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GROUPING IN RESOLVING CHROMATIC INTEROCULAR-SWITCH RIVALRY

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BY
WEI WANG

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ABSTRACT

Slowly alternating, instead of rapidly flickering, fused colors are perceived when two equiluminant but chromatically rivalrous stimuli (e.g. one “pink” and one “blue-green” disc) are presented separately to each eye and then swapped interocularly several times a second. This is a visual illusion induced by chromatic interocular-switch rivalry (CISR) (Christiasen, D’Antona & Shevell, 2014). Since CISR creates steady-state ambiguous neural representations of color beyond the level of the eye, it provides a novel approach to studying how the visual system interprets color in mid-level vision.

Experiment 1 investigated CISR at several different temporal frequencies to determine the frequency range over which relatively long-lasting color percepts are seen. The results showed that, in general, 3.13 Hz, 3.75 Hz and 4.69 Hz CISR resulted in stable long-duration color percepts.

Experiment 2 investigated whether grouping contributes to the long-lasting color percepts during CISR. This question was tested using two different paradigms with either two or four independent CISR stimuli. The results showed that grouping contributes to the resolution of the objects’ colors.

Experiments 3, 4 and 5 investigated what feature-based object properties contribute to grouping in the resolution of CISR. The features tested included synchronized temporal phase at a common frequency (experiment 3), identical temporal frequencies (experiment 4), and equal stereoscopic disparity (experiment 5). The results did not show evidence that grouping was affected by these object features.

Experiment 6 investigated whether ambiguity-based features affect grouping of two separate objects presented with CISR. Coherent ambiguity was tested with two CISR stimuli, compared to one object with CISR and the other object non-rivalrous (so no ambiguity). The results showed that the resolution of CISR by grouping depends on coherent ambiguity of the two objects.

Experiment 7 investigated chromatic adaptation during CISR to test whether a predominant color percept is related to the state of chromatic adaptation. The results showed that the color percept during CISR affected chromatic adaptation for two of the three observers.

Taken together, these experiments show that perceptual resolution of chromatic neural ambiguity, created with CISR, depends on object grouping. Therefore, the results demonstrate the importance of grouping for resolving ambiguous chromatic neural representations.

CHAPTER 1

LITERATURE REVIEW

At each moment, the human visual system receives an astonishing amount of sensory information. Sometimes, much of this information is ambiguous so that it can be interpreted in multiple ways. Fortunately, our brain is able to decipher this ambiguous sensory information successfully and form coherent percepts continuously (Sterzer & Kleinschmidt, 2007; Sterzer & Rees, 2008; Wolfe, 1996). To date, the mechanisms that contribute to interpreting ambiguous information and constructing coherent percepts from it are not well understood as many factors can affect the interpretation of ambiguous information.

This dissertation will investigate the role of a specific factor – grouping – in resolving chromatic interocular-switch rivalry, which contains perceptually ambiguous colors.

1.1 Perceptual Ambiguity

Perceptual ambiguity refers to two or more interpretations over time of the same stimulus pattern. The percept may be bi-stable for two interpretations or multi-stable for three or more interpretations. For instance, ambiguity often can be perceived as fluctuations in apparent depth when insufficient depth information is available in the image. Perceptual ambiguity occurs readily with monocular observation and the alternative percepts are experienced successively.

Perhaps the most well-known class of visual stimulus associated with perceptual ambiguity is the ambiguous figure. Such figures are most commonly bi-stable, so the percepts alternate over time between two interpretations sequentially (see examples in Fig. 1-1).

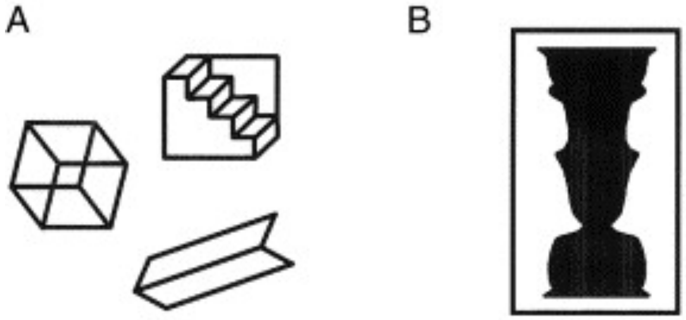

Figure 1-1. Examples of ambiguous figures (adapted from Leopold & Logothetis, 1999). (a) Perspective reversing figures. The Schroeder staircase (top) can be seen either as leading up to the left or as suspending from the ceiling. Similarly, the Necker cube (left) or the folded card (bottom) can be seen as two distinct three-dimensional configurations. (b) Figure-ground reversing figure. This figure can be seen as either a central black shape on a white background or two white half-silhouettes of a girl on a black background.

1.2 Binocular rivalry

Binocular rivalry is a well-studied form of bi-stable perception. It occurs when dissimilar stimuli are presented to the two eyes separately and produces perceptual alternation between one eye's stimulus and the other's stimulus (Blake & Logothetis, 2002). In normal viewing, the neural signals from the two eyes usually can create a single stable percept, even though the retinal images of a single stimulus differ slightly in the two eyes due to their physical positions. However, when these two images are very different, the neural signals from the two eyes do not give a single stable percept. Instead, only one of the images is perceived at a time and the percept alternates between the two images (Fig. 1-2).

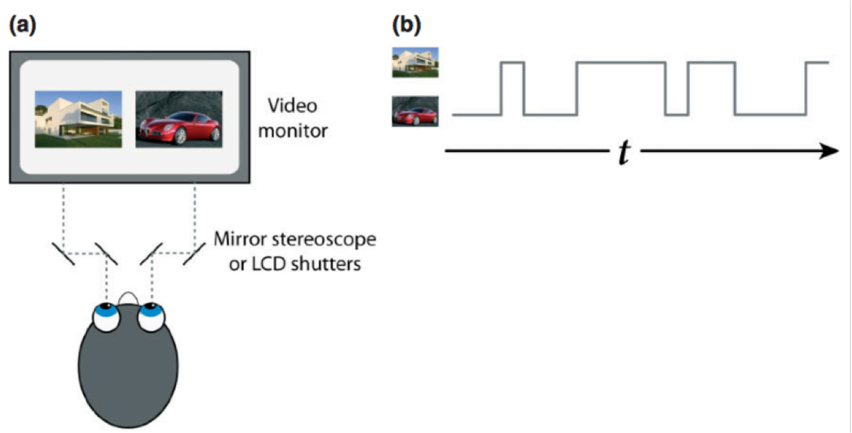

Figure 1-2. Binocular rivalry (adapted from Alais, 2012). (a) Two different images are presented to two eyes dichoptically, such as a house to the left eye and a car to the right eye. (b) Alternations occur between perceiving the car image and then the house image and back to the car image and so on, for as long as the images are presented. The perceptual alternations typically occur every few seconds.

Although binocular rivalry has much in common with other forms of bi-stable perception (e.g., ambiguous figures), several differences make binocular rivalry unique. First, binocular rivalry presents a different stimulus to each eye by a haploscope (illustrated in Fig. 1-3), while other forms of bi-stable perception involve only a single stimulus viewed by both eyes simultaneously. Second, the alternations during binocular rivalry are generally mutually exclusive, which means that only one interpretation is perceived at a given moment and the other is not; while other forms of bi-stable perception involve a single stimulus that supports two interpretations, and these two interpretations alternate even though the stimulus itself remains visible all the time. Third, binocular rivalry can be influenced locally (e.g., piecemeal rivalry), while other forms of bi-stable rivalry tend to alternate globally.

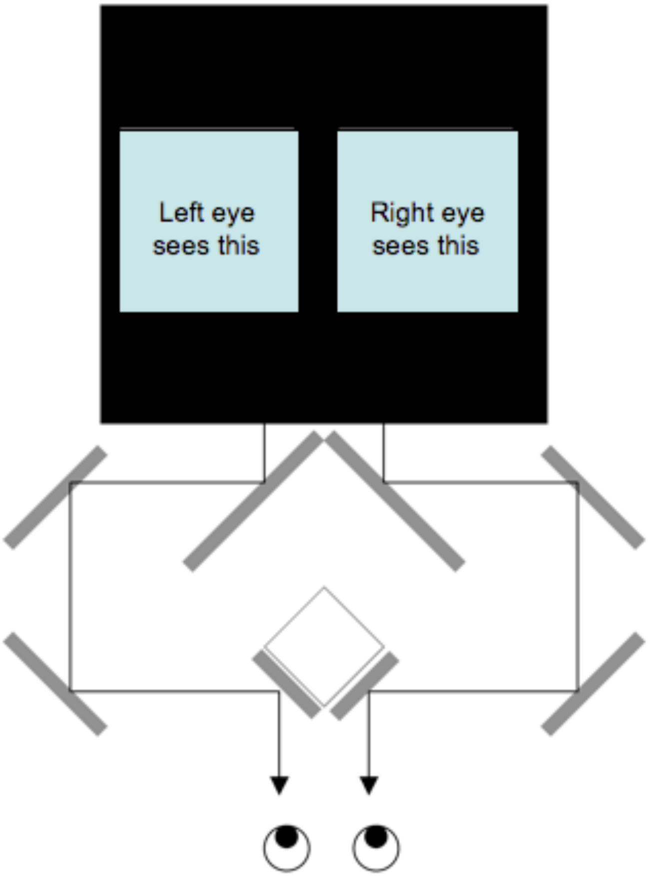

Figure 1-3. An illustration of a haploscope. It is widely used in the research area of binocular rivalry. This haploscope is composed of eight front-surface mirrors (gray bars) so that a different stimulus can be presented to each eye (solid lines with arrows).

1.2.1 Features

Two basic features characterize binocular rivalry over time: rate and predominance. Rate refers to how often one percept is replaced by the other. It is relatively stable within an observer but variable between observers (George, 1936; Aafjes, Hueting & Visser, 1966). Alternations of the dominant percepts have been shown to be stochastic over the viewing period (Fox & Herrmann, 1967). Predominance refers to the proportion of the total viewing time that a given stimulus is perceived within a given viewing period. It can be influenced by the stimulus properties, such as contrast (Mueller & Blake, 1989), luminance (Kaplan & Metlay, 1964), or spatial frequency (Fahle, 1982).

1.2.2 Mechanisms

In the past few decades, research in the area of binocular rivalry has aimed to understand the potential sites of neural competition and the types of visual representations that compete at these sites. That is, where and what rivals during binocular rivalry?

1.2.2.1 Interocular competition theory

The interocular competition theory proposes that perceptual alternation during binocular rivalry arises from competition between the two eyes among monocular neurons in the primary visual cortex (V1) or in the lateral geniculate nucleus (LGN) of the thalamus (Blake, 1989; Lehky, 1988; Tong, 2001). In other words, this theory proposes that binocular rivalry results from suppressing neural signals from one eye (see Fig. 1-4), which

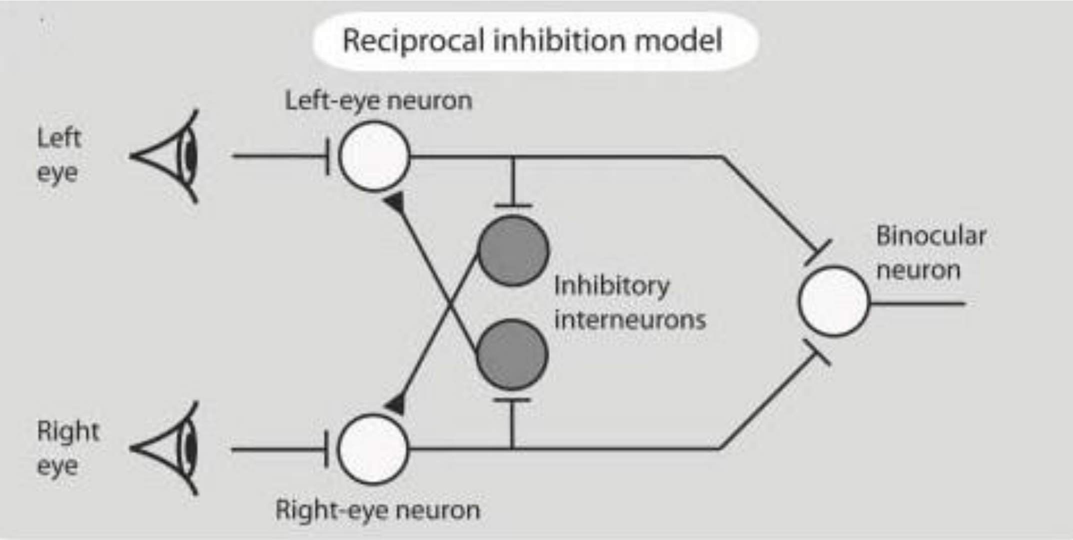

Figure 1-4. Reciprocal inhibition model of interocular competition theory (adapted from Alais, 2012). This classical model proposes that there is a reciprocal inhibition between the monocular channels, and explains how an image becomes suppressed during binocular rivalry.

is also referred as “eye” rivalry.

Psychophysical studies support the interocular competition theory based on evidence that the suppressed eye loses partial or full sensitivity to the visual information during binocular rivalry. For example, when a probe is presented with a stimulus during its phase of rivalry suppression, the detection probability of the probe is 20–30% less than that during the phase of rivalry non-suppression (Wales & Fox, 1970). Even large-scale changes are often not detected during translational and rotational motion when these changes are presented to one eye during the period of suppression (Blake, Yu, Lokey & Norman, 1998). In addition, when the dominant and suppressed orthogonally-oriented patterns are interchanged between the two eyes, observers continue seeing with the dominant eye, which indicates that the eye, not the pattern, is suppressed during rivalry (Blake, Westendorf & Overton, 1980).

Neuroimaging studies using fMRI also support the interocular competition theory. For example, when a low-contrast grating and a high-contrast grating are presented to the two eyes dichoptically, the neural activity in the primary visual cortex (V1) is coupled to the perceptual domination between the two gratings (Polonsky, Blake, Braun & Heeger, 2000). That is, the fMRI signals increase when the high-contrast grating is perceived and decrease when the low-contrast grating is perceived. Also, the amplitude of the fMRI signals during binocular rivalry is about 55% as large as that during physical stimulus alternation without rivalry, which suggests a partial resolution of binocular rivalry in V1. In another study, the magnitude of suppression in V1 during binocular rivalry is investigated by comparing the V1 neural activity in three stimulus conditions (Lee & Blake, 2002). First, in the “rivalry” condition, a pair of red and green orthogonal gratings is presented dichoptically, and the V1 activity represents the amount of neural activity during perceptual suppression of one grating. Second, in the “monocular-single alternation” condition, two monocular gratings, one red and one green, are physically alternated between the two eyes, mimicking the percepts in the “rivalry” condition, and the V1 activity represents the amount of neural activity during complete suppression of one grating. Third, in the “monocular-superimposed alternation” condition, a red and green plaid is physically alternated between the two eyes, and the V1 activity represents the amount of neural activity with no suppression of either grating. The results show that the V1 activity in the “rivalry” condition is midway between the lowest in the “monocular-single alternation” condition and the highest in the “monocular-superimposed alternation” condition, which implies perceptual suppression in V1 during binocular rivalry. In addition, the neural activity in a monocular region of V1 corresponding to the blind spot increases sharply when the ipsilateral eye becomes dominant (Tong & Engel, 2001). This is consistent with the prediction that if rivalry arises from interocular competition, then the ipsilateral neurons in the blind spot, which receive no contralateral-eye projection, should show increased activity when a stimulus is presented to the ipsilateral eye. Moreover, these fMRI signals are as large as those observed during physical alternations, which indicates that binocular rivalry may be fully resolved in monocular visual cortex. In general, all these findings support the interocular competition theory in that the V1 activity is partially, or even fully, correlated with the perceptual alternation.

1.2.2.2 Pattern competition theory

The pattern competition theory proposes that perceptual alternation during binocular rivalry arises from competition between incompatible patterns among pattern selective neurons at a higher level of visual processing than primary visual cortex (V1) (Kovacs, Papathomas, Yang & Feher, 1996; Leopold & Logothetis, 1996; Logothetis, Leopold, & Sheinberg, 1996). In other words, this theory proposes that binocular rivalry results from neural signals after responses from the two eyes are combined. It assumes the resolution of binocular rivalry has no, or at least less, involvement in V1. This is also referred to as "stimulus" rivalry.

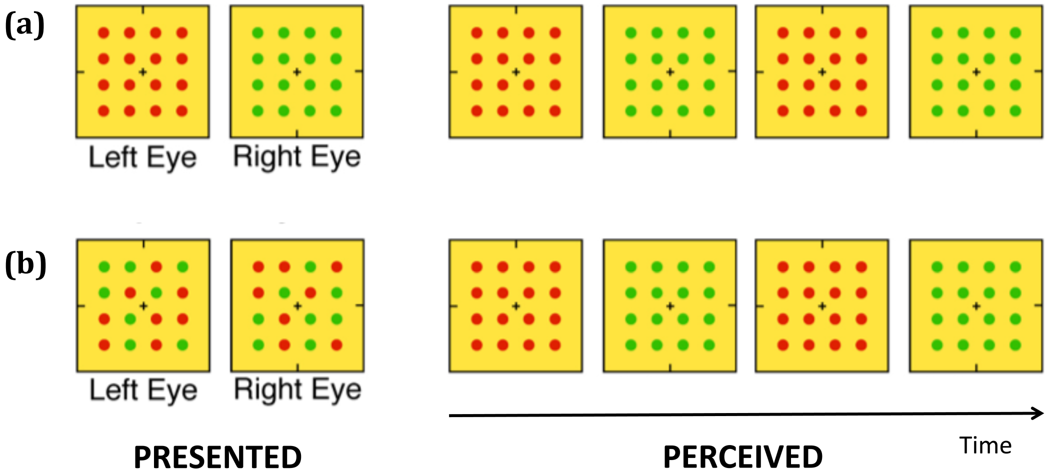

Figure 1-5. Interocular grouping (adapted from Kovacs, Papathomas, Yang & Feher, 1996). (a) Conventional color-rivalry. Each panel is presented to each eye separately. Viewing such stimuli results in alternations between perceiving all red dots and all green dots. (b) Patchwork stimuli with color-rivalry. Each panel is presented to each eye separately. Viewing such stimuli often results in the same percepts as (a).

Psychophysical studies support the pattern competition theory, based on two well-known visual phenomena that cannot be explained by the interocular competition theory. One is interocular grouping, in which the probability of perceiving all dots of the same color (all red or all green) from patchwork rivalrous stimuli (Fig. 1-5(b)) is similar to the probability of perceiving all dots in that color from conventional color-rivalry (Fig. 1-5(a); Kovacs, Papathomas, Yang & Feher, 1996). The much-higher-than-zero probability of perceiving all dots of one color in patchwork rivalry is not consistent with the prediction of interocular competition, which indicates that the visual system is able to select local elements from each eye and reorganize them into a perceptual representation of a coherent whole. This implies that the resolution of binocular rivalry is at a higher-level site than V1. The other phenomenon is interocular-switch rivalry (Logothetis, Leopold & Sheinberg, 1996). In this paradigm, orthogonal gratings are presented dichoptically as temporal square-waves at 18 Hz. In the case referred to as non-reversal rivalry, the orientation of the grating in each eye remains the same throughout the trial (Fig. 1-6(a)), while in the case of reversal rivalry the gratings in the left and the right eye are swapped at a rate of 3 Hz so that the orientations of the gratings are alternated between eyes (Fig. 1-6(b)). The rivalry between the two orthogonal gratings is continually and rapidly swapped between the two eyes but is nearly indistinguishable from conventional rivalry, which suggests that it is the "stimulus", instead of the "eye", that competes during binocular rivalry.

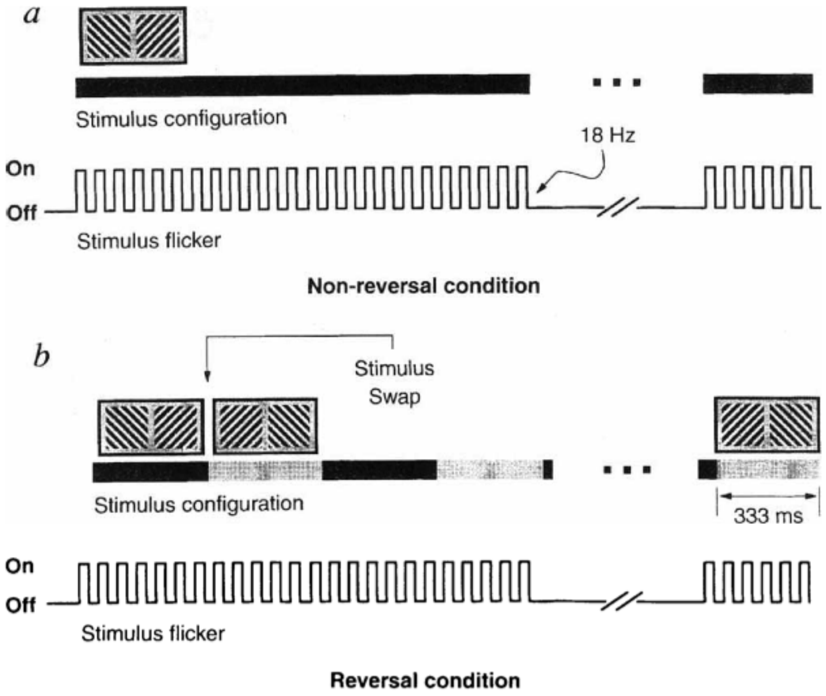

Figure 1-6. Interocular-switch rivalry (adapted from Logothetis, Leopold & Sheinberg, 1996). (a) Non-reversal rivalry. (b) Reversal rivalry.

Electrophysiological studies in monkeys also support the pattern competition theory. For example, some neurons in the monkey's cortical area, such as middle temporal (MT), show changes in activity during motion rivalry that reflects the perceived direction of motion (Logothetis & Schall, 1989). When monkeys report the perceived orientation of the orthogonal gratings presented dichoptically, the activity of the neurons in V4, but not V1 and V2, is correlated with the perceptual dominance and suppression of one grating (Leopold & Logothetis, 1996). That is, perception-related modulation of neural activity occurs in a higher visual cortical area, which suggests that binocular rivalry arises through interactions between the binocular neurons at several levels in the visual pathways. In addition, when monkeys view incongruent images dichoptically, the activity of most neurons (about 84%) in the inferior temporal cortex (IT) and the superior temporal sulcus (STS) are contingent on the perceptual dominance during binocular rivalry (Sheinberg & Logothetis, 1997). Thus, the temporal lobe plays a role in the visual awareness of rivalrous stimuli, which suggests that binocular rivalry arises even at this level of the visual hierarchy. In general, all these findings support the pattern competition theory in that V1 shows no or at least less activity, compared to the areas higher than V1, related to the resolution of binocular rivalry.

1.2.2.3 Hybrid model theory

Neither the interocular competition theory nor the pattern competition theory is able to provide a full account of binocular rivalry on its own, and many researchers have adopted a hybrid model theory involving the basic reciprocal inhibition framework reproduced at multiple stages (Alais, 2012; Dayan, 1998; Freeman, 2005; Leopold & Logothetis, 1999; Tong, Meng, & Blake, 2006; Wilson, 2003). In other words, this model proposes that inhibitory interactions take place between both monocular neurons and binocular pattern-selective neurons, and then strong inhibition between these two neurons alters the balance in the relative strengths of responses to the two stimuli, thus resulting in binocular rivalry.

Psychophysical studies support the hybrid model theory, including both monocular and binocular contributions to motion rivalry (Meng, Chen & Qian, 2004) and a monocular contribution to stimulus rivalry (Brascamp, Sohn, Lee & Blake, 2013). In addition, a neuroimaging study using TMS supports multilevel processing of binocular rivalry (Pearson, Tadin & Blake, 2007).

1.2.3 Factors

Binocular rivalry is due to a local competition, and this competition is evident at early sites and continues to occur at higher cortical sites (Tong, Meng & Blake, 2006). Therefore, both the local properties and global characteristics (e.g. grouping) of the stimulus play an important role in resolving binocular rivalry.

1.2.3.1 Local properties

Binocular rivalry is largely governed by the stimulus's local properties, such as luminance/chromaticity contrast, spatial frequency, and temporal frequency. It is not surprising that these properties affect binocular rivalry because they represent a change in the strength of the stimulus.

Luminance/chromaticity contrast: A high-contrast stimulus dominates longer and has shorter periods of suppression than a low-contrast one during binocular rivalry (Bossink, Stalmeier & de Weert, 1993; Kaplan & Metlay, 1964; Mueller & Blake, 1989). Aside from the contrast of the interocular luminance, increasing the luminance of both stimuli also increases their alternation rate (Kaplan & Metlay, 1964). In addition, interocular differences in chromaticity can trigger binocular rivalry (Kulikowski, 1992).

Spatial frequency: A densely contoured figure dominates longer than a sparsely contoured one during binocular rivalry (Fahle, 1982). In addition to the interocular difference of spatial frequency, high-spatial-frequency dichoptic stimuli are easier to fuse (Hollins, 1980) and induce more perceived rivalry (O'Shea, Sims & Govan, 1997) than low-spatial-frequency ones.

Temporal frequency: This is a controversial property because interocular differences in temporal frequency either can lead to binocular rivalry (Alais & Parker, 2012) or not (O'Shea & Blake, 1986). A possible reason for the range of the results is that different stimulus patterns, orthogonal gratings and random dots, have been used in these two studies separately. However, when the two stimuli oscillate at the same rate, temporal frequency is immune to binocular rivalry (Bower & Haley, 1964; Wolfe, 1983a, 1983b).

Motion: A moving contour has an advantage over a stationary one with longer dominance times during binocular rivalry (Breese, 1899), and the dominance time of a moving stimulus increases with speed (Wade, de Weert & Swanston, 1984). However, an interocular difference from speed is not evident when the stimuli move in the same direction (Blake, Zimba & Williams, 1985).

Stereopsis: Stereopsis is a controversial property. Wolfe (1986) developed a theory in which stereopsis and rivalry occur within parallel, independent pathways, whereas Blake, Yang and Wilson (1991) support the view that rivalry and stereopsis cannot coexist at the same spatial location. Other studies show instead that stereopsis and color rivalry can coexist (Hong & Shevell, 2008; Treisman, 1962).

1.2.3.2 Global properties

Spatially distributed stimulus features, such as luminance/chromaticity contrast, orientation, temporal frequency and motion, can be perceptually grouped together as a global form in accordance with Gestalt principles and simultaneously dominate during binocular rivalry (de Weert, Snoeren & Koning, 2005).

Luminance contrast: When dot arrays of opposite contrast relative to the background luminance are presented dichoptically, the uniform-luminance array produces significantly more unitary percepts than the mixed-luminance array during binocular rivalry (Silver & Logothetis, 2004). Specifically, one eye is shown a reference array that contains dots lighter than the background, and this array is held constant. The other eye views one of three types of array that contain dots darker than the background: uniform dark gray dots, uniform black dots (Fig. 1-7(a)), or a mixture of dark gray and black dots (Fig. 1-7(b)). The proportion of dark gray or black dots can be decreased to as little as 5% of the dots of the secondary luminance, which still reduces unitary perception of these

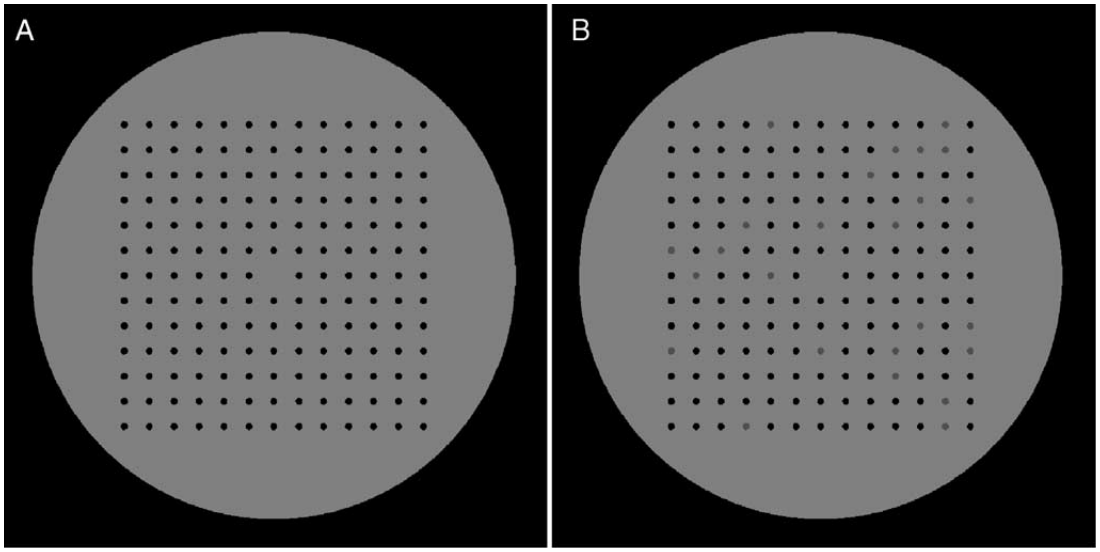

Figure 1-7. Grouping based on common luminance during binocular rivalry (adapted from Silver & Logothetis, 2004). (a) Test array with dots of uniform luminance. (b) Test array with dots of mixed luminance.

stimuli substantially compared to the arrays of uniform luminance. This indicates a grouping effect based on common luminance.

Chromaticity: When dots presented dichoptically to each eye are intermingled with two chromaticities (e.g. "red" and "green"), a unitary color, either red or green, is sometimes perceived in the fused percept of all the dots during binocular rivalry (Fig. 1-5(b); Kovacs, Papathomas, Yang & Feher, 1996). Because of the interocular distribution of the colors, a coherence of all dots in one color could only be formed by the simultaneous dominance of the spatially distributed dots in that color between both eyes. This implies that a grouping property based on the same chromaticity promotes predominance during binocular rivalry. In addition, when two rivalrous characters with different colors, either synesthetic or real, are presented dichoptically, these characters tend to group together and the perception of joint predominance is promoted (Kim, Blake & Palmeri, 2006). Despite a synesthetic or a real color, global coherence based on grouping occurs as long as the two rivalrous stimuli within each eye share the same color (Fig. 1-8).

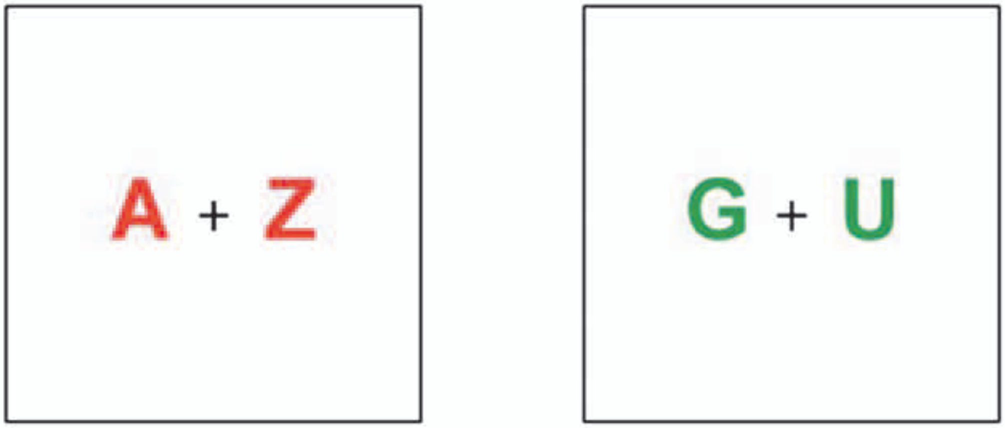

Figure 1-8. Stimulus paradigm of two characters presented dichoptically to the two eyes (adapted from Kim, Blake & Palmeri, 2006). The joint predominance of perceiving two characters with the same color is greater than by chance.

Orientation: The magnitude of the joint predominance has been investigated when two gratings are presented to the left eye and two sets of random dots are presented to the right eye dichoptically, with various orientations and contrast modulations (Alais & Blake, 1999). The joint predominance is the dominance time that both gratings are simultaneously perceived. The orientations of two gratings are varied among collinear, parallel and orthogonal (Fig. 1-9(a)), and their contrast modulations are varied between correlated (both gratings follow identical random patterns of contrast changes) and uncorrelated (each grating follows its own, independent pattern of contrast changes) (Fig. 1-9(b)). The results show that the strongest joint predominance is perceived from collinear gratings with correlated contrast modulation, which suggests that grouping based on collinear contours and correlated contrast can jointly increase dominance during binocular rivalry. In addition, good continuation of orientation has similar effects to promote simultaneous dominance of dichoptically presented stimuli (Ngo, Miller, Liu & Pettigrew, 2000).

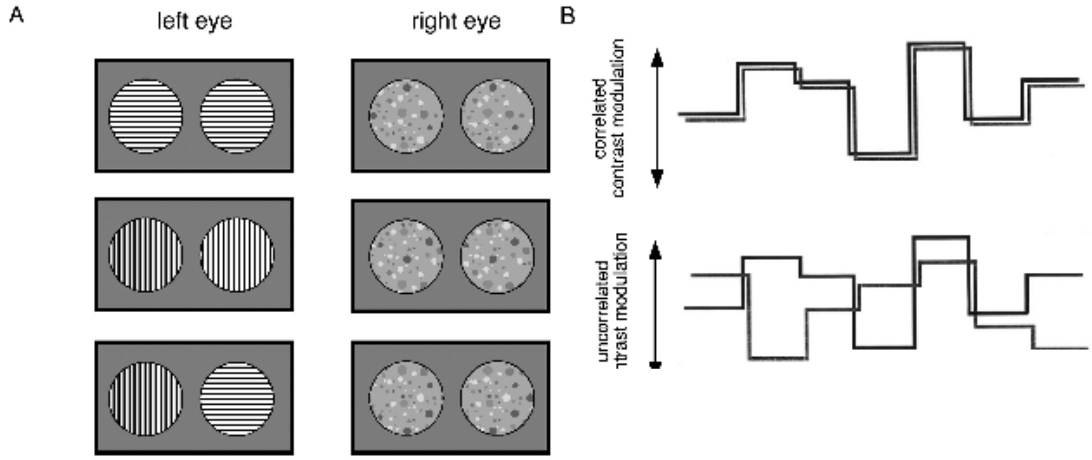

Figure 1-9. Grouping based on spatial and temporal factors influences predominance during binocular rivalry (adapted from Blake & Lee, 2005). (a) Orientations are collinear, parallel or orthogonal (from top to bottom) between two gratings. (b) Contrast modulations are correlated (top) or uncorrelated (bottom).

Temporal frequency: Suzuki and Grabowecky (2002) investigated the role of synchronized temporal frequencies on grouping during binocular rivalry by using overlapping visual features that flicker periodically: one is two pairs of orthogonally oriented bars and the other is a set of small circles. That is, the bars switch repetitively between two orientations of diagonal left or diagonal right, and the set of small circles flash periodically in synchrony with one orientation of the two pairs of bars (Fig. 1-10(a)). The results show that the set of small circles are perceived to be attached to the oriented bars with which those small circles are synchronously flashing; when the other orthogonally-oriented bars are dominant, the set of small circles appear to form a separate cluster of features seen transparently in relation to the bars (Fig. 1-10(b)). This implies that temporal frequency information can contribute to parse overlapping patterns during binocular rivalry.

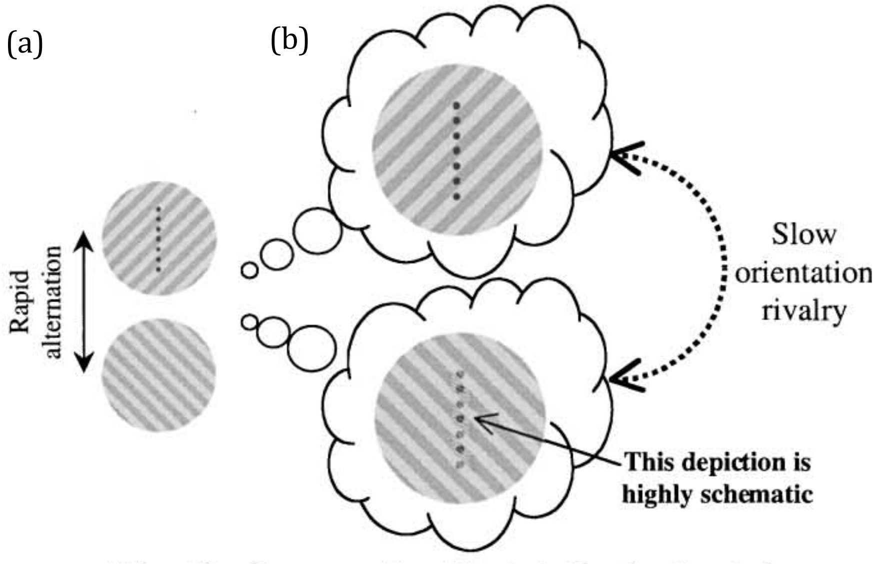

Figure 1-10. Feature parsing based on synchronized temporal frequencies (adapted from Suzuki & Grabowecky, 2002).

Motion: The predominance of a grating during binocular rivalry increases more in a global-motion pattern than in a local-motion pattern (Alais & Blake, 1998). By using a multiple-aperture motion stimulus, a global-motion pattern (Fig. 1-11(a)) has a target grating (e.g., the top-right one) and three non-rivalrous gratings presented in the left eye that form a larger global motion display. In this example, the global motion is upward. A local-motion pattern (Fig. 1-11(b)) has the target grating presented alone in the left eye. In both patterns, this target grating in the left eye is also rivaling with a set of random dots presented in the right eye. The high predominace of the target grating in a global pattern suggests that global coherence of motion plays a role in the predominance of a local component grating presented during binocular rivalry. Similar effects of a global motion context have also been found when a target grating is rivaling with a drifting grating (Sobel & Blake, 2002) or when all the local motions are coherent (Silver & Logothetis, 2004).

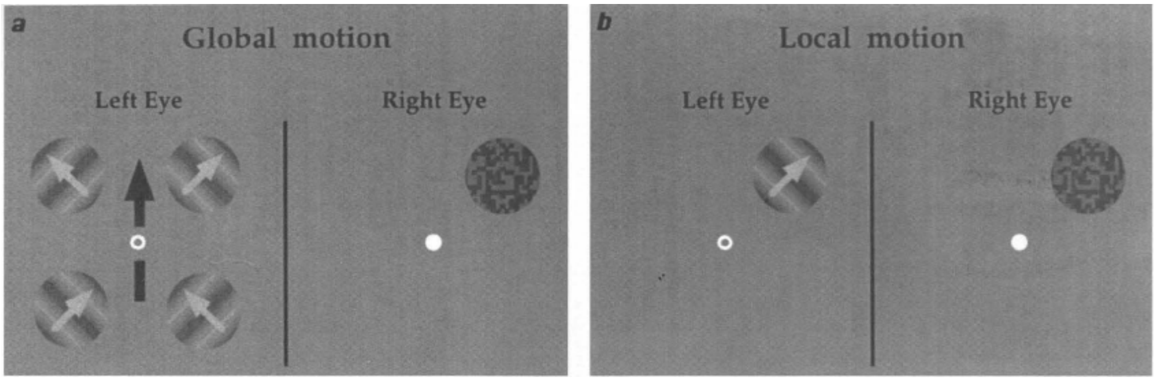

Figure 1-11. Global coherence of motion (adapted from Alais & Blake, 1998). (a) A global-motion pattern. (b) A local-motion pattern.

As a general rule of grouping during binocular rivalry, when two eyes are exposed to several distinct pairs of rivalrous stimuli, the members of each pair compete locally and rival independently. However, this independent competition can be broken down if any spatially distributed features of each rivalry are commonly connected, such as contour interactions (or association fields) (Alais, Lorenceau, Arrighi & Cass, 2006). That is, grouping of spatially separate stimuli may reflect that the neural representation of each independent rivalry interacts via lateral connections of the cortical hypercolumns (Alais & Blake, 1999; Lee & Blake, 2001). Furthermore, eye of origin gives a stronger cue for grouping than common features during binocular rivalry (Stuit, Paffen, van der Smagt & Verstraten, 2011). Thus, grouping of spatially rivalrous stimuli with common features tend to be dominant longer when they are presented in the same eye, compared to presenting them in different eyes.

1.3 Binocular color rivalry

As early as 1760, Dutour discovered that two different colors, despite unequal luminance, could cause binocular rivalry when the color difference is large enough. That is, perceptual alternation between two pieces of colored cloth was observed when a blue piece was presented to one eye and a yellow piece to the other eye. This perception of color raises a question about binocular color processing: what are the mechanisms mediating binocular color rivalry?

One popular view proposes that color rivalry results from competition between binocular neurons. Computational models that explain how the visual system produces slow alternations between stable percepts indicates that binocular neurons receive input from the left eye and right eye monocular neurons and produce a stable response based on the combination of these neural signals (Dayan, 1998; Freeman, 2005; Wilson, 2003).

An electrophysiological study supports a cortical binocular representation of color rivalry (Peirce, Solomon, Forte & Lennie, 2008). Using a spatially uniform field alternating between two equiluminant chromaticities presented dichoptically, the chromatic tuning of binocular neurons in monkeys’ V1 and V2 are measured. The results show that the binocular neurons preferring chromatic modulation have receptive fields that are well matched for chromatic tuning in the two eyes, while the binocular neurons preferring achromatic modulation have receptive fields that are poorly matched for chromatic tuning in the two eyes. This finding suggests that even in the early visual cortex, color-preferring neurons are binocularly driven. Other evidence comes from chromatic interocular-switch rivalry (Christiansen, D’Antona & Shevell, 2014). Chromatic interocular-switch rivalry

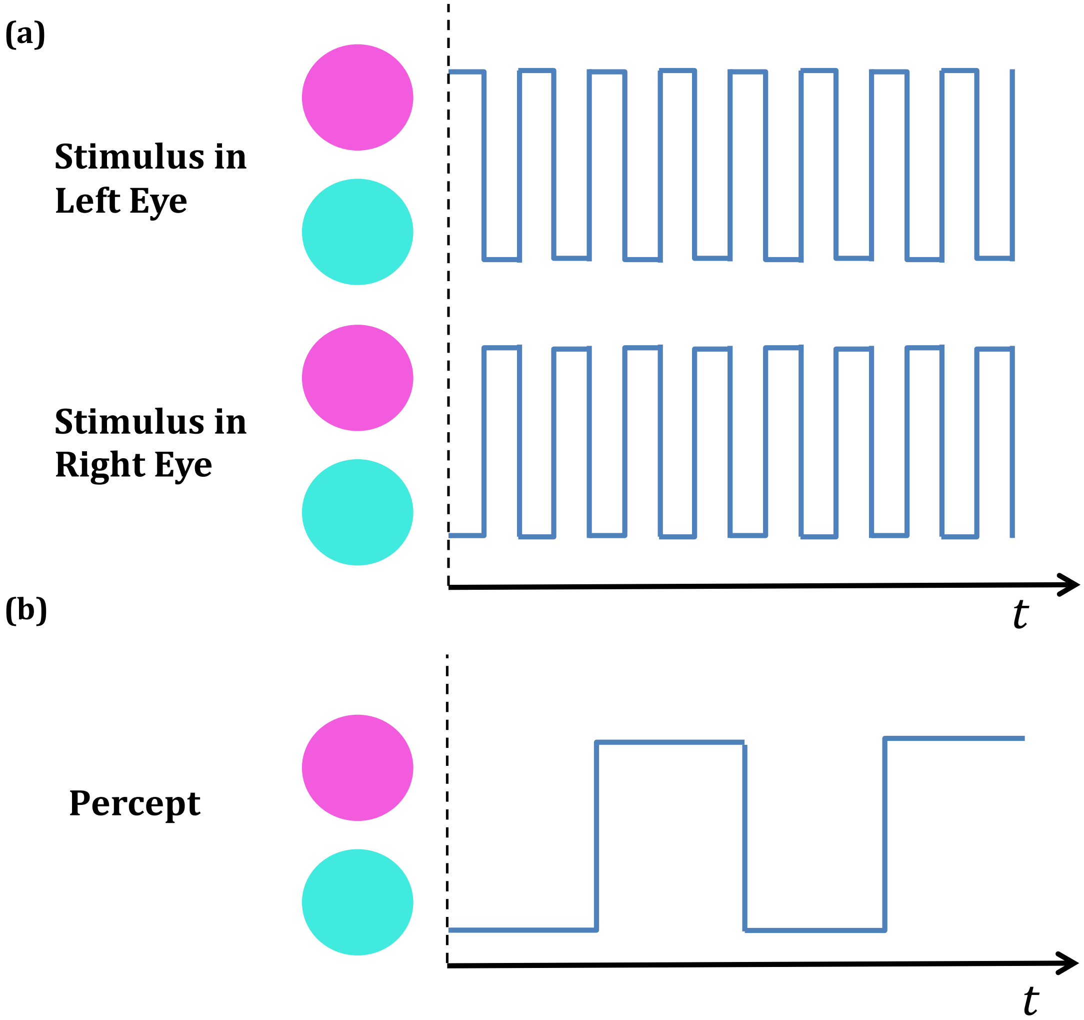

Figure 1-12. Chromatic interocular-switch rivalry. (a) Two equiluminant but chromatically rivalrous stimuli are presented dichoptically and swapped interocularly. (b) A longer-lasting color alternating between the two presented chromaticities is perceived.

occurs when two equiluminant but chromatically rivalrous stimuli (e.g., one “pink” disc and one “blue-green” disc) are presented separately to each eye, and then swapped interocularly several times a second (e.g., at 3.75Hz) (Fig. 1-12(a)). If a single neuron receives information from one eye and then the other, a rapid swap of monocular information should always be perceived. However, the percept is a longer-lasting color that alternates between the two chromaticities rather than seeing the fused disc switch colors rapidly (Fig. 1-12(b)). This implies that color rivalry can arise from competition among binocular neurons preferring one of the two chromaticities, not simply rivalry among monocular representations.

1.4 Color perception in mid-level vision

Research in human vision can be divided into three areas of investigation. Low-level vision is concerned with the analysis of the image falling on the retina in local regions. Color, lines and edges are represented at the level of the retina, LGN and parts of V1. High-level vision involves the mapping from visual representations to meaning (e.g. recognition of specific objects and events) and includes the study of processes and representations related to the interaction of perception and cognition (Henderson & Hollingworth, 1999). Mid-level vision, as its name implies, is an intermediate representation of surfaces and objects later than low-level vision (retinal representation of an image’s physical properties) but before high-level vision (object recognition). It represents the visual information only in a most general way, dealing primarily with surfaces and objects that can appear at different orientations, can be variously illuminated, and can be partially occluded (Nakayama, 1999; Nakayama, He & Shimojo, 1995).

Since mid-level vision can extract surfaces and objects that can be determined without regard to meaning, it is a process that can give ambiguous neural representations that lead to more than one interpretation. For example, if a Necker cube (Fig. 1-1(a)) is perceived, its orientation should have two possibilities depending on which part of the cube is focused on. Therefore, the neural representation of the cube in mid-level vision can be ambiguous in terms of the percept it evokes.

Previous research has confirmed that a slow alternation between two colors is perceived during chromatic interocular-switch rivalry (Christiansen, D'Antona & Shevell, 2014), which is consistent with the theory of "stimulus" rivalry. This slowly switching percept has two possible colors in mid-level vision, and is isolated from the clear retinal representations of the image's physical properties in low-level vision. Thus, chromatic interocular-switch rivalry creates steady-state ambiguous neural representations of color, which is a novel approach to studying how the visual system represents color in mid-level vision.

1.5 Specific aims

Gestalt psychologists proposed the idea that the whole is different than the sum of each component (Koffka, 1922; Kohler, 1959). The human visual system uses perceptual grouping to organize the visual world as structured and cohesive, rather than a group of isolated and independent fragments. Perceptual grouping refers to the fact the observers perceive some elements of the visual field as being parts of a single object more strongly than other elements, which is a particular kind of perceptual-organization phenomenon. In this dissertation, the concept of grouping is used to describe spatially neighboring objects that are perceived to take on the same feature (specially, the same color) when the chromatic neural representation of each object is ambiguous. By taking advantage of chromatic interocular-switch rivalry, this dissertation explores the role of such grouping in resolving ambiguous chromatic neural representations and advances the understanding of mechanisms for integrating information from separate visual regions in mid-level vision. Thus, grouping is examined with multiple objects presented nearby but that can change their color independently. Specifically, two or more spatially separated parts of the visual field, each with a distinct object, are presented simultaneously but independently using chromatic interocular-switch rivalry.

Aim 1: Is the color percept during chromatic interocular-switch rivalry related to the temporal frequency of swapping?

The percept from chromatic interocular-switch rivalry has previously been shown to be a longer-lasting alternation between two colors when these two chromaticities are swapped interocularly at a temporal frequency of 3.75 Hz (Christiansen, D'Antona & Shevell, 2014). Experiment 1 investigates several different temporal frequencies (including 3.75 Hz) over which longer-lasting color percepts can be seen, to seek a wide and optimal range of temporal frequency for following experiments.

Aim 2: Does grouping contribute to the longer-lasting color percepts during chromatic interocular-switch rivalry?

Grouping previously has been shown to promote the predominant percept during binocular rivalry (Alais & Blake, 1998, 1999; Kim, Blake & Palmeri, 2006; Kovas, Papathomas, Yang & Feher, 1996; Silver & Logothetis, 2004; Sobel & Blake, 2002; Suzuki & Grabowecky, 2002). Experiment 2 investigates whether grouping contributes to the longer-lasting color percepts during chromatic interocular-switch rivalry. This question is tested using two different paradigms that have a group of two independent objects (experiment 2a) or four independent objects (experiment 2b).

Aim 3: What features of grouped objects contribute to the longer-lasting color percepts during chromatic interocular-switch rivalry?

Previous research has shown that spatially distributed features of grouped objects can contribute to the predominant percept during binocular rivalry. These grouping features include common luminance (Silver & Logothetis, 2004), collinear contours and correlated contrast (Alais & Blake, 1999). Assuming two-object grouping promotes the longer-lasting color percepts during chromatic interocular-switch rivalry (as found in pilot experiments), experiments 3, 4 and 5 investigate which feature-based grouping relations contribute to this. The possible features include grouped objects with synchronized temporal phase at a common temporal frequency (experiment 3), grouped objects with different temporal frequencies (experiment 4), and grouped percepts with unequal stereoscopic disparity (experiment 5).

Aim 4: Does coherent ambiguity of grouped objects contribute to the longer-lasting color percepts during chromatic interocular-switch rivalry?

Previous research has shown that global motion coherence of non-rivalrous objects promotes the predominant motion percept of a locally rivalrous object during binocular rivalry (Alais & Blake, 1998; Silver & Logothetis, 2004; Sobel & Blake, 2002). Given a group formed by a rivalrous object and a non-rivalrous object, experiment 6 investigates whether an ambiguous rivalrous color percept is grouped with a non-rivalrous color percept during chromatic interocular-switch rivalry.

Aim 5: To what is the visual system adapting when resolving chromatic interocular-switch rivalry?

With the aid of chromatic adaptation, experiment 7 investigates whether the predominant longer-lasting color percept during chromatic interocular-switch rivalry is related to the state of chromatic adaptation.

CHAPTER 2

GENERAL METHODS

2.1 Experimental setup

Three basic stimulus paradigms were tested in all the experiments (Fig. 2-1). In the first paradigm, one spatially homogeneous disc was presented in the center to each eye at a corresponding retinal location and then one fused disc was perceived (Fig. 2-1(a)); in the second paradigm, two spatially homogeneous discs, arranged vertically (one above the

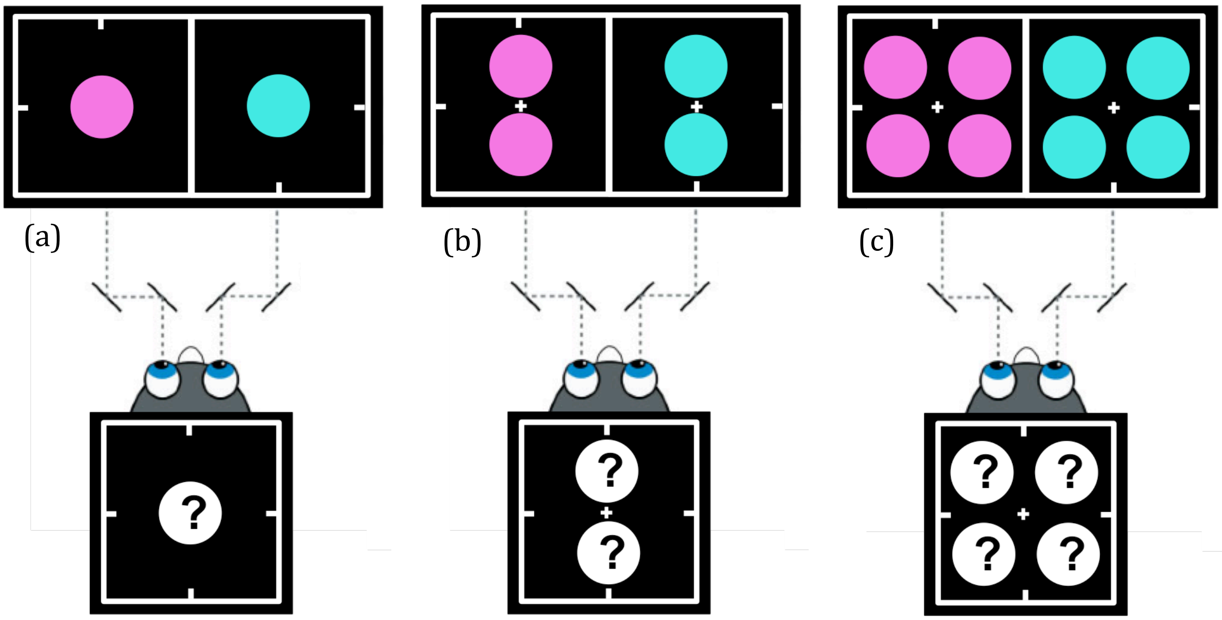

Figure 2-1. Stimulus paradigm with (a) one disc, (b) two discs, and (c) four discs are demonstrated with two colors ("pink" and "blue-green") embedded.

fixation cross, one below), were presented in the center to each eye at corresponding retinal locations and then two fused discs were perceived (Fig. 2-1(b)); in the third paradigm, four spatially homogeneous discs, each at the corner of a square which was centered by the fixation cross, were presented to each eye at corresponding retinal locations and then four fused discs were perceived (Fig. 2-1(c)).

The stimulus presented to each eye was composed of three parts. The first part was a rivalry-inducing pattern, usually presented with square-wave temporal exchange of the chromaticity of the uniform disc(s) in each eye. The size of each disc was 1.5° in diameter in all stimulus paradigms. The distance between the centers of the two discs was 2° in the two-disc paradigm and four-disc paradigm (both in the vertical and horizontal directions). The second part was a surrounding square white "guideline" that aided stable fixation of the rivalry-inducing patterns presented to the two eyes. The third part included top and left nonius lines presented to the left eye and bottom and right nonius lines presented to the right eye, so the two eyes could be pointed at exactly the same location in the visual field by horizontally and vertically aligning the lines in each eye. In the multiple-disc paradigms, an additional fixation cross was presented in the center of each eye's stimulus (see fixation cross in Figs. 2–1 (b)(c)).

Each disc in the stimulus paradigm alternated over time between two equiluminant chromaticities. The time-average chromaticity was always metameric to equal-energy-spectrum (EES) "white". In experiment 1, eight pairs of chromaticities were tested in total, two pairs along each of the two cardinal chromatic directions (either l = L/(L+M) or s = S/(L+M)) and two pairs along each of the two diagonal directions that varied in both L/(L+M) and S/(L+M) simultaneously. These chromaticities (l, s) were: [1] (0.690, 1.0) &

(0.640, 1.0); [2] (0.715, 1.0) & (0.615, 1.0); [3] (0.665, 1.4) & (0.665, 0.6); [4] (0.665, 1.8) & (0.665, 0.2); [5] (0.690, 1.4) & (0.640, 0.6); [6] (0.715, 1.8) & (0.615, 0.2); [7] (0.690, 0.6) & (0.640, 1.4); or [8] (0.715, 0.2) & (0.615, 1.8) (Fig. 2-2). In the other experiments, only two pairs of chromaticities were tested in total, one pair along each of the two cardinal chromatic directions (either *l* = L/(L+M) or *s* = S/(L+M)). These chromaticities (*l*, *s*) were (0.715, 1.0) & (0.615, 1.0) and (0.665, 1.8) & (0.665, 0.2). The luminance of all the discs was fixed at 7.85 cd/m^2 and the background was dark (<0.01 cd/m^2).

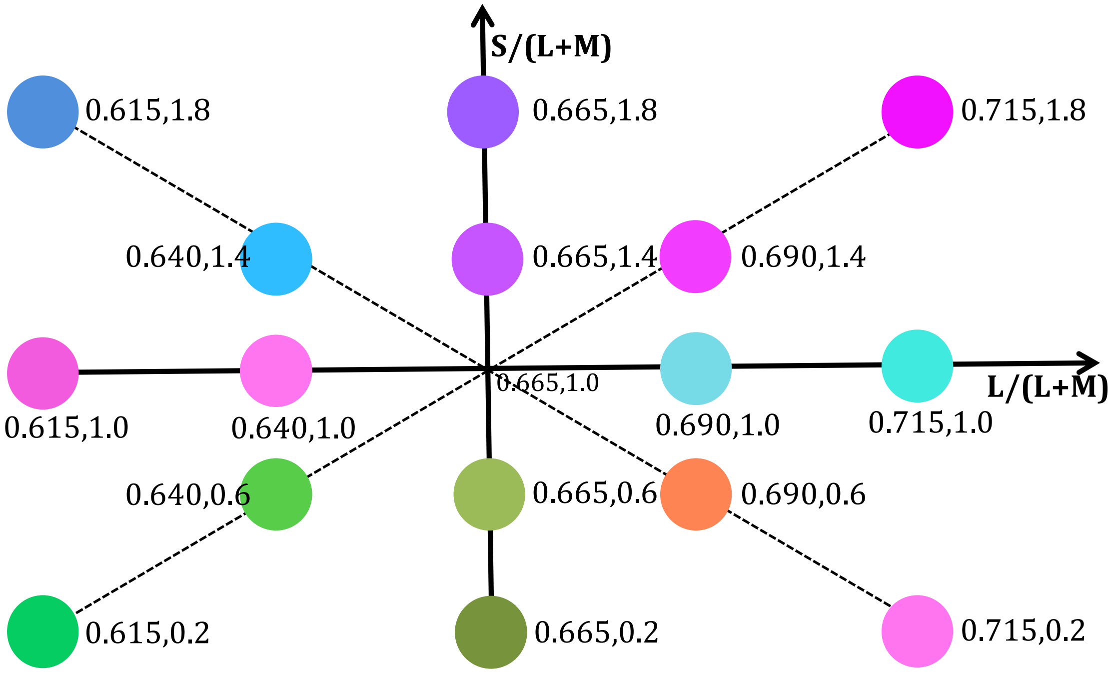

Figure 2-2. Eight pairs of (sixteen) chromaticities tested in experiment 1. Two pairs of chromaticities, along each of the two cardinal chromatic directions (either *l* = L/(L+M) or *s* = S/(L+M)) or along each of the two diagonal directions that varied both L/(L+M) and S/(L+M) simultaneously, were tested. One pair of chromaticities along the *l* axis, (0.715, 1.0) and (0.615, 1.0), is selected for demonstration in all the figures of this dissertation.

The temporal oscillation of each disc in the left eye was always at the same square-wave frequency but in the opposite phase compared to the disc in the right eye at the corresponding retinal location (Fig. 2-3), except for some experimental conditions in experiments 6 and 7. This pattern held whether there were single or multiple discs presented in each eye.

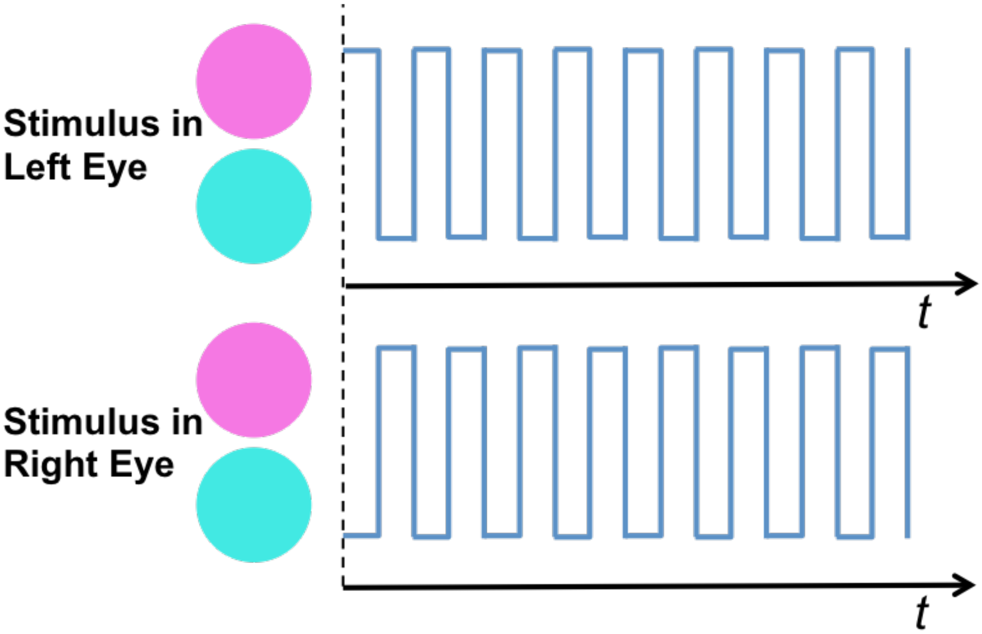

Figure 2-3. Temporal chromatic exchange of the disc in the left eye (above) and right eye (below) at the corresponding retinal location. The chromaticity of the disc in the left eye was in opposite phase relative to the disc in the right eye (for most experiments, the two discs were always chromatically rivalrous in the two eyes).

2.2 General procedure

Prior to each experiment, equiluminant settings were determined for each observer using heterochromatic flicker photometry (HFP). The HFP field size was 1.6° in diameter, the temporal frequency was 12.5 Hz and the luminance was 5 cd/m^2.

Each observer practiced the experimental procedure for two days and no data from the practice sessions were included in the analyses.

Each session was composed of a certain number of trials, and each trial had chromatic interocular-switch rivalry with one pair of chromaticities (described above, except for experiment 7). All pairs of chromaticities were repeated once in a random sequence within each session under all the experimental conditions. On each trial, chromatic interocular-switch rivalry began with an instruction of how to respond to each perceived color using a gamepad. Then, after a beep, the discs were presented for 70 seconds with only the last 60 seconds of responses recorded to avoid missing responses at the beginning. Each session began with a 2-minute period of dark adaptation and then fusion/alignment of the vertical and horizontal nonius lines (and also the fixation cross, if presented in the experiment).

The observer’s task was always to report the color of the fused binocular disc (Fig 2-1(a)); the color of the top and the bottom disc in the fused binocular percept when they both were the same color (Fig 2-1(b)); or the color of all four discs in the fused binocular percept when they all were the same color (Fig 2-1(c)). Pre-assigned button presses were used for the responses. The observer’s possible button-press responses were limited to the color of one of the chromaticities presented alone (e.g., “pink” or “blue-green” in Fig. 2-1) and neither.

Two dependent variables were determined for chromatic interocular-switch rivalry (except for experiment 7). One was the total dominance time (Alais, 2012), which was defined as the cumulative duration of perceiving each color. The other was the mean duration time (Alais, 2012), which was defined as the average duration of perceiving a color before a perceptual alternation occurred (excluded in experiment 2). They were both calculated from the raw data based on the button presses of each color recorded every 200 msec. The dependent variable used in experiment 7 was the chromaticity that gave, for example, a neither red nor green percept as described later.

2.3 Apparatus

All the stimuli were generated using an iMac computer and presented on a calibrated Sony color cathode-ray tube (CRT) display (GDM-F520). This display had a 1360 × 1024 pixel resolution at a refresh rate of 75Hz non-interlaced. The stimuli presented on the CRT were projected to the two eyes separately through a haploscope (Fig 1-3). During the experiments, observers were seated at a fixed optical distance of 1.1 m from the computer monitor, and a chinrest was used to minimize head movements and to center gaze on the monitor screen.

The CRT color display was calibrated before the experiments. The calibration included three steps for each phosphor: linearization of the radiance, measurement of the spectral emission, and measurement of the maximum luminance.

A radiometer (IL-1700, International Light Technologies) was used for the linearization of the radiance. 1000-step lookup tables were constructed to linearize each of R (red), G (green), and B (blue) guns of the color CRT. The energy values for each phosphor were measured in an ascending and descending sequence of the corresponding digital values, and then averaged.

The spectral emission was measured using a spectroradiometer (PR-670, Photo Research). The full spectrum of energy values was measured as a function of wavelength, which was used to calculate chromaticity coordinates (CIE 1931 and Judd).

A luminance meter (LS-100, Minolta) was used to measure the overall luminance of each phosphor at its maximum. The absolute luminance value was determined in units of cd/m^2.

2.4 Observers

Four observers participated in these experiments. Observer 1, the author, had prior experience with binocular rivalry experiments, and observer 2, 3 and 4 were naïve about the design and the purpose of all the experiments. Specifically, observers 1 and 2 participated in all the experiments, observer 3 participated in experiments 1, 2a, 3 and 4, and observer 4 participated in experiments 2b, 5, 6 and 7. A small number of observers was used so each observer could participate in many experiments. Therefore, for each single experiment, each observer's results could be assessed in comparison to the results from other experiments.

All observers had normal or corrected-to-normal visual acuity, and normal color vision (assessed by the Rayleigh Matching) and binocular vision (assessed by the Titmus Stereo Test). Consent forms were completed in accordance with the policy of the University of Chicago's Institutional Review Board.

CHAPTER 3

EXPERIMENT 1: RELATION BETWEEN STABLE COLOR PERCEPT DURING CHROMATIC INTEROCULAR-SWITCH RIVALRY AND TEMPORAL FREQUENCY OF SWAPPING

3.1 Rationale

The purpose of this experiment is to investigate the relation between the stable color percepts during chromatic interocular-switch rivalry (CISR) and the temporal frequency of swapping, and then to discover a range of temporal frequencies that induces relatively slow perceptual alternations between the two color percepts. The experimental question, therefore, is whether the perceptual resolution of CISR is influenced by the temporal frequency of swapping. If so, then both the total dominance and/or mean duration time of perceiving each color in the fused binocular percept should change when the discs are oscillating at different temporal frequencies.

When two equiluminant but chromatically rivalrous discs are presented dichoptically and swapped interocularly at a temporal frequency of 3.75Hz, a relatively long-lasting single color percept of the fused disc is perceived before a change to another color percept of a similar duration. The perceived colors are those of the two chromaticties presented with chromatic interocular-switch rivalry (CISR) (Fig. 1-12; Christiansen, D'Antona & Shevell, 2014). Therefore, the visual illusion of persisting colors suggests CISR would be a useful visual illusion to investigate how the visual system resolves perceptual ambiguity of object colors. However, 3.75Hz is the only temporal frequency tested by Christiansen *et al.* (2014), and whether this frequency is optimal for inducing long-duration color percepts during CISR is unclear. Thus, a wider range of temporal frequencies is tested to determine the one best suited for observing sustained color percepts.

Interocular switching of orthogonal gratings at a temporal frequency of 3 Hz (Fig. 1-6b) can result in perceptual alternations between the two orientations (Logothetis, Leopold & Sheinberg, 1996). This visual illusion is called interocular-switch rivalry, and it has been found to occur only within a limited range of temporal frequencies when two orthogonal gratings are swapped (Lee & Blake, 1999a). For example, CISR might give a fused percept (as in HFP), instead of distinct alternating color percepts, if the temporal frequency of swapping is too high. In this situation, the percept from each eye becomes the time average and the perceptual alternation of the fused percept would not occur. Therefore, it is important to determine whether the same limited range of temporal frequencies exists during CISR when equiluminant chromaticities of uniform discs are swapped interocularly.

3.2 Methods

A stimulus paradigm with one disc was tested. That is, one spatially homogeneous disc was presented in the center to each eye at a corresponding retinal location and then one fused disc was perceived (see Fig. 2-1(a)).

In this experiment, each session was composed of eight trials in a random sequence, and each trial tested one of the eight pairs of chromaticities (described in Chapter 2) at a given temporal frequency. Thus, CISR was repeated eight times in a random sequence with each disc alternating between two chromaticities. The task was to report the color of the disc in the fused binocular percept. The total dominance time of each color percept during each trial and the mean duration time of each color percept during that trial were calculated.

In separate sessions, four different square-wave temporal frequencies were tested: 3.13Hz, 3.75Hz, 4.69Hz and 6.25Hz. Each observer ran each frequency in each of five sessions on different days, so twenty sessions were completed in total.

3.3 Results

The total dominance time of each color percept is shown in Figure 3-1 (vertical axis) as a function of the chromaticities (horizontal axis) and the temporal frequency (open symbols). The chromaticities are grouped as variation along the *l*, *s* chromatic directions and then the two diagonal chromatic directions that varied both *l* and *s* simultaneously (left to right on the horizontal axis). Within each group, the chromaticities are arranged as pairs from low to high contrast along each chromatic direction. The temporal frequencies are indicated with various open symbols. The symbol color is the approximate color of the tested chromaticity. Each panel shows results for one observer. Figure 3-2 shows the mean dominance time of each color percept in the same format as the total dominance time in Figure 3-1.

Total dominance time and mean duration time are analyzed separately for each observer, by completing two-way analysis of variance (ANOVA). The two factors are the

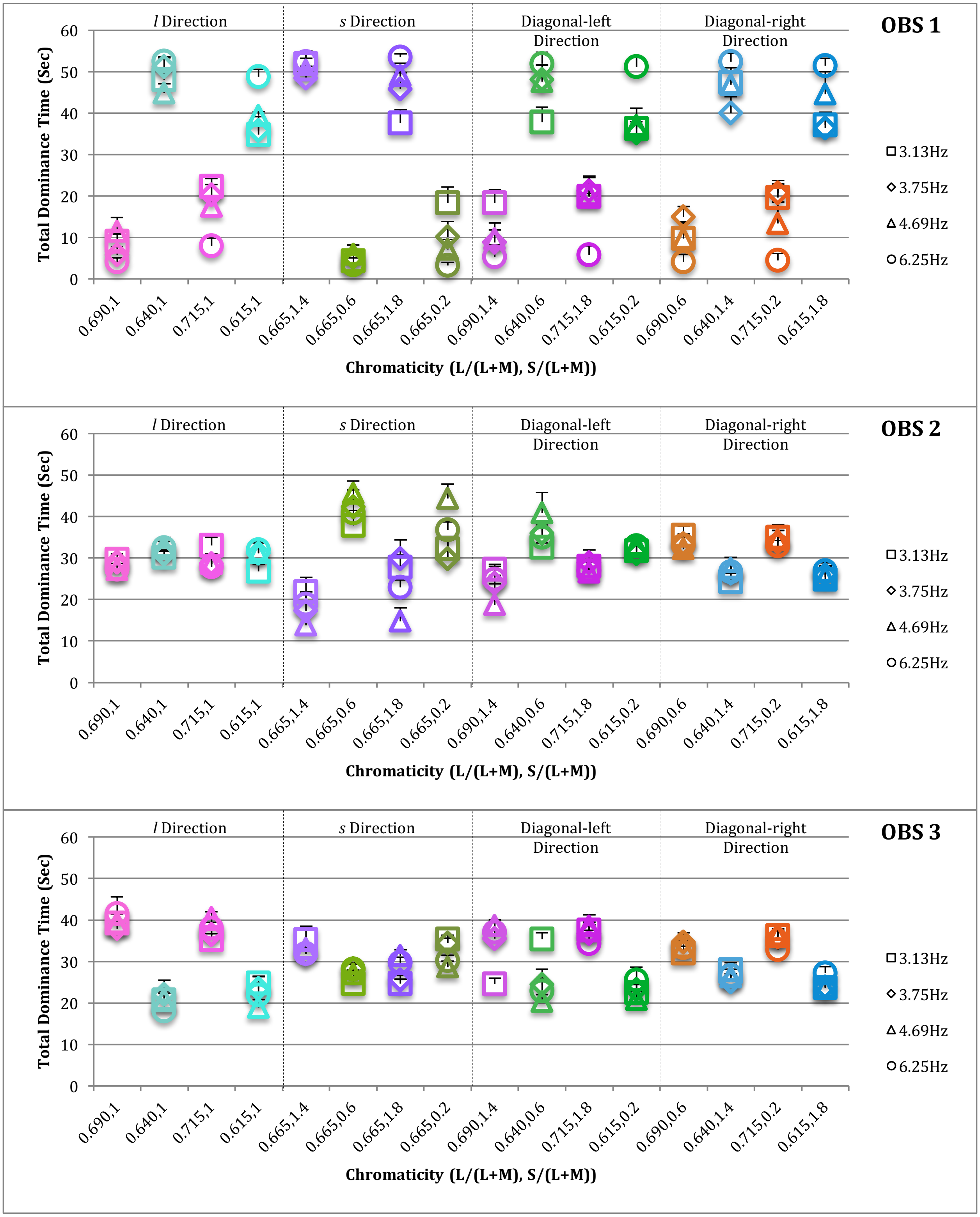

Figure 3-1. Total dominance time of sixteen (eight pairs of) color percepts at four temporal frequencies. The chromaticities on the horizontal axis are grouped as variation along the "*l* direction", "*s* direction", "diagonal-left direction" and "diagonal-right direction".

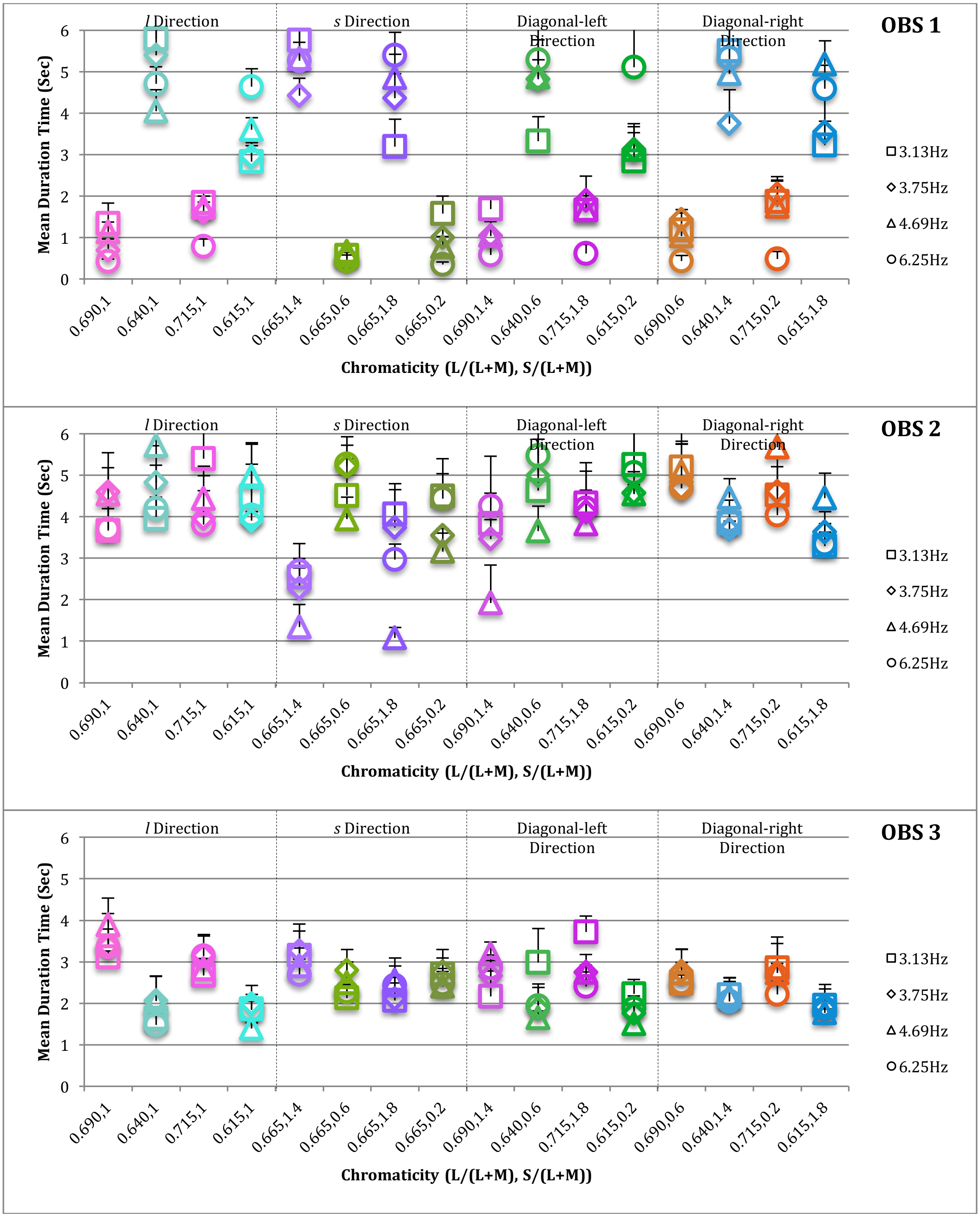

Figure 3-2. As Figure 3-1, but for mean duration time of sixteen (eight pairs of) color percepts at four temporal frequencies.

color (sixteen levels) and the temporal frequency (four levels).

For each observer, the results show that the total dominance time is not significantly different for the four temporal frequencies (see Table 3-1 and Figure 3-3). Further, there is no significant effect of frequency on the mean duration time (see Table 3-2 and Figure 3-4).

Table 3-1. Results of the total dominance time.

Observer	Temporal Frequency	Average Total Dominance Time	F (3, 256)	*p*
1	3.13 Hz	28.28 sec	0.24	0.86
	3.75 Hz	27.98 sec		
	4.69 Hz	28.40 sec		
	6.25 Hz	28.28 sec		
2	3.13 Hz	29.89 sec	0.01	0.99
	3.75 Hz	29.87 sec		
	4.69 Hz	29.81 sec		
	6.25 Hz	29.88 sec		
3	3.13 Hz	29.99 sec	0.06	0.97
	3.75 Hz	29.94 sec		
	4.69 Hz	29.82 sec		
	6.25 Hz	29.94 sec		

* Average total dominance time indicates the mean value of the total dominance time among sixteen (eight pairs of) color percepts (maximum time is 30 sec).

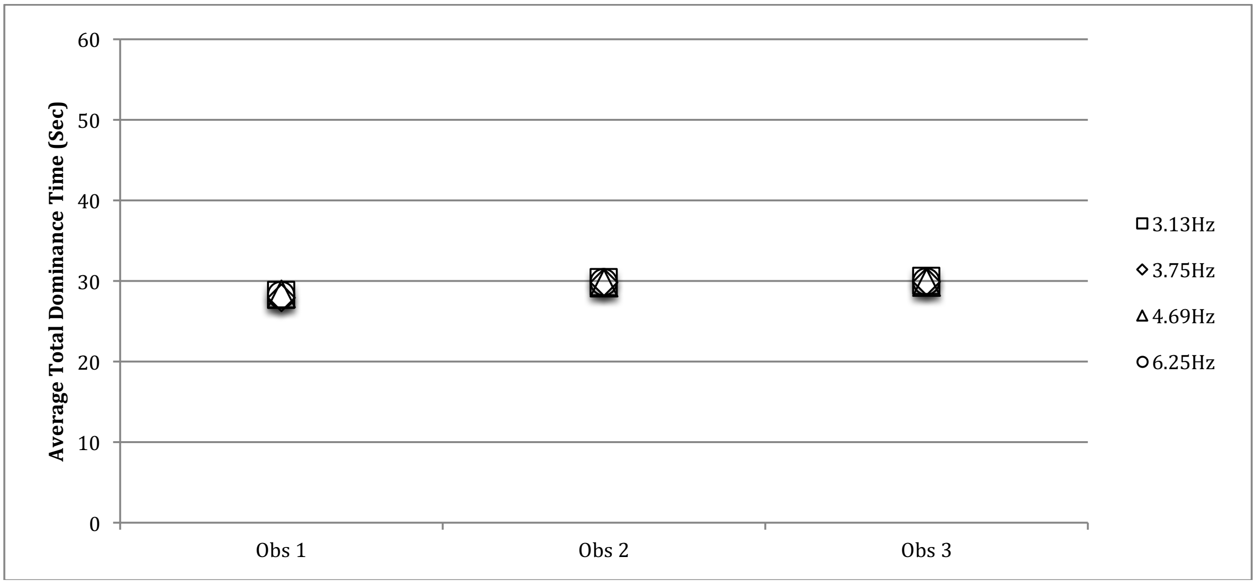

Figure 3-3. Average total dominance time at four temporal frequencies. Each open symbol indicates the average total dominance of the sixteen chromaticities at a given temporal frequency for each observer.

Table 3-2. Results of the mean duration time.

Observer	Temporal Frequency	Average Mean Duration Time	F (3, 256)	*p*
1	3.13 Hz	2.76 sec	1.60	0.19
	3.75 Hz	2.65 sec		
	4.69 Hz	2.85 sec		
	6.25 Hz	2.77 sec		
2	3.13 Hz	4.25 sec	1.96	0.12
	3.75 Hz	4.11 sec		
	4.69 Hz	3.92 sec		
	6.25 Hz	4.12 sec		
3	3.13 Hz	2.49 sec	1.88	0.13
	3.75 Hz	2.50 sec		
	4.69 Hz	2.43 sec		
	6.25 Hz	2.33 sec		

* Average Mean duration time indicates the mean value of the mean duration time among sixteen (eight pairs of) color percepts (maximum time is 30 sec).

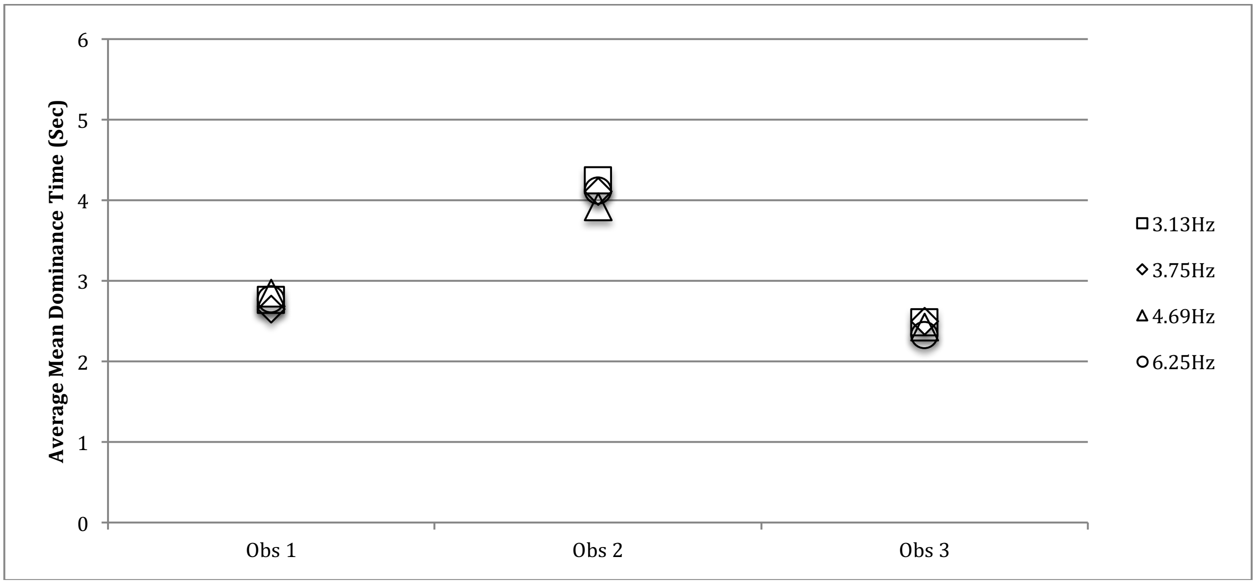

Figure 3-4. As Figure 3-3, but for the average mean duration time.

As expected, both the total dominance time and mean duration time show significant difference among the sixteen colors for each observer ($p < .001$). In addition, for both the total dominance time and mean duration time, there is a statistically significant interaction between the color and the temporal frequency for each observer ($p < .001$). It indicates that the effect of the temporal frequency depends on the color of the stimulus. This discovery is consistent with the temporal properties of the parvocellular (PC) and koniocellular (KC) pathways (Derrington & Lennie, 1984; Xu, Ichida, Allison, Boyd, Bonds & Casagrande, 2001), since chromatic neural signals are mainly processed in these two pathways (Lee, 2011).

Thus, there is not enough evidence to support the conclusion that the resolution of CISR varies, in general, over the range of tested temporal frequencies, though a significant interaction between temporal frequency and color of the stimulus implies temporal frequency depends on the color of the stimulus. Since 3.75 Hz has been demonstrated to be a temporal frequency inducing longer-lasting color percepts between the two chromaticities (Christiansen, D'Antona & Shevell, 2014), the results of this experiment further show that the other three temporal frequencies, 3.13Hz, 4.69Hz and 6.25Hz, induce similar color percepts during CISR.

For observer 1, both the total dominance time and mean duration time at 6.25Hz shows a more dominant distribution for only one of the two color percepts, compared to

Table 3-3. Results of the average time ratio.

Observer	Temporal Frequency	Average Total Dominance Time Ratio	Average Mean Duration Time Ratio
1	3.13 Hz	0.42	0.43
	3.75 Hz	0.42	0.42
	4.69 Hz	0.40	0.41
	6.25 Hz	0.30	0.31

* Average total dominance time ratio indicates the proportion between the cumulative duration of perceiving one color and the total duration of perceiving both colors in each pair.
** Average mean duration time ratio indicates the proportion between the mean duration of perceiving one color and the summed mean duration of perceiving both color in each pair

those at other temporal frequencies (see Table 3-3). That is, both the average total dominance time and mean duration time ratios at 6.25 Hz are smaller compared to the other temporal frequencies. In addition, the color percept sometimes appears to be fused between the two chromaticities if the temporal frequency of oscillation is 6.25 Hz, which is unfavorable for inducing longer-lasting color percepts during CISR. Therefore, 6.25Hz is removed from the list of the tested temporal frequencies, and only 3.13Hz, 3.75Hz and 4.69Hz are used to induce stable color percepts in the later experiments.

CHAPTER 4

EXPERIMENT 2: CONTRIBUTION OF GROUPING TO THE RESOLUTION OF CHROMATIC INTEROCULAR-SWITCH RIVALRY

4.1 Rationale

The purpose of this experiment is to investigate whether grouping contributes to the resolution of chromatic interocular-switch rivalry (CISR). In part (a), grouping is assessed by aligning two discs vertically, one above the other, in the central visual field. If grouping makes a contribution to color perception, then the total dominance time of simultaneously perceiving two spatially separated discs of the same color would be greater than the total dominance time predicted from the independent probabilities of perceiving each of the discs with that color. In part (b), grouping is assessed by using four discs, each presented in one quadrant of a square. Applying similar logic, if grouping contributes to color perception, then the total dominance time of simultaneously perceiving four spatially separated discs of the same color would be greater than the total dominance time predicted from the independent probabilities of perceiving the color of each disc.

As discussed previously, one accepted view of binocular rivalry is “stimulus” rivalry or pattern competition theory. It posits that binocular rivalry arises from a competition between neural stimulus representations rather than a competition between the two eyes' signals to the brain. Two well-known visual phenomena, interocular-switch rivalry (Logothetis, Leopold & Sheinberg, 1996) and interocular grouping (Kovas, Papathomas, Yang & Feher, 1996), suggest that there must be higher-level mechanisms contributing to the percepts that are experienced during binocular rivalry.

One of these mechanisms, grouping, has been shown to promote dominance during binocular rivalry (Alais & Blake, 1998, 1999; Kim, Blake & Palmeri, 2006; Kovas, Papathomas, Yang & Feher, 1996; Silver & Logothetis, 2004; Sobel & Blake, 2002; Suzuki & Grabowecky, 2002). However, these grouping studies employ either a stimulus pattern of achromatic gratings (Alais & Blake, 1998, 1999; Sobel & Blake, 2002; Suzuki & Grabowecky, 2002) or dot arrays (Silver & Logothetis, 2004). Although grouping contributes to binocular color rivalry (Kim, Blake & Palmeri, 2006; Kovas, Papathomas, Yang & Feher, 1996), previous studies used only conventional binocular rivalry (no interocular switching). No line of research has explored the contribution of grouping to the perception of colors during binocular rivalry.

4.2 Methods

Different stimulus paradigms were used. In part (a), a stimulus paradigm with two discs was tested. That is, two spatially homogeneous discs were aligned vertically in each eye at the corresponding retinal locations so that two fused discs were perceived (Fig. 4-1(a)). Based on this paradigm, two additional control conditions were tested with one disc alone in either the top or the bottom location while the other disc was removed. Thus, one fused disc was perceived either in the top or the bottom location (see Fig. 4-1(b) and(c)). In part (b), a stimulus paradigm with four discs was tested. That is, four spatially

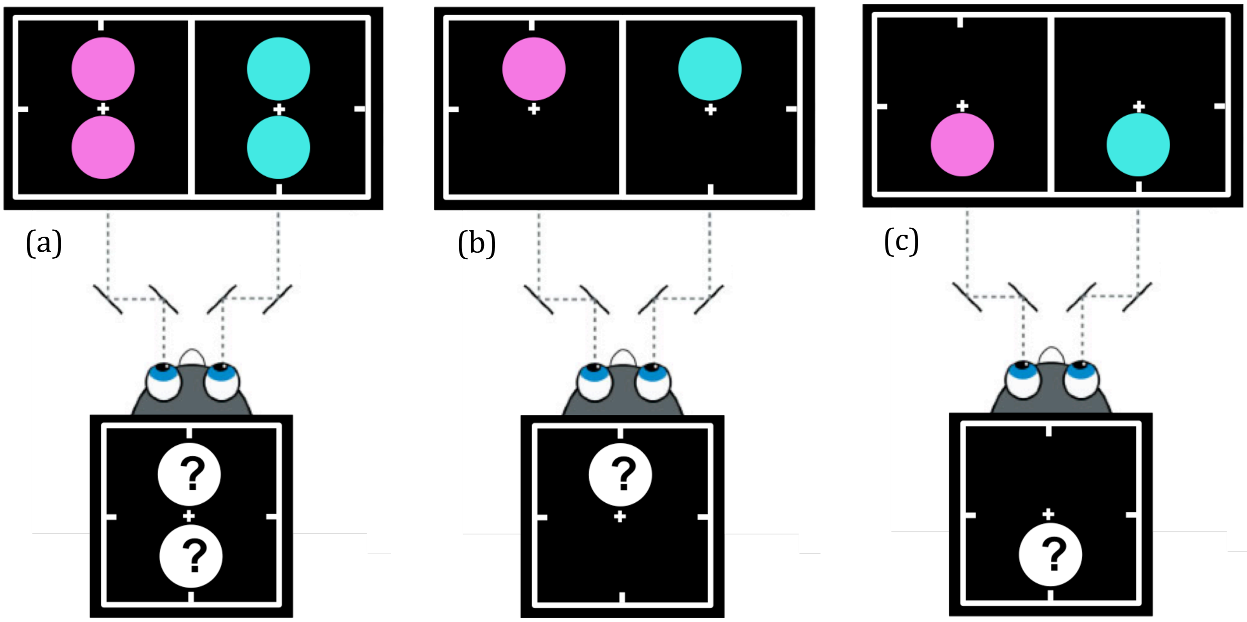

Figure 4-1. Stimulus paradigms for experiment 2a. (a) Both, (b) only the top, or (c) only the bottom discs are presented to each eye.

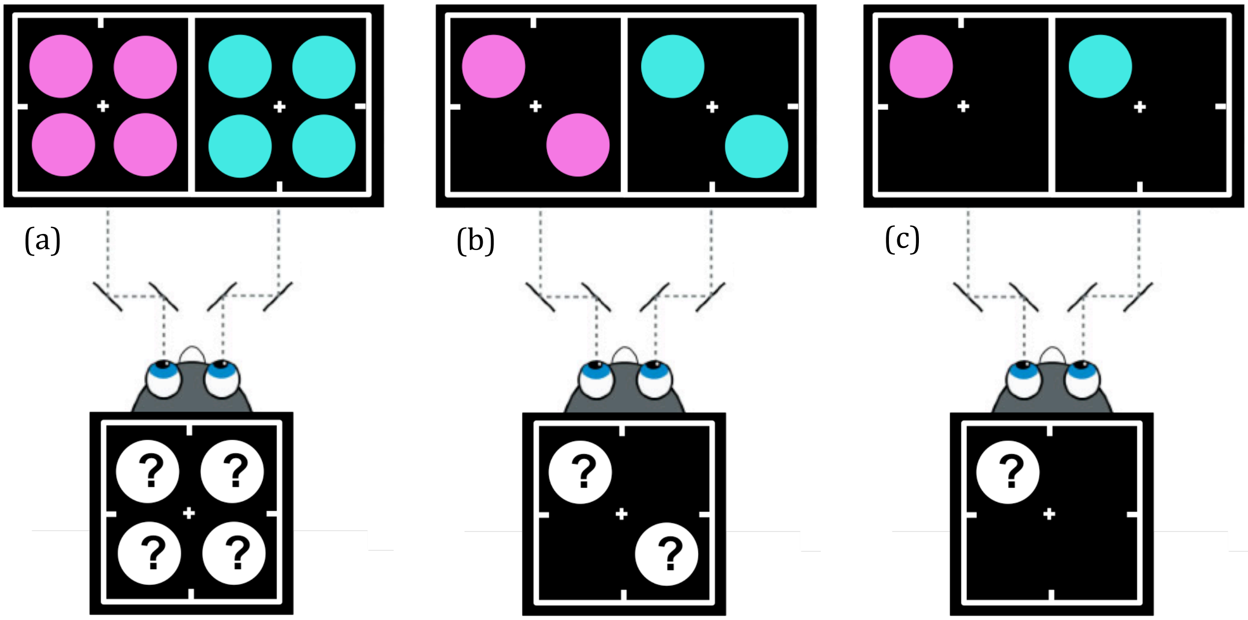

Figure 4-2. Stimulus paradigms for experiment 2b. (a) All four, (b) only diagonal-left (top-left and bottom-right), or (c) only the top-left discs are presented to each eye.

homogeneous discs were presented to each eye within the quadrants of a square. Then four fused discs were perceived (Fig. 4-2(a)). Based on this paradigm, six more control conditions also were tested with either two diagonal discs alone or only one disc alone in one of the quadrants. Thus, two or one fused disc was perceived, either in the diagonal direction or in a corner of the square (see Fig. 4-2(b) and (c)). All the discs in the stimulus paradigms oscillated at the same temporal phase within each eye.

Due to different stimulus paradigms, the predicated total dominance times in the two- and four-disc stimulus were calculated separately. In part (a), since only one spatially homogeneous disc was presented in the control conditions, either above the fixation cross (Fig. 4-2(b)) or below it (Fig. 4-2(c)), the independent probability of each color at each spatial location (top or bottom) was the ratio between the total dominance time of that color at that location and the total presentation time (60 seconds). Therefore, the joint probability of both discs simultaneously having each color, based on independence, was the product of the two independent probabilities of the same color at the two locations (top and bottom). The predicted total dominance time of each color for both discs, then, was the product of the joint probability and 60 seconds.

In part (b), when two spatially homogeneous discs were presented diagonally in the control conditions, either along a diagonal-left (135°) direction (Fig. 4-2(b)) or a diagonal-right (45°) direction, the two-disc independent probability of each color along each diagonal direction was the ratio between the total dominance time of that color at that direction and 60 seconds. With only one disc presented in the control conditions (e.g., the top-left disc in Fig. 4-2(c)), the independent probability of each color in each corner was the ratio between the total dominance of that color and 60 seconds. Thus, one joint probability of each color based on two-disc independence was the product of the two independent probabilities of the same color along the two diagonal directions. The other joint probability based on four-disc independence was the product of the four independent probabilities in each corner location. The predicated independent total dominance times, therefore, were the product of the joint probabilities and 60 seconds in both parts.

Similarly, the experimental procedure depended on the stimulus paradigm in this experiment. In part (a), each session was composed of six trials in a random sequence, and each trial tested one of the two pairs of chromaticities (described in Chapter 2) in each of the three experimental conditions (see Fig. 4-1(a) two discs, (b) only the top disc, and (c) only the bottom disc) at a given temporal frequency. In part (b), each session was composed of fourteen trials in a random sequence, and each trial tested one of the two pairs of chromaticities (same as part (a)) in each of the seven experimental conditions (see Fig 4-2(a) four discs, (b) diagonal-left discs and the other (unshown) diagonal-right discs, and (c) top-left disc and other three (unshown) corner discs). In other words, CISR was repeated either six times in part (a) or fourteen times in part (b) randomly with each disc alternating between two chromaticities. The task was to report the color of the disc (if one disc was perceived) or the color of all the discs simultaneously (if multiple discs were perceived to be the same color) in the fused binocular percept. The total dominance time of each color percept during each trial was the dependent measure for the experiment.

In separate sessions, three different square-wave temporal frequencies were tested: 3.13Hz, 3.75Hz and 4.69Hz. Each observer ran each frequency in each of five sessions on different days, so fifteen sessions were completed in total for each part.

4.3 Results

The total dominance time of each color percept in part (a) is shown in Figure 4-3 (vertical axis) as a function of the chromaticities (horizontal axis) and the temporal frequency (open symbols). The chromaticities are grouped as “two discs measured”, “top disc alone”, “bottom disc alone” and “two disc expected” (left to right along the horizontal axis). Within each group, the chromaticities are arranged as one pair along the l and s chromatic directions [(l = 0.715, s = 1.0) & (l = 0.615, s = 1.0) and (l = 0.665, s = 1.8) & (l = 0.665, s = 0.2)]. The temporal frequencies are indicated with various open symbols, with solid lines indicating experimental measurements and dotted lines indicating theoretical predictions. The symbol color is the approximate color of the tested chromaticity in the experimental conditions. Each panel shows results for one observer. Figure 4-4 shows the total dominance time of each color percept in part (b) in a similar format as the total dominance time in Figure 4-3, but the chromaticities are grouped as “four (discs) measured”, “diagonal-left (discs)”, “diagonal-right (discs)”, “top-left (disc) alone”, “top-right (disc) alone”, “bottom-left (disc) alone”, “bottom-right (disc) alone”, “four (discs) expected (based on diagonal discs)” and “four (discs) expected (based on corner discs)” (from left to right along the horizontal axis).

The total dominance times are analyzed separately for each observer at each temporal frequency in each part, by completing two-way analysis of variance (ANOVA). One factor is the color (four levels) and the other is the selected experimental condition (two levels in part (a): “two discs measured” and “two discs expected”; three levels in part (b): “four discs measured”, “four discs expected (based on diagonal discs)” and “four discs expected (based on corner discs)”).

For each observer in part (a), the results show that the total dominance time of perceiving two spatially separated discs having the same color is significantly greater than predicted by independence, at each of the three temporal frequencies (see Table 4-1 and

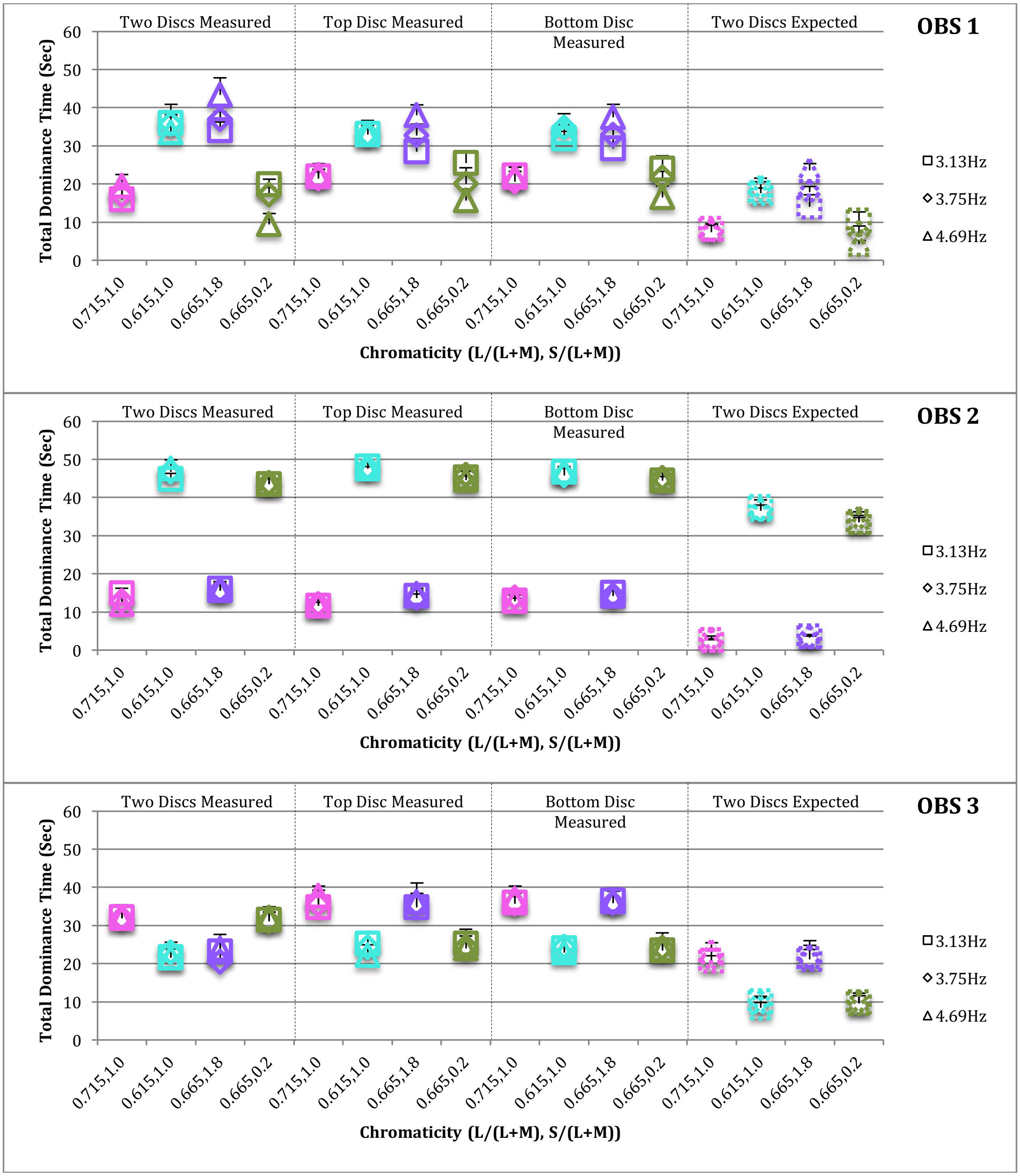

Figure 4-3. Total dominance time of four (two pairs of) color percepts at three temporal frequencies when two discs are viewed simultaneously. The chromaticities are grouped as "two discs measured", "top disc alone", "bottom disc alone" and "two discs expected". Within each group, the chromaticities (*l*, *s*) are arranged as (0.715, 1.0), (0.615, 1.0), (0.665, 1.8) and (0.665, 0.2). Open symbols with solid lines indicate experimental measurements and open symbols with dotted lines indicate theoretical predictions.

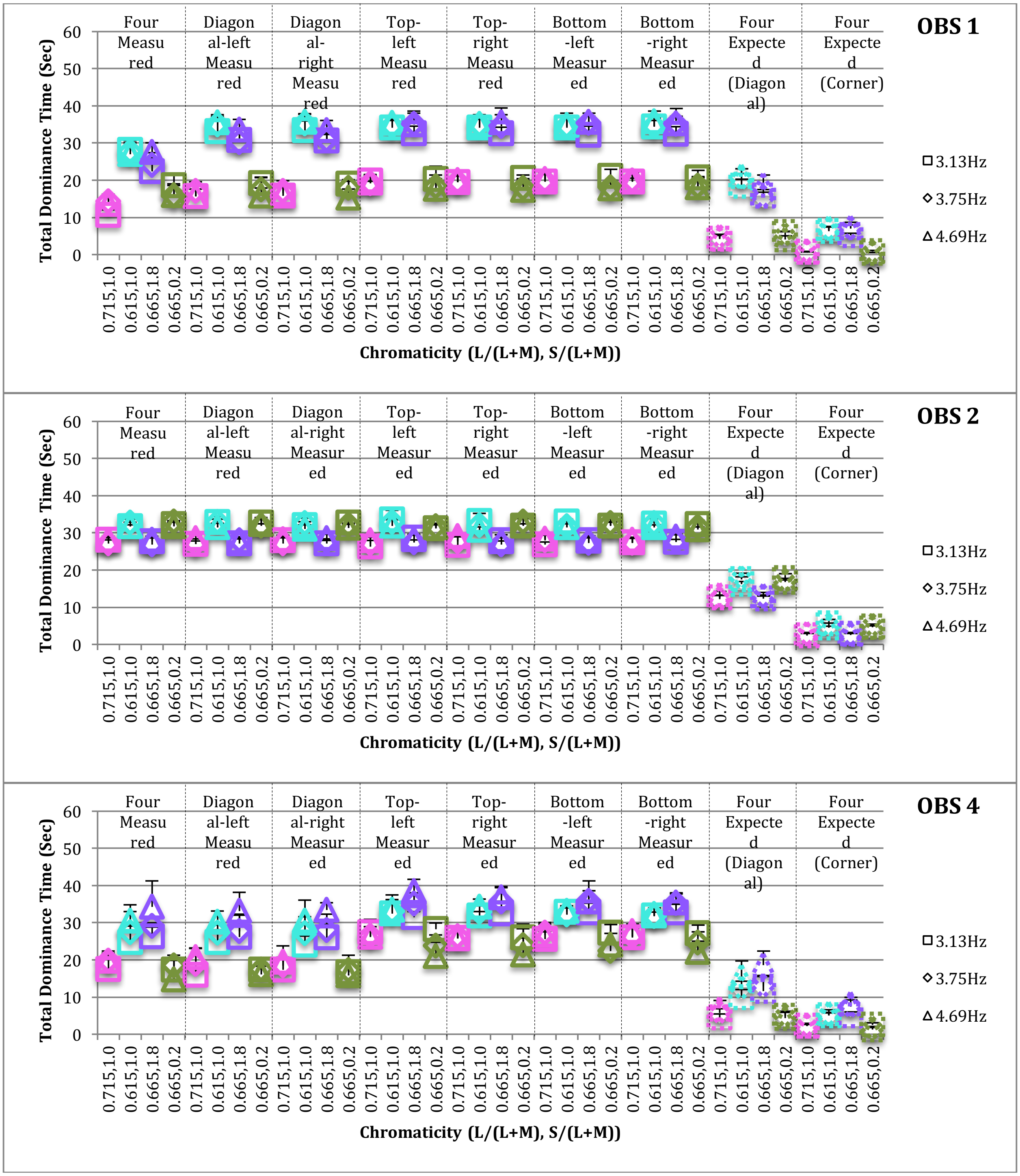

Figure 4-4. As Figure 4-3, but chromaticities are grouped as “four (discs) measured”, “diagonal-left (discs)”, “diagonal-right (discs)”, “top-left (disc) alone”, “top-right (disc) alone”, “bottom-left (disc) alone”, “bottom-right (disc) alone”, “four (discs) expected (based on diagonal discs)”, “four (discs) expected (based on corner discs)”.

Table 4-1. Results of the total dominance time in part (a)

Observer	Temporal Frequency	Experimental Condition	Average Total Dominance Time	F (1, 32)	*p*
1	3.13 Hz	Two discs measured	26.43 sec	205.6	<.001
		Two discs expected	12.52 sec		
	3.75 Hz	Two discs measured	26.67 sec	398.9	<.001
		Two discs expected	12.90 sec		
	4.69 Hz	Two discs measured	26.42 sec	159.8	<.001
		Two discs expected	13.60 sec		
2	3.13 Hz	Two discs measured	29.77 sec	535.3	<.001
		Two discs expected	19.25 sec		
	3.75 Hz	Two discs measured	29.73 sec	272.1	<.001
		Two discs expected	19.26 sec		
	4.69 Hz	Two discs measured	29.73 sec	297.3	<.001
		Two discs expected	19.12 sec		
3	3.13 Hz	Two discs measured	27.07 sec	199.6	<.001
		Two discs expected	15.44 sec		
	3.75 Hz	Two discs measured	26.57 sec	124.1	<.001
		Two discs expected	15.54 sec		
	4.69 Hz	Two discs measured	27.31 sec	117.6	<.001
		Two discs expected	15.76 sec		

* Average total dominance time indicates the mean value of the total dominance time among four (two pairs of) color percepts (maximum time is 30 sec).

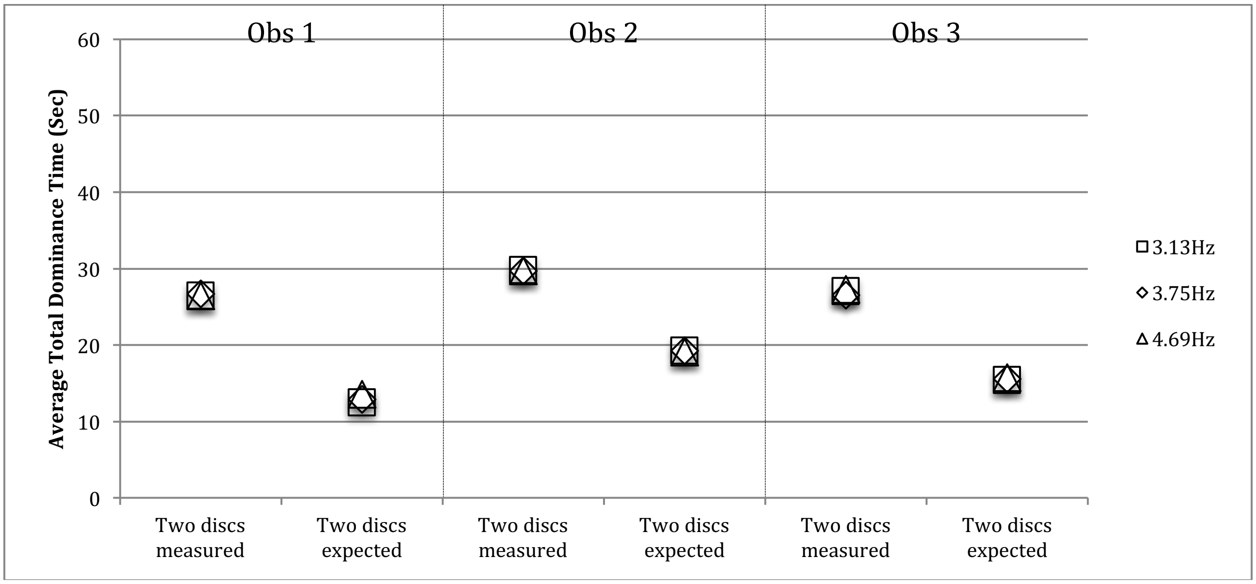

Figure 4-5. Average total dominance time when two discs are measured or expected. Each open symbol indicates the average total dominance of the four chromaticities at a given temporal frequency for each observer.

Figure 4-5). Furthermore, there is a statistically significant interaction between the color and the selected experimental conditions for observer 1 and 3 at 3.13 Hz, 3.75 Hz and 4.69 Hz, observer 2 at 3.13 Hz (*p* < .05). This indicates that the effect of the deviation from independence depends on the particular colors used. Overall, the measurements clearly

Table 4-2. Results of the total dominance time in part (b)

Observer	Temporal Frequency	Experimental Condition	Average Total Dominance Time	F (2, 48)	*p*
1	3.13 Hz	Four discs measured	19.95 sec	389.9	<.001
		Four discs expected^{2}	11.11 sec		
		Four discs expected^{4}	3.25 sec		
	3.75 Hz	Four discs measured	20.43 sec	342.3	<.001
		Four discs expected^{2}	11.43 sec		
		Four discs expected^{4}	3.69 sec		
	4.69 Hz	Four discs measured	21.00 sec	311.0	<.001
		Four discs expected^{2}	12.04 sec		
		Four discs expected^{4}	3.88 sec		
2	3.13 Hz	Four discs measured	29.93 sec	3600.8	<.001
		Four discs expected^{2}	15.03 sec		
		Four discs expected^{4}	3.88 sec		
	3.75 Hz	Four discs measured	29.89 sec	2397.7	<.001
		Four discs expected^{2}	15.00 sec		
		Four discs expected^{4}	3.81 sec		
	4.69 Hz	Four discs measured	29.89 sec	5387.4	<.001
		Four discs expected^{2}	14.90 sec		
		Four discs expected^{4}	3.76 sec		
4	3.13 Hz	Four discs measured	21.44 sec	198.2	<.001
		Four discs expected^{2}	7.72 sec		
		Four discs expected^{4}	3.71 sec		
	3.75 Hz	Four discs measured	23.65 sec	357.0	<.001
		Four discs expected^{2}	8.96 sec		
		Four discs expected^{4}	4.07 sec		
	4.69 Hz	Four discs measured	24.77 sec	165.5	<.001
		Four discs expected^{2}	11.34 sec		
		Four discs expected^{4}	4.37 sec		

* Average total dominance time indicates the mean value of the total dominance time among four (two pairs of) color percepts (maximum time is 30 sec).

** Four discs expected^{2} indicates the total dominance time of the four discs expected based on two diagonal discs, and four discs expected^{4} indicates the total dominance time of the four discs expected based on four corner discs.

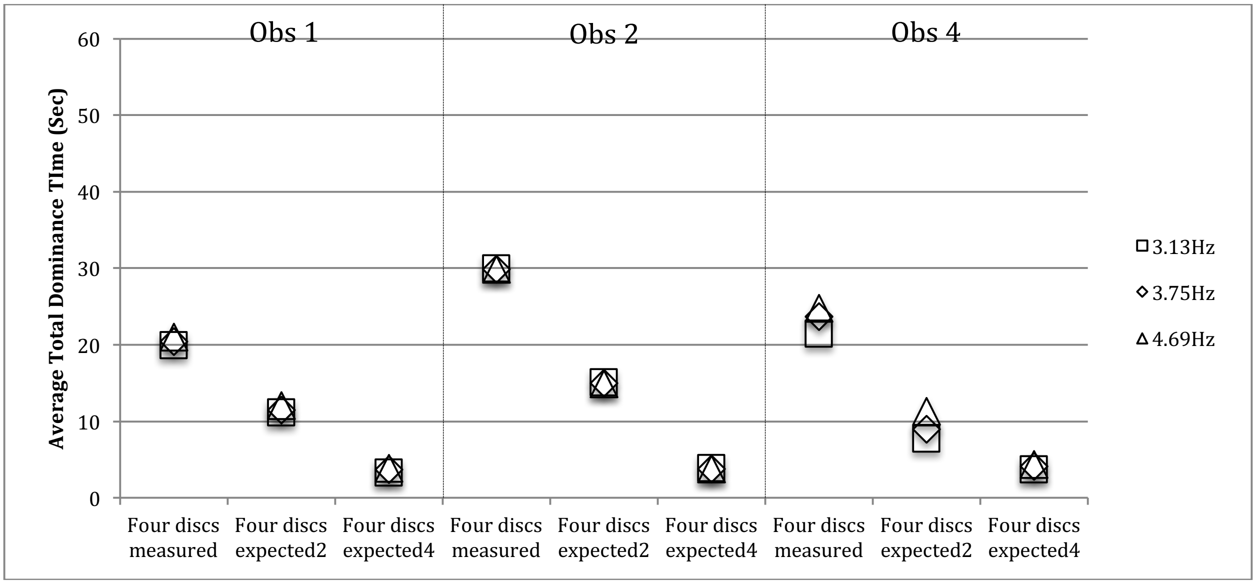

Figure 4-6. As Figure 4-5, but when four discs are measured, expected based on two diagonal discs, or expected based on four corner discs.

differ from the independence conditions, which demonstrates that grouping contributes to the resolution of chromatic interocular-switch rivalry when two discs are viewed simultaneously.

For each observer in part (b), similar results also show that the total dominance time of perceiving four spatially separated discs having the same color is significantly different across the three experimental conditions, at each of the three temporal frequencies (see Table 4-2 and Figure 4-6). Post-hoc Fisher-Hayter tests reveal that both the predicted total dominance times of four discs based on the two diagonal discs and four corner discs are significantly lower than the total dominance time of perceiving all four discs of the same color simultaneously for all the observers at all three temporal frequencies ($p < .05$). Therefore, the total dominance time of perceiving four spatially separated discs having the same color is significantly greater than predicted by each of the two possible independent representations of color, at each of the three temporal frequencies. Furthermore, there is a statistically significant interaction between the color and the selected experimental condition for observers 1 and 2 at 3.13 Hz, 3.75 Hz and 4.69 Hz and observer 4 at 4.69 Hz ($p < .05$). This indicates that the deviation from independence depends on stimulus color. Overall, grouping is shown to contribute to the resolution of CISR when four discs are viewed simultaneously.

In sum, the results of both parts indicate that grouping contributes to resolving CISR. That is, "stimulus"-based neural ambiguity induced by CISR is resolved in part by a higher–level grouping mechanism.

4.4 Supplementary Experiment

The purpose of this supplementary experiment is to check whether an observer responded based on a reliable percept when grouped discs oscillated between distinct pairs of chromaticities. If an observer's responses reflect reliable percepts, then the total dominance time of simultaneously perceiving two spatially separated discs of the same color are predicted to be low (e.g., close to zero) if the top and bottom discs never have the same physical chromaticity. If so, this also would show that observers do not respond randomly or without paying attention to the percepts in previous experiments.

The stimulus paradigm with two discs was used in this supplementary experiment (Fig 2-1(b)). That is, two discs were aligned vertically, one above the other, to each eye. One disc alternated over time between two equiluminant chromaticities along one cardinal chromatic direction (e.g., l = L/(L+M)), and the other disc alternated along the other cardinal chromatic direction (e.g., s = S/(L+M)). The time-average chromaticity was always equal-energy-spectrum (EES) "white" for both discs. Thus, two pairs of chromaticities (l, s) were tested: (0.715, 1.0) & (0.615, 1.0) in the top disc and (0.665, 1.8) & (0.665, 0.2) in the bottom disc. The observer's task was to report when the color of the top disc was the same as the bottom disc. In a counterbalanced design, the chromaticities in the top and bottom discs were switched in separate trials.

The total dominance time perceiving both discs with the same color is shown in Figure 4-7 (vertical axis) for each observer (horizontal axis), with the temporal frequency indicated by symbol shape (open symbols). Here, the total dominance time is averaged from the two experimental conditions with either the top or the bottom disc oscillating along the *l* chromatic direction.

The total dominance time is analyzed separately for each observer, by completing a two-sample t test. One sample is the total dominance time in this supplemental experiment, in which the two discs oscillated between different pairs of chromaticities; the other is the total dominance time in experiment 2(a), in which the two discs oscillated between the same pair of chromaticities.

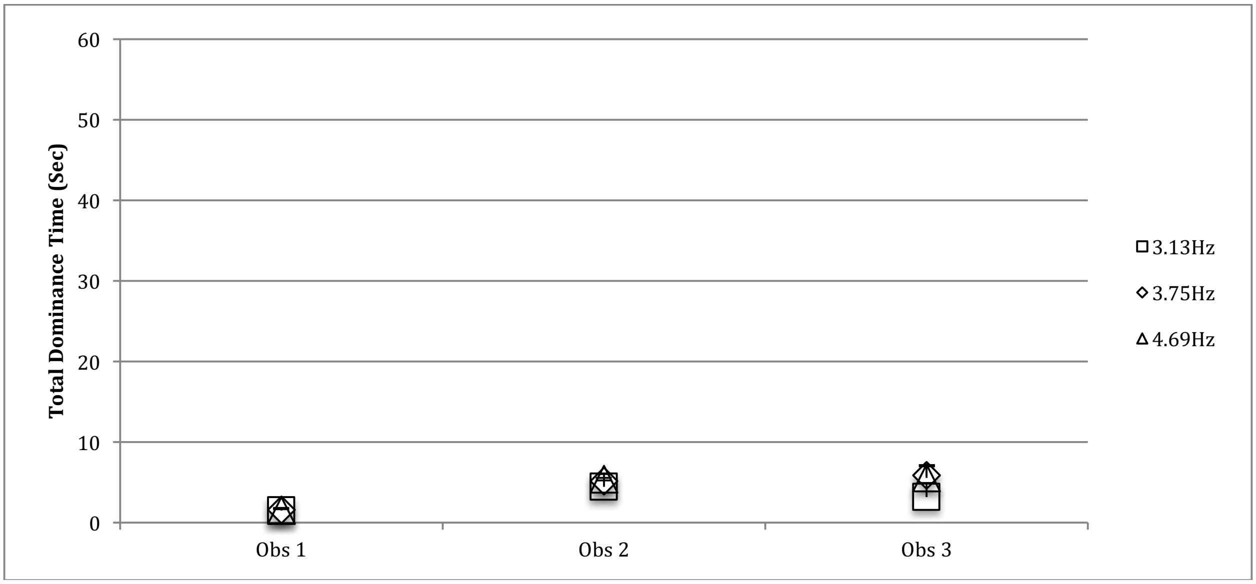

Figure 4-7. Total dominance time of supplementary experiment, at three temporal frequencies.

Table 4-3. Results of the supplementary experiment

Observer	Temporal Frequency	Experimental Condition	Total Dominance Time	t (8)	*p*
1	3.13 Hz	Different chromaticities	1.54 sec	54.37	<.001
		Same chromaticities	26.43 sec		
	3.75 Hz	Different chromaticities	1.59 sec	283.37	<.001
		Same chromaticities	26.67 sec		
	4.69 Hz	Different chromaticities	1.50 sec	60.26	<.001
		Same chromaticities	26.42 sec		
2	3.13 Hz	Different chromaticities	4.47 sec	144.85	<.001
		Same chromaticities	29.77 sec		
	3.75 Hz	Different chromaticities	5.19 sec	146.55	<.001
		Same chromaticities	29.73 sec		
	4.69 Hz	Different chromaticities	5.43 sec	86.88	<.001
		Same chromaticities	29.73 sec		
3	3.13 Hz	Different chromaticities	3.16 sec	21.70	<.001
		Same chromaticities	27.07 sec		
	3.75 Hz	Different chromaticities	5.90 sec	26.11	<.001
		Same chromaticities	26.57 sec		
	4.69 Hz	Different chromaticities	5.53 sec	48.07	<.001
		Same chromaticities	27.31 sec		

* "Different chromaticities" indicate two discs oscillating between different pairs of chromaticities in the supplementary experiment, and "same chromaticities" indicates two discs oscillating between same pairs of chromaticities in experiment 2(a).

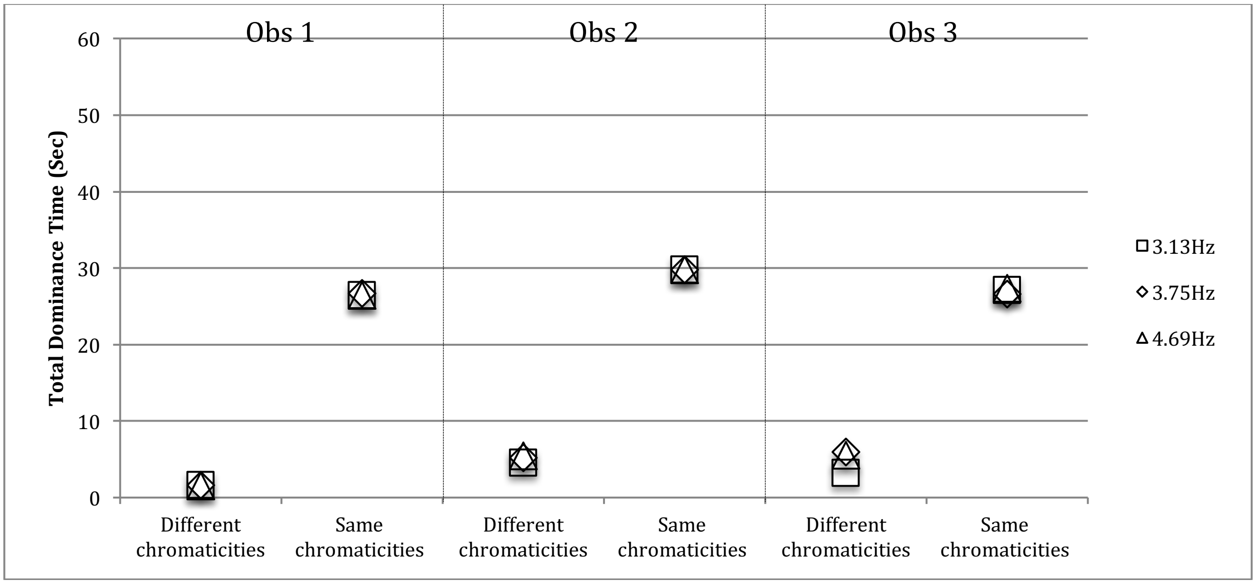

Figure 4-8. Total dominance time of supplementary experiment and experiment 2(a), at three temporal frequencies.

For each observer, the results show that the total dominance time in the supplemental experiment always is near zero and, of course, significantly lower than the total dominance time when two discs have the same pair of chromaiticicities (experiment 2(a)). This holds at each of the three temporal frequencies (see Table 4-3 and Figure 4-8).

Thus, the resolution of CISR for each observer is not based on random responding or on viewing only one of the two discs. Instead, the results are consistent with a reliable report of the color percept of both discs.

CHAPTER 5

EXPERIMENT 3: CONTRIBUTION TO GROUPING OF OBJECTS FROM SYNCHRONIZED TEMPORAL FREQUENCIES IN CHROMATIC INTEROCULAR-SWITCH RIVALRY

5.1 Rationale

The purpose of this experiment is to investigate the contribution of temporal phase synchrony to grouping of objects at a common temporal frequency during chromatic interocular-switch rivalry (CISR). Grouping is assessed by aligning two discs vertically, one above the other, in each eye. If temporal phase synchrony affects grouping, then both the total dominance and mean duration times of simultaneously perceiving two spatially separated discs of the same color would depend on the temporal phase differences between the two discs.

Previous research has shown that spatially distributed stimulus features can be simultaneously dominant during binocular rivalry when those features are perceptually grouped together as a coherent form, including common luminance contrast (Silver & Logothetis, 2004), collinear contours and correlated contrast modulations (Alais & Blake,

1999) and coherent motion (Alais, & Blake, 1998; Silver & Logothetis, 2004; Sobel & Blake, 2002). As a result, simultaneous dominance is promoted during binocular rivalry. However, all these grouping features are luminance-based and cannot be defined in the equiluminant uniform fields during CISR. A possible feature affecting resolution of CISR is the temporal chromatic structure of the grouped objects.

One simple way of manipulating the temporal chromatic structure is to introduce a temporal phase difference between the grouped objects presented with square wave flicker. If grouping depends on a common phase, then the grouped objects flickering at different temporal phase would not form a coherent group. Studies in perceptual binding and segmentation provide some interesting clues to the role of temporal phase in grouping. For example, Usher and Donnelly (1998) discovered that binding is enhanced when a set of dots is presented at the same time as another set of dots, compared to if two sets of dots are presented with temporal asynchrony. Similar effects are found with temporal synchrony in perceptual binding (Blake & Yang, 1997), though opposite effects were uncovered with temporal asynchrony in perceptual segmentation (Lee & Blake, 1999b; Motoyoshi, 2004). Other lines of research show that temporal asynchrony is unrelated to the processes of perceptual segmentation (Fahle & Koch, 1995; Kiper, Gegenfurtner & Movshon, 1996).

5.2 Methods

A stimulus paradigm with two discs was tested. That is, two spatially homogeneous discs were aligned vertically in each eye at the corresponding retinal locations so that two fused discs were perceived (see Fig. 2-1(b)).

Based on this paradigm, the top disc oscillated at 0°, 90°, 180° or 270° temporal phase difference relative to the bottom disc within each eye. In the left eye, for example, 0° phase difference (called "in phase") means the top and bottom discs were always presented with the same chromaticities, and 180° phase difference (called "out of phase") means the top and bottom discs were always presented with two different chromaticities. 90° and 270° phase differences were designed to remove synchrony of rectified chromatic changes. At the same time, all discs in the right eye oscillated with the same temporal phase difference as the left eye but with opposite chromaticity. Thus, four experimental conditions were tested (Fig. 5-1).

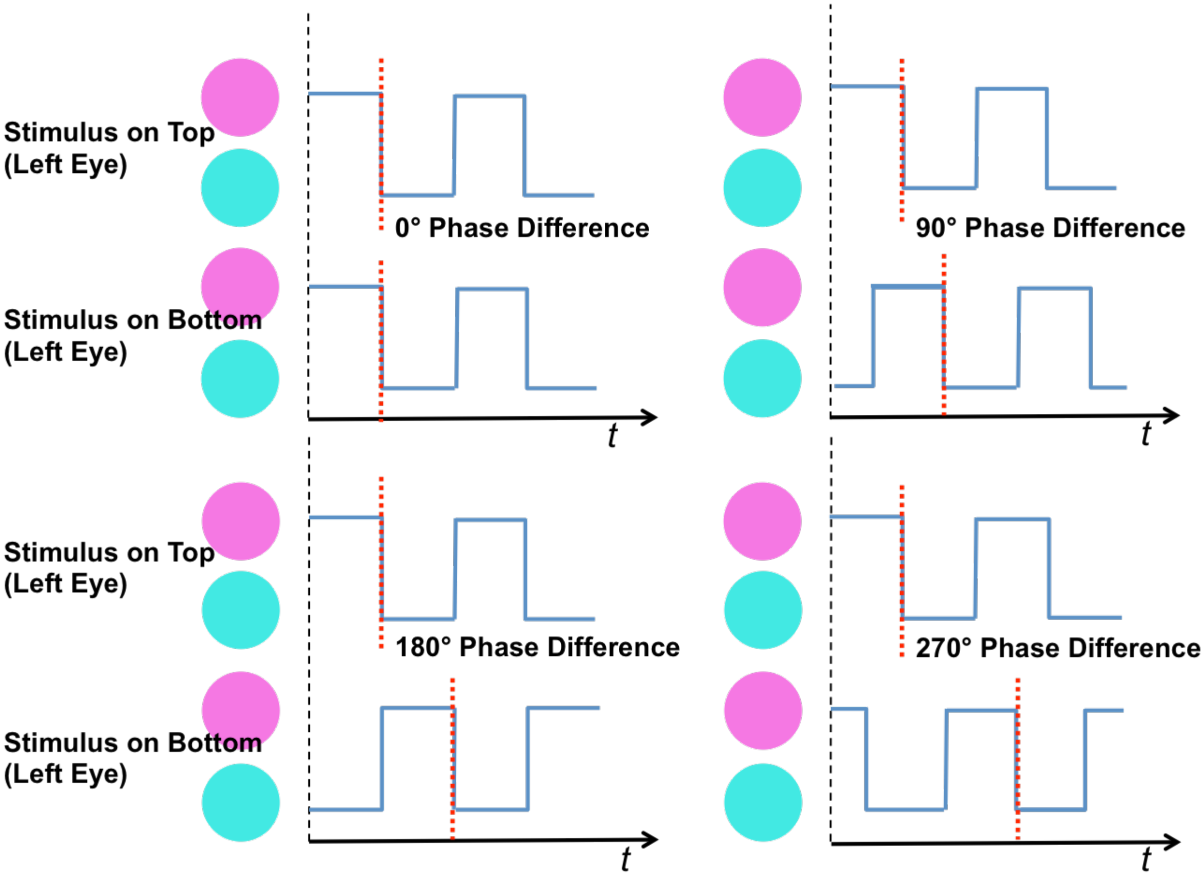

Figure 5-1. Experimental conditions in experiment 3. Top disc oscillates at 0°, 90°, 180° or 270° temporal phase difference relative to the bottom disc in each eye (only left eye shown). Red dash lines indicate the phase difference between the top and bottom discs.

In this experiment, each session was composed of eight trials in a random sequence, and each trial tested one of the two pairs of chromaticites (described in Chapter 2) in each of the four experimental conditions (see Fig. 5-1) at a given temporal frequency. In other words, CISR was repeated eight times, randomly ordered, with each disc alternating between two chromaticities. The task was to report the color of the top and bottom discs in the fused binocular percept. The total dominance time and the mean duration time of each color percept during each trial was calculated.

In separate sessions, three different square-wave temporal frequencies were tested: 3.13Hz, 3.75Hz and 4.69Hz. Each observer ran each frequency in each of five sessions on different days, so fifteen sessions were completed in total.

5.3 Results

The total dominance time of each color percept is shown in Figure 5-2 (vertical axis) as a function of the chromaticities (horizontal axis) and the temporal frequency (open symbols). The chromaticities are grouped as "0° phase difference", "90° phase difference", "180° phase difference" or "270° phase difference" (left to right along the horizontal axis). Within each group, the chromaticities are arranged as one pair along the l and s chromatic directions [(l = 0.715, s = 1.0) & (l = 0.615, s = 1.0) and (l = 0.665, s = 1.8) & (l = 0.665, s = 0.2)]. The temporal frequencies are indicated with various open symbols. The symbol color is the approximate color of the tested chromaticity. Each panel shows results for one observer. Figure 5-3 shows the mean duration time of each color percept in the same format as the total dominance time in Figure 5-2.

Total dominance time is on a different scale than the mean duration time, so they are analyzed separately for each observer at each temporal frequency, with a two-way

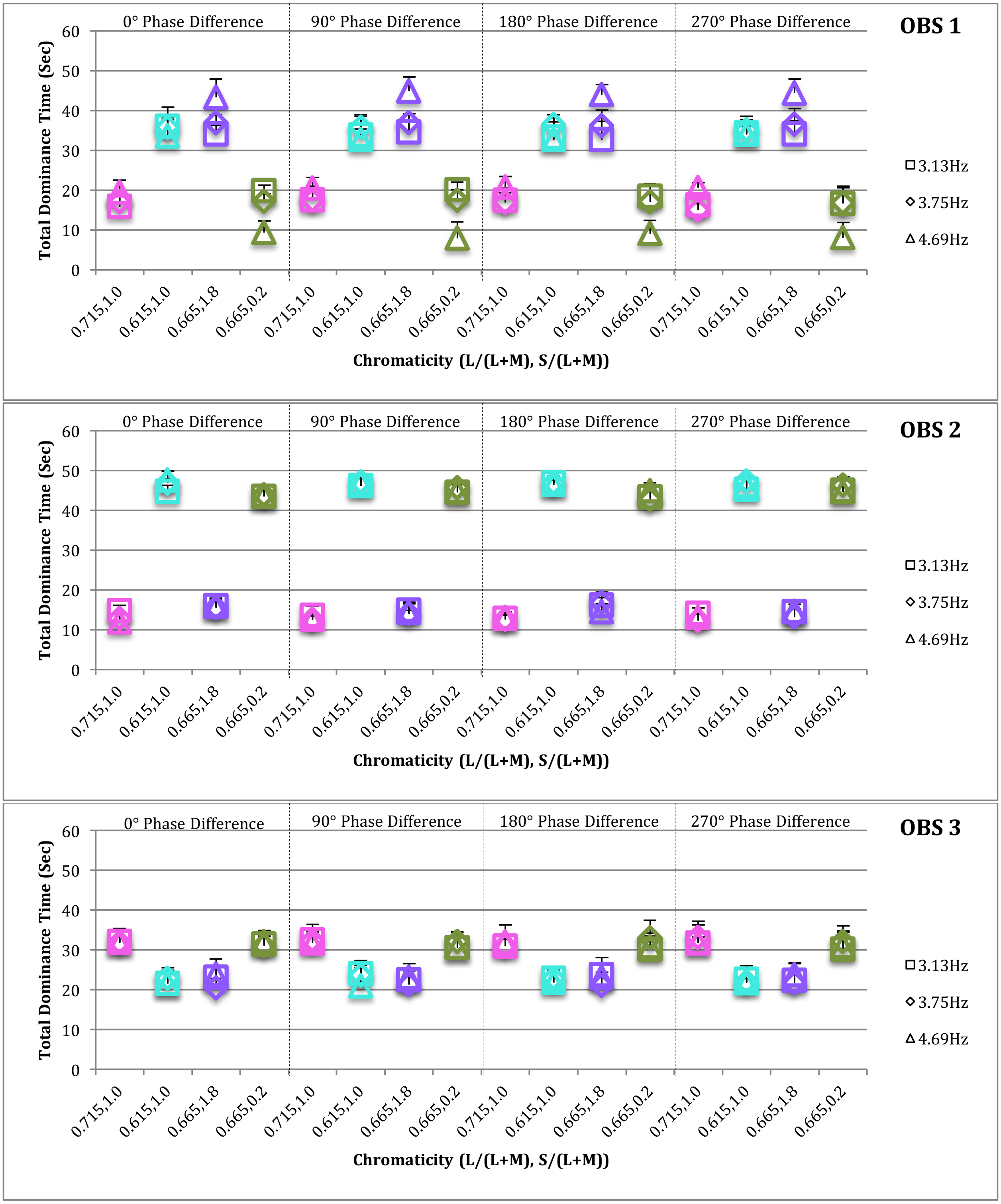

Figure 5-2. Total dominance time of four (two pairs of) color percepts at three temporal frequencies. The results are shown for “0° phase difference”, “90° phase difference”, “180° phase difference” and “270° phase difference”. Within each group, the chromaticities (*l*, *s*) are arranged as (0.715, 1.0), (0.615, 1.0), (0.665, 1.8) and (0.665, 0.2).

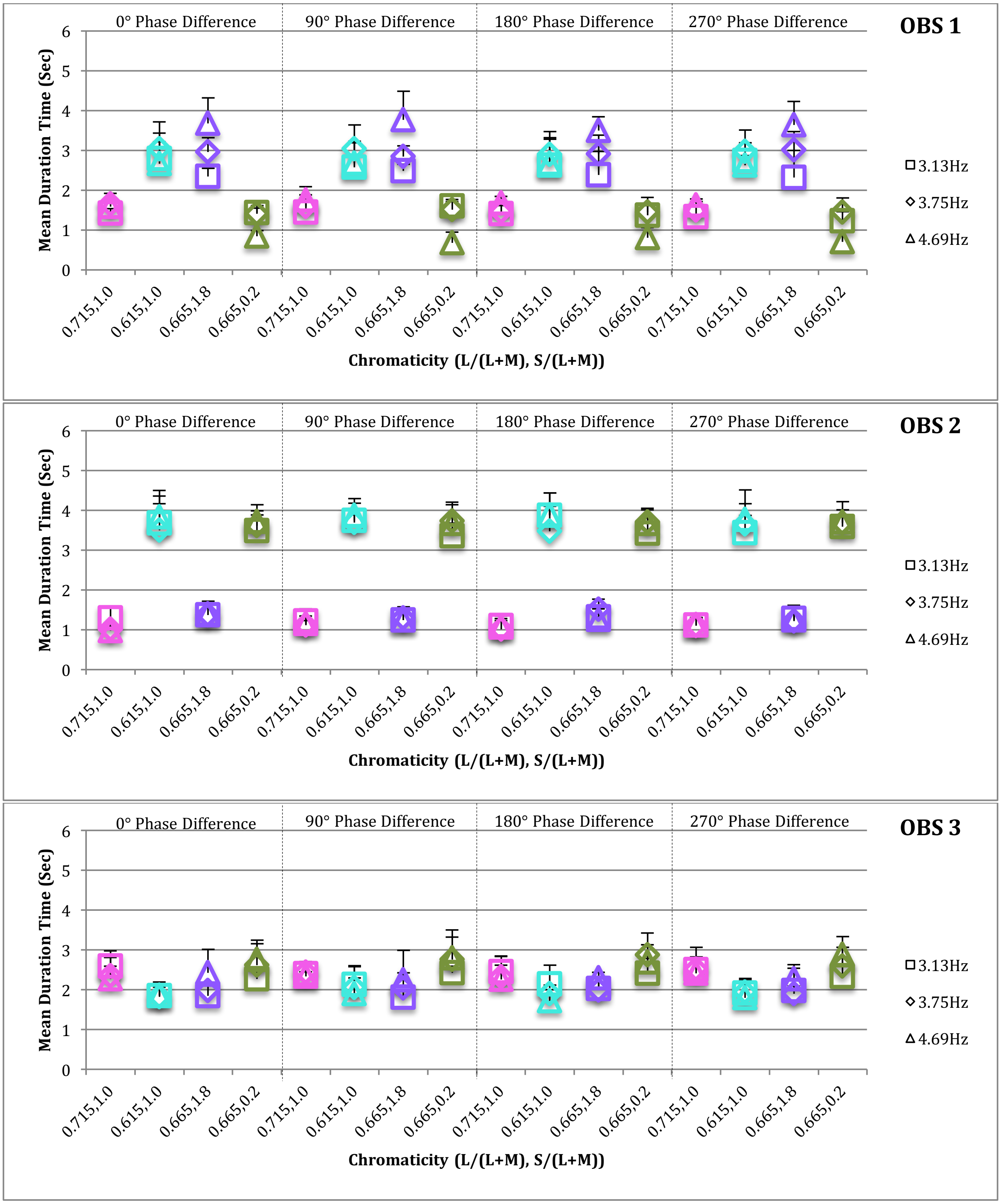

Figure 5-3. As Figure 5-2, but mean duration time of four (two pairs of) color percepts at three temporal frequencies.

analysis of variance (ANOVA). One factor is the color (four levels) and the other is the

Table 5-1. Results for the total dominance time

Observer	Temporal Frequency	Experimental Condition	Average Total Dominance Time	F (3, 64)	*p*
1	3.13 Hz	0° difference	26.43 sec	0.52	0.66
		90° difference	26.47 sec		
		180° difference	25.42 sec		
		270° difference	25.31 sec		
	3.75 Hz	0° difference	26.67 sec	0.35	0.78
		90° difference	26.83 sec		
		180° difference	26.60 sec		
		270° difference	25.83 sec		
	4.69 Hz	0° difference	26.42 sec	0.02	0.99
		90° difference	26.47 sec		
		180° difference	26.58 sec		
		270° difference	26.70 sec		
2	3.13 Hz	0° difference	29.78 sec	0.01	0.99
		90° difference	29.79 sec		
		180° difference	29.79 sec		
		270° difference	29.70 sec		
	3.75 Hz	0° difference	29.73 sec	0.01	0.99
		90° difference	29.81 sec		
		180° difference	29.72 sec		
		270° difference	29.77 sec		
	4.69 Hz	0° difference	29.73 sec	0.01	0.99
		90° difference	29.66 sec		
		180° difference	29.72 sec		
		270° difference	29.61 sec		
3	3.13 Hz	0° difference	27.07 sec	0.11	0.95
		90° difference	27.39 sec		
		180° difference	26.94 sec		
		270° difference	26.74 sec		
	3.75 Hz	0° difference	26.57 sec	0.21	0.89
		90° difference	27.36 sec		
		180° difference	26.98 sec		
		270° difference	27.24 sec		
	4.69 Hz	0° difference	27.31 sec	0.09	0.96
		90° difference	26.62 sec		
		180° difference	26.93 sec		
		270° difference	27.05 sec		

* Average total dominance time indicates the mean value of the total dominance time among four (two pairs of) color percepts (maximum time is 30 sec).

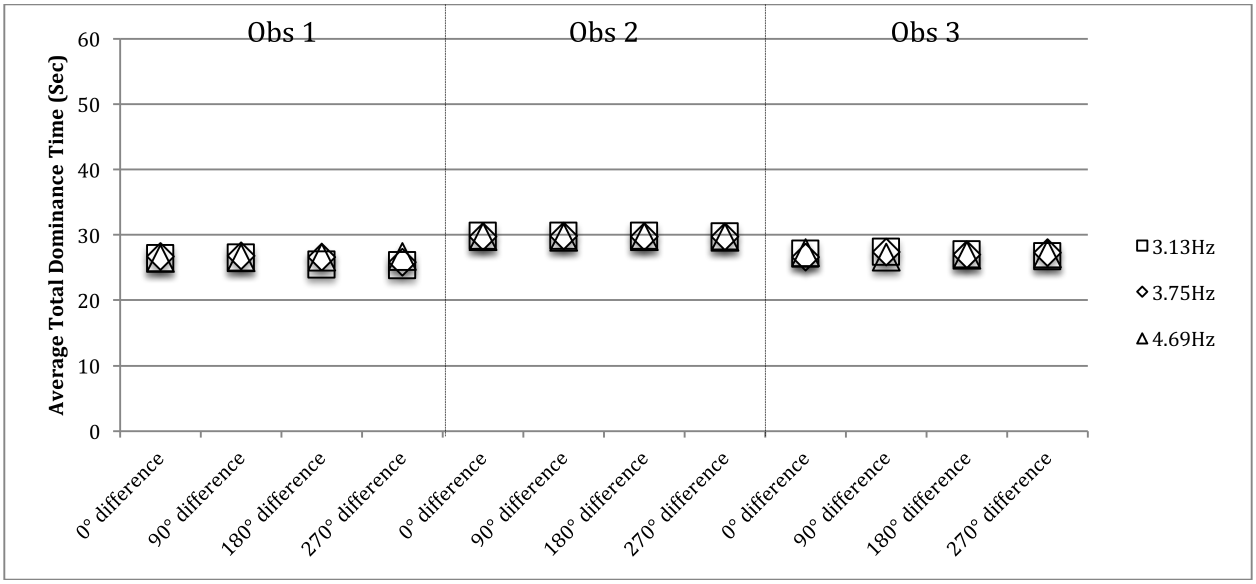

Figure 5-4. Average total dominance time when two discs are oscillated with 0°, 90°, 180° or 270° temporal phase difference. Each open symbol indicates the average total dominance time of the four chromaticities at a given temporal frequency for each observer.

experimental condition (four levels of phase).

For each observer, the results show that the total dominance time is not significantly different among the four different phase conditions, at each of the three temporal frequencies (see Table 5-1 and Figure 5-4). The same result is found for the mean

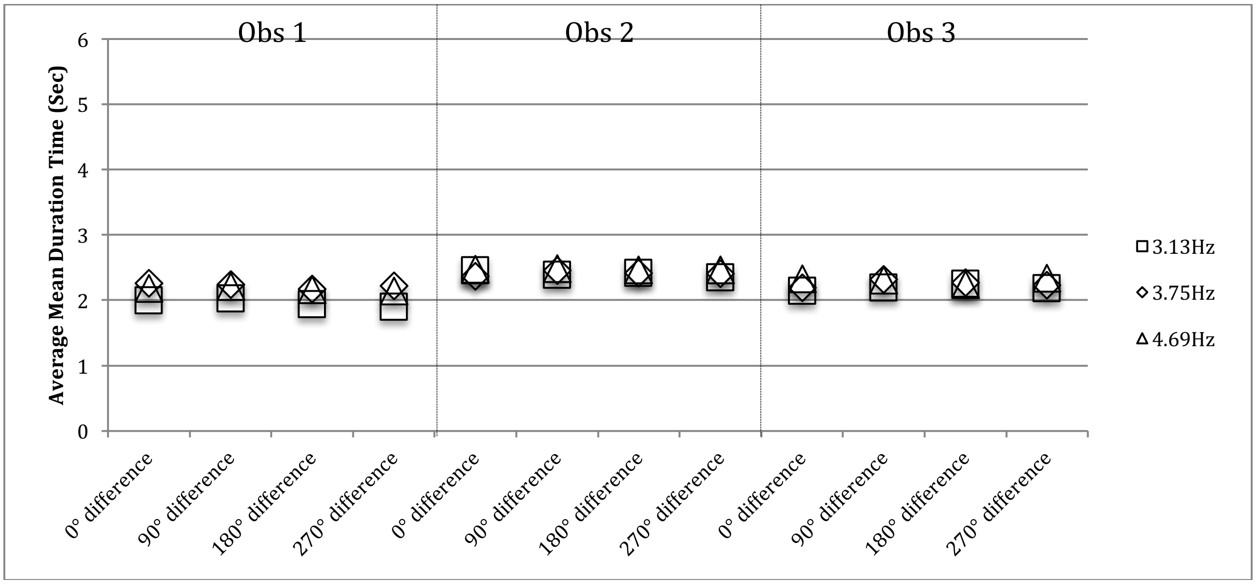

Figure 5-5. As Figure 5-4, but for average mean duration time.

Table 5-2. Results for the mean duration time

Observer	Temporal Frequency	Experimental Condition	Average Mean Duration Time	F (3, 64)	*p*
1	3.13 Hz	0° difference	1.99 sec	0.31	0.82
		90° difference	2.02 sec		
		180° difference	1.94 sec		
		270° difference	1.90 sec		
	3.75 Hz	0° difference	2.26 sec	0.13	0.94
		90° difference	2.24 sec		
		180° difference	2.17 sec		
		270° difference	2.22 sec		
	4.69 Hz	0° difference	2.18 sec	0.07	0.97
		90° difference	2.21 sec		
		180° difference	2.16 sec		
		270° difference	2.14 sec		
2	3.13 Hz	0° difference	2.45 sec	0.15	0.93
		90° difference	2.39 sec		
		180° difference	2.42 sec		
		270° difference	2.35 sec		
	3.75 Hz	0° difference	2.37 sec	0.16	0.92
		90° difference	2.45 sec		
		180° difference	2.42 sec		
		270° difference	2.41 sec		
	4.69 Hz	0° difference	2.47 sec	0.02	0.99
		90° difference	2.48 sec		
		180° difference	2.46 sec		
		270° difference	2.46 sec		
3	3.13 Hz	0° difference	2.14 sec	0.28	0.83
		90° difference	2.19 sec		
		180° difference	2.25 sec		
		270° difference	2.18 sec		
	3.75 Hz	0° difference	2.19 sec	0.27	0.84
		90° difference	2.32 sec		
		180° difference	2.27 sec		
		270° difference	2.23 sec		
	4.69 Hz	0° difference	2.33 sec	0.16	0.92
		90° difference	2.31 sec		
		180° difference	2.24 sec		
		270° difference	2.34 sec		

* Average mean duration time indicates the mean value of the mean duration time among four (two pairs of) color percepts (maximum time is 30 sec).

duration time (see Table 5-2 and Figure 5-5). For the total dominance time, there is a statistically significant interaction between the color and the phase for only observer 3 at 3.75 Hz ($p < .05$). This indicates that the effect of the color depends on the temporal phase difference between the two discs for observer 3 at 3.75 Hz.

Thus, there is no evidence to support the conclusion that grouping in the resolution of CISR depends on the temporal phase synchrony of the grouped objects presented at a common temporal frequency. The results of this experiment indicate that, regardless of each component's flickering temporal phase, objects can be grouped as long as the temporal frequency of flicker is identical.

CHAPTER 6

EXPERIMENT 4: CONTRIBUTION TO GROUPING OF OBJECTS FROM IDENTICAL TEMPORAL FREQUENCIES IN CHROMATIC INTEROCULAR-SWITCH RIVALRY

6.1 Rationale

The purpose of this experiment is to investigate the contribution of equal temporal frequencies to grouped objects during chromatic interocular-switch rivalry (CISR). Grouping is assessed by aligning two discs vertically, one above the other, in each eye. If temporal frequency equality affects grouping, then both the total dominance and mean duration times of simultaneously perceiving two spatially separated discs of the same color would depend on whether the temporal frequencies of the two discs are same.

When flickering objects are grouped together, one way to manipulate their temporal relation is to vary the temporal synchrony of the grouped objects at a common temporal frequency. In the previous experiment, temporal synchrony was varied by changing the phase difference between the two objects. The resolution of CISR was not found to depend on temporal phase synchrony. In addition, the temporal relation between the grouped objects may be altered by using non-identical temporal frequencies. The frequency-difference in temporal structure may induce an incoherence of the global temporal structure and thereby reduce grouping.

If grouping depends on equal temporal frequencies, then the grouped objects flickering at different temporal frequencies would not form a coherent form. Studies in figure/ground segregation support the idea that there exists an influence of a temporal frequency difference. For example, Fahle (1993) found that the temporal frequency difference to separate figure and ground is about 5 ms for both sharply focused and blurred points. When luminance and motion information are removed, however, the temporal difference is about 10 ms for figure/ground segregation (Kandil & Fahle, 2001). Similar effects from temporal frequency differences are also found in border segregation (Rogers-Ramachandran & Ramachandran, 1998), texture segregation (Leonards, Singer & Fahle, 1996), or segregation of random textures composed of high spatial frequencies (Kojima, 1998). All these lines of research suggest that objects' identical temporal frequencies may be a critical factor for grouping.

6.2 Methods

A stimulus paradigm with two discs was tested. That is, two spatially homogeneous discs were aligned vertically in each eye at the corresponding retinal locations so that two fused discs were perceived (see Fig. 2-1(b)).

Based on this paradigm, the top and bottom discs oscillated at either different or the same temporal frequencies within each eye. In the left eye, for example, the top and bottom discs could oscillate at 3.13 Hz and 3.75 Hz, respectively. This was compared to two conditions, one with both discs at 3.13 Hz and the other with both at 3.75 Hz. All discs in the right eye oscillated at the same temporal frequency as in the left eye. Thus, four experimental conditions were tested (Fig. 6-1).

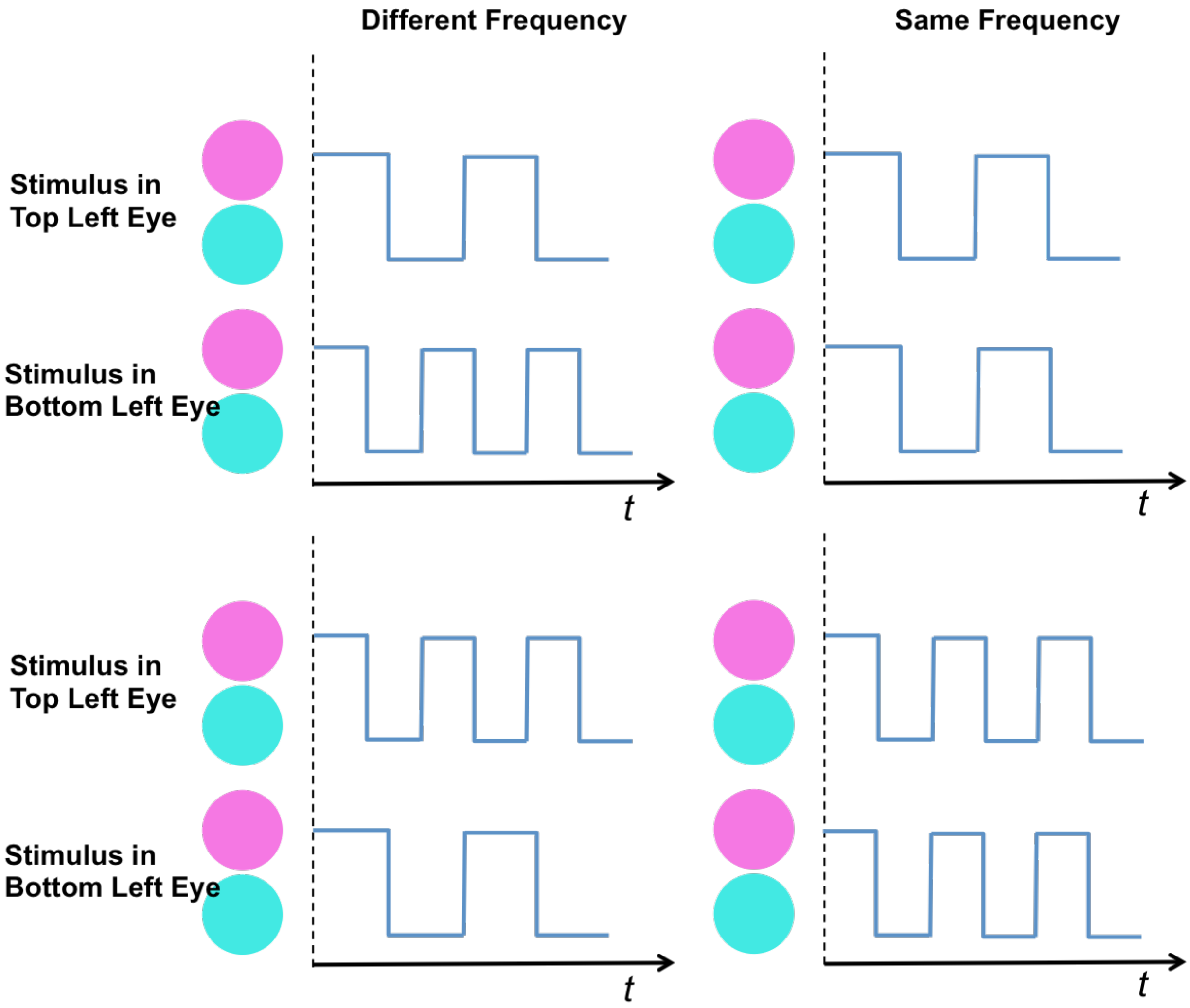

Figure 6-1. Experimental conditions in experiment 4. In the different-frequency conditions, the top disc oscillates at either a slower (top-left) or faster (bottom-left) temporal frequency, compared to the bottom disc. In the same-frequency case, the top and bottom discs both oscillate at the same slower (top-right) or faster (bottom-right) temporal frequency used in the different-frequency conditions.

In this experiment, each session was composed of eight trials in a random sequence, and each trial tested one of the two pairs of chromaticities (described in Chapter 2) in each of the four experimental conditions (see Fig. 6-1). In other words, CISR was repeated eight times randomly with each disc alternating between two chromaticities. The task was to report the color of the top and bottom discs in the fused binocular percept. The total dominance time and mean duration time of each color percept during each trial was calculated.

In separate sessions, two pairs of square-wave temporal frequencies were tested: (1) 3.13 Hz and 3.75 Hz and (2) 3.75 Hz and 4.69 Hz. Each observer ran each frequency-pair in each of five sessions on different days, so ten sessions were completed in total.

6.3 Results

The total dominance time of each color percept is shown in Figure 6-2 (vertical axis) as a function of the chromaticities (horizontal axis) and the pair of temporal frequencies (open symbols). The chromaticities are grouped as “different frequencies”, “same low frequency” and “same high frequency” (left to right along the horizontal axis). Here, “different frequencies” is the average of the two experimental conditions with different temporal frequencies (see Fig. 6-1). Within each group, the chromaticities are arranged as one pair along the l and s chromatic directions [(l = 0.715, s = 1.0) & (l = 0.615, s = 1.0) and (l = 0.665, s = 1.8) & (l = 0.665, s = 0.2)]. The pairs of temporal frequencies are indicated with various open symbols. The symbol color is the approximate color of the tested chromaticity. Each panel shows results for one observer. Figure 6-3 shows the mean duration time of each color percept in the same format as the total dominance in Figure 6-2.

Total dominance time is on a different scale than the mean duration time, so the two dependent measures are analyzed separately for each observer, by completing two-way analysis of variance (ANOVA). One factor is the color (four levels) and the other is the

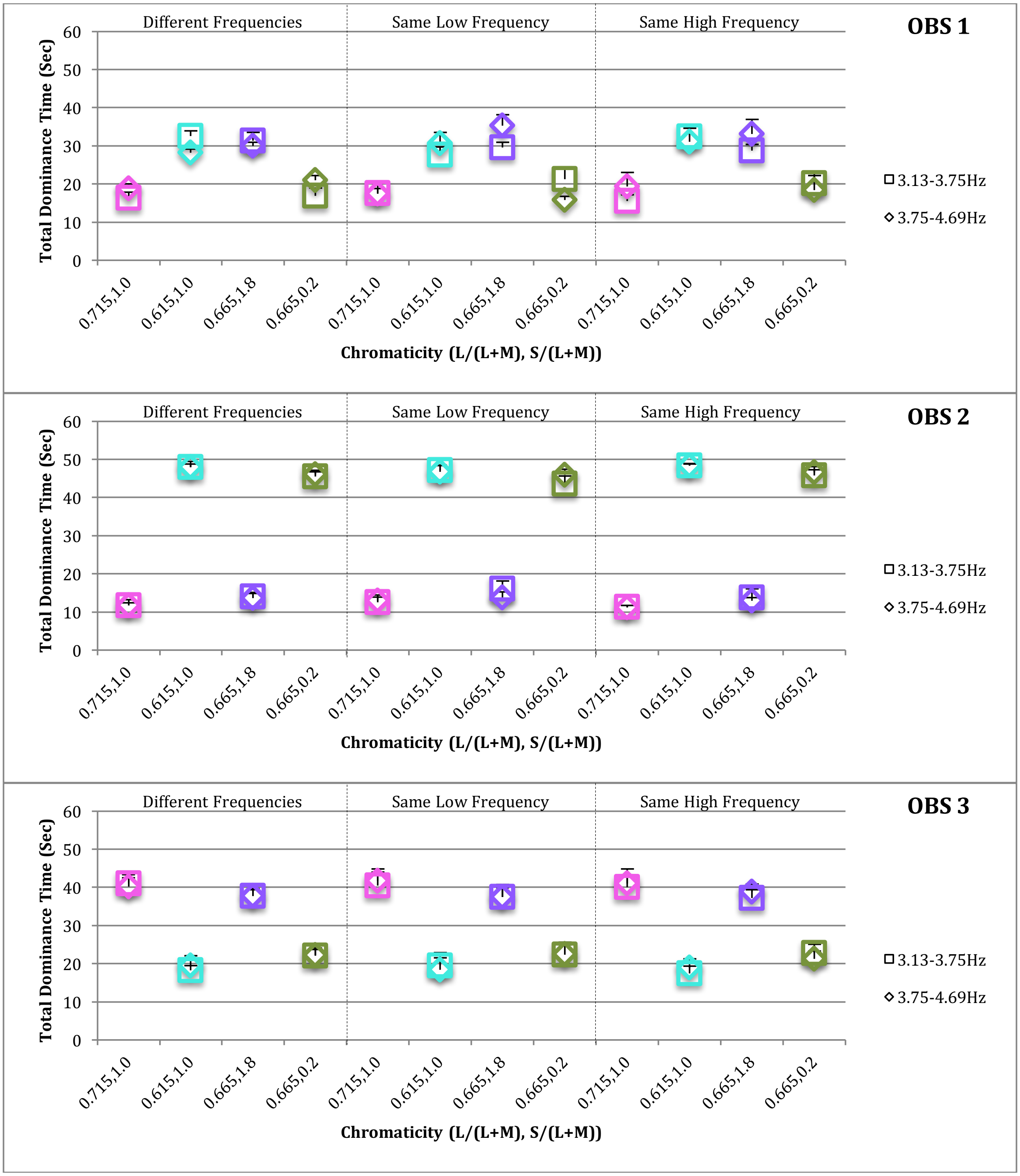

Figure 6-2. Total dominance time of four (two pairs of) color percepts at two pairs of temporal frequencies. The chromaticities are grouped as “different frequencies”, “same low frequency” and “same high frequency”. Within each group, the chromaticities (*l*, *s*) are arranged as (0.715, 1.0), (0.615, 1.0), (0.665, 1.8) and (0.665, 0.2).

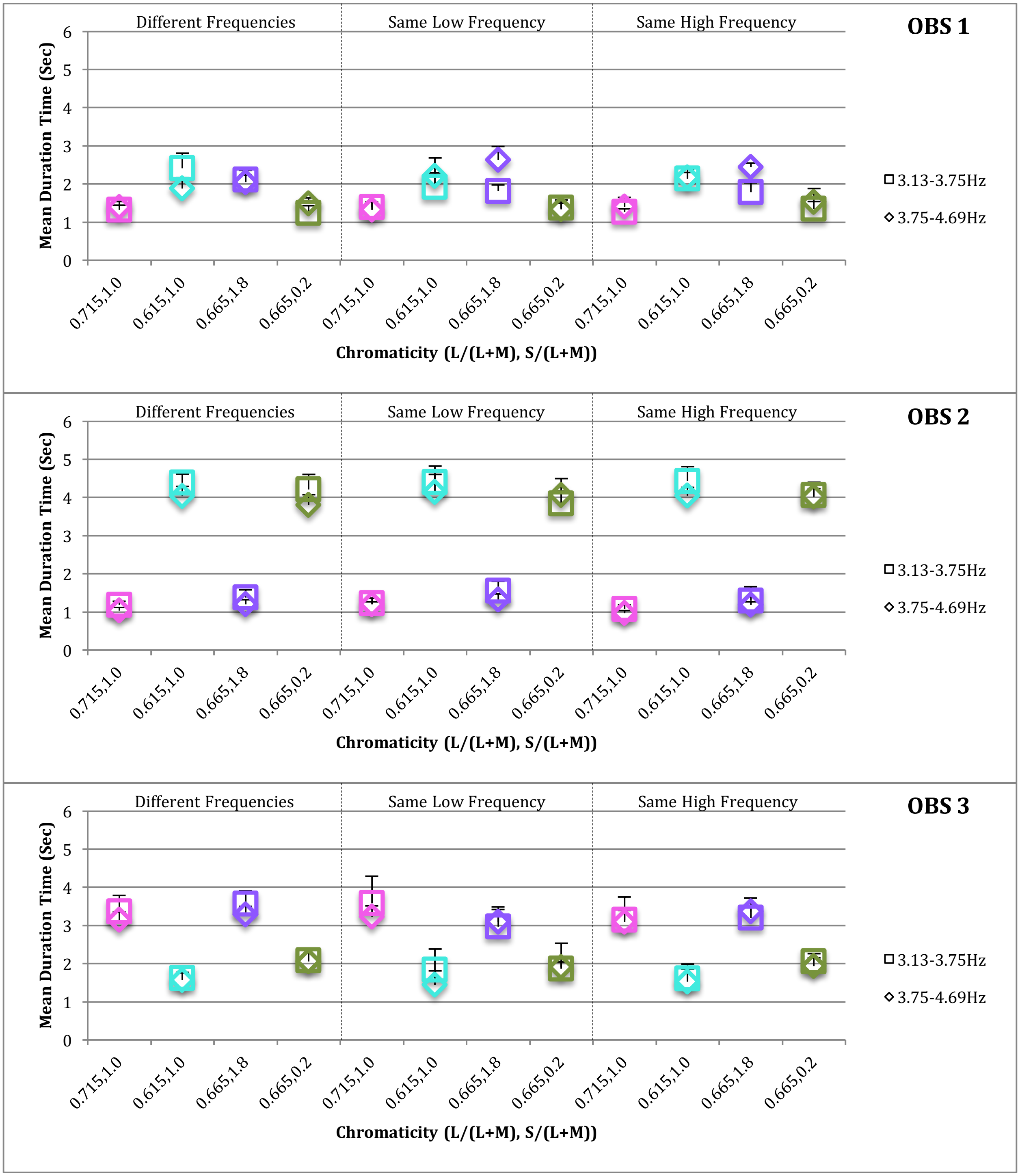

Figure 6-3. As Figure 6-2, but mean duration time of four (two pairs of) color percepts at two pairs of temporal frequencies.

experimental condition (unequal temporal frequency, equal slower frequency and equal faster frequency).

For each observer, the results show that the total dominance time is not significantly different for the various temporal frequency conditions, for each of the temporal frequency pairs (see Table 6-1 and Figure 6-4). The same results are found for the mean duration time (see Table 6-2 and Figure 6-5). For the total dominance time, there is also a statistically significant interaction between the color and the temporal condition for observer 1 at both pairs of temporal frequencies ($p <. 05$). This indicates that the effect of color depends on whether the temporal frequencies are identical or not for observer 1.

Table 6-1. Results for the total dominance time

Observer	Temporal Frequency Pair	Experimental Condition	Average Total Dominance Time	F (2, 48)	*p*
1	3.13-3.75 Hz	Different frequency	24.31 sec	0.09	0.91
		Same low frequency	23.99 sec		
		Same high frequency	24.17 sec		
	3.75-4.69 Hz	Different frequency	24.49 sec	0.64	0.53
		Same low frequency	24.77 sec		
		Same high frequency	25.49 sec		
2	3.13-3.75 Hz	Different frequency	29.80 sec	0.01	0.99
		Same low frequency	29.82 sec		
		Same high frequency	29.79 sec		
	3.75-4.69 Hz	Different frequency	29.84 sec	0.01	0.99
		Same low frequency	29.81 sec		
		Same high frequency	29.78 sec		
3	3.13-3.75 Hz	Different frequency	29.74 sec	0.16	0.85
		Same low frequency	29.92 sec		
		Same high frequency	29.37 sec		
	3.75-4.69 Hz	Different frequency	29.91 sec	0.01	0.99
		Same low frequency	29.98 sec		
		Same high frequency	29.97 sec		

* Average total dominance time indicates the mean value of the total dominance time among four (two pairs of) color percepts (maximum time is 30 sec).

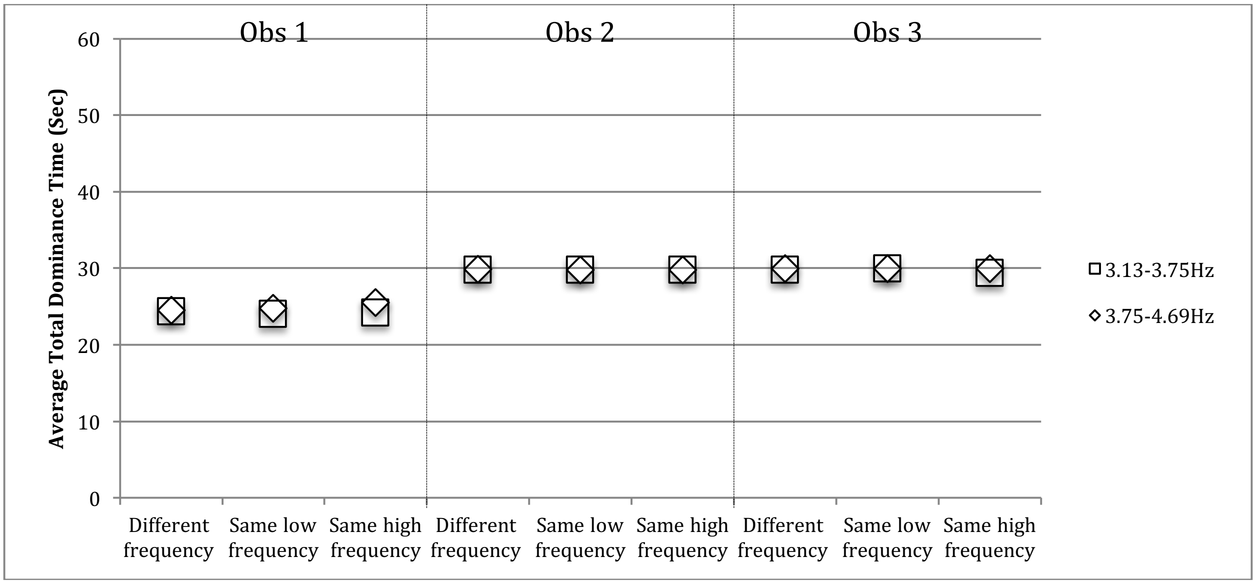

Figure 6-4. Average total dominance time when two discs are oscillated at different frequencies, the same low frequency or the same high frequency. Each open symbol indicates the average total dominance of the four chromaticities at a given pair of temporal frequencies for each observer.

Table 6-2. Results for the mean duration time

Observer	Temporal Frequency Pair	Experimental Condition	Average Mean Duration Time	F (2, 48)	*p*
1	3.13-3.75 Hz	Different frequency	1.77 sec	1.87	0.16
		Same low frequency	1.62 sec		
		Same high frequency	1.64 sec		
	3.75-4.69 Hz	Different frequency	1.69 sec	2.48	0.09
		Same low frequency	1.87 sec		
		Same high frequency	1.88 sec		
2	3.13-3.75 Hz	Different frequency	2.79 sec	0.27	0.76
		Same low frequency	2.75 sec		
		Same high frequency	2.71 sec		
	3.75-4.69 Hz	Different frequency	2.51 sec	2.04	0.14
		Same low frequency	2.68 sec		
		Same high frequency	2.55 sec		
3	3.13-3.75 Hz	Different frequency	2.65 sec	0.42	0.65
		Same low frequency	2.56 sec		
		Same high frequency	2.50 sec		
	3.75-4.69 Hz	Different frequency	2.51 sec	0.45	0.64
		Same low frequency	2.42 sec		
		Same high frequency	2.48 sec		

* Average mean duration time indicates the mean value of the mean duration time among four (two pairs of) color percepts (maximum time is 30 sec).

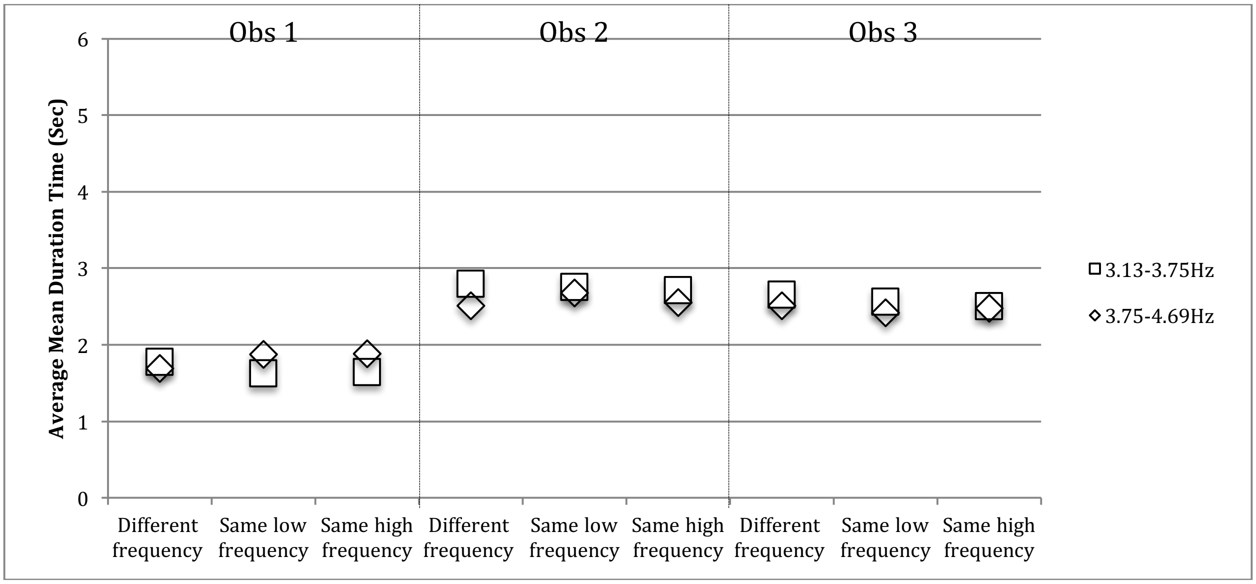

Figure 6-5. As Figure 6-3, but for mean duration time.

Overall, the results do not support the conclusion that the resolution of CISR depends on the same temporal frequency for the grouped objects. The results of this experiment indicate that objects can be grouped together, even when each object's temporal frequency is different.

CHAPTER 7

EXPERIMENT 5: CONTRIBUTION TO GROUPING OF OBJECTS FROM EQUAL STEREOSCOPIC DISPARITY IN CHROMATIC INTEROCULAR-SWITCH RIVALRY

7.1 Rationale

The purpose of this experiment is to investigate the contribution of stereoscopic disparity to grouped percepts during chromatic interocular-switch rivalry (CISR). Grouping is assessed by aligning two discs vertically, one above the other, in each eye. If stereoscopic disparity affects grouping, then both the total dominance and mean duration times of simultaneously perceiving two spatially separated discs of the same color would depend on the stereoscopic disparity difference between the two percepts. In addition, this experiment explores a possible influence from the stereoscopic disparity of the fixation point relative to the grouped percepts. If fixation depth affects grouping, then the total dominance and mean duration times would depend on the fixation disparity as well.

Although the previous experiments do not show that color percepts of grouped objects depend on the temporal properties of CISR, there is another relation among grouped objects, spatial structure, that may affect color perception. For example, the two-dimensional spatial relation (layout) of the grouped objects has been explored and the results show that same-eye grouping gives the longest effect of simultaneous dominance during binocular rivalry (Stuit, Paffen, van der Smart & Verstraten, 2011). Another possibility for spatial relations among objects is the depth information of the grouped objects.

One way to vary the depth relations among objects is to introduce different stereoscopic disparity among the grouped percepts viewed under binocular fusion. If grouping depends on stereoscopic disparity, then the grouped percepts seen in different depth planes would not form a coherent form. Studies in image segmentation and grouping show that intrinsic borders (inherent to the object itself) aid in image segmentation and prevent grouping, while extrinsic borders (defined by occlusion) provide a link to other extrinsic borders and promote grouping (Nakayama, Shimojo & Silverman, 1989). This suggests that stereoscopic disparity of borders, either intrinsic or extrinsic, might influence grouping, regardless of the controversy of whether stereopsis and binocular rivalry occur together (Blake, Yang & Wilson, 1991; Wolfe, 1986).

7.2 Methods

A stimulus paradigm with two discs was tested. That is, two spatially homogeneous discs were aligned vertically in each eye at the corresponding retinal locations so that two fused discs were perceived (see Fig. 2-1(b)).

Based on this paradigm, the top or/and bottom disc in the left and right eye was shifted 3' toward the center of the field (e.g. the disc in the left eye moved 3' rightward and the disc in the right eye moved 3' leftward), which created 6' of disparity for the fused binocular percept of the disc relative to the background. These manipulations resulted in four conditions: “no disparity”, “6’ on top”, “6’ on bottom” and “6’ on both”. Here, “no disparity” means no shifts of the discs in either eye so that the fused binocular percepts of both discs were perceived in the background plane; “6’ on top” means shifts for only the top disc in both eyes so that the fused binocular percept of the top disc popped out relative to the fused binocular percept of the bottom disc and the background plane; similarly, “6’ on bottom” means the fused binocular percept of the bottom disc popped out relative to the top one and the background plane, and “6’ on both” means the fused binocular percepts of the top and bottom discs popped out relative to the background plane. In the meantime, the fixation cross was located on the background plane without disparity. In addition to these four conditions, the fixation cross in the left and right eyes was shifted 1.5’ toward the center (e.g. the fixation cross in the left eye moved 1.5’ rightward and the fixation cross in the right eye moved 1.5’ leftward), which created 3’ of disparity for the fused binocular percept of the fixation cross relative to the background (half way between the depth of the top and bottom disc in the “6’ on top” and “6’ on bottom” conditions). This created another four conditions with the same manipulations of the discs, but with 3’ of disparity for the fused binocular percept of the fixation cross. Thus, eight experimental conditions were tested (Fig. 7-1 has a side view). For small visual stimuli, the maximum range of disparity giving fusion in the human foveal area is about 10’ (Patterson and Martin, 1992). Therefore, in separate sessions, the same eight experimental conditions were tested again with 10’ of disparity for the fused percept of the discs and 5’ for the fused percept of the fixation cross.

In this experiment, each session was composed of sixteen trials in a random sequence, and each trial tested one of the two pairs of chromaticities (described in Chapter2) in each of the eight experimental conditions (see Fig. 7-1) at a given temporal frequency. In other words, CISR was repeated eight times randomly with each disc alternating between two chromaticities. The task was to report the color of the top and bottom discs in the fused binocular percept. The total dominance time and mean duration time of each color percept during each trial was calculated.

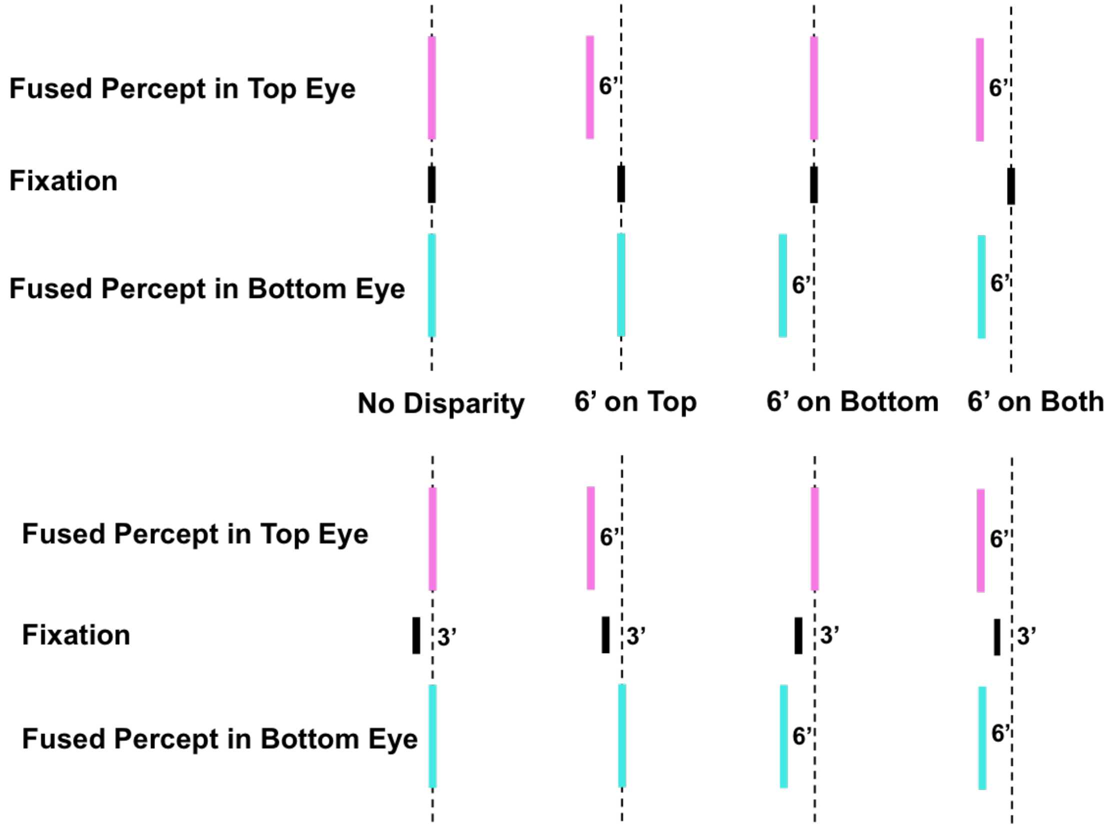

Figure 7-1. Experimental conditions in experiment 5 (side view). Fused percept of the top disc (pink solid line) or/and the bottom disc (blue solid line) pops up 6' relative to the background plane (black dashed line), which creates four conditions: "no disparity", "6' on top", "6' on bottom" and "6' on both". Fused percept of the fixation cross (black solid line) either does not pop out or pops out 3' relative to the background plane, which creates two conditions for the fixation cross: "no disparity" and "3' disparity". Thus, eight experimental conditions were tested in total.

In separate sessions, three different square-wave temporal frequencies were tested: 3.13Hz, 3.75Hz and 4.69Hz. Each observer ran each frequency in each of five sessions on different days, so thirty sessions were completed in total for both parts.

7.3 Results

In the case of 6’ disparity for the discs and either 0’ or 3’ on for the fixation cross, the total dominance time of each color percept is shown in Figure 7-2 (vertical axis) as a function of the chromaticities (horizontal axis) and the temporal frequency (open symbols). The chromaticities are grouped as “no disparity (F0’)”, “6’ on top (F0’)”, “6’ on bottom (F0’)”, “6’ on both (F0’)”, “no disparity (F3’)”, “6’ on top (F3’)”, “6’ on bottom (F3’)”, and “6’ on both (F3’)” (left to right along the horizontal axis). Here, “(F0’)” indicates no disparity for the fixation cross and “(F3’)” indicates 3’ disparity for the fixation cross. Within each group, the chromaticities are arranged as one pair along the l and s chromatic directions [(l = 0.715, s = 1.0), (l = 0.615, s = 1.0), (l = 0.665, s = 1.8) and (l = 0.665, s = 0.2)]. The temporal frequencies are indicated with various open symbols. The symbol color is the approximate color of the tested chromaticity. Each panel shows results for one observer. Figure 7-3 shows the mean duration time of each color percept in the same format as the total dominance time in Figure 7-2.

In the case of 10’ disparity for the discs and either 0’ or 5’ for the fixation cross, the total dominance and mean duration times of each color percept are shown in Figure 7-4 and Figure 7-5, respectively, in the same format as Figure 7-2 and Figure 7-3. In these figures, the chromaticities are grouped as “no disparity (F0’)”, “10’ on top (F0’)”, “10’ on bottom (F0’)”, “10’ on both (F0’)”, “no disparity (F5’)”, “10’ on top (F5’)”, “10’ on bottom (F5’)”, and “10’ on both (F5’)” (left to right in the horizontal axis). Here, “(F0’)” indicates no

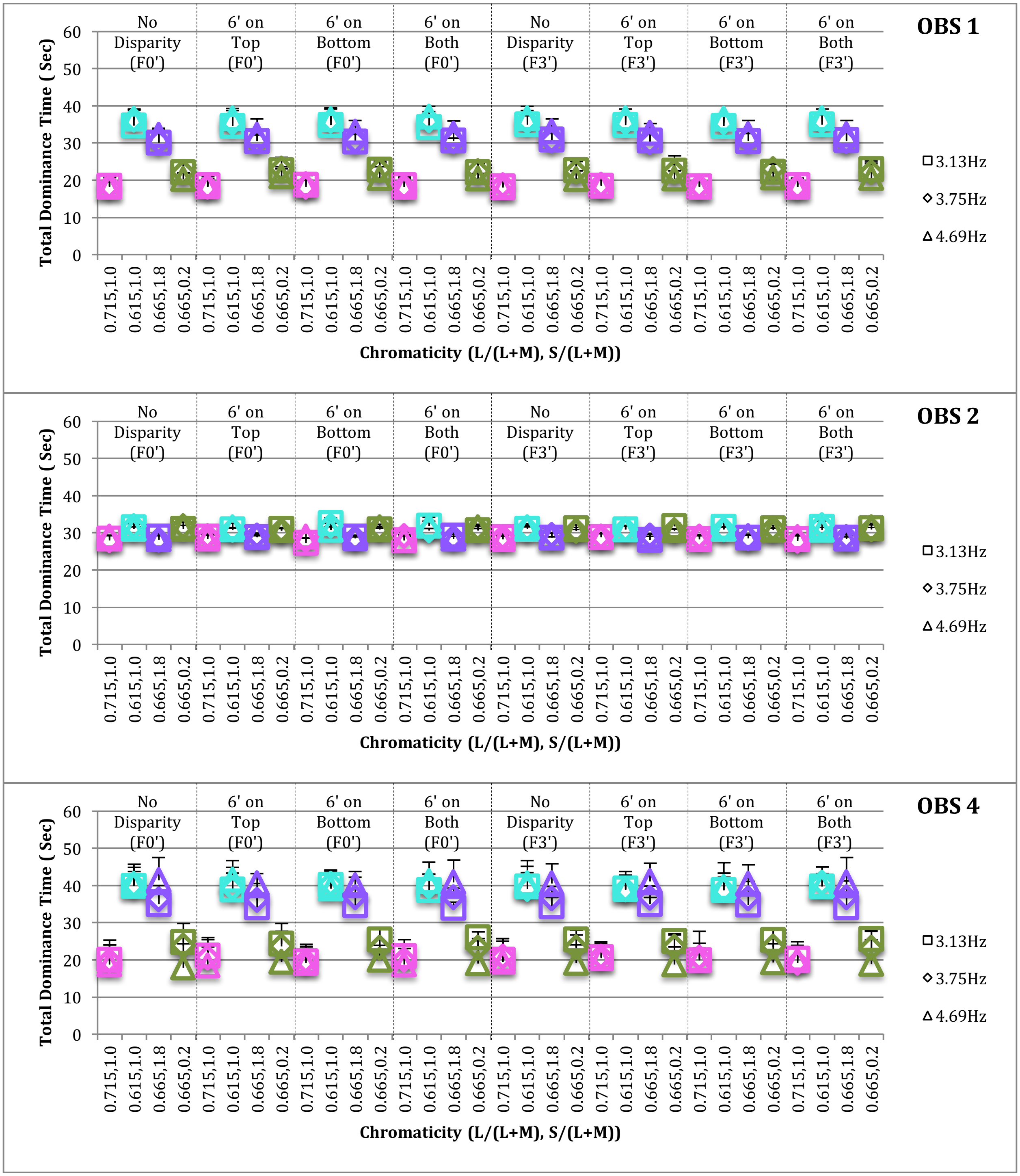

Figure 7-2. Total dominance time of four (two pairs of) color percepts at three temporal frequencies. The chromaticities are grouped as “no disparity (F0’)”, “6’ on top (F0’)”, “6’ on bottom (F0’)”, “6’ on both (F0’)”, “no disparity (F3’)”, “6’ on top (F3’)”, “6’ on bottom (F3’)” and “6’ on both (F3’)”. Within each group, the chromaticities (*l*, *s*) are arranged as (0.715, 1.0), (0.615, 1.0), (0.665, 1.8) and (0.665, 0.2).

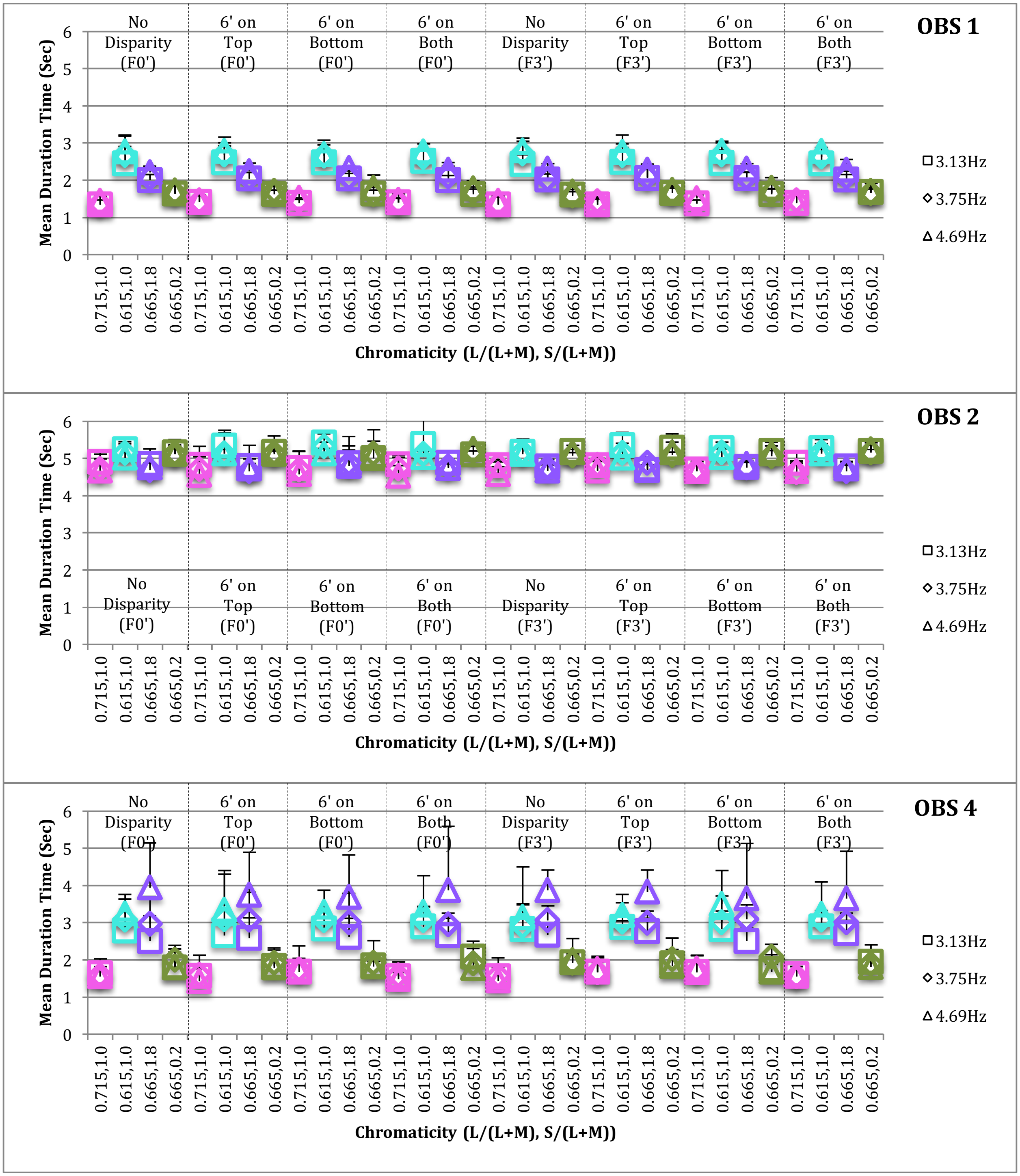

Figure 7-3. As Figure 7-2, but for mean duration time of four (two pairs of) color percepts at three temporal frequencies.

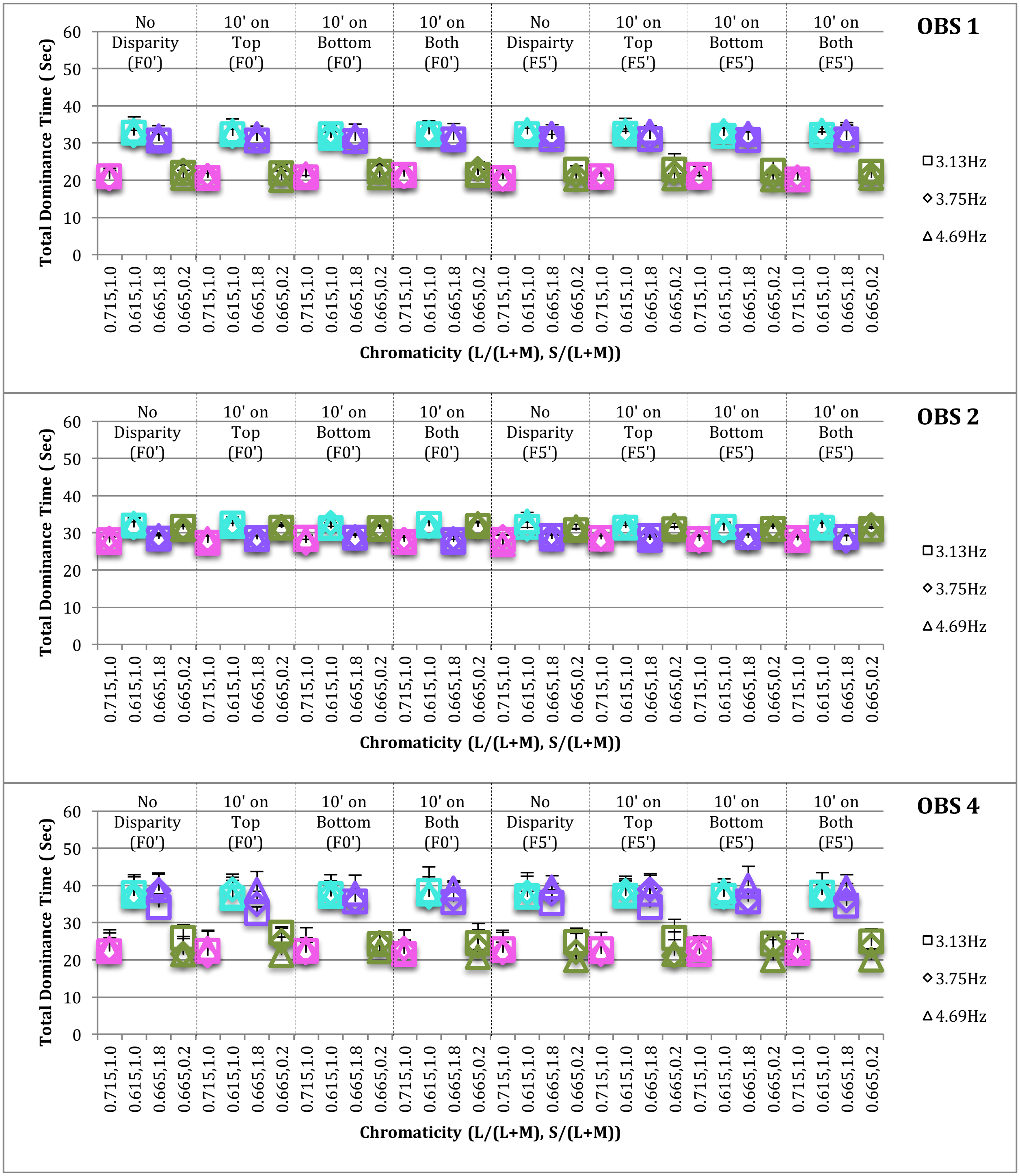

Figure 7-4. As Figure 7-2, but the chromaticities are grouped as “no disparity (F0’)”, “10’ on top (F0’)”, “10’ on bottom (F0’)”, “10’ on both (F0’)”, “no disparity (F5’)”, “10’ on top (F5’)”, “10’ on bottom (F5’)” and “10’ on both (F5’). “(F0’)” indicates no disparity for the fixation cross and “(F5’)” indicates 5’ disparity for the fixation cross.

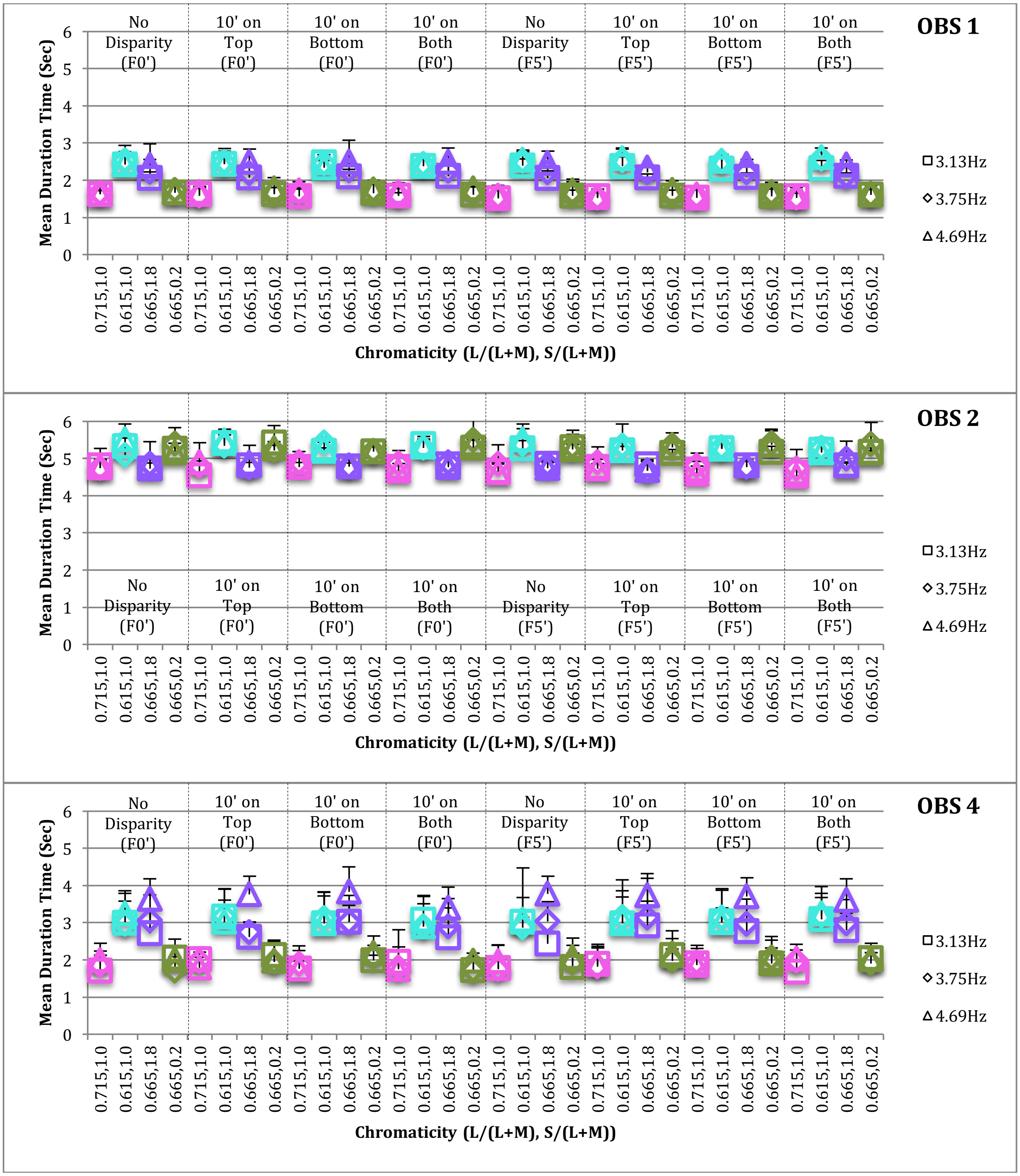

Figure 7-5. As Figure 7-4, but for mean duration time of four (two pairs of) color percepts at three temporal frequencies.

disparity for the fixation cross and “(F5’)” indicates 5’ disparity for the fixation cross.

The total dominance time is on a different scale than the mean duration time, so they are analyzed separately for each observer at each temporal frequency, by completing three-way analysis of variance (ANOVA). The first factor is the color (four levels), the second factor is the disparity of the discs (four levels, described in the previous section) and the third factor is the disparity of the fixation cross (two levels, described in the previous section). The two sets of disc disparity parameters (6’ or 10’) are analyzed separately as well.

For each observer who perceived 6’ of disc disparity and 3’ of fixation disparity, the results show that the total dominance time is not significantly different among the experimental conditions of disc disparity (see Table 7-1 and Figure 7-6). The same results are found for the mean duration time (see Table 7-2 and Figure 7-7). In addition, the results also show that the total dominance time is not significantly different for the experimental conditions of fixation disparity (see Table 7-3 and Figure 7-8), and the same result holds for the mean duration time (see Table 7-4 and Figure 7-9).

For each observer who perceived 10’ of disc disparity and 5’ of fixation disparity, the results again show that the total dominance time is not significantly different among the experimental conditions of disc disparity (see Table 7-5 and Figure 7-10). The same results are found for the mean duration time (see Table 7-6 and Figure 7-11). In addition, the results show that the total dominance time is not significantly different for the experimental conditions of fixation disparity (see Table 7-7 and Figure 7-12). The mean duration time shows the same result (see Table 7-8 and Figure 7-13).

Table 7-1. Results for the total dominance time (6’ disparity for the discs)

Observer	Temporal Frequency	Experimental Condition	Average Total Dominance Time	F (3, 128)	*p*
1	3.13 Hz	No disparity	26.52 sec	0.33	0.81
		6’ on top	26.57 sec		
		6’ on bottom	26.53 sec		
		6’ on both	26.62 sec		
	3.75 Hz	No disparity	26.75 sec	0.04	0.99
		6’ on top	26.68 sec		
		6’ on bottom	26.82 sec		
		6’ on both	26.67 sec		
	4.69 Hz	No disparity	26.88 sec	0.24	0.87
		6’ on top	27.04 sec		
		6’ on bottom	27.03 sec		
		6’ on both	26.93 sec		
2	3.13 Hz	No disparity	29.91 sec	0.01	0.99
		6’ on top	29.90 sec		
		6’ on bottom	29.91 sec		
		6’ on both	29.91 sec		
	3.75 Hz	No disparity	29.90 sec	0.01	0.99
		6’ on top	29.90 sec		
		6’ on bottom	29.90 sec		
		6’ on both	29.88 sec		
	4.69 Hz	No disparity	29.91 sec	0.01	0.99
		6’ on top	29.89 sec		
		6’ on bottom	29.91 sec		
		6’ on both	29.89 sec		
4	3.13 Hz	No disparity	29.87 sec	0.01	0.99
		6’ on top	29.76 sec		
		6’ on bottom	29.77 sec		
		6’ on both	29.92 sec		
	3.75 Hz	No disparity	29.93 sec	0.01	0.99
		6’ on top	29.89 sec		
		6’ on bottom	29.90 sec		
		6’ on both	29.93 sec		
	4.69 Hz	No disparity	29.77 sec	0.02	0.99
		6’ on top	29.89 sec		
		6’ on bottom	29.70 sec		
		6’ on both	29.90 sec		

* Average total dominance time indicates the mean value of the total dominance time among four (two pairs of) color percepts under two disparities of the fixation cross (maximum time is 30 sec).

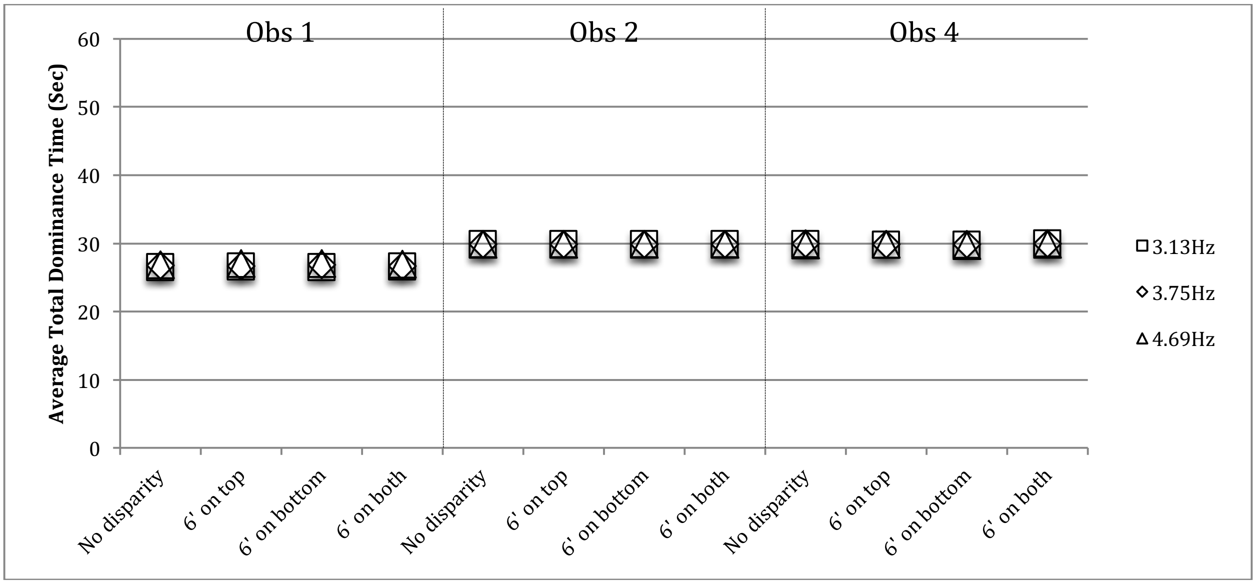

Figure 7-6. Average total dominance time when two discs are oscillated with no disparity, 6' on top disc, 6' on bottom disc and 6' on both discs. Each open symbol indicates the average total dominance time of the four chromaticities at a given temporal frequency for each observer.

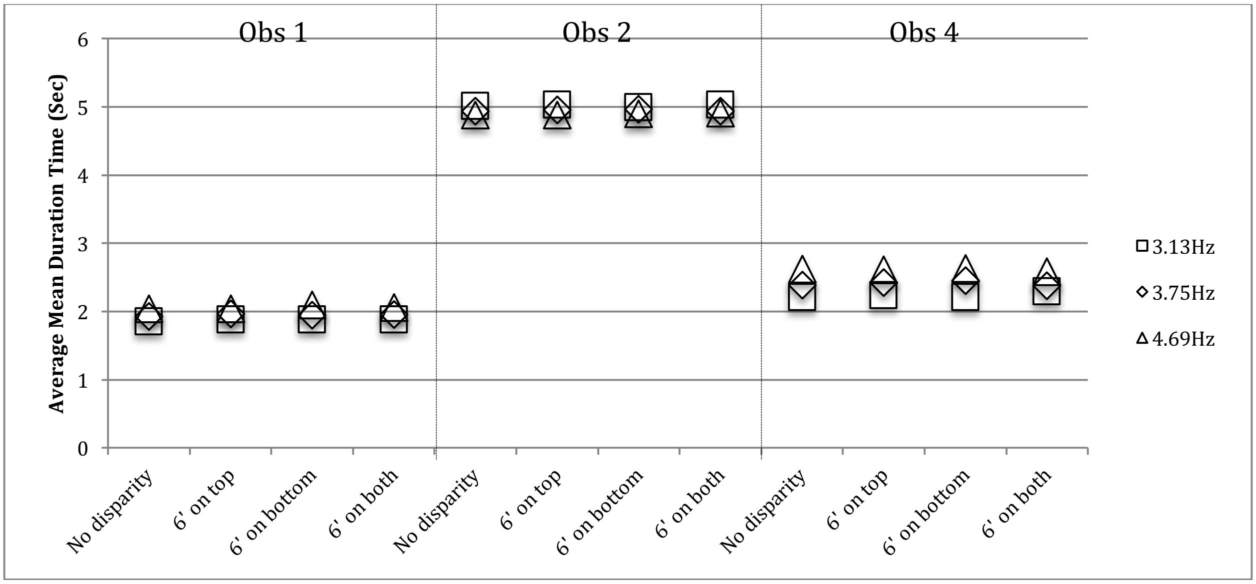

Figure 7-7. As Figure 7-6, but for average mean duration time.

Table 7-2. Results for the mean duration time (6’ disparity for the discs)

Observer	Temporal Frequency	Experimental Condition	Average Mean Duration Time	F (3, 128)	*p*
1	3.13 Hz	No disparity	1.85 sec	0.09	0.96
		6’ on top	1.88 sec		
		6’ on bottom	1.88 sec		
		6’ on both	1.88 sec		
	3.75 Hz	No disparity	1.92 sec	0.16	0.93
		6’ on top	1.96 sec		
		6’ on bottom	1.94 sec		
		6’ on both	1.95 sec		
	4.69 Hz	No disparity	2.04 sec	0.33	0.80
		6’ on top	2.04 sec		
		6’ on bottom	2.09 sec		
		6’ on both	2.06 sec		
2	3.13 Hz	No disparity	5.01 sec	0.20	0.89
		6’ on top	5.03 sec		
		6’ on bottom	4.99 sec		
		6’ on both	5.03 sec		
	3.75 Hz	No disparity	4.93 sec	0.13	0.94
		6’ on top	4.95 sec		
		6’ on bottom	4.96 sec		
		6’ on both	4.93 sec		
	4.69 Hz	No disparity	4.88 sec	0.11	0.95
		6’ on top	4.88 sec		
		6’ on bottom	4.90 sec		
		6’ on both	4.91 sec		
4	3.13 Hz	No disparity	2.21 sec	0.27	0.84
		6’ on top	2.23 sec		
		6’ on bottom	2.21 sec		
		6’ on both	2.29 sec		
	3.75 Hz	No disparity	2.38 sec	0.34	0.79
		6’ on top	2.42 sec		
		6’ on bottom	2.45 sec		
		6’ on both	2.37 sec		
	4.69 Hz	No disparity	2.62 sec	0.03	0.99
		6’ on top	2.61 sec		
		6’ on bottom	2.63 sec		
		6’ on both	2.58 sec		

* Average mean duration time indicates the mean value of the mean duration time among four (two pairs of) color percepts under two disparities of the fixation cross (maximum time is 30 sec).

Table 7-3. Results for the total dominance time (3’ disparity for the fixation cross)

Observer	Temporal Frequency	Experimental Condition	Average Total Dominance Time	F (1, 128)	*p*
1	3.13 Hz	No disparity	26.50 sec	0.17	0.68
		3’ disparity	26.62 sec		
	3.75 Hz	No disparity	26.74 sec	0.05	0.83
		3’ disparity	26.72 sec		
	4.69 Hz	No disparity	26.98 sec	0.27	0.60
		3’ disparity	26.97 sec		
2	3.13 Hz	No disparity	29.91 sec	0.01	0.97
		3’ disparity	29.91 sec		
	3.75 Hz	No disparity	29.89 sec	0.01	0.98
		3’ disparity	29.90 sec		
	4.69 Hz	No disparity	29.91 sec	0.02	0.88
		3’ disparity	29.89 sec		
4	3.13 Hz	No disparity	29.82 sec	0.01	0.96
		3’ disparity	29.85 sec		
	3.75 Hz	No disparity	29.94 sec	0.01	0.95
		3’ disparity	29.88 sec		
	4.69 Hz	No disparity	29.76 sec	0.02	0.89
		3’ disparity	29.88 sec		

* Average total dominance time indicates the mean value of the total dominance time among four (two pairs of) color percepts under four disparities of the discs (maximum time is 30 sec).

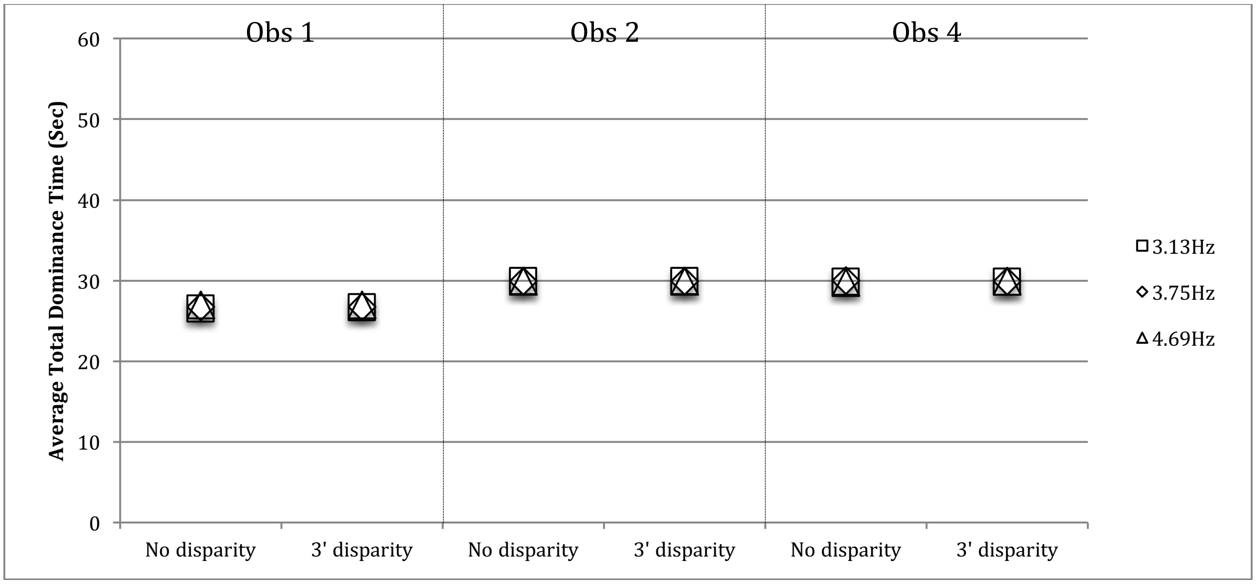

Figure 7-8. As Figure 7-6, but the fixation cross is presented with no disparity and 3’ disparity.

Table 7-4. Results for the mean duration time (3’ disparity for the fixation cross)

Observer	Temporal Frequency	Experimental Condition	Average Mean Duration Time	F (1, 128)	*p*
1	3.13 Hz	No disparity	1.88 sec	0.01	0.89
		3’ disparity	1.87 sec		
	3.75 Hz	No disparity	1.95 sec	0.01	0.89
		3’ disparity	1.94 sec		
	4.69 Hz	No disparity	2.06 sec	0.04	0.84
		3’ disparity	2.06 sec		
2	3.13 Hz	No disparity	5.03 sec	0.59	0.44
		3’ disparity	5.00 sec		
	3.75 Hz	No disparity	4.94 sec	0.04	0.83
		3’ disparity	4.94 sec		
	4.69 Hz	No disparity	4.88 sec	0.10	0.75
		3’ disparity	4.90 sec		
4	3.13 Hz	No disparity	2.22 sec	0.27	0.60
		3’ disparity	2.25 sec		
	3.75 Hz	No disparity	2.41 sec	0.01	0.94
		3’ disparity	2.41 sec		
	4.69 Hz	No disparity	2.61 sec	0.03	0.86
		3’ disparity	2.61 sec		

* Average mean duration time indicates the mean value of the mean duration time among four (two pairs of) color percepts under four disparities of the discs (maximum time is 30 sec).

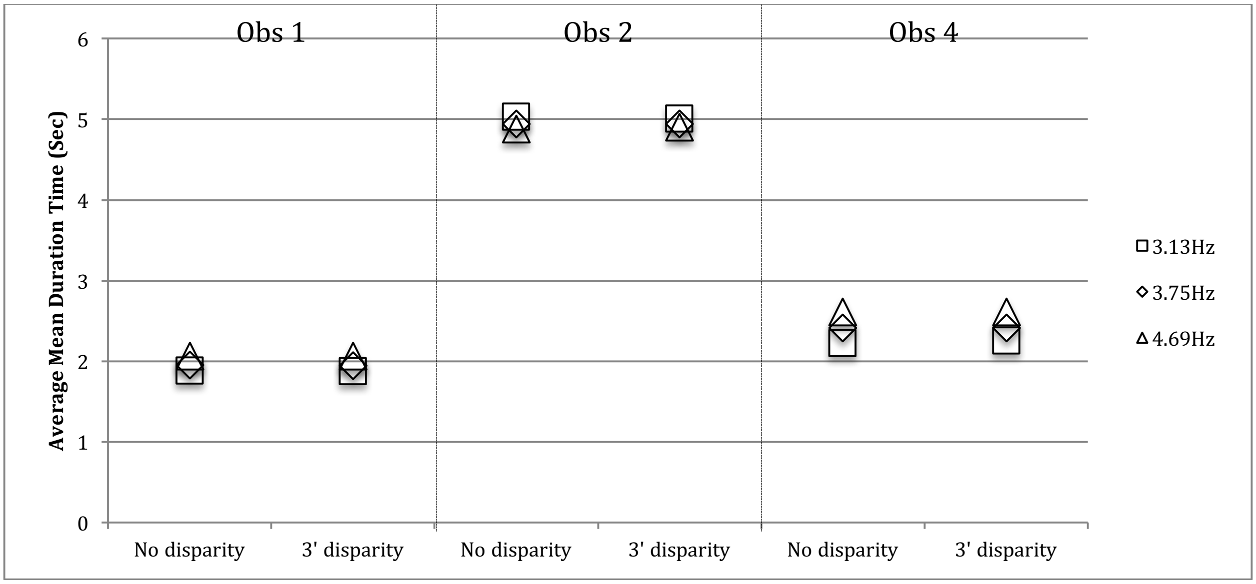

Figure 7-9. As Figure 7-8, but for average mean duration time.

Table 7-5. Results for the total dominance time (10’ disparity for the discs)

Observer	Temporal Frequency	Experimental Condition	Average Total Dominance Time	F (3, 128)	*p*
1	3.13 Hz	No disparity	26.61 sec	0.04	0.98
		10’ on top	26.58 sec		
		10’ on bottom	26.54 sec		
		10’ on both	26.42 sec		
	3.75 Hz	No disparity	26.39 sec	0.45	0.71
		10’ on top	26.51 sec		
		10’ on bottom	26.69 sec		
		10’ on both	26.72 sec		
	4.69 Hz	No disparity	26.63 sec	0.12	0.95
		10’ on top	26.73 sec		
		10’ on bottom	26.50 sec		
		10’ on both	26.79 sec		
2	3.13 Hz	No disparity	29.89 sec	0.01	0.99
		10’ on top	29.89 sec		
		10’ on bottom	29.92 sec		
		10’ on both	29.90 sec		
	3.75 Hz	No disparity	29.90 sec	0.21	0.89
		10’ on top	29.91 sec		
		10’ on bottom	29.74 sec		
		10’ on both	29.89 sec		
	4.69 Hz	No disparity	29.94 sec	0.01	0.99
		10’ on top	29.93 sec		
		10’ on bottom	29.94 sec		
		10’ on both	29.93 sec		
4	3.13 Hz	No disparity	29.95 sec	0.01	0.99
		10’ on top	29.83 sec		
		10’ on bottom	29.98 sec		
		10’ on both	29.89 sec		
	3.75 Hz	No disparity	29.96 sec	0.01	0.99
		10’ on top	29.99 sec		
		10’ on bottom	29.95 sec		
		10’ on both	29.93 sec		
	4.69 Hz	No disparity	29.85 sec	0.01	0.99
		10’ on top	29.90 sec		
		10’ on bottom	29.93 sec		
		10’ on both	29.83 sec		

* Average total dominance time indicates the mean value of the total dominance time among four (two pairs of) color percepts under two disparities of the fixation cross (maximum time is 30 sec).

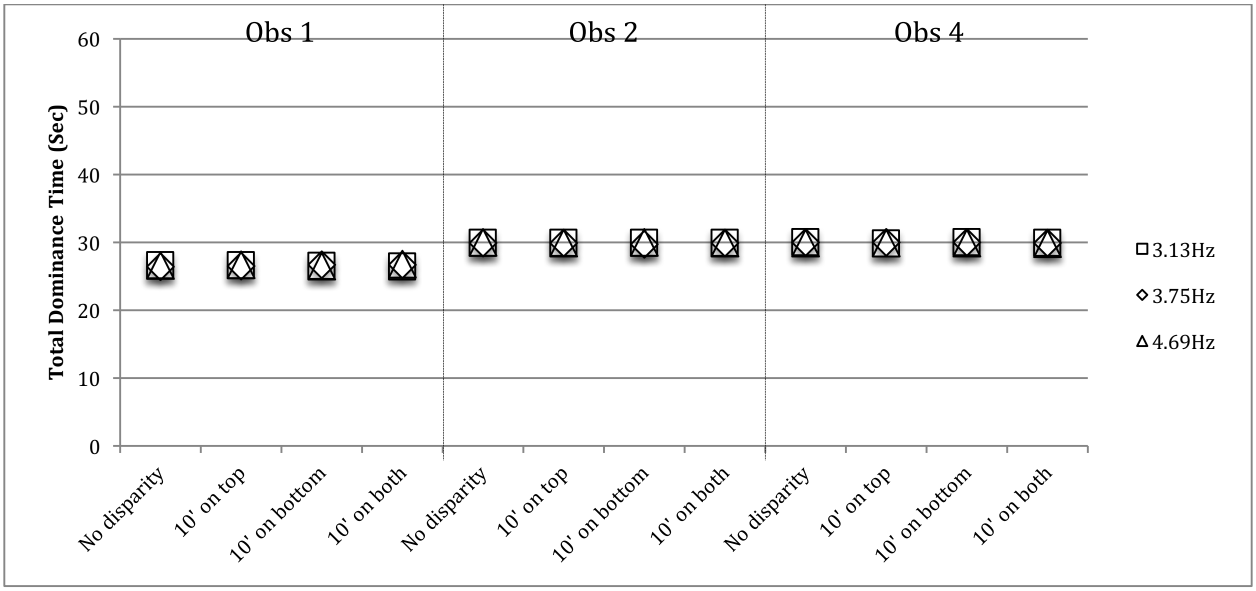

Figure 7-10. Average total dominance time when two discs are oscillated with no disparity, 10’ on top disc, 10’ on bottom disc and 10’ on both discs. Each open symbol indicates the average total dominance time of the four chromaticities at a given temporal frequency for each observer.

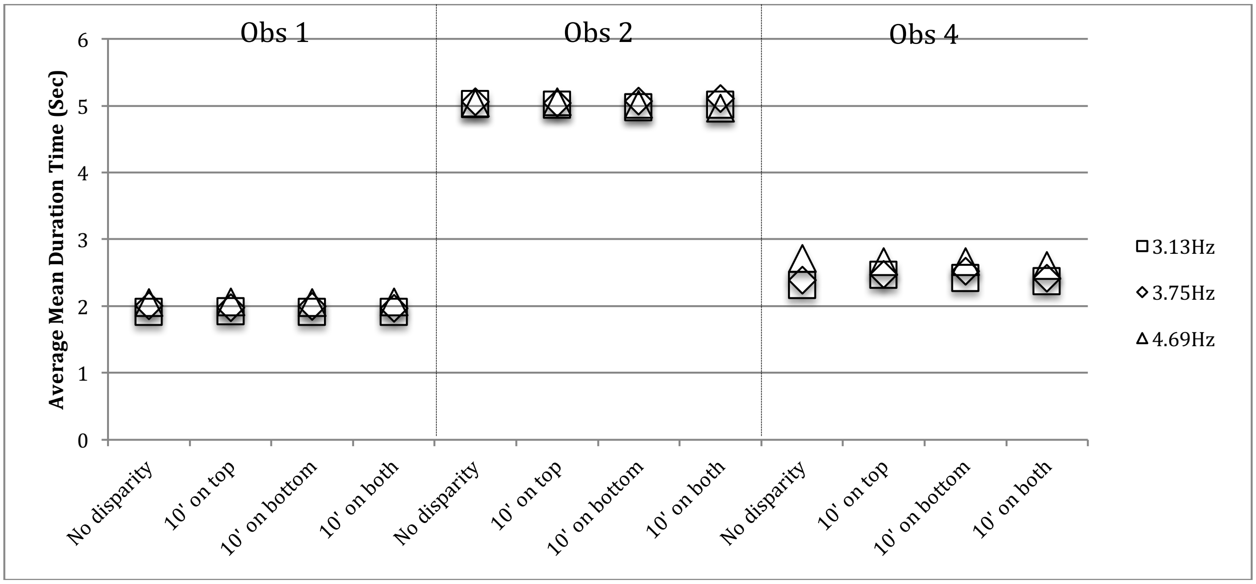

Figure 7-11. As Figure 7-10, but for average mean duration time.

Table 7-6. Results for the mean duration time (10’ disparity for the discs)

Observer	Temporal Frequency	Experimental Condition	Average Mean Duration Time	F (3, 128)	*p*
1	3.13 Hz	No disparity	1.91 sec	0.23	0.87
		10’ on top	1.92 sec		
		10’ on bottom	1.91 sec		
		10’ on both	1.91 sec		
	3.75 Hz	No disparity	2.01 sec	0.35	0.79
		10’ on top	1.98 sec		
		10’ on bottom	2.00 sec		
		10’ on both	1.97 sec		
	4.69 Hz	No disparity	2.06 sec	0.89	0.45
		10’ on top	2.07 sec		
		10’ on bottom	2.06 sec		
		10’ on both	2.07 sec		
2	3.13 Hz	No disparity	5.02 sec	0.19	0.90
		10’ on top	5.01 sec		
		10’ on bottom	4.98 sec		
		10’ on both	5.01 sec		
	3.75 Hz	No disparity	5.06 sec	0.73	0.54
		10’ on top	5.04 sec		
		10’ on bottom	5.07 sec		
		10’ on both	5.11 sec		
	4.69 Hz	No disparity	5.04 sec	0.79	0.49
		10’ on top	5.06 sec		
		10’ on bottom	5.02 sec		
		10’ on both	4.97 sec		
4	3.13 Hz	No disparity	2.31 sec	0.24	0.87
		10’ on top	2.47 sec		
		10’ on bottom	2.42 sec		
		10’ on both	2.37 sec		
	3.75 Hz	No disparity	2.39 sec	0.77	0.51
		10’ on top	2.48 sec		
		10’ on bottom	2.53 sec		
		10’ on both	2.42 sec		
	4.69 Hz	No disparity	2.72 sec	0.29	0.83
		10’ on top	2.67 sec		
		10’ on bottom	2.67 sec		
		10’ on both	2.61 sec		

* Average mean duration time indicates the mean value of the mean duration time among four (two pairs of) color percepts under two disparities of the fixation cross (maximum time is 30 sec).

Table 7-7. Results for the total dominance time (5’ disparity for the fixation cross)

Observer	Temporal Frequency	Experimental Condition	Average Total Dominance Time	F (1, 128)	*p*
1	3.13 Hz	No disparity	26.46 sec	0.77	038
		5’ disparity	26.62 sec		
	3.75 Hz	No disparity	26.57 sec	0.14	0.71
		5’ disparity	26.59 sec		
	4.69 Hz	No disparity	26.59 sec	0.12	0.72
		5’ disparity	26.73 sec		
2	3.13 Hz	No disparity	29.89 sec	0.01	0.92
		5’ disparity	29.90 sec		
	3.75 Hz	No disparity	29.91 sec	0.32	0.57
		5’ disparity	29.81 sec		
	4.69 Hz	No disparity	29.93 sec	0.01	0.97
		5’ disparity	29.93 sec		
4	3.13 Hz	No disparity	29.90 sec	0.02	0.92
		5’ disparity	29.93 sec		
	3.75 Hz	No disparity	29.97 sec	0.01	0.98
		5’ disparity	29.95 sec		
	4.69 Hz	No disparity	29.95 sec	0.04	0.84
		5’ disparity	29.80 sec		

* Average total dominance time indicates the mean value of the total dominance time among four (two pairs of) color percepts under four disparities of the discs (maximum time is 30 sec).

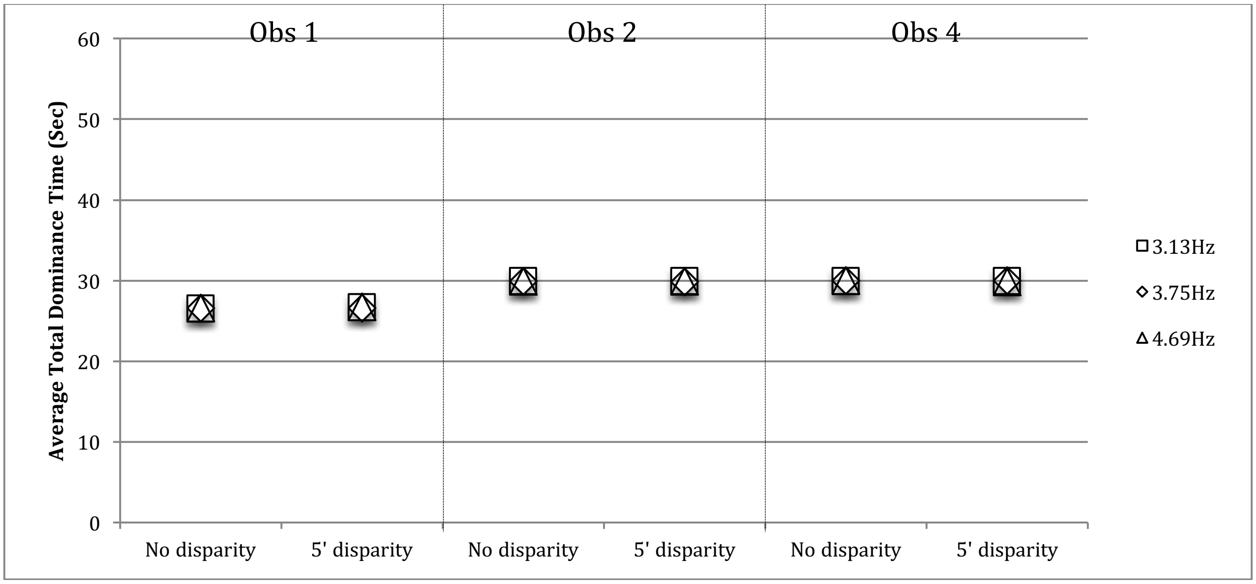

Figure 7-12. As Figure 7-10, but the fixation cross is presented with no disparity and 5’ disparity.

Table 7-8. Results for the mean duration time (5’ disparity for the fixation cross)

Observer	Temporal Frequency	Experimental Condition	Average Mean Duration Time	F (1, 128)	*p*
1	3.13 Hz	No disparity	1.94 sec	1.47	0.23
		5’ disparity	1.89 sec		
	3.75 Hz	No disparity	2.01 sec	0.65	0.42
		5’ disparity	1.98 sec		
	4.69 Hz	No disparity	2.07 sec	0.07	0.78
		5’ disparity	2.06 sec		
2	3.13 Hz	No disparity	5.03 sec	1.31	0.25
		5’ disparity	4.99 sec		
	3.75 Hz	No disparity	5.06 sec	0.17	0.68
		5’ disparity	5.08 sec		
	4.69 Hz	No disparity	5.06 sec	2.98	0.08
		5’ disparity	4.98 sec		
4	3.13 Hz	No disparity	2.40 sec	0.41	0.52
		5’ disparity	2.38 sec		
	3.75 Hz	No disparity	2.42 sec	0.39	0.54
		5’ disparity	2.48 sec		
	4.69 Hz	No disparity	2.64 sec	1.58	0.21
		5’ disparity	2.69 sec		

* Average mean duration indicates the mean value of the mean duration time among four (two pairs of) color percepts under four disparities of the discs (maximum time 30 sec).

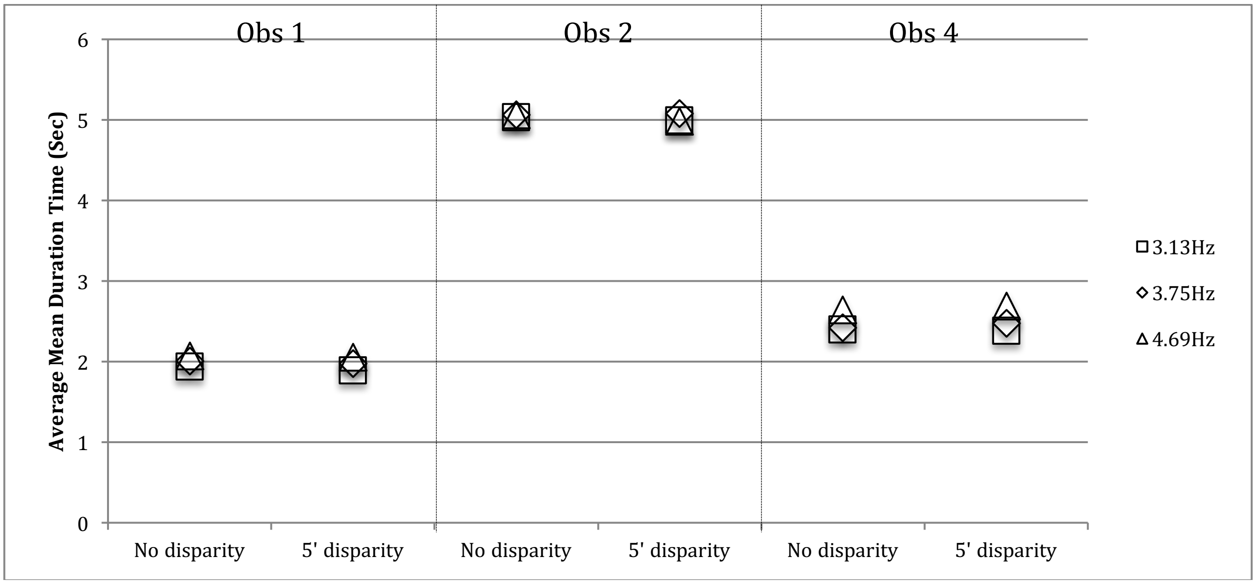

Figure 7-13. As Figure 7-12, but for average mean duration time.

All the F values from the tables are very small, especially for observer 2 and 4. This is because they nearly always perceive both discs as the same color, so that the average total dominance time is almost 30 seconds, meaning there was a ceiling effect.

Based on the disparities of the grouped percepts under binocular fusion, there is no evidence to support the conclusion that grouping in the resolution of CISR depends on identical stereoscopic disparity of the grouped objects presented at a common temporal frequency. In addition, there is no evidence to support that grouping in resolving CISR depends on the same disparity of the fixation cross and the grouped objects. In sum, the results of this experiment indicate no evidence to support that objects can be grouped based on equal stereoscopic percept between grouped objects or between the group and the fixation cross.

CHAPTER 8

EXPERIMENT 6: CONTRIBUTION TO GROUPING OF OBJECTS FROM COHERENT AMBIGUITY IN CHROMATIC INTEROCULAR-SWITCH RIVALRY

8.1 Rationale

The purpose of this experiment is to investigate the contribution of coherent ambiguity to grouped percepts during chromatic interocular-switch rivalry (CISR). Coherent ambiguity is defined as similar retinal stimulus features. It is constructed by aligning two discs vertically in each eye and flickering them at the same temporal phase synchrony at a common temporal frequency. To eliminate the coherence, the two discs in this experiment are changed from both ambiguous to one non-rivalrously clear and the other ambiguous. To implement it, the temporal phase difference between the two eyes is eliminated for one disc, so it is never rivalrous. The other disc still has CISR. Thus, an incoherent ambiguity of the grouped percepts has been created based on one disc with periodic non-rivalrous chromaticity changes and one disc with CISR. The experimental question is whether the resolution of CISR is influenced by the non-rivalrous disc. If so, and the two discs' percepts are grouped, then both the total dominance and mean duration time of simultaneously perceiving two spatially separated discs of the same color should be above chance.

The previous experiments do not support the view that the resolution of CISR by grouping depends on either the temporal relations or the stereoscopic disparity among the grouped objects. In those studies, the discs were always flickering in the opposite temporal phases between the two eyes, so that the fused percepts were rivalrous and therefore produced the identical perceptual ambiguity for color. It is possible that this *equality of ambiguity* forms a global coherence contributing to the grouping. Other lines of research suggest the importance of a globally coherent percept for grouping. For example, the dominance time of a local grating viewed during binocular rivalry is increased by a global coherence of motion from three additional non-rivalrous gratings with the same direction of motion (Alais & Blake, 1998; Sobel & Blake, 2002). This grouping effect has also been found in perceptual fading (Vergeer & van Lier, 2007) and feature binding (Wang & Shevell, 2014; Shevell & Wang, 2016).

8.2 Methods

A stimulus paradigm with two discs was tested. That is, two spatially homogeneous discs were aligned vertically in each eye at the corresponding retinal locations so that two fused discs were perceived (see Fig. 2-1(b)).

Based on this paradigm, the top or the bottom disc in both eyes was always identical and changed in chromaticity non-rivalrously (periodical flickering) at 0.17Hz, while the other disc oscillated with CISR. Thus, the non-rivalrous disc was switching between two colors slowly once every 3 seconds, while the rivalrous disc was oscillating much more quickly, as in the previous experiments. This experiment also included a control condition, in which both discs were presented with the usual CISR at the same phase and temporal frequency. Thus, three experimental conditions were tested (Fig. 8-1).

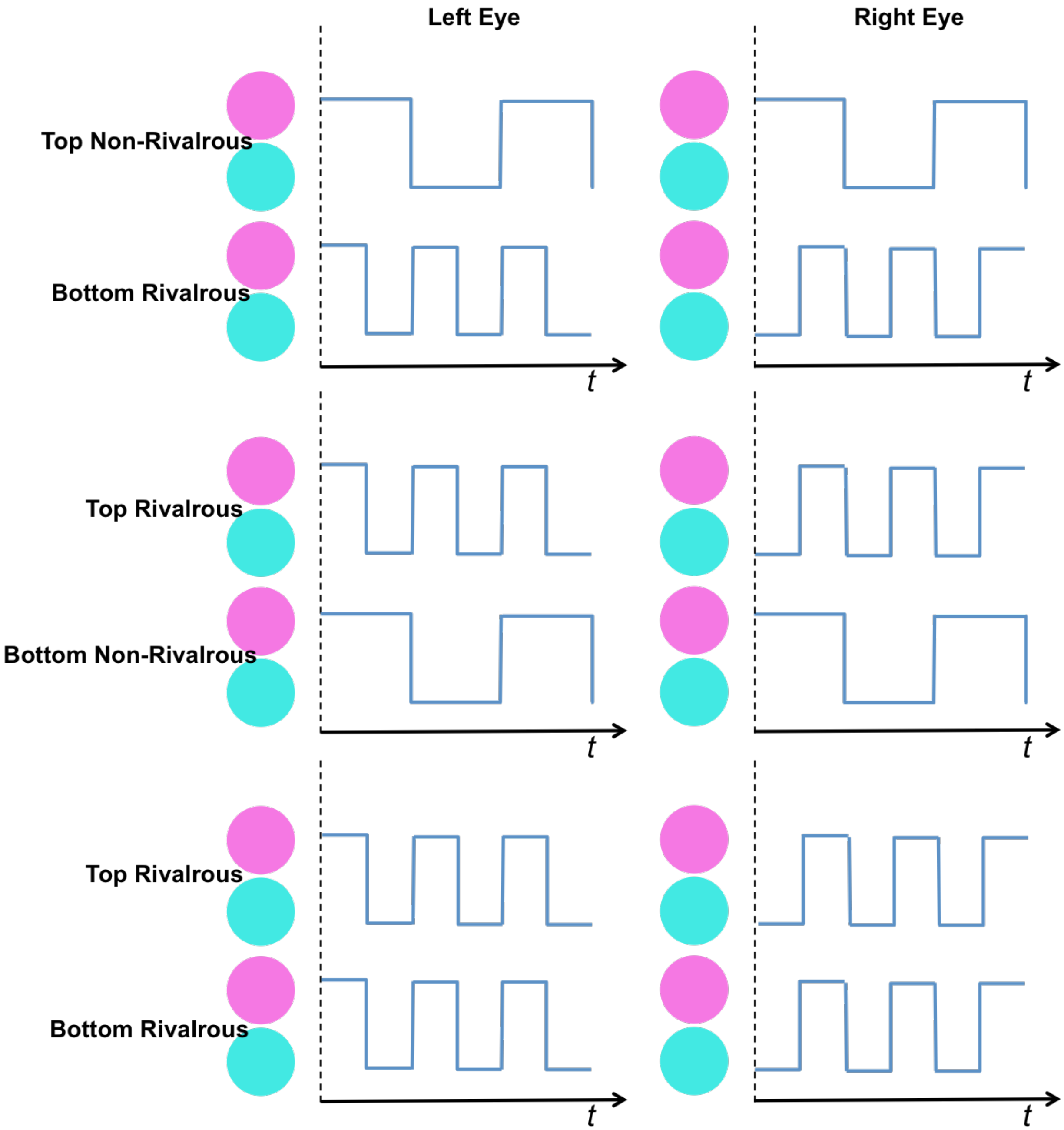

Figure 8-1. Experimental conditions in experiment 6. Top and middle rows represent how the top and bottom discs oscillate, one with chromatic inteocular-switch rivalry (CISR) and the other without rivalry. The bottom row represents both discs oscillating with typical CISR. Left and right columns represent stimuli oscillating in the left and right eye, respectively.

In this experiment, each session was composed of six trials in a random sequence, and each trial tested one of two pairs of chromaticities (described in Chapter 2) in each of the three experimental conditions (see Fig. 8-1) at a given temporal frequency. In other words, either a combination of one non-rivalrous flickering disc and one CISR disc or two CISR discs were repeated six times randomly with each disc alternating between two chromaticities. The task was to report the color of the top and the bottom discs in the fused binocular percept. The total dominance time and mean duration time of each color percept during each trial was calculated.

In separate sessions, three different square-wave temporal frequencies were tested: 3.13hz, 3.75Hz and 4.69Hz. Each observer ran each frequency in each of five sessions on different days, so fifteen sessions were completed in total.

8.3 Results

The total dominance time of each color percept is shown in Figure 8-2 (vertical axis) as a function of the chromaticities (horizontal axis) and the temporal frequency (open symbols). The chromaticities are grouped as “nonrivalry and CISR” and “both CISR” (left to right along the horizontal axis). Here, “nonrivalry and CISR” is the average of two experimental conditions with either the top or the bottom disc oscillating non-rivalrously. Within each group, the chromaticities are arranged as one pair along the l and s chromatic directions [(l = 0.715, s = 1.0), (l = 0.615, s = 1.0), (l = 0.665, s = 1.8) and (l = 0.665, s = 0.2)]. The temporal frequencies are indicated using various open symbols. The symbol color is the approximate color of the tested chromaticity. Each panel shows results for one observer. Figure 8-3 shows the mean duration time of each color percept the same format as the total dominance time in Figure 8-2.

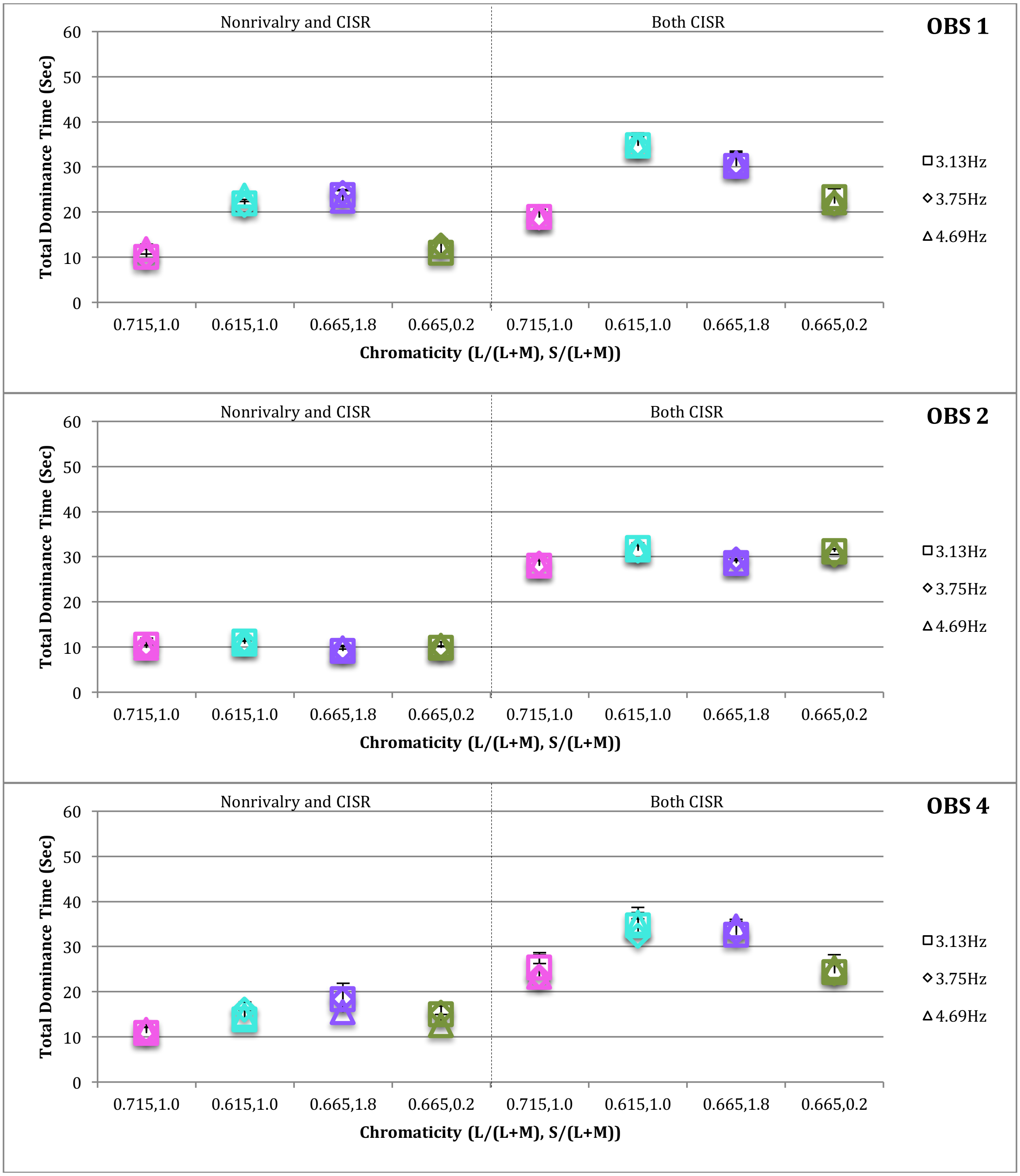

Figure 8-2. Total dominance time of four (two pairs of) color percepts at three temporal frequencies. The chromaticities are grouped as “nonrivalry and CISR” and “both CISR”. Within each group, the chromaticities (*l*, *s*) are arranged as (0.715, 1.0), (0.615, 1.0), (0.665, 1.8) and (0.665, 0.2).

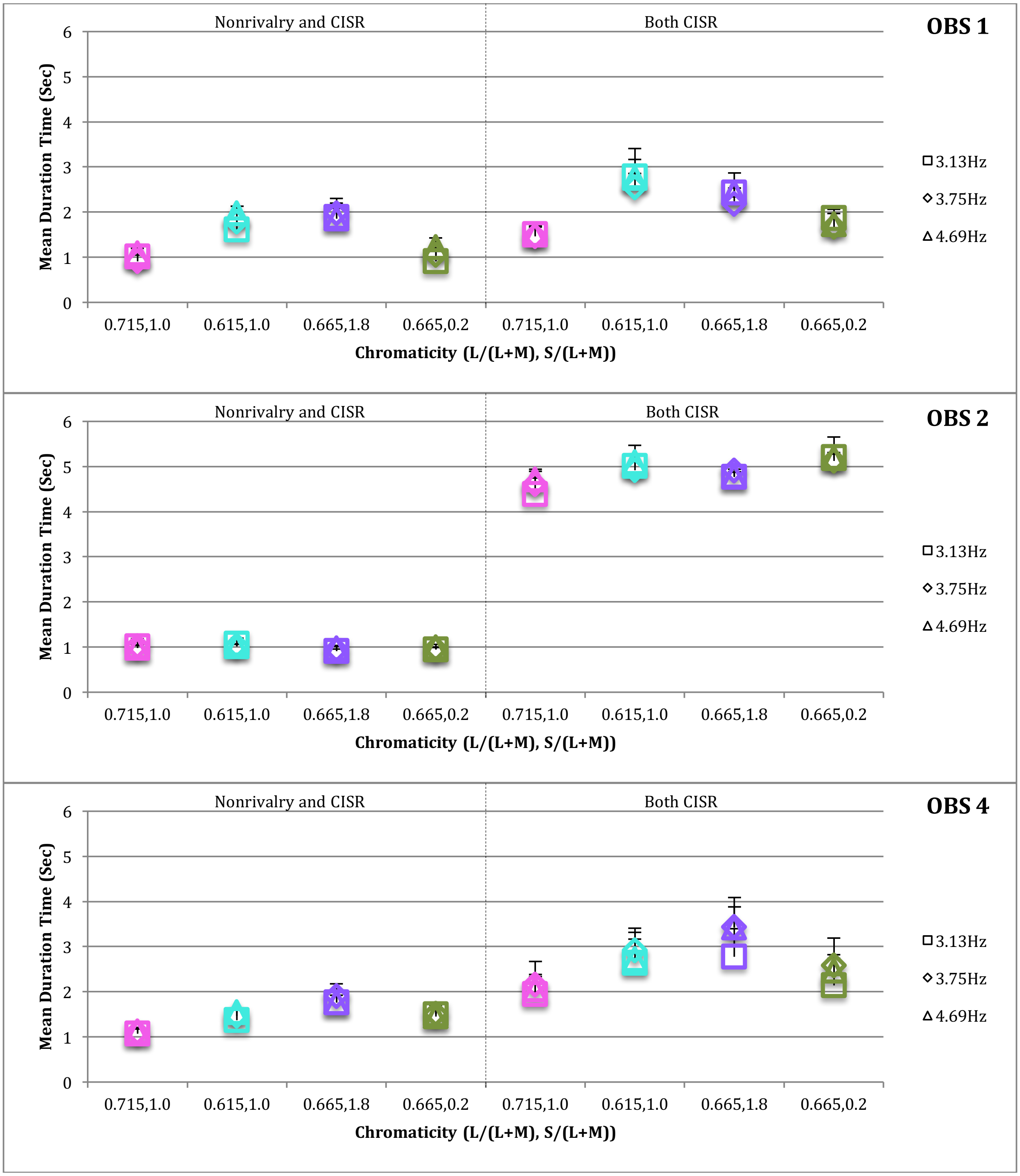

Figure 8-3. As Figure 8-2, but for mean duration time.

The total dominance time and the mean duration time are analyzed separately for each observer at each temporal frequency, by completing two-way analysis of variance (ANOVA). One factor is the color (four levels) and the other is the selected experimental condition (two levels: “nonrivalry and CISR” and “both CISR”, as described in the previous section).

For each observer, the results show that the total dominance time is significantly different for the two experimental conditions (see Table 8-1 and Figure 8-4). The same finding holds for the mean duration time (see Table 8-2 and Figure 8-5). For the total dominance time, there is a statistically significant interaction between the color and the experimental condition for observer 1 at 3.13 Hz and 3.75 Hz, observer 2 at 3.13 Hz, 3.75

Table 8-1. Results of the total dominance time

Observer	Temporal Frequency	Experimental Condition	Average Total Dominance Time	F (1, 32)	*p*
1	3.13 Hz	Nonrivalry and CISR	16.62 sec	189.16	<.001
		Both CISR	26.78 sec		
	3.75 Hz	Nonrivalry and CISR	17.10 sec	217.09	<.001
		Both CISR	26.45 sec		
	4.69 Hz	Nonrivalry and CISR	17.55 sec	152.76	<.001
		Both CISR	26.59 sec		
2	3.13 Hz	Nonrivalry and CISR	10.14 sec	3079.56	<.001
		Both CISR	29.90 sec		
	3.75 Hz	Nonrivalry and CISR	10.13 sec	6685.27	<.001
		Both CISR	29.88 sec		
	4.69 Hz	Nonrivalry and CISR	10.13 sec	5106.83	<.001
		Both CISR	29.88 sec		
4	3.13 Hz	Nonrivalry and CISR	14.50 sec	312.45	<.001
		Both CISR	29.22 sec		
	3.75 Hz	Nonrivalry and CISR	15.19 sec	118.58	<.001
		Both CISR	28.19 sec		
	4.69 Hz	Nonrivalry and CISR	13.51 sec	449.40	<.001
		Both CISR	29.54 sec		

* Average total dominance time indicates the mean value of the total dominance time among four (two pairs of) color percepts (maximum time is 30 sec).

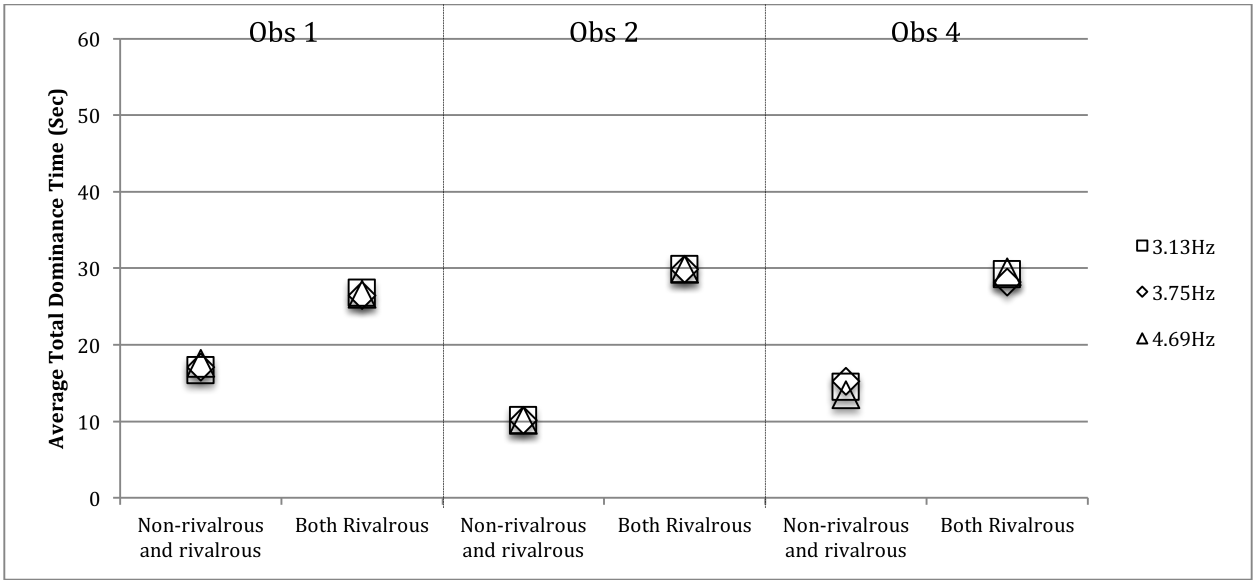

Figure 8-4. Average total dominance time when two discs are “nonrivalry and CISR” or “both CISR”. Each open symbol indicates the average total dominance time of the four chromaticities at a given temporal frequency for each observer.

Table 8-2. Results of the mean duration time

Observer	Temporal Frequency	Experimental Condition	Average Mean Duration Time	F (1, 32)	*p*
1	3.13 Hz	Nonrivalry and CISR	1.36 sec	90.96	<.001
		Both CISR	2.15 sec		
	3.75 Hz	Nonrivalry and CISR	1.44 sec	40.16	<.001
		Both CISR	1.96 sec		
	4.69 Hz	Nonrivalry and CISR	1.53 sec	23.44	<.001
		Both CISR	2.10 sec		
2	3.13 Hz	Nonrivalry and CISR	0.99 sec	2043.77	<.001
		Both CISR	4.84 sec		
	3.75 Hz	Nonrivalry and CISR	0.98 sec	1823.35	<.001
		Both CISR	4.88 sec		
	4.69 Hz	Nonrivalry and CISR	0.99 sec	10481.9	<.001
		Both CISR	4.94 sec		
4	3.13 Hz	Nonrivalry and CISR	1.42 sec	33.71	<.001
		Both CISR	2.37 sec		
	3.75 Hz	Nonrivalry and CISR	1.49 sec	76.59	<.001
		Both CISR	2.77 sec		
	4.69 Hz	Nonrivalry and CISR	1.47 sec	136.04	<.001
		Both CISR	2.66 sec		

* Average mean duration time indicates the mean value of the mean duration time among four (two pairs of) color percepts (maximum time is 30 sec).

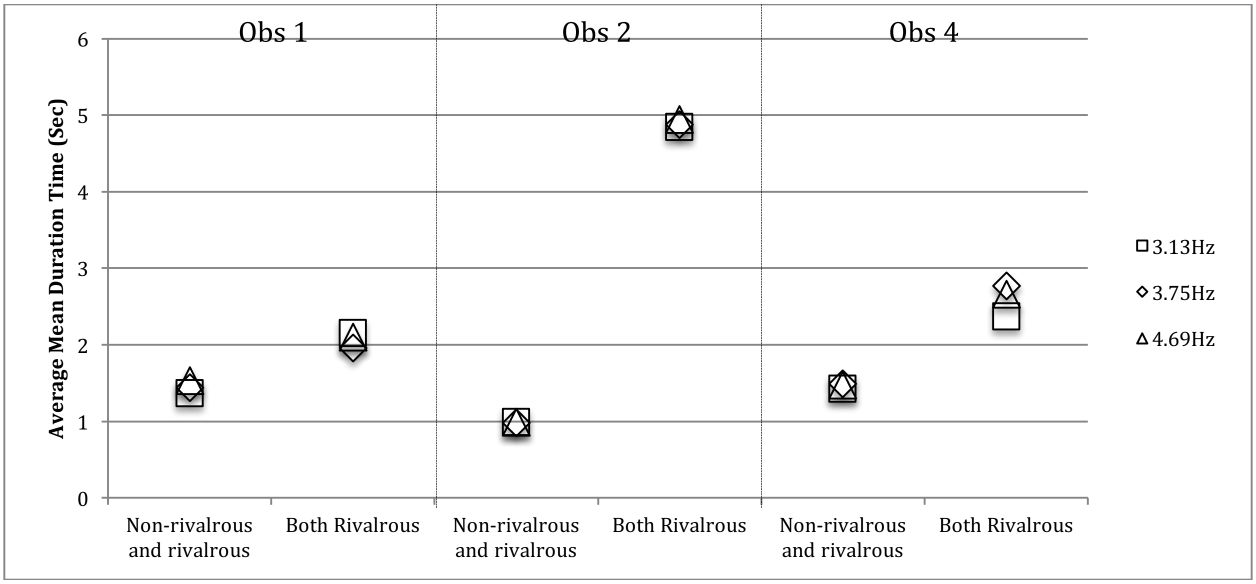

Figure 8-5. As Figure 8-4, but for average mean duration time.

Hz and 4.69 Hz, and observer 4 at 3.13 Hz and 4.69 Hz ($p < .05$); for the mean duration time, there is also a statistically significant interaction between the color and the experimental condition for observer 1 at 3.13 Hz and 3.75 Hz, and observer 2 at 3.13 Hz and 3.75 Hz ($p < .05$). This indicates that the time for each color percept depends to a different extent whether one of the discs is rivalrous or not.

In sum, when one disc flickers non-rivalrously, the dominance time of simultaneously perceiving two discs with the same color is substantially decreased, compared to that when viewing both discs with CISR. Thus, the resolution of CISR has been found to depend on the coherent ambiguity of the grouped objects. The results of this experiment indicate that corresponding coherent rivalry between objects determines the degree to which the objects are grouped to give the same color percept.

CHAPTER 9

EXPERIMENT 7: EFFECT OF PERCEPT DURING CHROMATIC INTEROCULAR-SWITCH RIVALRY ON CHROMATIC ADAPTATION

9.1 Rationale

The purpose of this experiment is to investigate whether the percept during chromatic interocular-switch rivalry (CISR) affects chromatic adaptation. The experimental question, therefore, is whether the predominant hue percept during CISR affects the state of chromatic adaptation more than the less dominant hue. If the visual system adapts to a slowly alternating color percept - for example, a color predominantly “pink”- then a greenish hue would be perceived when an equal-energy-spectrum (EES) “white” light is presented right after chromatic adaptation. Alternatively, if adaptation depends on a rapidly flickering stimulus, then the time average (EES) “white” chromaticity would cause the same chromatic adaptation, regardless of the predominant percept.

In the past few decades, a great deal of research in the area of binocular rivalry has focused on a fundamental question: what rivals during binocular rivalry? Some studies support “eye” rivalry while others point to “stimulus” rivalry. According to each of these theories, during CISR, either a fast flicker between two chromaticities or a slow alternation between two colors is perceived, respectively. Recently, it was confirmed that the percept is a slow alternation between two colors (Christiansen, D'Antona & Shevell, 2014), which is consistent with "stimulus" rivalry originating at a cortical level. However, it is still unclear what neural response controls adaptation during CISR. Is the visual system adapting to a fast flickering stimulus in each eye or a slowly alternating percept? The answer to this question can be determined by the visual phenomenon of chromatic adaptation, in which color appearance changes relatively slowly and can last for a few minutes following the effect of chromatic adapting light (Shevell, 2000).

9.2 Methods

A stimulus paradigm with one disc was used. That is, one spatially homogeneous disc was presented in the central field of each eye at a corresponding retinal location so that one fused disc was perceived (see Fig. 2-1(a)).

Based on this paradigm, two control conditions were tested to measure the degree of chromatic adaptation for each chromaticity viewed alone. In the first condition, with chromatic adaptation to a static disc of "pink", a disc was presented in the left and right eye that was always the chromaticity giving the percept of "pink". After viewing this solid color percept for 60 seconds, these stimuli disappeared and the screen was dark for 500 ms. Then a test disc with a randomly assigned chromaticity (varied along only the *l* chromatic direction) was presented with a beep and the task was to report whether the test disc appeared "reddish" or "greenish". After the judgment, the same stimulus disc (static "pink") was viewed again for 10 seconds, then the 500 ms dark period, and then the same task was performed with the test disc whose chromaticity had been adjusted based on the previous judgment on the *l* chromatic direction (Fig. 9-1). The chromaticity of the test was varied on each trial using a staircase procedure, which was designed to find a balance point at which the chromaticity appeared neither "reddish" nor "greenish". Each staircase continued for ten reversals, which were defined as switching of judgments (e.g. from "reddish" to "greenish"). The initial step size of changing chromaticity was 0.02 along the *l* chromatic direction, and on each turnaround of the staircase the step decreased to half of the previous size until reaching a minimum of 0.0025. The balance point was calculated as the average chromaticity of the last six reversals. Two randomized interleaved staircases were used to estimate the balance point. In the second condition, with chromatic adaptation to a static disc that appeared "blue-green", the adapting disc in the left and right eyes was always

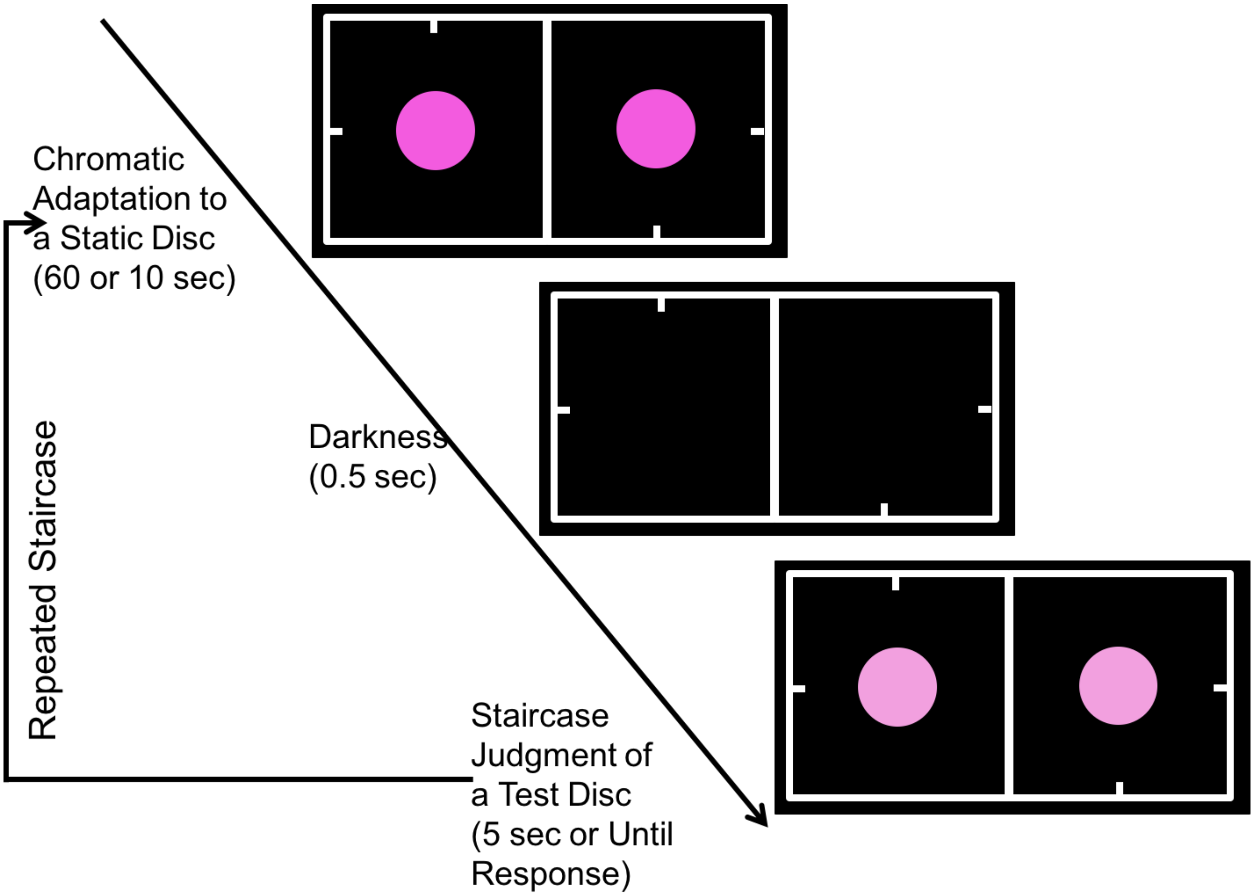

Figure 9-1. Experimental procedure for chromatic adaptation to a static disc of "pink" in experiment 7. The stimulus disc in the left and right eye was always static with the same color of "pink". After adaptation to this solid color, the test disc was judged to be either "reddish" or "greenish".

presented with the same chromaticity giving the percept of “blue-green”. The staircase procedure generally was the same as in the first condition. In addition, two similar control conditions were conducted as the adapting chromaticities varied along the *s* chromatic direction. That is, the adapting disc was either a “purple” disc in one condition, or a “lime” disc in the other condition (equal to the “purple” in *l* value but with much lower *s* value). The test disc was varied along the *s* chromatic direction in each step using the same staircase procedure as for the *l* chromatic direction, except the initial step size for *s* was 0.2, decreasing by half on each turnaround until it reached 0.025.

Three more experimental conditions were tested using essentially the same paradigm. In the first condition, chromatic adaptation was to a disc with CISR. While viewing this percept (e.g., slow alternation between “pink” and “blue-green” colors) for 60 seconds, the observer was asked to report the color of the disc in the fused binocular percept (as in previous experiments). Then the adapting disc disappeared and the screen was dark for 500 ms. After that, a test disc with a randomly assigned chromaticity (varied along the *l* chromatic direction) was presented with a beep and the task was to report whether the test disc appeared “reddish” or “greenish”. After the judgment, the same CISR adapting discs (rivaling between “pink” and “blue-green”) were viewed again for 10 seconds while reporting the perceived color of the disc in the fused binocular percept. Then the screen went dark for 500 ms and the same task was performed with the test (Fig 9-2). The staircase procedure was the same as for the control conditions with the test disc varied along the *l* chromatic direction. In the second condition, with chromatic adaptation to a non-rivalrous disc, the temporal oscillation of the disc in the left eye was always at the same square-wave frequency and same phase, compared to the disc in the right eye at the

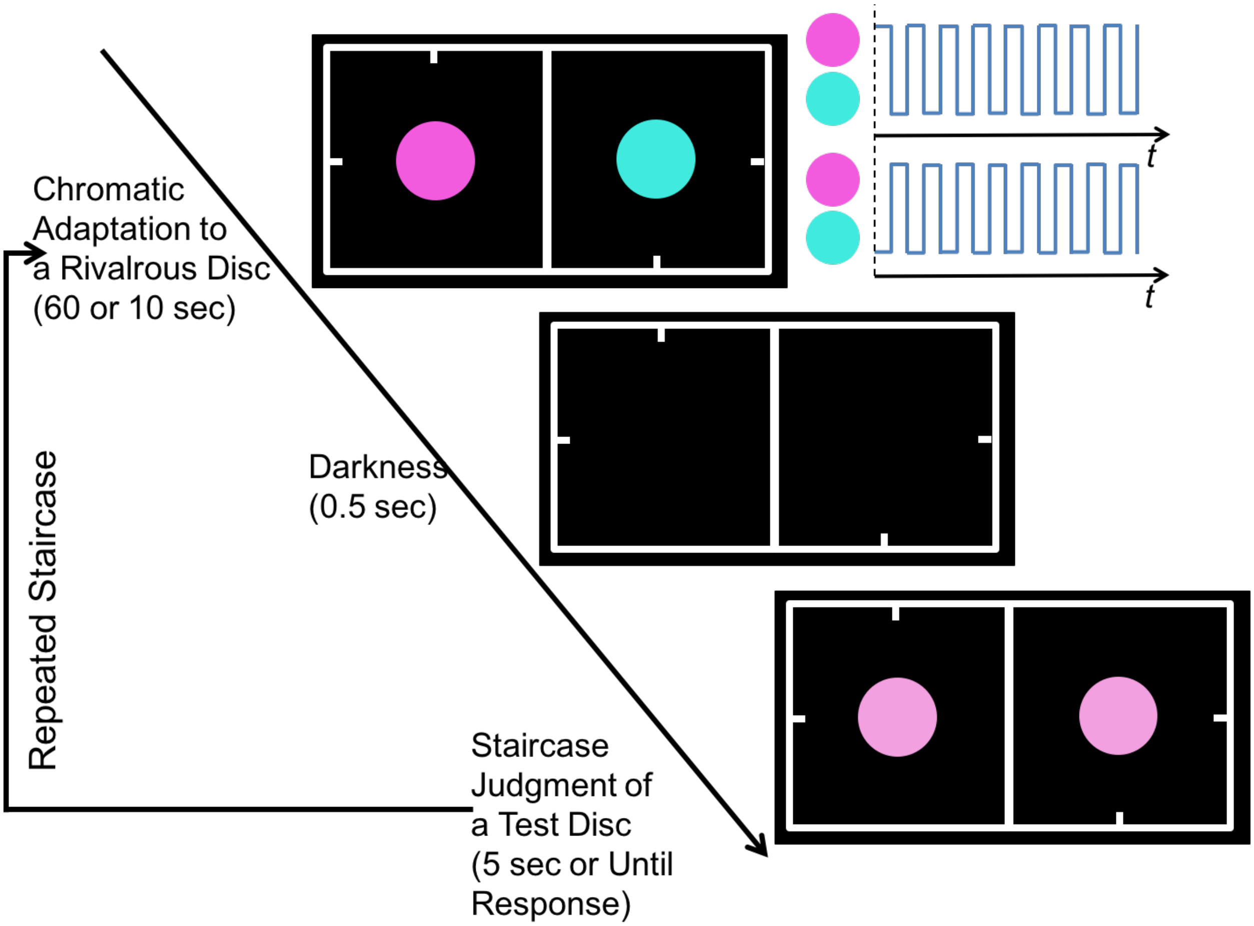

Figure 9-2. Experimental procedure for chromatic adaptation to a rivalrous disc oscillating between "pink" and "blue-green" in experiment 7. As Figure 9-1, but the adaptating disc in the left eye always oscillates at the same square-wave frequency but in opposite phase relative to the disc in the right eye at the corresponding retinal location.

corresponding retinal location. The staircase procedure was the same as the first experimental condition except without reporting the color of the disc in the fused binocular percept during adaptation (Fig. 9-3). In the third condition, with chromatic adaptation to a static disc at EES "white" (the time average adapting chromaticity in all other conditions), the disc in the left and right eye was always presented at the same EES chromaticity, and the staircase procedure was the same as for the control conditions. In addition, the same three experimental conditions were repeated as the adapting disc and the test were varied

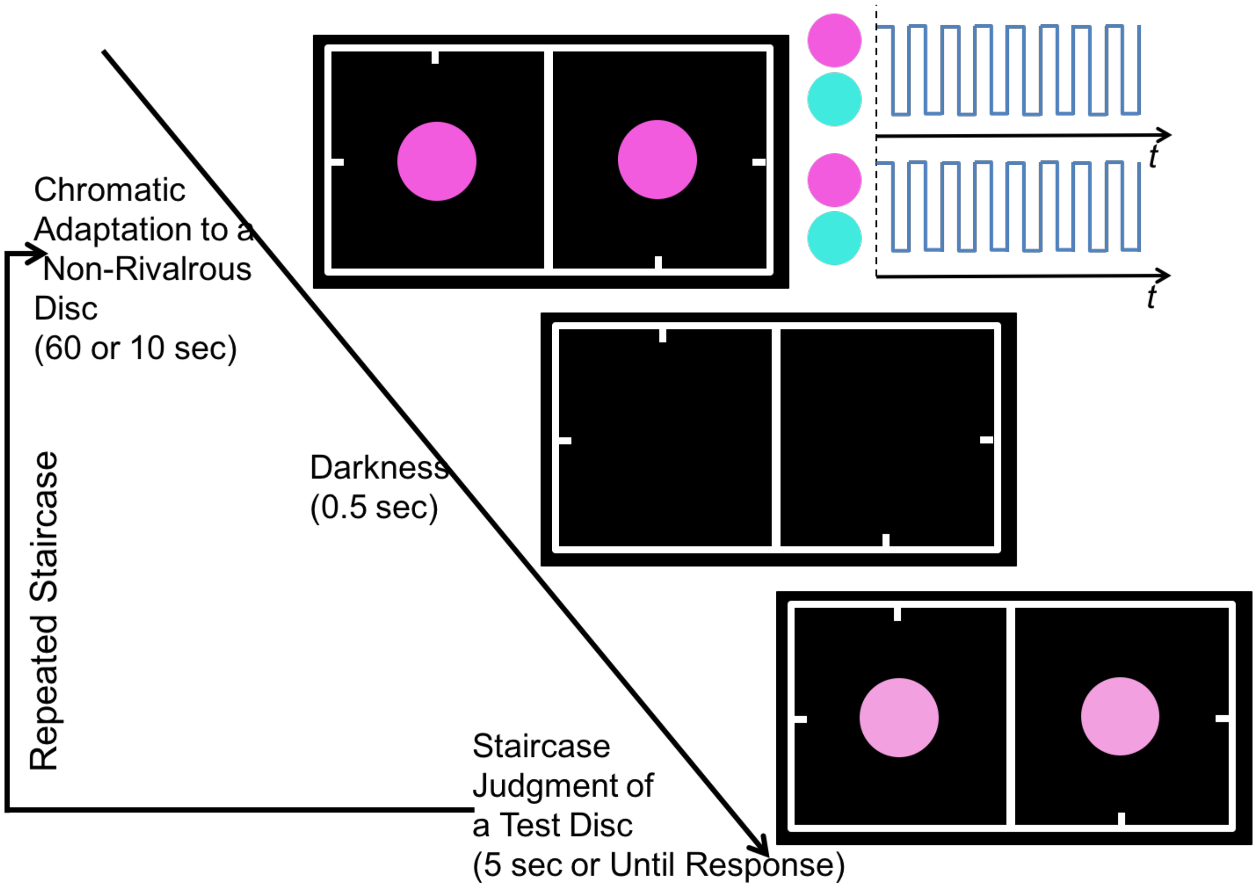

Figure 9-3. Experimental procedure of chromatic adaptation to a non-rivalrous disc oscillating between “pink” and “blue-green” in experiment 7. Same as Figure 9-2, but the adapting disc in the left eye always oscillated at the same square-wave frequency and same phase relative to the disc in the right eye at the corresponding retinal location.

along the *s* chromatic direction. That is, the stimulus disc was flickering between “purple” and “lime”, and the test disc was varied along the *s* chromatic direction in all three conditions.

In this experiment, each session was composed of five trials, and each trial tested one pair of chromaticities in one of the five conditions. Thus, the same pair of chromaticities was repeated five times under the same condition in each session. The chromaticity of the balance point perceived to be, for example, neither “reddish” nor "greenish" when the test disc varied along the *l* chromatic direction, was determined from the staircases.

In separate sessions, two different pairs of chromaticities (described in Chapter 2) in all five conditions were tested (the control conditions were tested before the experimental conditions, described in the previous section). Only one temporal frequency was used for non-static discs (3.75Hz). Thus, each observer ran ten sessions in total.

9.3 Results

The chromaticity that appeared achromatic after adaptation is shown in Figure 9-4 (vertical axis) as a function of the control-condition adapting chromaticity (horizontal axis). The control conditions are grouped as "static (0.715, 1.0)" and "static (0.615, 1.0)" in the left columns (as the adapting chromaticity is varied along the *l* chromatic direction) or "static (0.665, 1.8)" and "static (0.665, 0.2)" in the right columns (adapting chromaticities varied along the *s* chromatic direction), along the horizontal axis. The symbol color is the approximate color of the adapting chromaticity. Each panel shows results for one observer.

The quantitative measure of chromaticity along the *l* chromatic direction is in different units than the chromaticity along the *s* chromatic direction, so the chromaticities of the test are analyzed separately for each chromatic direction and each observer by completing two-tailed t tests.

For each observer, the results show that the chromaticity of the test after adapting to a static disc of "pink" ($l = 0.715$) is significantly higher than time-average EES "white" (dashed line). Also the chromaticity of the test after adapting to a static disc of "blue-green" ($l = 0.615$) is significantly lower than EES "white". The results also show that the chromaticity after adapting to a static disc of "purple" ($s = 1.8$) is significantly higher than

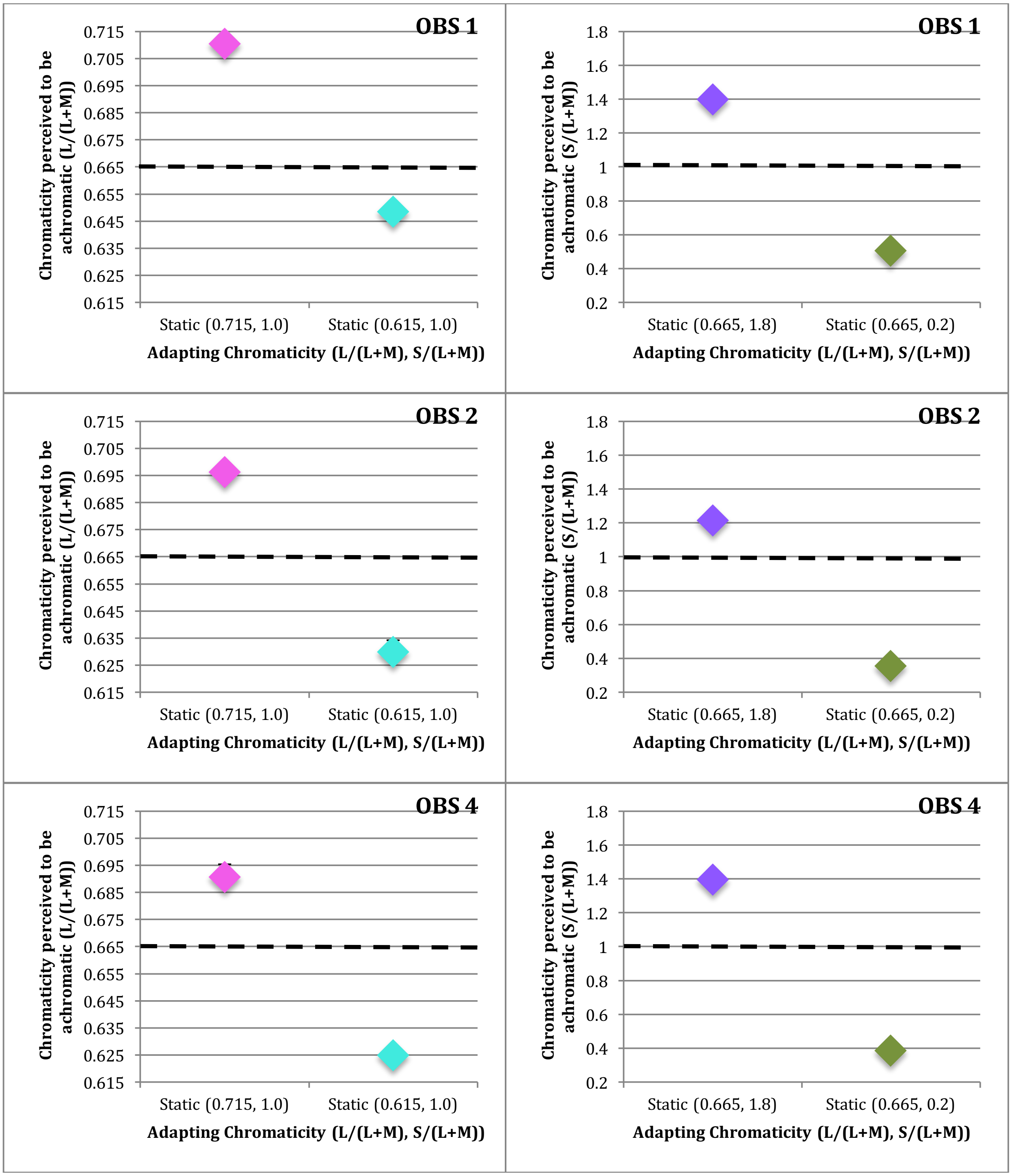

Figure 9-4. Chromaticity perceived to be achromatic at the (0.715, 1.0) or (0.615, 1.0) adapting chromaticity (left columns), or the (0.665, 1.8) or (0.665, 0.2) adapting chromaticity (right columns). The measured chromaticity along either the *l* or *s* chromatic direction is well away from EES "white" (dashed line).

EES “white”, and the chromaticity after adapting to a static disc of “lime” (*s* = 0.2) is significantly lower than EES “white” (see Table 9-1).

Table 9-1. Results of the control conditions

Observer	Chromatic Direction	Chromaticity of stimulus disc	Chromaticity of test disc	t (8)	*p*
1	*l*	Static (0.715, 1.00)	(0.710, 1.00)	27.57	< .001
		Static (0.615, 1.00)	(0.648, 1.00)	11.23	< .001
	s	Static (0.665, 1.80)	(0.665, 1.40)	16.24	< .001
		Static (0.665, 0.20)	(0.665, 0.51)	27.41	< .001
2	*l*	Static (0.715, 1.00)	(0.696, 1.00)	28.75	< .001
		Static (0.615, 1.00)	(0.630, 1.00)	16.07	< .001
	s	Static (0.665, 1.80)	(0.665, 1.21)	8.9	< .001
		Static (0.665, 0.20)	(0.665, 0.36)	29.80	< .001
4	*l*	Static (0.715, 1.00)	(0.691, 1.00)	10.47	< .001
		Static (0.615, 1.00)	(0.625, 1.00)	53.21	< .001
	s	Static (0.665, 1.80)	(0.665, 1.39)	15.29	< .001
		Static (0.665, 0.20)	(0.665, 0.39)	53.20	< .001

* Chromaticity of test disc indicates the average chromaticity of the final balanced percept when adapting to a static disc

Thus, all the observers experience clear and substantial chromatic adaptation from these chromaticities, which is a pre-requisite for the following experiments on chromatic adaptation during CISR.

The chromaticity that appeared achromatic after adaptation to a rivalrous disc, a non-rivalrous disc and a static disc of EES “white” is shown in Figure 9-5 (vertical axis) as a function of the experimental adapting chromaticity (horizontal axis). Here, “rivalrous” indicates CISR (see Figure 9-2), while “non-rivalrous” indicates periodic flickering at 3.75 Hz without rivalry (see Figure 9-3). On the horizontal axis, the experimental conditions are grouped as “rivalrous (0.715, 1.0) to (0.615, 1.0)”, “non-rivalrous (0.715, 1.0) to (0.615, 1.0)” and “static EES (time average)” in the left columns (as the adapting chromaticity is varied along the *l* chromatic direction); or “rivalrous (0.665, 1.8) to (0.665, 0.2)”, “non-

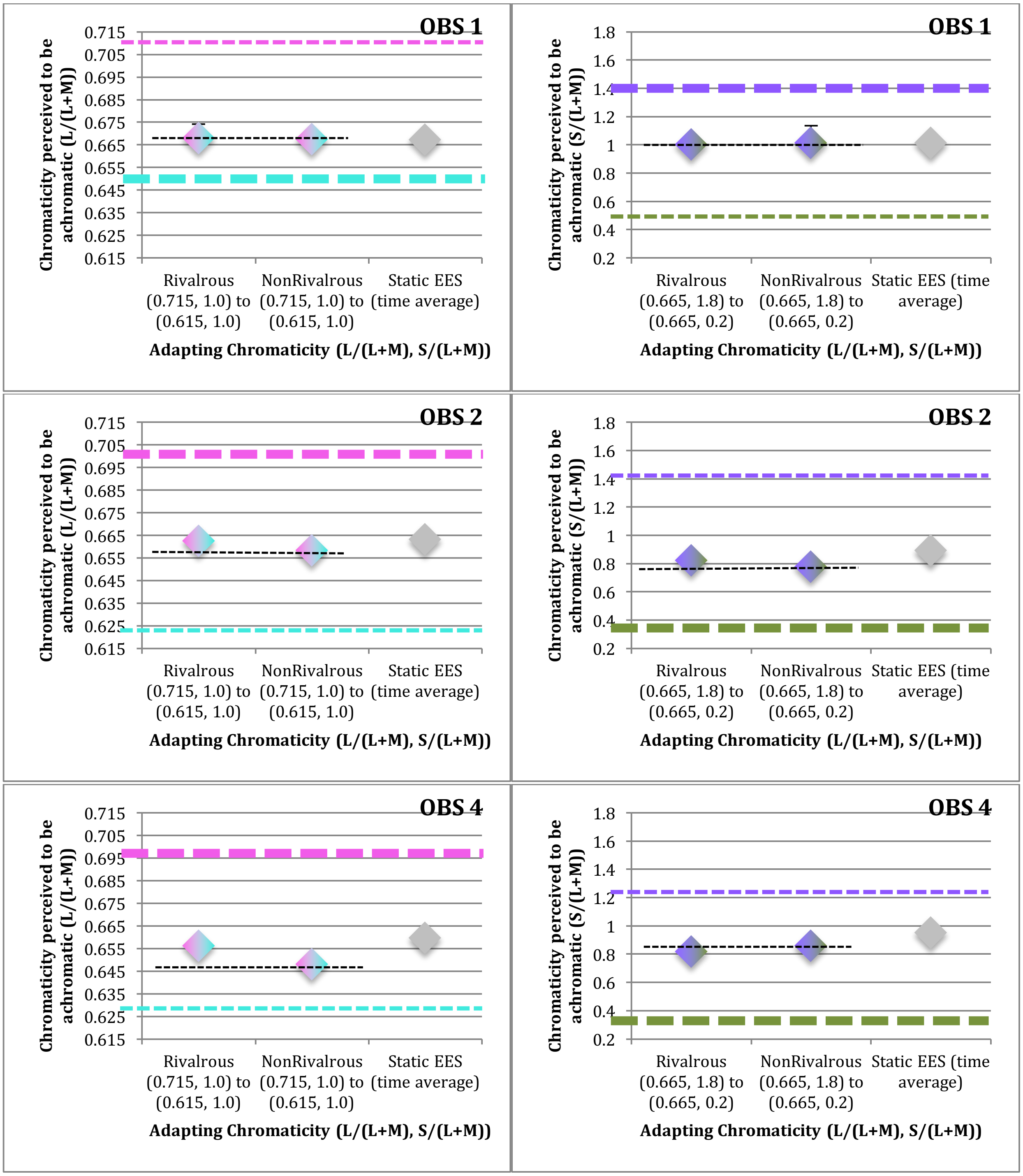

Figure 9-5. Chromaticity perceived to be achromatic to “rivalrous (0.715, 1.0) to (0.615, 1.0)”, “nonrivalrous (0.715, 1.0) to (0.615, 1.0)” or “static EES” (left columns); and “rivalrous (0.665, 1.8) to (0.665, 0.2)”, “nonrivalrous (0.665, 1.8) to (0.665, 0.2)” or “static EES” (right columns). The black dashed lines indicate the chromaticity difference between CISR and non-rivalry. The color dashed lines indicate the measured chromaticity perceived to be achromatic to (0.715, 1.0) or (0.615, 1.0), and (0.665, 1.8) or (0.665, 0.2). The color of the thick lines indicate the predominant percept during CISR.

rivalrous (0.665, 1.8) to (0.665, 0.2)" and "static EES (time average)" in the right columns (adapting chromaticities varied along the *s* chromatic direction). The symbol color is the approximate color of the adapting chromaticity (a mixture indicates oscillation between two colors). Each panel shows results for one observer. The percentage of each color percept during chromatic interocular-switch rivalry is shown in Table 9-2. Here, the percentage is calculated as the ratio between the total dominance time of each color percept over the total presentation time.

Table 9-2. Percentage of each adapting color percept during CISR

Observer	Chromatic Direction	Adapting Chromaticities during Chromatic Interocular-Switch Rivalry	Percentage of Total Dominance Time
1	*l*	(0.715, 1.0)	30.8%
		(0.615, 1.0)	44.6%
	s	(0.665, 1.8)	42.3%
		(0.665, 0.2)	26.8%
2	*l*	(0.715, 1.0)	53.1%
		(0.615, 1.0)	39.9%
	s	(0.665, 1.8)	44.7%
		(0.665, 0.2)	49.9%
4	*l*	(0.715, 1.0)	44.4%
		(0.615, 1.0)	34.8%
	s	(0.665, 1.8)	38.7%
		(0.665, 0.2)	40.6%

The quantitative measure of chromaticity along the *l* chromatic direction is in different units than the chromaticity along the *s* chromatic direction, so the chromaticities of the test are analyzed separately for each chromatic direction and each observer by completing one-way analysis of variance (ANOVA). The factor is the experimental condition, which had three levels (rivalrous, non-rivalrous, and static EES "white").

The results show that the chromaticity of the test after adapting to a rivalrous disc oscillating between (0.715, 1.0) and (0.615, 1.0), a non-rivalrous disc oscillating between

(0.715, 1.0) and (0.615, 1.0) and a static disc of EES “white” is not significantly different for observer 1, but is significantly different for observers 2 and 4. Similar results are found for the chromaticity of the test after adapting to a rivalrous disc oscillating between (0.665, 1.8) and (0.665, 0.2), a non-rivalrous disc oscillating between (0.665, 1.8) and (0.665, 0.2) and a static disc of EES “white” (see Table 9-3). Post-hoc Fisher-Hayter tests for observers

Table 9-3 One-way ANOVA results of the experimental conditions (rivalrous, non-rivalrous and EES “white”)

Observer	Chromatic Direction	Chromaticity of stimulus disc	Chromaticity of test disc	F (2, 12)	*p*
1	*l*	Rivalrous (0.715, 1.0) to (0.615, 1.0)	(0.668, 1.00)	0.03	0.97
		Nonrivalrous (0.715, 1.0) to (0.615, 1.0)	(0.667, 1.00)		
		Static EES (time average)	(0.667, 1.0)		
	s	Rivalrous (0.665, 1.8) to (0.665, 0.2)	(0.665, 1.00)	0.02	0.98
		Nonrivalrous (0.665, 1.8) to (0.665, 0.2)	(0.665, 1.01)		
		Static EES (time average)	(0.665, 1.01)		
2	*l*	Rivalrous (0.715, 1.0) to (0.615, 1.0)	(0.662, 1.00)	30.26	< .001
		Nonrivalrous (0.715, 1.0) to (0.615, 1.0)	(0.658, 1.00)		
		Static EES (time average)	(0.663, 1.00)		
	s	Rivalrous (0.665, 1.8) to (0.665, 0.2)	(0.665, 0.82)	39.26	< .001
		Nonrivalrous (0.665, 1.8) to (0.665, 0.2)	(0.665, 0.78)		
		Static EES (time average)	(0.665, 0.89)		
4	*l*	Rivalrous (0.715, 1.0) to (0.615, 1.0)	(0.656, 1.00)	86.43	< .001
		Nonrivalrous (0.715, 1.0) to (0.615, 1.0)	(0.648, 1.00)		
		Static EES (time average)	(0.660, 1.00)		
	s	Rivalrous (0.665, 1.8) to (0.665, 0.2)	(0.665, 0.82)	48.34	< .001
		Nonrivalrous (0.665, 1.8) to (0.665, 0.2)	(0.665, 0.86)		
		Static EES (time average)	(0.665, 0.95)		

2 and 4 reveal that the achromatic chromaticity of the test after adapting to a rivalrous disc oscillating between (0.715, 1.0) and (0.615, 1.0) is significantly different than adapting to a non-rivalrous disc oscillating between the same chromaticities for both observers ($p < .05$). The results also show that the achromatic chromaticity of the test after adapting to a rivalrous disc oscillating between (0.665, 1.8) and (0.665, 0.2) is significantly different than adapting to a non-rivalrous disc oscillating between the same chromaticities for both observers ($p < .05$). In addition, post-hoc Fisher-Hayter tests reveal that the achromatic chromaticity of the test after adapting to a rivalrous disc oscillating between (0.715, 1.0) and (0.615, 1.0) is significantly different than adapting to a static EES "white" field for observer 4 ($p < .05$), and that the achromatic chromaticity of the test after adapting to a rivalrous disc oscillating between (0.665, 1.8) and (0.665, 0.2) is significantly different than adapting to a static EES "white" field for both observers ($p < .05$) (see Table 9-4).

Table 9-4 Post-hoc Fisher-Hayter test results of the experimental conditions

Observer	Chromatic Direction	R	NR	White	Chromaticity Difference (R vs. NR)	Chromaticity Difference (R vs. White)	Critical Difference ($p = .05$)
2	l	0.662	0.658	0.663	0.004*	0.001	0.0015
	s	0.82	0.78	0.89	0.04*	0.07*	0.0289
4	l	0.656	0.648	0.660	0.008*	0.004*	0.0020
	s	0.82	0.86	0.95	0.04*	0.13*	0.0302

* R, NR and White indicates the chromaticity of test disc adapting to a rivalrous disc, a non-rivalrous disc and a static EES "white" disc, respectively.

Thus, the results of this experiment show adaptation to CISR for two of the three observers is different than for flickering discs that are not rivalrous and for a steady EES "white" field (the time average chromaticity of the flickering adapting discs).

As Figure 9-5 and Table 9-2 shows, observer 1 has a predominant color percept of "blue-green" (44.6%) or "purple" (42.3%) when chromaticity is varied along the *l* or *s* chromatic directions separately, so a shift in the achromatic setting is predicted in the "blue-green" and "purple" directions for the perceived achromatic chromaticity after adapting to CISR. However, for observer 1 the achromatic chromaticity under CISR is not significantly different compared to the non-rivalrous periodic flicker or static EES "white" adapting field along either chromatic direction.

Observer 2 has a predominant color percept of "pink" (53.1%) or "lime" (49.9%) when chromaticity is varied along the *l* or *s* chromatic directions separately (see Figure 9-5 and Table 9-2), so a shift in the achromatic setting is predicted in the "pink" and "lime" directions for the perceived achromatic chromaticity after adapting to CISR. For observer 2, the achromatic chromaticity under CISR moves significantly toward "pink" compared to the non-rivalrous periodic flicker but slightly toward "blue-green" compared to the static EES "white" adapting field along the *l* chromatic direction; the achromatic chromaticity under CISR moves significantly toward "purple" compared to the non-rivalrous periodic flicker but significantly toward "lime" compared to the static EES "white" adapting field along the *s* chromatic direction.

Observer 4 has a predominant color percept of "pink" (44.4%) or "lime" (40.6) when chromaticity is varied along the *l* or *s* chromatic directions separately (see Figure 9-5 and Table 9-2), so a shift in the achromatic setting is predicted in the "pink" and "lime" directions for the perceived achromatic chromaticity after adapting to CISR. For observer 4, the achromatic chromaticity under CISR moves significantly toward "pink" compared to the non-rivalrous periodic flicker but significantly toward "blue-green" compared to the static

EES “white” adapting field along the *l* chromatic direction; the achromatic chromaticity under CISR moves significantly toward to “lime” compared to both the non-rivalrous periodic flicker and the static EES “white” adapting field along the *s* chromatic direction.

CHAPTER 10

GENERAL DISCUSSION

Slow-alternating color percepts induced by chromatic interocular-switch rivalry (CISR) result from ambiguous chromatic neural representations (Christiansen, D'Antona & Shevell, 2014). The experiments in this dissertation examined how the human visual system converts an ambiguous representation into a sustained percept. The temporal properties of CISR (experiment 1), the relation between grouping and the resolution of CISR (experiments 2 - 6), and chromatic adaptation following CISR (experiment 7) were investigated.

Experiment 1 showed that the resolution of CISR does not depend on a specific temporal frequency of swapping (3.13 Hz – 6.25 Hz).

Experiment 2 showed a much longer duration when two or more CISR discs have the identical color compared to the expectation if each disc's color was resolved independently. This indicates grouping of two or more discs contributes to resolving their perceived color.

Experiments 3, 4 and 5 tested whether feature-based object relations contribute to grouping in the resolution of CISR, including synchronized temporal phase at a common frequency (experiment 3), identical temporal frequencies (experiment 4), and equal stereoscopic disparity (experiment 5) of the two objects. The results did not support the proposition that grouping is influenced by any of these features.

Experiment 6 tested whether the properties of the ambiguous representation itself contribute to grouping in the resolution of CISR. Coherent ambiguity was constructed with two identical CISR stimuli. Results showed that grouping is affected by whether one of the two objects has an ambiguous representation (CISR) and the other an unambiguous representation.

Experiment 7 tested whether the state of chromatic adaptation during CISR depends on the perceived predominant color. The results suggested that two of the three observers had color percepts that depended on the perceptual resolution of CISR.

Taken together, these findings show that perceptual resolution of neural ambiguity for color depends on object grouping. This strongly suggests the importance of grouping for resolving mid-level ambiguous visual neural representations.

10.1 Neural mechanism of chromatic interocular-switch rivalry

The potential site of neural competition and the type of visual representations that compete at this site during binocular rivalry is still controversial. Some studies support "eye" rivalry which suggests that perceptual alternation arises from competition between the two eyes' monocular neurons, while others point to "stimulus" rivalry which suggests that perceptual alternation arises from competition between binocular pattern selective neurons.

Chromatic interocular-switch rivalry (CISR) causes a relatively longer-lasting single color percept before switching to another color percept of a similar duration, compared to the duration of stimulus alteration. This suggests a cortical representation of color at the level beyond the retina, in which the neural ambiguity of color induced by CISR is based on a combination of neural signals from the two eyes. The slowly alternating color percept is consistent with the chromatic analog of a pattern competition mechanism of “stimulus” rivalry at a cortical level (Logothetis, Leopold & Sheinberg, 1996), and cannot be explained by sustained (say, 1/2 sec or longer) complete suppression of neural responses from one or the other eye (Blake, 1989; Lehey, 1988; Tong, 2001).

The results of experiment 1 show that the resolution of CISR does not depend on a specific temporal frequency of swapping. This shows that the sustained color percepts from CISR are not dependent on a particular frequency; it also serves as useful preliminary experiment for selecting frequencies for the following studies. Based on the neural representations combining two eyes’ signals, the results of experiment 2 show that grouping multiple CISR “stimuli” contributes to the resolution of their color percepts during CISR. A binocular neural integration model for resolution of CISR should predict little or no effect on grouping multiple neural representations when the “stimuli” in view are unsynchronized in temporal phase at a common frequency (experiment 3), unequal in temporal frequency (experiment 4), or unequal in stereoscopic depth from rental disparity (experiment 5). This is because the integrated neural representations of these “stimuli” should be insensitive to these temporal phase/frequency differences. Similarly, these neural representations can be insensitive to the stereoscopic depth as well. Finally, the results of experiment 7 show that the dominant color percept during CISR may affect chromatic adaptation, though it was found here for only two of the three observers. For these two observers, they adapted, at least in part, to the slow alternating color percepts, not to the rapidly changing (3.75 Hz) stimuli, which have a time-average chromaticity metameric to EES "white".

Overall, all the findings of these experiments are consistent with binocular color rivalry resulting from competition between binocular neurons preferring one of the two colors, not simple rivalry among monocular chromatic representations. This is consistent with pattern competition theory for "stimulus" rivalry (Kovcas et al., 1996; Leopold et al., 1996; Logothetis et al., 1996).

Although stimulus rivalry can be explained by eye-independent neural processes at a binocular stage of cortical processing, it does not rule out the possibility of an eye-specific neural contribution to stimulus rivalry at early monocular stages of cortical processing (Brascamp, Sohn, Lee & Blake, 2013). This idea has been tested using the threshold elevation aftereffect (TEAE), a contrast adaptation caused by eye-specific neural activity at early cortical stages and characterized by diminished detection of a grating that is similar to the inducing ones. The results of their study show that TEAE becomes weaker when the adapting gratings were engaged in stimulus rivalry than when not, which indicates that eye-specific neural suppression of a grating at a given moment specifically diminished adaptation associated with the eye viewing the grating during stimulus rivalry at that moment. A monocular adapting effect, however, does not rule out a subsequent eye-independent binocular mechanism.

10.2 Resolving neural ambiguity in mid-level vision

Mid-level vision is an intermediate representation of surfaces and objects later than low-level vision (a retinal representation of an image's physical properties) but before high-level vision (object recognition), so is an intermediate step in the transition from physical light encoding to object perception (Nakayama, 1999; Nakayama, He & Shimojo, 1995). Before mid-level vision, neural responses represent local information from small regions of an image, so that the whole image is represented by multiple neural responses at different retinotopic locations. At a later stage after mid-level vision, object-based recognition occurs.

Since the neural representations of surface and object in mid-level vision can be determined without object meaning, these ambiguous neural representations may lead to more than one interpretation. Therefore, resolving implicit ambiguity in the integrated neural representations from separate visual regions is considered to be an essential aspect of mid-level vision (Nakayama, 1999; Nakayama, He & Shimojo, 1995).

However, it is unclear what kinds of processes contribute to reducing ambiguity in mid-level neural representations. Emerging evidence has shown that creating a coherent and stable visual percept from ambiguous stimuli depends on a variety of cognitive factors, such as working memory (Allen, Beilock & Shevell, 2011, 2012), prior experience (Kersten, Mamassian & Yuille, 2004; Leopold, Wilke, Maier & Logothetis, 2002), and reward expectation (Botha, 1963).

This dissertation proves that one more factor, grouping, contributes to resolving the ambiguous chromatic neural representations created by chromatic interocular-switch rivalry (CISR). In other words, each ambiguous representation of an object within a group is not resolved independently. When multiple objects are presented simultaneously, the neural response of each object is encoded separately from small regions of an image in low-level vision. Once the whole image is constructed by multiple neural responses, mid-level vision integrates local information into larger surfaces and objects. The results here show that the chromatic representations of mid-level surfaces depend on grouping multiple objects together. This finding is consistent with the property of a "surface" as a meaningful representation in mid-level vision (Peirce, 2015). That is, human observers need to understand the meaning of an image in order to describe the characteristics of the objects in the image. Results here indicate a meaningful representation is constructed by grouping objects sharing the same ambiguous properties (that is, coherent ambiguity).

During visual information processing, a surface representation is an explicit stage of visual analysis. Surface-level representations encode the physical world in terms of segmented objects or regions with specific properties (for example, color or transparency). Although this level of neural representation is not as well understood as low-level visual processing, this dissertation sheds some light on the mechanisms that mediate surface representations in mid-level vision.

10.3 General implications for visual information processing

In order to explain how the visual system integrates visual information into a whole percept, Gestalt psychologists proposed several classic laws of perceptual grouping (Koffka, 1922; Kohler, 1959). The law of similarity states that similar elements tend to be grouped together as a whole unit. In studies of binocular rivalry, grouping is posited to depend on facilitation among neural circuits that respond to similar features, such as a common direction of motion (Alais & Blake, 1998). That is, rivalrous objects can be perceptually grouped together as a global form in accordance with similarity of a spatially distributed stimulus feature and then simultaneously dominate during binocular rivalry (de Weert, Snoeren & Koning, 2005). Alternatively, the interpretation of an image with rivalrous objects may be constrained by an unambiguous part of the scene available to the perceptual system (Gillam, 1976).

This dissertation shows evidence that a common property like coherent ambiguity, rather than common features like temporal relations and stereoscopic depth, plays a critical role in grouping multiple chromatically rivalrous objects. Coherent ambiguity is constructed as a group of two CISR discs that have the same ambiguous components. One way to break down this coherence is to introduce an unambiguous component in the group. For example, one CISR disc in view is changed to a periodically alternating stimulus but with no rivalry, so that this disc is always perceived to have its unambiguous colors. Results from experiment 6 showed a steep reduction of the viewing time with a single dominant color percept for the group when it consisted of both a CISR and non-rivalrous discs. This suggests that corresponding ambiguous neural representations of color increase the degree to which the discs are grouped. In addition, this interpretation was confirmed by another incoherent ambiguity constructed with two CISR objects having different ambiguous components in the supplementary experiment of chapter 4. That is, one CISR disc had color percepts alternating between "pink" and "blue-green" while the other between "purple" and "lime"; in this case the total dominance time of perceiving both discs with the same color was near zero. Both findings suggest that the same ambiguous properties of the rivalrous objects contribute to the grouping mechanism, which can be understood in terms of lateral excitatory connections between neurons tuned to similar features implicit in coherent ambiguity (Tong, Meng & Blake, 2006).

Although coherent ambiguity has been shown to contribute to grouping, it does not rule out the possibility that non-ambiguous objects can be grouped together. For example, grouping can be constructed by non-ambiguous objects based on common luminance (Alais & Blake, 1999). When two gratings are presented to the left eye and two sets of random dots are presented to the right eye separately, both gratings are perceived simultaneously with the longest dominance time for collinear gratings with correlated contrast modulation. Even in the situation with the shortest dominance time when the orientations of the gratings are orthogonal and their contrast modulations are uncorrelated, there is still about 20% of the total presentation time accounted by a grouping effect.

This dissertation, however, found no evidence to show that features such as relative temporal phase difference, temporal frequency difference and stereoscopic disparity difference are important factors that affect grouping ambiguous colors. This suggests that the ambiguity property has a higher priority than the tested features for a grouping mechanism during mid-level visual information processing. In other words, what the visual system groups depends more on coherent ambiguity of the objects than their features in common.

10.4 Broader implications of resolving ambiguous neural representations

An image in natural viewing generates ambiguous neural representations that may be interpreted in two or more ways. For example, the Necker cube and face-vase figures are the well-known examples of bi-stable ambiguity that result in fluctuation between two percepts. Bi-stability reveals that the visual system can generate multiple perceptual solutions based on a single neural representation of an image in early stages and then, at a later stage, resolve the interpretation of the lower-level representation.

Binocular rivalry is a well-studied form of bi-stable perception. Based on binocular rivalry, chromatic interocular-switch rivalry (CISR) provides a technique to generate ambiguous neural representations for a color percept. Therefore, this technique establishes an ambiguous neural representation at a level higher than each eye's monocular information. This dissertation demonstrates that grouping based on coherent ambiguity plays an important role in resolving ambiguous neural representations of colors induced by CISR. It also suggests that the color percept induced by CISR can affect chromatic adaptation (for two of the three observers).

In addition to normal vision of human observers, the discoveries here about resolving ambiguous neural representations may provide some insights to understand human visual impairments. For example, patients with Alzheimer's disease can have perceptual deficits affecting integration of information from separate visual regions (Kurylo, Corken & Growon, 1994; Paxton, Peavy, Jenkins, Rice, Heindel & Salmon, 2007); patients with schizophrenia can have perceptual organization dysfunction so that they cannot integrate contextually related information across space and time (Uhlhaas & Silverstein, 2005). Therefore, the capability to resolve ambiguity may be useful for understanding some visual impairments.

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