the gap, vs a wave is terminated at one side of the gap but another wave occurs spontaneously at the opposite side of the gap. It is also difficult to categorize the following two cases: 1) a wave arrives at one side of the gap and triggers another wave at the opposite side with some temporal delay and 2) a wave arrives at one side of the gap but another wave occurs spontaneously at the opposite side with some temporal delay. More importantly, it is unknown whether the dynamics associated with spontaneous alternations also change with increasing gap size. In the periodic perturbation technique, instead of categorizing a series of perceptual switches over the rival figure as a traveling wave, the propagation dynamics of the waves can be inferred based on any trigger-locked perceptual alternations. Therefore, the objective criterion is not a concern, and the spontaneous alternations should also be reflected in the switch function.

I have investigated whether triggers given, for example, at the upper region of the suppressed stimulus, produce perceptual dominance within a lower region below the gap change in response to those triggers. Observers were asked to maintain fixation at the center of the stimuli and to track rivalry occurring in either the upper or the lower region of the rival figure. Note that during each tracking session the monitoring region was fixed and perceptual dominance periods associated with the triggers at the opposite side of the monitoring region were considered for analysis because they reflected whether the traveling waves were disrupted by the gap.

As in Experiment 5.1, the switch function was derived to infer the propagation dynamics of the traveling waves. Based on previous studies (Kim, Blake, & Lee, 2005; Wilson et al., 2001), it was expected that modulation of the switch function would decrease with increasing gap size, meaning that the incidence of trigger-locked perceptual alternations decreased. To quantify the incidence of perception switches in response to the trigger, a switch probability P_S, as shown equation [5-2], was obtained as follows. Remember that the switch function represents the mean perceptual state as a function of the trigger phase, $M(\theta)$. If we assume that the perceptual dominance at the triggering location is the same as that within the monitoring region at the trigger onset, the proportion of the trigger given to the suppression phase of the carrier is $1 - M(0)$. It is also assumed that a trigger given during the suppression phase always produces a perceptual switch at the monitoring region with delay T if there is no disruption associated with the physical gap. For simplicity, the delay T is the trigger phase $\theta = \pi/2$ in this analysis. In contrast, a trigger given during the dominant phase does not produce any state change. This relation leads to equation [5-1] in which the mean perceptual state at T can be represented with the switch probability P_S and the mean perceptual state at the trigger onset $M(0)$. Using this relation [5-1], the switch probability is obtained as shown in equation [5-2]. In the switch function, this switch probability basically equals the difference in mean perceptual states between the two different trigger onsets divided by the proportion of triggers given to the carrier in the suppression phase.

$$M(T) = P_S(1 - M(0)) + M(0) \qquad [5\text{-}1]$$

$$P_S = \frac{M(T) - M(0)}{1 - M(0)} \qquad [5\text{-}2]$$

Note that the periodic perturbation technique produces two types of qualitatively different waves when a physical gap is introduced to one of the two rival stimuli (Figure 5.6). In one case, the stimulus with a gap is being suppressed initially but it emerges from suppression and propagates. This case, termed jump propagation, gives some impression that the carrier at one region, the physical gap and the carrier at the other region appear in series. In the other case, the stimulus with the gap is initially dominant, and it is the stimulus without a gap that emerges from suppression and propagates along the rival figure. This case, termed bridge propagation, gives some impression that the propagating waves connect the two disconnected regions. To study the propagation dynamics disrupted by the gap, only jump propagation was considered as in previously studies (Kim, Blake, & Lee, 2005; Wilson et al., 2001). Nevertheless, I expected that bridge propagations were rarely disrupted by the gap because there is no competing stimulus against the propagation, and the result was consistent with this expectation (data are not shown).

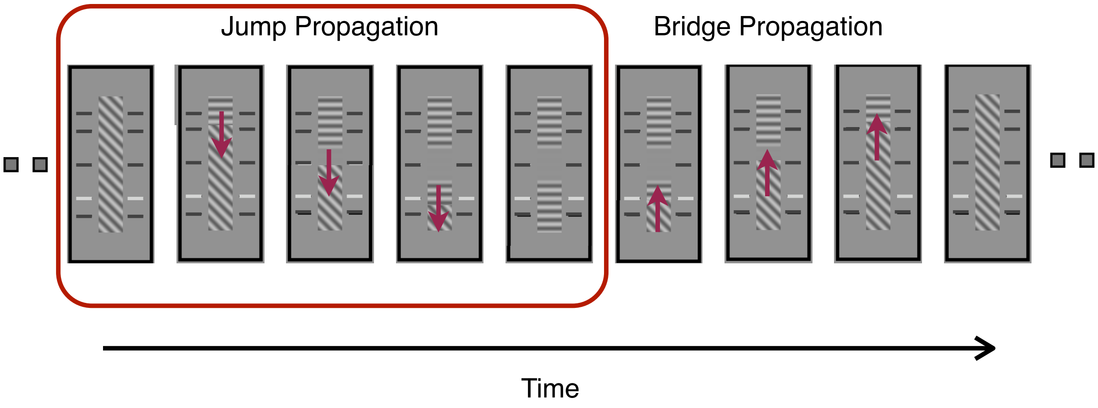

Figure 5.6 Illustration of jump propagation. The traveling wave within the red box indicates the jump propagation in which the stimulus with a gap is being suppressed initially but it emerges from suppression and propagates. In this figure, the white side bars at the lower region indicate the monitoring region.

5.4.1 Method

Observers who participated in Experiment 5.1 and 5.2 also participated in this experiment. The stimuli and the experimental conditions were identical to those used in Experiment 5.2 except for the following. The triggers were periodically presented within the upper and lower regions of each rival stimulus. For each observer, the optimal trigger period determined in Experiment 5.1 was used for this experiment. In order to assess disruption of traveling waves by the physical gap, the monitoring region was either in the upper or the lower region of the stimuli. Observers were instructed to maintain fixation at the center of rival stimuli but to report fluctutions in the perceptually dominant pattern within that monitoring region. Side markers at the monitoring region were colored in white. Note that unlike Experiment 5.2, perception within the monitoring region comprised the diagonal grating, vertical/horizontal grating and the mixture of these two. For each gap stimulus condition (GwD or GwVH), a total of 48 tracking sessions were given, divided into 4 blocks. Each block consists of 3 gap sizes, 2 collinearity conditions (V and H) and 2 repetitions. The order of these 12 trials was randomized within each block. The monitoring region was placed at the upper region for two blocks and at the lower region for the other two blocks with the order was counterbalanced.

5.4.2 Result

Figure 5.7 shows the switch probability of the jump propagation, condition where wave propagation must jump a gap to arrive monitoring point. For all four conditions, the switch probability decreased with increasing physical gap [$F(1,4)=28.03$, $p<0.01$], implying that the traveling waves were interrupted by the presence of physical gap. In addition, on a number of trials that increased with gap size there was a significant effect of the collinearity [$F(1,4)=12.26$, $p< 0.05$] but the effect of the two gap conditions (GwVH and GwD) was not significant [$F(1,4)=1.63$, $p=0.27$]. Importantly, the interaction between the collinearity and the gap size showed only marginal significance [$F(1,4)=5.14$, $p=0.08$], implying that the modulation in the switch probability was slightly larger for the H collinearity condition compared to the V collinearity condition with increasing gap size.

Although the interaction between the collinearity and the gap size was marginally significant, this result shows the tendency that modulation in the switch probability was larger for the H condition than for the V condition, for both GwVH and GwVH conditions. This result is consistent with the previous two experiments. How can we explain these counterintuitive results? At least, these results showed that the recurrent excitation associated with collinearity of rival pattern alone cannot explain the present empirical results. In the following Discussion, I explain these results in the context of suppressive interactions of the collinear flanker (instead of facilitation) along with long-range recurrent excitation.

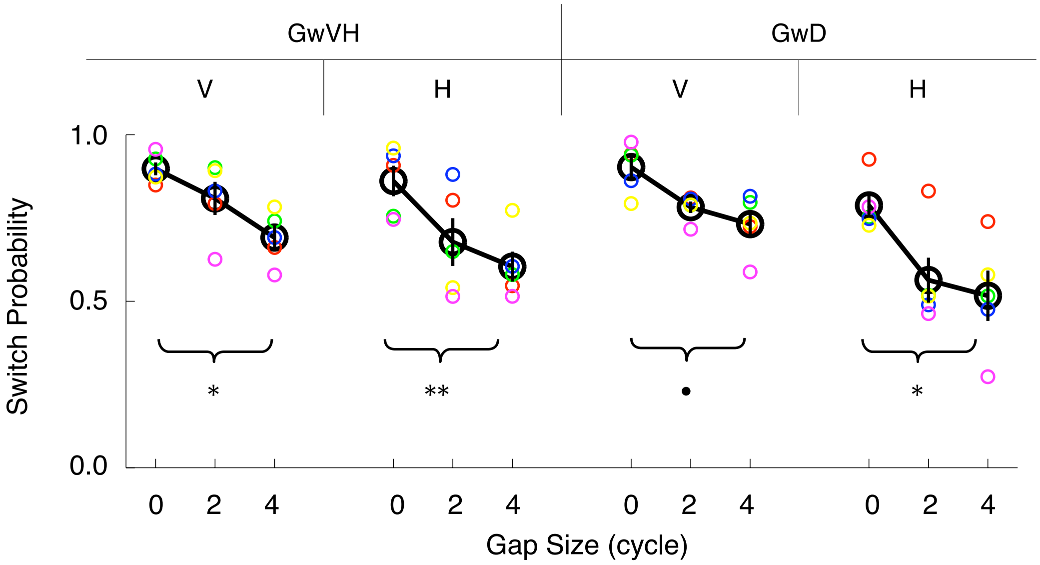

Figure 5.7 Results of Experiment 5.3. For four conditions (two gap conditions and two collinearity conditions), the switch probability is drawn as a function of gap size. The large black circles indicate the averaged switch probability of the five observers and the colored small circles indicate the switch probability of individual observers. The error bars indicate the ±1 S.E. The statistical significance of the effect of gap size for each condition is indicated as * for 0.05 and ** for 0.01.

5.5 Discussion

Across all three experiments, compared to the horizontal grating (low collinearity), the vertical grating (high collinearity) more successfully promoted perceptual switches over the extended region of a rival figure. Specifically, in Experiment 5.1, traveling waves were faster when the vertical grating was paired with the diagonal grating than when the horizontal grating was presented with the diagonal grating. This pattern of result was true for both carriers: vertical grating and the diagonal grating. In Experiment 5.2, when a physical gap was introduced within one of the two rival stimuli, perceptual dominance of the continuous stimulus was higher for any given physical gap size when the horizontal grating was paired with the diagonal grating than when the vertical grating was presented with the diagonal grating. This pattern of result was true for both GwVH and GwD conditions. In Experiment 5.3, the switch probability associated with the jump propagation condition also showed that traveling waves were more resilient when the vertical grating was presented with the diagonal grating than when the horizontal grating was presented with the diagonal grating. This pattern of result was also true for both GwVH and GwD conditions.

How, then, can we explain these counterintuitive results? One may propose that fast neural adaptation associated with the collinear stimulus might account for the present results, because adaptation reduces the neural response associated with the collinear pattern. However, considering the slow time scale of the adaptation, I think that the role of neural adaptation is limited. Instead, I first discuss both physiological and psychophysical evidence showing suppressive interactions associated with the collinear flankers, and then provide an account regarding how long-range recurrent excitation and collinear suppression might explain traveling wave dynamics characterized in this chapter.

5.5.1 Collinear facilitation and collinear suppression

Besides the neurophysical evidence for the collinear facilitation which was discussed in the Introduction, evidence for collinear suppression has also been reported:

stimuli of similar orientation presented outside a neuron's the receptive field can suppress its neural response (Angelucci et al., 2002; Cavanagh, Bair & Movshon, 2002; Levitt & Lund, 1997; Mizobe, 2001; Polat et al., 1998; Sceniak et al., 1999; 2001). In particular, Polat and colleagues (1998; 2001) reported that neural responses in V1 were facilitated at low contrast levels but were suppressed at high contrast levels when activity was evoked by collinear stimuli like those used in the lateral interaction paradigm discussed in Introduction. The physiological origin of this contrast dependent facilitation and suppression remains to be identified, but it is thought that fast feedback connections from higher visual areas, along with the slow long-range horizontal connections in V1 are involved with both facilitation and suppression (Angelucci & Bullier, 2003).

Consistent with these physiological findings, there are a number of psychophysical studies showing that concurrent presentation of surrounding stimuli suppress the visibility of a target stimulus (Ejima & Takahashi, 1985; Meese, Summers, Homes, & Willis, 2007; Xing & Heeger, 2000; Yu, Klein & Levi, 2003). In particular, Chen and Tyler (2000; 2002; 2008) psychophysically identified the contrast dependent facilitation and suppression using a variant of the lateral interaction paradigm. In their experiments, observers had to detect a target stimulus (a vertical grating) superimposed on a pedestal stimulus (also vertical grating) in a 2 interval forced choice (2IAFC) experiment. Note that both target stimulus and pedestal stimulus are identical except for their contrasts so that observers had to discriminate the contrast between the two presentations. In the absence of flanker stimuli, the incremental threshold decreased moderately at low contrasts (less than 1%) but increased in log-log scale at high contrasts. The curve plotting threshold contrast as a function of pedestal contrast (TvC curve) showed a well established ‘dipper’ shape (Legge & Foley, 1980; Ross, Speed & Morgan, 1993). Now, with the concurrent presentation of the two vertical gratings, Chen and Tyler (2000; 2002; 2008) found that the detection threshold decreased at low contrasts but increased at high contrasts compared to the detection threshold measured with target stimulus presentation in isolation. However, the influence of flanker stimuli whose orientation was orthogonal to the orientation of target stimulus tended to disappear over all contrast levels. This is consistent with the physiological studies mentioned above (Polat et al., 1998; Mizobe et al., 2001). Chen and Tyler (2000; 2002; 2008) proposed that lateral interactions modulate the contrast gain control mechanisms, resulting in this contrast dependent facilitation/suppression.

This contrast-dependent facilitation and suppression is consistent not only with the physiological findings mentioned above but also with a recent binocular rivalry study (Paffen, Tadin, te Pas, Blake & Verstraten, 2006). In this study, the rival stimuli, the left- and right-tilted gratings, were presented within a central region and an annulus stimulus filled with right-tilted grating was dioptically presented. In this experiment, the perceptual dominance of the rival stimulus whose orientation was identical to the surrounding stimulus increased at low contrasts (˜1.5%) but decreased at high contrasts (˜100%). Considering that the gain-control mechanisms still operate during suppression phases of binocular (Watanabe, Paik & Blake, 2004), I can conclude that similar gain-control mechanisms associated with contrast dependent collinear facilitation and suppression operate before the stage where binocular rivalry occurs.

One may remember the implication of results from the path paradigm in which gratings with similar orientation were perceptually salient even at suprathreshold levels

(Field, Hayes, & Hess, 1993). Why does facilitatory contour integration revealed by the path paradigm still operate at suprathreshold levels whereas the collinear facilitation in the lateral interaction paradigm only operates near detection threshold levels? Recent psychophysical studies have shown that these two paradigms reflect different integration mechanisms (Hess & Dakin, 1998; Hess & Field, 1999; Huang, Hess & Dakin, 2006; Huang & Hess, 2007). In particular, Huang et al. (2006) compared the path paradigm and the lateral interaction paradigm over monocular, binocular and dichoptic presentations. They found that contour integration revealed by the path paradigm operated over all three conditions whereas the lateral interaction paradigm produced no facilitation for the dichoptic condition. They concluded that collinear facilitation associated with the lateral interaction paradigm operates largely within a monocular level.

5.5.2 Mechanisms producing the traveling waves during binocular rivalry

Putting all these results together, I propose that a stimulus-dependent modulation of neural responses operates over two stages during binocular rivalry. Figure 5.8a illustrates this model in which the contrast and pattern-dependent gain control occur in the first gain-control stage (Watanabe et al., 2004), whereas reciprocal inhibition and pattern dependent recurrent excitation occur in a second stage (Wilson et al., 2001; see Chapter 2 to review how this gain-control and this binocular rivalry stage are relevant to the previous studies of binocular rivalry). Note, however, that this does not necessarily mean a feed-forward model because the gain-control depicted in the first stage can be governed by both the feed-forward and feed-back inputs (Angelucci & Bullier, 2003).

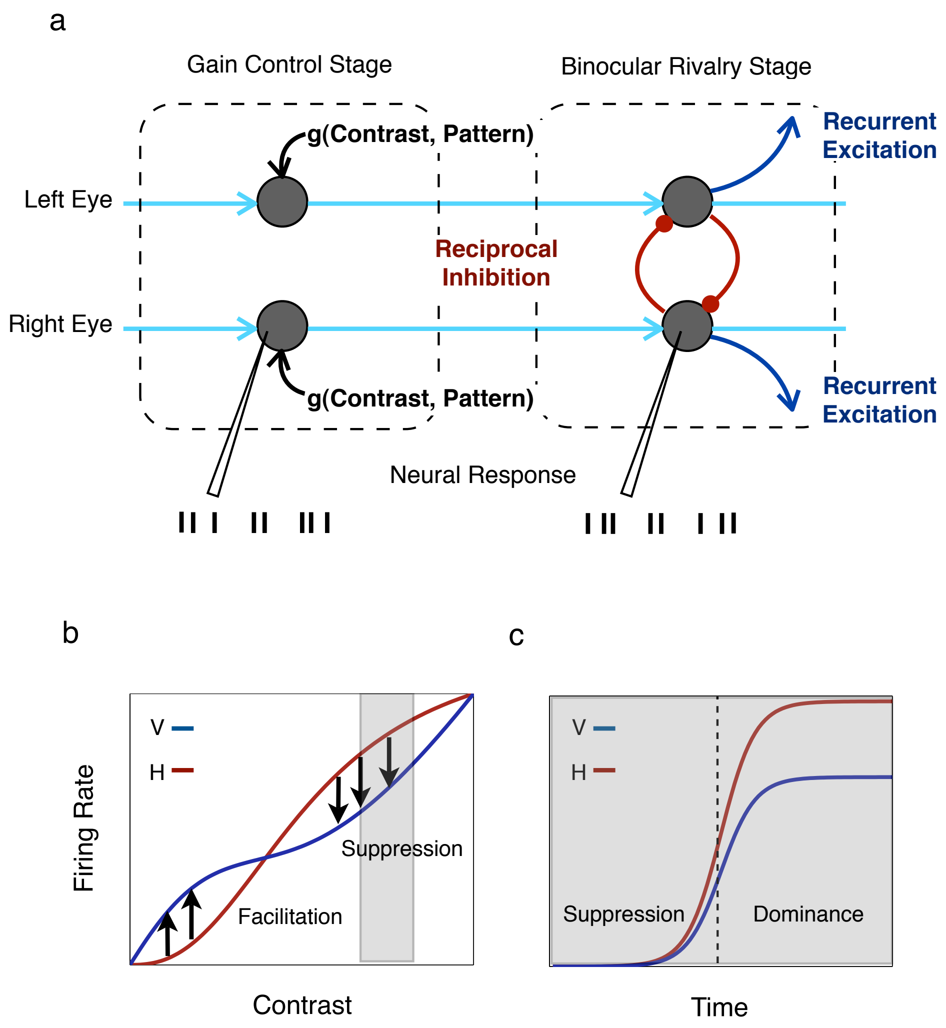

Figure 5.8 Illustration of gain-control and binocular rivalry stages. a) Illustration of the proposed model in which the contrast and pattern dependent gain control occurs in the first gain-control stage whereas the reciprocal inhibition and the pattern dependent recurrent excitation occur in the second binocular rivalry stage. b) They hypothetical neural response at the gain-control stage. The neural response is represented as a function of contrast for two types of stimuli. Collinear facilitation occurs in low contrast level and collinear suppression occurs in high contrast level. c) The hypothetical neural response in the binocular rivalry stage as a function of time. The contrast of the stimuli corresponds to the shaded area in Figure 5.8b, showing weak neural response of the vertical stimulus in the dominant phase of binocular rivalry.

Figure 5.8b shows hypothetical neural responses at the gain-control stage, illustrating the hypothetical neural responses as a function of stimulus contrast. The blue curve indicates the hypothetical neural response for a vertical grating (high collinearity) and the red line shows the hypothetical neural response for a horizontal grating (low collinearity). As indicated by the arrows, facilitation occurs within the low contrast range and suppression occurs within the high contrast range. Note that the contrast range where facilitation occurs was less than 10% (usually around 1%) in psychophysical studies. Considering that the stimulus contrasts used in all three experiments of this chapter are around 20%, they are within the suppression regime. The shaded area indicates the contrast range of the present experiment.

Figure 5.8c illustrates the hypothetical neural response in the binocular rivalry stage as a function of time. The contrast of the stimuli corresponds to the shaded area in Figure 6.8b: the neural response during the dominance phase of the vertical grating (blue) is smaller than the horizontal grating (red). Importantly, despite this decreased neural response of the vertical grating (high collinearity condition), the extent of recurrent excitation of the neurons representing the vertical grating is larger than the horizontal grating in this binocular rivalry stage.

With this collinear suppression in mind, I will now offer an explanation for why the traveling waves emerging from a diagonal carrier propagate faster when paired with a vertical suppressor (high collinearity) than when paired with a horizontal suppressor (low collinearity). As illustrated in Figure 5.1c (page 102), the increased extent of recurrent excitation decreases the propagation speed of traveling waves. However, collinear suppression reduces the overall response of vertical grating in dominant phases so that the inhibition to the carrier pattern is reduced accordingly. This collinear suppression, therefore, increases the traveling wave speed. This means that the collinear suppression interacts with the recurrent excitation in opposite directions in modulating the traveling wave speed, predicting that the propagation of the waves emerging from the diagonal carrier is not necessarily slower with the vertical grating suppressor compared to the horizontal pattern suppression.

5.5.3 Final thoughts

The present results challenge the model of binocular rivalry in which the extent of recurrent excitation represents the pattern-dependent lateral interaction. Instead, I proposed an alternative network model in which the pattern and contrast dependent gain-control operates along with recurrent excitation. This study sheds light on how spatial patterns affect rivalry alternations over space and time

CHAPTER VI

CONCLUSIONS

6.1 Summary

Perception is not always a veridical record of the physical world, as exemplified by various visual illusions. Viewed from this perspective, binocular rivalry is particularly revealing because it dissociates how the brain reorganizes visual inputs and reconstructs the perceptual experiences that differ from the invariant physical stimulation presented to the two eyes. This dissociation of perception from visual inputs is especially conspicuous during the periods of mixed dominance of binocular rivalry. Prior to this dissertation, however, the spatiotemporal dynamics of these periods of mixture have been largely uncharacterized. Thus, the study of dynamics associated with spontaneous perceptual alternations has been largely separated from the consideration of the dynamics associated with the periods of mixed dominance such as traveling waves.

The objective of this dissertation was to consider a broad range of aspects of binocular rivalry, with a particular emphasis on its spatiotemporal dynamics, and in doing so to initiate a coherent framework in which binocular rivalry occurs through cooperative and competitive interactions within a multi-zone network model (MZNM). To achieve this goal, I developed several techniques for studying spatiotemporal dynamics and refined the perceptual characteristics of binocular rivalry within spatiotemporal domain. In doing so, I have advanced the theoretical framework in the following ways:

The neural adaptation in the dominant phase of binocular rivalry indeed operates for producing perceptual alternations (Chapter 2). In addition to this neural adaptation, previous studies have suggested that abrupt fluctuations of neural response in the suppression phase operate simultaneously for perceptual switches.

Level't 2nd proposition has been considered the hallmark phenomenon of binocular rivalry dynamics but its generality has been controversial. In Chapter 3, I showed that this controversy regarding Levelt's 2nd proposition can be resolved by considering that the perceptual dominance is the outcome of cooperative and competitive interaction among local zones of rivalries, emphasizing the spatiotemporal nature of binocular rivalry dynamics.

Extending the partial tracking strategy developed in Chapter 3 and the potency of contrast increment trigger, a novel stimulus technique called periodic perturbation was described in Chapter 4. Using this technique, I identified the relation between the dominance durations associated with the spontaneous perceptual alternations and the speed of traveling waves of binocular rivalry. The result suggested that the strength of spatial interactions is involved in this correlation.

In Chapter 5, the role of the extent of recurrent excitation was investigated by varying the stimulus pattern and its perceptual phase during binocular rivalry. The results suggest that reciprocal inhibition operates during binocular rivalry after the contrast gain-control stage. In addition, the same neural circuitry operates differently depending on the perceptual phase, refining the functional role of recurrent excitation in producing traveling waves during binocular rivalry.

Besides the individual points of theoretical importance summarized above, the overall results from this dissertation have provided two general implications. First, the states of perceptual dominance of the rival stimuli and their alternations over time are the outcome of cooperative and competitive interactions of neural events transpiring within discrete zones. Thus, the spatiotemporal dynamics provides the fundamental building blocks for understanding the temporal dynamics, the traditional characterization of binocular rivalry as shown in Chapter 3 and 4. Second, the theoretical framework embodied in **MZNM** of binocular rivalry is informative because 1) it provides testable hypotheses (Chapter 5) and 2) its biologically plausible structure (e.g. the strength and the extent of spatial interaction) provides a useful framework for data interpretation.

6.2 Future directions

One barometer estimating how well we understand a given phenomenon is to reproduce that phenomenon with a set of rules. For decades, experimenters have used so called mimic conditions to attempt to physically reproduce perceptual experiences of binocular rivalry by physically presenting and removing two rival stimuli in a reciprocal manner over time. However, no mimic condition was sufficiently realistic; observers readily see the difference between binocular rivalry and its mimic conditions mainly because of the abrupt transitions between the two rival stimuli. Is it now possible to reproduce more realistic mimic conditions with the increased understanding of spatiotemporal dynamics provided by work?

For example, as briefly discussed in Chapter 3, the spatial interactions between two complex images like a human face and house are largely unknown. It would be challenging to characterize the perceptual experiences of the rivalry between any two natural images. If characterized, the next challenge would be whether those characterized spatiotemporal dynamics could be understood in terms of known early visual mechanisms such as spatial frequency and orientations. Although daunting, I believe we can eventually reproduce realistic and perceptually indistinguishable rivalry mimic conditions between any two dissimilar images. And the present dissertation suggests that it is important to understand the underlying neural circuitry and their functional role. With this goal in mind, I consider a number of psychophysical studies.

The partial tracking strategy was useful as shown in Chapter 3 through 5. This strategy can be also useful for characterizing the spatiotemporal dynamics of binocular rivalry between the two complex images combined with the periodic perturbation technique. For example, consider binocular rivalry in which one stimulus is a left-tilted grating whose spatial frequency changes gradually over space and the other stimulus is a right-tilted grating whose orientation gradually changes from slightly-tilted to dramatically-tilted. How these different stimulus variables interact remains unknown. If observers can track at least two monitoring regions simultaneously, the tracking records associated with those two monitoring regions would reveal the interaction structure over space and time. The same strategy can be applied to binocular rivalry between two more complex images such as a human face and house.

The influence of spatial attention should be investigated. As briefly discussed in Chapter 4, considering that it may be difficult to distribute attention equally over the entire spatial extent of rival stimuli, the role of attention in spatiotemporal dynamics needs to be investigated. In a related vein, it is also interesting and relevant to ask how eye movements modulate spatiotemporal dynamics. Recently, van Dam and van Ee (2006) have showed that eye movements modulate the incidence of perceptual switches. One relevant question, then, is whether eye movements alter perceptual experiences during periods of mixed dominance. This question is particularly important for two theoretical perspectives. First, the interocular grouping paradigm demonstrates that high-level grouping processes are involved with the binocular rivalry. However, interactions between high- and low-level processes are poorly understood (Lee & Blake, 2004; Papthomas, Kovács, & Conway, 2005). Eye-movements and retinal image shifts associated with them could provide additional information about how the low-level processes interact with the high-level processes. Second, a number of theoretical studies regarding network dynamics have shown that it is possible, but difficult, to maintain coherent states across all networks in noisy environments (Acebórn, Bonilla, Pérez Vicente, Ritort & Spigler, 2005). In most cases, all constituents of such a network can start from the same state, but they eventually disintegrate into incoherent states. Similar to this, Stollenwerk and Bode (2003) reported that coherent perceptual dominance could be produced with correlated noise within a MZNM of binocular rivalry. I conjecture that occasional eye movements may serve an external trigger to produce coherent perceptual state over the entire rival figure.

Finally and most importantly, besides the empirical studies, it is necessary to pursue the computational modeling works as shown in Chapter 3. In the context of spatial network of binocular rivalry, any empirical results suggest some rules associated with the constituents of the networks such as the extent or the strength of spatial interaction. But, it may be limited to manipulate a particular factor related to those constituents. The computational evidence along with empirical evidence would enlarge our understanding of binocular rivalry.

6.3 Concluding remarks

Binocular rivalry is an important phenomenon for number of reasons. To name a few, its ability to suppress one eye's view from visual awareness has received a wide range of attention for its promise that this dissociation of perception from physical inputs reveals the neural correlate of consciousness (Crick & Koch, 1995). Binocular rivalry is also important for studying how we perceive 3-dimensional information from the 2-dimensional retinal inputs (Howard, 2005; Shimojo & Nakayama, 1990; 1994)

In addition, as shown in this dissertation, the spatiotemporal dynamics associated with the periods of mixed dominance reveals how the perceptual organization behaves over such a slow time scale so that we can actually trace the changes. Considering that binocular rivalry is the most powerful tool for manipulating the visual awareness (Kim & Blake, 2003), it may be also possible to study how the same perceptual organization operates depending on visual awareness and eventually reveal how the brain produces our perceptual experiences.

APPENDIX

A. SIMULATION DETAILS

The overall simulation procedure and many details are similar to those of Moreno-Bote et al. (2007), and the units in the simulations are arbitrary. The energy model is defined by a double-well energy function shown in equation [3-1]. This energy model has been used to describe bistable systems (Brascampe et al., 2006; Kim et al., 2006; Moreno-Bote et al., 2007) in which two energy minima correspond to two stable states. The fourth order equation shown in equation [3-1] was chosen because it produces two local minima and a single local maxima symmetric at the axis where $r = 0$ (Figure A.1a).

Equation [3-2] describes the dynamics of individual local rivalry. The dynamics governed by a given energy model satisfies $\tau \frac{dr}{dt} = -\frac{dE(r)}{dr}$. This relation means that the dependent variable r moves along the energy landscape toward the location of the closest energy minimum (as the minus sign indicates) with a velocity proportional to the slope of the energy function at a given r. In addition to this deterministic rule, the interaction term among local rivalries shown in Equation 3-3 and noise source are added in equation [3-2]. The noise produces stochastic transitions between the two energy minima. The time constant τ=10. Figure A.1b shows the trace of difference firing rate r of a local rivalry with no interaction ($\eta = 0$).

According to Moreno-Bote et al., (2007), the noise term $n_i(t)$ in equation [3-2] follows Ornstein-Uhlenbeck process $\dot{n}_i = -n_i/\tau_s + \sigma\sqrt{2/\tau_s}\xi_i(t)$ whose amplitude was increased by ω=5. In this equation, the time constant τ_s=100, deviation term σ=0.7 and $\xi_i(t)$ represents a white noise randomly selected from a normal distribution. Euler's method was used for all numerical integration with time step δt equals 0.1 for 10^6 time unit, which means for 10^7 iterations. Matlab (Mathworks, MA) running in Machintosh G5 computer (Apple, CA) was used for the simulation.

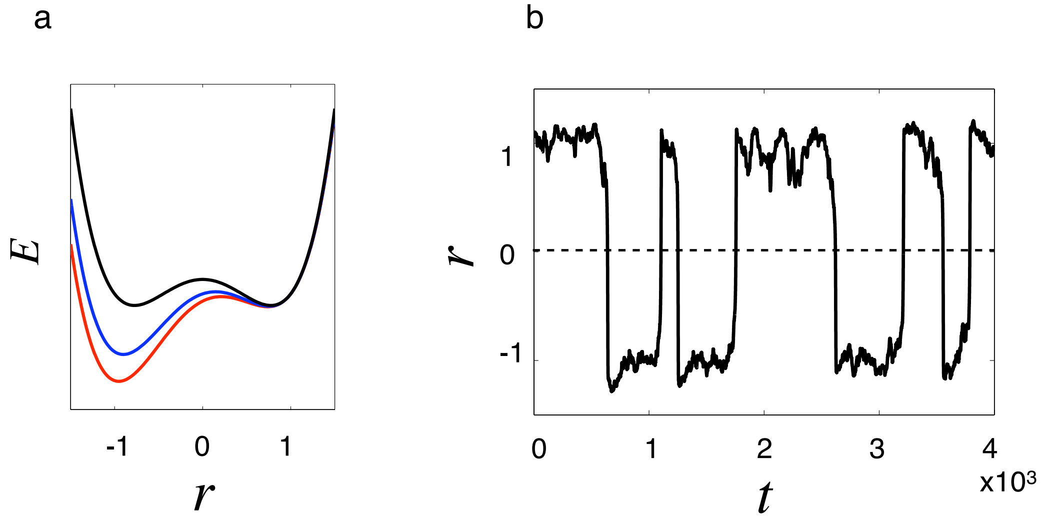

Figure A.1 Energy model and dynamics of local rivalry model. a) Equation [3-1] is drawn for a fixed $g_B = 0.4$. Three lines correspond to energy models for $g_A = 0.1$ (red), $g_A = 0.2$ (blue) and $g_A = 0.4$ (black) respectively. b) Trace of difference firing rate r of a local rivalry is drawn over time when the coupling strength $\eta = 0$.

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