Perceptual Combination of Binocular Luminance and Orientation

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Abstract:

This thesis contains two projects. Project one was inspired, in part, by findings by Baker and Graf (2009). Baker and Graf (2009) found that decreasing the difference in orientation between dichoptic gratings shown to each eye, increased the length of binocular rivalry dominance durations and increased masking thresholds during dichoptic masking. They also found significant individual differences in masking threshold and rivalry rate and that those individuals with the slowest rivalry also had the strongest masking. We set out to replicate these findings with a few novel modifications. When we examined the effects of changing the orientation difference between stimuli in binocular rivalry and dichoptic masking, we replicated the findings of Baker and Graf (2009). These findings indicate that decreasing the orientation difference between two stimuli, increases cortical inhibition and slows rivalry rate. We tested another masking condition, half-binocular masking, and found the same trend for this type of masking as for dichoptic masking. This implies that our findings are relevant for masking generally. Based on our lab's interest in binocular rivalry and masking for stimuli with homogenous luminance, we created luminance-only analogue experiments to the oriented grating experiments. We tested luminance rivalry experiments where the stimuli varied in luminance level between conditions. Similarly, in our dichoptic and half-binocular masking experiments, the luminance level of the mask varied across conditions. Overall, we found that strong stimuli, those that have a luminance level far from background luminance, exhibit the fastest rivalry and the strongest masking. Since in the case of luminance rivalry, slow rivalry conditions are associated with weak masking and high amounts of mixed percepts, we concluded that slow luminance rivalry corresponds with weak inhibition. This is opposite from the conclusion for oriented rivalry and so we hypothesize that these two types of stimuli use distinct mechanisms to achieve rivalry and masking. For project two, we systematically explored the dynamics of luminance-only binocular rivalry. Based on the data obtained from our four experiments, we showed that the pattern of results associated with luminance only rivalry agrees with those characterized in the revised Levlt's propositions (Brascamp, Klink, & Levelt, 2015).

Résumé:

Cette thèse inclut deux projets. Le premier projet a été inspiré en partie par les résultats de Baker et Graf (2009). Baker et Graf (2009) ont démontré que diminuer la différence d'orientation entre chacun des réseaux sinusoïdaux présentés aux deux yeux individuellement, augmentait les durées de dominance de la rivalité binoculaire et de la puissance de masquage dichoptique. Ils ont aussi démontré une différence individuelle significative de puissance de masquage et de vitesse de rivalité. Les participants dont la vitesse de rivalité était des plus lentes présentaient aussi un masquage plus fort. Nous avons voulu reproduire les résultats de Baker and Graf (2009) avec quelques changements dans leur méthodologie. Quand nous avons examiné les effets du changement d'orientation entre les stimuli pour la rivalité binoculaire et le masquage dichoptique, nous avons reproduit les résultats de Baker and Graf (2009). Ces résultats indiquaient que si la différence d'orientation entre les deux stimuli etait réduite, l'inhibition corticale augmentait et la vitesse de rivalité ralentissait. Nous avons testé une autre condition de masquage, qui s'appelle le masquage demi-binoculaire. Nous avons trouvé la même tendance pour les deux types de masquage. Ceci indique que nos résultats ne sont pas spécifiques au masquage dichoptique, mais s'appliquent au masquage en général. De plus, notre laboratoire est intéressé par la rivalité binoculaire et le masquage dans le cas des stimuli à luminosité homogène. Nous avons donc créé des expériences avec des stimuli à luminosité homogène qui sont analogues aux expériences de stimuli orientés. Pour les expériences de rivalité entre stimuli à luminosité homogène, la luminosité des stimuli était différente entre chaque condition. De même, la luminosité des masques était différente entre chaque condition pour les expériences de masquage dichoptique ainsi que demi-binoculaire. Dans l'ensemble, nous avons démontré que les stimuli les plus forts (ceux dont le niveau de luminosité était très loin de la luminosité de l'arrière-plan) causaient la rivalité la plus rapide et le masquage le plus fort. Pour la rivalité des stimuli à luminosité homogène, les conditions qui provoquaient la rivalité lente étaient aussi celles associées au masquage faible et aux longues durées de perception combinée. Nous avons conclu que la rivalité des stimuli à luminosité homogène lente correspondait à une faible inhibition corticale. Ceci est la conclusion opposée à celle que nous avons tirée de notre expérience sur la rivalité d'orientation. Donc, nous avons fait l'hypothèse que ces deux types de stimuli recrutent deux mécanismes corticaux différents pour accomplir la rivalité et le masquage. Pour le deuxième projet, nous avons exploré systématiquement les dynamiques de la rivalité

entre stimuli à luminosité homogène. Les résultats que nous avons obtenus pour les quatre expériences portant sur la rivalité sont en accord avec les résultats prévus par les propositionsrévisées de Levelt (Brascamp, Klink, & Levelt, 2015).

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Introduction & Literature Review:

1. Binocular Rivalry:

1.1. Introduction to Binocular Rivalry (psychophysics and physiology):

Binocular rivalry (BR) is a perceptual phenomenon that occurs when two irreconcilable images are shown, one to each eye, to an observer. The stimuli are too different for the eyes to fuse into a single perceptual image (Alais, 2012). If the incongruous stimuli are presented for a long enough period of time, in an attempt to resolve the visual ambiguity, the brain causes one image to dominate perception while suppressing the other (Alais, 2012). After a short period of one image dominating, perception shifts, and the formerly suppressed stimulus dominates perception (Alais, 2012). Without any change in visual input, visual perception continues to alternate (Alais, 2012). Classically, the two stimuli used for BR are orthogonal, sinusoidal gratings (Said & Heeger, 2013). BR alternations are stochastic and it is therefore unpredictable when during the BR trial an individual will experience an alternation (Arnold, Law, & Wallis, 2007; Ling, Hubert-Wallander, & Blake, 2010; Pearson & Clifford, 2005). Often with large BR stimuli, the transitions between the stimuli are perceived to occur in a "travelling wave" (Genç, Bergmann, Singer, & Kohler, 2015; Lee, Blake, & Heeger, 2007) During the travelling wave, the newly dominant stimulus' percept originates at one location and then spreads in a wave across the visual field until the formerly dominant stimulus is no longer visible (Genç et al., 2015; Lee et al., 2007). Although BR has long been studied, there still remains uncertainty about the mechanisms which underlie the phenomenon (Brascamp et al., 2015). Some researchers have concluded that the mechanisms underlying BR are also active during day to day vision to resolve ambiguity or competing sensory information in normal visual input (Lunghi, Burr, & Morrone, 2011; Zadbood, Lee, & Blake, 2011).

As mentioned above, during BR, subjects' perception is changing without any change in visual input. This means that although their eye is being shown a stimulus, the observer is not perceptually aware that stimulus. This has led to BR being characterized as alternations conscious awareness (e.g. Baker & Cass, 2013; Brascamp, Sohn, Lee, & Blake, 2013; Lee et al., 2007). Consequently, BR has often been used to study the neural correlates of conscious perception as well as unconscious visual processing (Carter & Cavanagh, 2007; van Boxtel, van Ee, & Alais, 2008). Similarly, the role of attention in controlling BR alternations has been investigated since the work of Helmholtz (Alais, 2012). Generally, it has been found that attention does play a role in modulating rivalry dominance duration length and when alternations occur but it is not causally responsible for BR (Alais, 2012).

Rivalry is often considered alongside stereopsis because both involve showing different images to each eye that the brain must reconcile and interpret. In the case of stereopsis, this conflict is resolved through the perception or illusion of depth. Because of this similarity, it has often been thought that BR results when the two eyes' images are too different to provoke stereopsis (Blake, 1989, 2001). Many studies have indicated that BR and stereopsis arise from an overlapping neural mechanism. For example, using fMRI, Buckthought and Mendola (2011) showed that depth and rivalry result in similar cortical activity.

In addition to BR, there are several other types of rivalry. Monocular rivalry occurs when two patterns superimposed on the same image are shown to one (or both) eye(s) (Alais, 2012). Unlike BR, during monocular rivalry, neither one of the competing patterns disappears from conscious awareness, rather the two patterns alternate in visual saliency to the observer (Alais, 2012; van Boxtel, Knapen, Erkelens, & van Ee, 2008). Additionally, monocular rivalry occurs exclusively between patterns in one eye whereas BR occurs between the two eyes (inter-ocular versus within-eye completion) (van Boxtel et al., 2008b). A second type of rivalry is stimulus rivalry (or flicker-swap rivalry). During stimulus rivalry, as with BR, irreconcilable images are shown to each eye but throughout the trial these images are swapped between the two eyes (Logothetis, Leopold, & Sheinburg, 1996). Since the conscious percept experienced by the subject does not change when the stimuli are swapped between the eyes, stimulus rivalry has been used to test whether BR dynamics and perception are independent of eye origin (Brascamp et al., 2013). van Boxtel et al. (2008b) have argued that these three types of rivalry share common neural processes and the apparent differences between the phenomena arise from differing monocular interactions (van Boxtel et al., 2008b). They find that when these monocular interactions are removed, the three forms of rivalry are statistically identical (van Boxtel et al., 2008b). One final form of rivalry used experimentally is successive rivalry. During successive rivalry, rivalrous stimuli are not presented simultaneously (van Boxtel, van Ee, & Erkelens, 2007). Instead, the left eye's stimulus and the right eye's stimulus are presented successively (van Boxtel et al., 2007). The stimulus is flickered continuously for the duration of the BR trial to mask when the stimuli are swapped between eyes (van Boxtel et al., 2007). Interestingly, with exception of the flicker, the subject's percept still resembles that of classic BR (van Boxtel et al., 2007).

fMRI has allowed researchers to observe the neural activation that correlates with experiencing BR and to track the patterns of activation associated with percept changes (Haynes & Rees, 2005). Zadbood et al. (2011) found that although subjects failed to discriminate perceptually between a situation when a stimulus was suppressed during rivalry and when it was physically removed, there were significant differences in cortical activation. Generally, BR has often been associated with activity in the primary visual areas (V1, V2 and V3) and the lateral geniculate nucleus (LGN) (Buckthought, Jessula, & Mendola, 2011; Genç et al., 2015). As discussed above, the perceptual experience of BR often occurs in a travelling wave (Genç et al., 2015; Lee et al., 2007). Using fMRI, this travelling wave percept has been linked to a corresponding wave in cortical activity in V1 (Arnold, James, & Roseboom, 2009; Lee et al., 2007). Lee et al. (2007) found that when subjects' attention was diverted from the perceptual alternation, the waves of activity in V1 remained but were no longer present in V2 and reversed direction in V3. The authors therefore concluded that the waves of activity in V1 are associated with experiencing perceptual rivalry and are not affected by not attending to the stimuli (Lee et al., 2007). In addition to these lower visual areas, higher visual areas are also active during rivalry, such as the occipito-parietal areas V3a, V4d-topo and V7; ventral temporal and frontal regions; the superior parietal lobe, and the caudal intraparietal sulcus (Buckthought et al, 2011; Lumer, Friston, & Rees, 1998). BR activation also appears to be lateralized to the right hemisphere (Lumer et al., 1998). The wide-spread cortical activation during BR has led to the theory that BR alternations, or at least the active reporting of a BR alternation, involves a whole brain network (Benrimoh, Buckthought, Dawson, Shmuel, & Mendola, 2016). The brain area responsible for triggering BR alternations is contentious. One dominant view is that fronto-parietal networks are responsible for perceptual alternations (e.g. Leopold & Logothetis, 1999; Sterzer & Kleinschmidt, 2007). However recent studies, using modified techniques, have not supported this hypothesis (Frässle, Sommer, Jansen, Naber, & Einhäuser, 2014; Knapen, Brascamp, Pearson, van Ee, & Blake, 2011). Additionally, some studies have found that TMS on regions of the parietal lobe, such as the superior parietal lobe (SPL) and the intraparietal sulcus (IPS), slows dominance durations of multistable stimuli, which implies these areas play a causal role (Kanai, Carmel, Bahrami, & Rees, 2011; Zaretskaya, Thielscher, Logothetis, and Bartels, 2010). However, another TMS study found the opposite effect (Carmel, Walsh, Lavie, and Rees, 2010). These inconclusive findings support the conclusion that fronto-parietal activation during rivalry, while not causal, may play an important role in attending to the rivalry transitions, judging when an alternation has occurred or self-monitoring of one's perceptual state (Frässle et al., 2014; Kanpen et al., 2011; Zaretskaya & Narinyan, 2014).

1.2. Rivalry and Orientation (psychophysics and physiology):

BR has been evoked using many different stimulus features such as motion, spatial frequency, color and orientation (Stuit, Cass, Paffen, & Alais, 2009). As mentioned above, classic BR stimuli are sinusoidal gratings which are orthogonal in orientation (Said & Heeger, 2013) and it has been long known than neurons in the primary visual cortex (V1) are orientation tuned and respond maximally to their preferred direction (Alais, 2012). This has led researchers to investigate whether different orientations experience different levels of suppression during BR.

Many researchers found psychophysical evidence that the orientations of the BR stimuli have no effect on the amount of suppression exhibited during BR (e.g. Blake & Lema, 1978; Nguyen, Freeman, & Wenderoth, 2001). However other studies have found the opposite. For example, O'Shea and Crassini (1981) observed that during rivalry, a small change in the orientation of the suppressed stimulus resulted in more suppression than a large orientation change. Stuit et al. (2009) examined this conflict using rivalry stimuli with a fixed, orthogonal orientation difference. Instead, they changed the orientation of a monocular probe stimulus which was presented in the middle of right eye's stimulus (Stuit et al., 2009). The probe's orientation conditions were: ±10°, ±20°, ±30° and ±45° (relative to the rivaling grating stimuli) (Stuit et al., 2009). They found that discrimination thresholds, for the probe during BR suppression, increased as the orientation difference between the probe and the suppressed BR image decreased (Stuit et al., 2009). Specifically, when the probe was 10° from the rivaling stimulus, suppression thresholds were six times higher than they were when the probe and rivaling stimulus differed by 45° (Stuit et al., 2009). The researchers therefore concluded that suppression is greatest for probes that have an orientation similar to that of the suppressed grating and this effect decreases as the difference increases (Stuit et al., 2009). Based on these findings, Stuit et al. (2009) concluded that the orientation tuning function for suppression during BR is centered around the orientation of the rivalrous stimuli and has a half-width of ~26° (Stuit et al., 2009). This value has also been found physiologically using single-unit recording (Stuit et al., 2009).

Another line of exploration has looked at how different stimulus orientations effect the dynamics of BR. Fahle (1982) examined the effects of changing the grating in one eye from vertical to horizontal and the grating in the other eye from horizontal to vertical. He concluded that the vertical grating was preferred by the visual system because it was dominant more often during BR (Fahle, 1982). In an experiment designed to determine if monocular rivalry and binocular rivalry arose from different mechanisms, Kitterle and Thomas (1980) conducted BR with grating stimuli oriented 10, 20, 30, 45, 60 and 90°. In this experiment the orientation of the stimuli was the same in both eyes and it was the color of the gratings that differed between eyes (Kitterle & Thomas, 1980). They found that for both monocular and binocular rivalry as the orientation approached 90°, the rivalry alternation rate increased (Kitterle & Thomas, 1980). These findings indicate that rivalry rate changes with changes in orientation.

These studies did not however explore the effects of changing the orientation difference between eyes. Most commonly, changing the orientation difference between eyes has been used to explore which inter-ocular conditions lead to stereopsis and which lead to BR (e.g. Buckthought, Kim, & Wilson, 2008; Buckthought & Wilson, 2007; Chopin, Mamassian, & Blake, 2012). Buckthought et al., (2008), as a part of a study on this topic, measured BR dominance durations over a range of inter-ocular orientation differences (2°, 4°, 6°,…,40°). They found that rivalry did not occur with inter-ocular orientation differences smaller than 26° for stimuli at 100% contrast and this increased to 32° when the stimuli were at 25% contrast (Buckthought et al., 2008). Additionally, they found that as the inter-ocular orientation difference increased, the length of rivalry dominance durations decreased (Buckthought et al., 2008). These findings and those of Kitterle and Thomas (1980) indicate that BR is sensitive to changes in stimulus orientation and as the inter-ocular orientation difference increases, the length of rivalry dominance durations decreases and the rate of alternation increases.

In a recent study, Baker and Graf (2009) directly and systematically tested the effects inter-ocular orientation difference on BR dominance durations. They used Gabor patches with a range inter-ocular orientation differences between 30° and 90° in 5° steps (Baker & Graf, 2009). They found, for all their observers, as the orientation difference between the rivalry stimuli approached 30°, the length of rivalry dominance durations increased (Baker & Graf, 2009). It should be noted that for the case when the orientation difference is equal to zero, this results in the perceptual fusion of the target and the mask.

Physiologically, Roeber (2012) conducted an EEG study to investigate the neural activity, as measured using event-related potentials (ERPs), associated with inter-ocular orientation differences. His orientation differences between the eyes varied from 0° to 90° and he presented his sine-wave grating stimuli dichoptically for 200 ms (Roeber, 2012). Overall, Roeber (2012) found two neural signatures sensitive to inter-ocular orientation differences. One was a positive peak 100 ms after stimulus onset (P100) and the other was a negative peak 170 ms after stimulus onset (N170) (Roeber, 2012). When Roeber did a global activity analysis, he found that for both P100 and N170 activity varied significantly based on orientation difference. For P100, the function of activity was a U-shape, with maximal activity for the 0° difference condition, activity decreasing for small orientation differences and increasing again for large orientation differences. For N170, activity increased as orientation difference increased (Roeber, 2012). He hypothesized that the P100 activity is related to initial binocular processing and the N170 activity is the stage at which the binocular input in evaluated (Roeber, 2012). More specifically, for the N170, Roeber postulates that larger inter-ocular orientation differences result in more activation because they are atypical and require re-evaluation, and this re-evaluation results in a larger neural response. An interpretation more directly tied to neural inhibition will be considered in the Discussion Section.

1.3. Models of Binocular Rivalry:

Early models of BR assumed rivalry was a solely eye-based, low level process. Eye-based models proposed that BR arose from mutual inhibition between the competing eyes' monocular neurons in combination with eye based adaptation to the stimulus (Alais, 2012; Bartels and Logothetis, 2010; Bhardwaj and O'Shea, 2012; Buckthought et al., 2011; Stuit et al., 2009; van Boxtel et al., 2008a; van Boxtel et al., 2008b; van Boxtel, Alais, Erkelens, van Ee, 2008). Briefly, the neural pool with the strongest response to its eye's stimulus also exerts more inhibition on the other eye's neural pool than that other eye's neural pool exerts on it (Alais, 2012). This results in one stimulus becoming exclusively dominant (Alais, 2012). Over time, neural adaptation results in the dominant eye's neurons responding less strongly to the stimulus and exerting less inhibition on the other eye's neurons. The other eye's response to its stimulus and its inhibition of the other eye's neurons are therefore stronger and an alternation takes place (Alais, 2012).

However, there is much evidence to suggest that image-based, higher order mechanisms are also involved (Alais, 2012; Bartels and Logothetis, 2010; Bhardwaj and O'Shea, 2012; Buckthought et al., 2011; Stuit et al., 2009; van Boxtel et al., 2008a; van Boxtel et al., 2008b; van Boxtel et al., 2008c). The discovery of stimulus rivalry especially challenged the eye-based model because rapidly swapping the stimuli between the two eyes should would disrupt the inter-ocular monocular iterations on which the eye-based models are based (Bhardwaj and O'Shea, 2012; Patel, Stuit, & Blake, 2015; Stuit et al., 2009; van Boxtel et al., 2008c). Consequently, the current, prevailing model for BR is hierarchical, assuming that BR arises from multiple processes, including both eye-based and image-based mechanisms (Alais, 2012; Bartels and Logothetis, 2010; Bhardwaj and O'Shea, 2012; Buckthought et al., 2011; Cater and Cavanagh, 2007; Stuit et al., 2009; van Boxtel et al., 2008a; van Boxtel et al., 2008b; van Boxtel et al., 2008c). To investigate the respective contributions of the eye-based and stimulus-based mechanisms, Bartels and Logothetis (2010) used a technique that introduced disruptions during BR trials. These disruptions were introduced at varying points during the dominant phase and were sometimes accompanied by swapping the stimuli between eyes (Bartels and Logothetis, 2010). They found that both eye-based and image-based mechanisms act to stabilize the dominant image (Bartels and Logothetis, 2010). During a dominance duration, both eye-based and image-based percept stabilizing effects decline (Bartels and Logothetis, 2010). The influences of both mechanisms decline in parallel over the dominance duration, however since the stabilization provided by the eye-based mechanism is stronger, it is the image-based input that first acts to destabilize the dominant percept (Bartels and Logothetis, 2010). This mechanism was further validated by Bhardwaj and O'Shea (2012) who found that image-based rivalry contributes to suppression early in the dominance duration but later suppression results from eye-based suppression. The hierarchical model of BR is also validated by physiology. As detailed above, fMRI studies have shown that while lower-level visual areas, such as the LGN and V1, are active during BR, higher order areas, such as those associated with pattern representation, are also involved (Buckthought et al., 2011; Lee et al., 2007).

Abadi (1976) suggested a model for orientation rivalry using the concept of orientation selective neural columns in the cortex. In his model, since orientation preference changes systematically across the columns, neighboring columns respond maximally to similar but not identical orientations (Abadi, 1976). He therefore assumed that orientation rivalry occurs through lateral inhibition between these orientation columns (Abadi, 1976). Using his model, BR between stimuli with similar orientations would result in the most lateral inhibition whereas there would be less lateral inhibition between stimuli with larger orientation differences (Abadi, 1976). However, as discussed above, many researchers questioned the validity of this model because BR suppression was thought not to be orientation tuned (Alais, 2012; Blake and Lem, 1977; Stuit et al., 2009). However, the previous discussed studies by O'Shea and Crassini (1981) and Stuit et al. (2009) did find different amounts of BR suppression based orientation, which suggests that BR suppression is orientation tuned. Interestingly, Stuit et al. (2009) did not find orientation tuned suppression for stimulus rivalry (Stuit et al., 2009). Since stimulus rivalry is thought to originate exclusively from higher order, image-based rivalry mechanisms, these findings suggest that orientation tuning in BR suppression arises from eye-based mechanisms, such as those suggested by Abadi (1976).

Another problem with BR models based on competition between orientation selective neurons is that these models predict that strong rivalry between the components of plaid stimuli (Said and Heeger, 2013). In practice these components undergo, the much weaker, cross-orientation suppression (Said and Heeger, 2013). Cross-orientation suppression is the attenuation of the neural response to a stimulus by the presence of a superimposed grating of an orthogonal orientation (Said and Heeger, 2013). To rectify this problem with BR models, Said and Heeger (2013) introduce ocular opponency neurons into the model. Ocular opponency neurons respond to differences between the two eyes, and would therefore be active when the eyes are presented with dichoptic gratings (Said and Heeger, 2013). Once activated, ocular opponency neurons, through feedback, strengthen the competition between the two eyes' neural pools and this results in strong rivalry (Said and Heeger, 2013). In contrast, there is no inter-ocular stimulus difference for binocular plaids, so the ocular opponency neurons are silent and cross-orientation suppression occurs rather than rivalry (Said and Heeger, 2013). Said and Heeger (2013) psychophysically tested this model by presenting either monocular or binocular grating stimuli during adaptation under the assumption that monocular adaptation will involve ocular opponency neurons but binocular adaptation will not. As predicted by the ocular opponency model, monocular adaptation resulted in more mixed perception during rivalry due to the adaptation of the ocular opponency neurons (Said and Heeger, 2013). Rivalry models that lack ocular opponency neurons predict more mixed percept for binocular adaptation, which does not agree with the findings of Said and Heeger (2013).

2. Masking:

2.1. Introduction to Masking:

Masking is a psychophysical technique during which one visual stimulus alters the perception of another. Dichoptic masking refers to the situation where one stimulus, called the "target" is presented to one eye and another stimulus, called the "mask" is presented to the other eye (Legge, 1979). As in BR, the images presented to the two eyes are irreconcilable. However, unlike BR, the presentation of the stimuli is too brief for rivalry to occur. Instead, the observer sees a combined percept of the two stimuli, and effectively, the masking stimulus reduces the observer's sensitivity for the target stimulus (Legge, 1979; Baker & Graf, 2009). There are several other types of masking used psychophysically. During monocular masking, one eye is presented both the mask and the target while the other eye is shown the mean luminance of the stimulus background (Meese, Georgeson & Baker, 2006). The term "binocular masking" is used to describe a situation where both the mask and the target are shown to both eyes (Meese et al., 2006). Finally, during "half-binocular masking" the mask stimulus is shown to both eyes, but the target stimulus is only shown to one eye (Meese et al., 2006). Several other masking paradigms are used to study visual suppression and inhibition physiologically. One of these is "continuous flash suppression" (CFS) which occurs when a low contrast target image in one eye is rendered invisible to the observer by a high contrast, continuously flashing mask in the other eye (Tsuchiya & Koch, 2005; Arnold et al., 2007; Yamashiro et al., 2013; Yuval-Greenburg & Heeger, 2013). This technique is also often used to study BR because like rivalry, one eye's stimulus is suppressed from conscious perception by the other eye's stimulus (Arnold et al., 2007; Yamashiro et al., 2013; Yuval-Greenburg & Heeger, 2013). However, the suppression induced by CFS has a longer duration and is more predictable than that of BR (Arnold et al., 2007; Yamashiro et al., 2013; Yuval-Greenburg & Heeger, 2013). Arnold et al. (2007) proposed an alternate method of suppressing one eye's image called binocular switch suppression (BSS). Similar to CFS, one eye's stimulus is more salient than the other but the suppression is maintained by swapping the images between the two eyes (Arnold et al., 2007). This acts to reduce the neural adaptation, which is thought to play a role in perceptual switches during BR, while inducing long lasting suppression of the target stimulus (Arnold et al., 2007).

2.2. Past Findings – Psychophysics:

It has long been known that the detection threshold for the target stimulus during dichoptic masking increases as the spatial frequency of the stimuli increases (Legge, 1979; Levi, Harwerth, & Smith, 1979). Legge (1979) also showed dichoptic tuning functions for a range spatial frequency values. Interestingly, the spatial frequency channels thought to be responsible for these findings also show orientation selectively in masking (Legge, 1979). Campbell and Kulikoski (1966) showed that, for monocular masking, as the orientation difference increased between the target grating and the mask grating, the effect of masking decreased. Based on these observations and those found in his study, Legge (1979) suggested that dichoptic masking may also be orientation specific. Indeed, the findings of Levi et al., (1979) indicated that for dichoptic masking, the maximal masking occurred when the target and the mask had the same orientation and that there was no obvious masking when the target and mask were orthogonal to each other. Similar to Legge (1979), Baker and Meese (2007) found, using dichoptic masking, orientation tuning with a bandwidth of ±33°. Recently, Yang and Blake (2012) found that, during CFS, observers' sensitivity was higher for obliquely orientated stimuli than for cardinally orientated stimuli.

Baker and Graf (2009) also examined the effect of orientation differences between the target and mask on subjects' dichoptic masking thresholds. They tested a range of orientation differences from 30° to 90° in 5° increments as a systematic investigation of the effects of orientation difference on dichoptic masking threshold (Baker & Graf, 2009). Each subjects' baseline detection threshold was obtained using a 45° target grating (Baker & Graf, 2009). To determine subjects' threshold elevation for various orientation differences, the contrast of the mask was fixed at 32% and the contrast of the target was controlled using a staircase (Baker & Graf, 2009). For all observers, Baker and Graf (2009) found that as the orientation difference between the target and the mask approached zero, the detection threshold for the target stimulus increased. Their data are also Gaussian in form and therefore their data agrees with previous findings (Baker & Graf, 2009). However contrary to previous findings, they found significant threshold elevation for all orientation conditions, even when the mask and target were orthogonal (Baker & Graf, 2009).

2.4. Models:

The findings of both psychophysical and physiological studies are used as a basis for modelling the neural interactions that underlie masking. One model, proposed by Heeger (1992), is called the normalization model. This model is used to explain the effects of cross-orientation suppression (Brouwer & Heeger, 2011; Yuval-Greenberg & Heeger, 2013). The model postulates that the amount of excitatory activation in a neural population from a target stimulus of its preferred orientation depends on the stimulus strength of the target (for example the amount of contrast in the grating stimulus, referred to as "contrast energy") (Yuval-Greenberg & Heeger, 2013). This excitatory activation can be suppressed or "normalized" by the summed activity of a pool of neurons (the normalization pool) that are activated by the mask stimulus (Yuval-Greenberg & Heeger, 2013). The response of the normalization pool neurons to the mask also depends on the contrast energy on the mask (Yuval-Greenberg & Heeger, 2013). Therefore, adding a mask on top of a target stimulus reduces the effective contrast energy of the target (referred to as a reduction of "contrast gain") and produces a similar effect to reducing the contrast of the target (Yuval-Greenberg & Heeger, 2013). Others describe the phenomenon of masking using the similar but more general concept of lateral inhibition. Lateral inhibition is a process by which the excitation of a neuron acts to inhibit the activation of proximal neurons in a lateral direction.

Another approach to modelling uses computational designs to determine the mathematical processes underlying psychophysical data. In attempt to identify the optimal computational model for masking, Meese et al. (2006) compared how several different models account for psychophysical data on several common masking tasks (detection and discrimination thresholds and contrast matching) for the four types of masking (monocular, binocular, half-binocular and dichoptic). They ultimately found that two models, the two-stage model of contrast gain control and the twin summation model preform the best under this range of conditions (Meese et al., 2006). In the twin summation model, non-linear monocular inputs and binocular summation occur before contrast gain control (Meese et al., 2006). What is unique in this model is that the first two steps (non-linear monocular inputs and binocular summation) occur in two separate pathways, one excitatory and one inhibitory (Meese et al., 2006). These two pathways are then combined during contrast gain control (Meese et al., 2006). In the two stage model, the first stage is monocular input which, unlike the twin summation model, is subject to divisive suppression in both eyes (Meese et al., 2006). Then binocular summation occurs (stage two) (Meese et al., 2006). Binocular summation is high in this model because there is a low exponent on the excitatory monocular input (Meese et al., 2006). Stage two is also subject to divisive suppression (Meese et al., 2006). Both models account for a region of facilitation at low mask contrasts in the dichoptic masking data (Meese et al., 2006). This property both contributed to the two stage model and the twin summation model emerging as the best fits for masking data and the rejection of the other models as insufficient (Meese et al., 2006). Finally, the authors discuss which of two most effective models can explain cross-orientation suppression (Meese et al., 2006). Based on previous psychophysical data, they conclude that cross-orientation suppression must occur in their models before binocular summation (Meese et al., 2006). In that case, the two-stage model accounts for cross-orientation suppression data whereas the twin summation model, in its current form, cannot (Meese et al., 2006).

Based on their masking data described above, Baker and Graf (2009) adopt the models just discussed of Meese et al. (2006) because these models contain a parameter that estimates the magnitude of inter-ocular suppression. Large values for the inter-ocular parameter result in strong masking effects such as these seen in the dichoptic masking experiments of Baker and Graf (2009).

3. Evidence for Comparison of Rivalry and Masking:

It has often been proposed that masking and rivalry arise from the same suppressive neural mechanisms (Baker, Meese, & Summers, 2007; Brown, Candy, & Norcia, 1999; Sengpiel, Blakemore, & Harrad, 1995) For example, both phenomenon disrupt the conscious perception of presented stimuli (van Boxtel et al., 2007). Additionally, the strength of a masking effect decreases with increased number of trials, which resembles the immergence of the suppressed stimulus during a BR trial (van Boxtel et al., 2007). Yamashiro et al. (2013) demonstrate the assumed similarity between masking and rivalry by using a masking technique called continuous flash suppression (CFS) as a means to study BR. In their experiment they consider CFS a "special case" of BR because of their similar perceptual dynamics (Yamashiro et al., 2013). Baker et al. (2007) used cross-orientation masking to explore two suppressive neural pathways, one within-eye and one inter-ocular. Based on their psychophysical evidence, they conclude that these pathways occur before binocular summation, the within-eye pathway at a pre-cortical location and the inter-ocular pathway occurring cortically (Baker et al., 2007). The authors note that their proposed model can also provide a framework for interpreting BR data (Baker et al., 2007). Specifically, this model provides an underlying biological mechanism for cross-orientation BR since it fits with previous, hierarchical theories of BR (Baker et al., 2007). van Boxtel et al. (2007) link BR and dichoptic masking using successive rivalry, a technique which induces rivalry using intermittent stimulation. The authors have previously found that successive rivalry ceases to resemble BR if the inter-stimulus intervals exceed ~350 ms and instead the percepts resemble dichoptic masking (van Boxtel et al., 2007). Based on these findings, van Boxtel et al. (2007) wished to investigate whether successive rivalry and dichoptic masking met their three perceptual criteria for BR. The criteria were as follows: 1) the dominance durations must follow a gamma distribution, 2) the dominance durations are temporally uncorrelated between stimuli and, 3) the stimuli dynamics follow Levelt's second proposition, which states that increasing the salience of one stimulus affects the dominance durations of the other eye's stimulus but does not change that stimulus' dominance durations (van Boxtel et al., 2007). As expected, the results of the study confirmed that dichoptic masking meets the three perceptual conditions for BR and van Boxtel et al. (2007) concluded that dichoptic masking and BR arise, at least partially, from the same neural mechanism. Another interesting finding of this study was that the initial percept typically resembled dichoptic masking, even under conditions when the percept subsequently resembled rivalry (van Boxtel et al., 2007). These findings are similar to those of Carter and Cavanagh (2007) who found that the initial rivalry percept is different from those perceived during the subsequent rivalry dominance durations. In fact, they state that the "onset" rivalry percept shares characteristics with masking (Carter & Cavanagh, 2007). Coming from the opposite side, Baker et al. (2007) state that the strength dichoptic masking, but not monoptic making, increases with stimulus duration, resembling BR.

Based on these previous findings, Baker and Graf (2009) designed a set of psychophysical experiments to directly compare BR and dichoptic masking using the same stimuli and the same group of subjects. It has been previously shown that the greatest amount of masking occurs when the target and the mask have the same orientation and the masking effect decreases to a minimum when the mask and target are orthogonal to each other (Baker & Meese, 2007). Similarly, in BR, the length of mean dominance durations increases as the orientations of the two stimuli become more similar (Buckthought et al., 2008). Baker and Graf (2009) therefore hypothesized that those stimuli that result in a strong dichoptic masking effect (small orientation difference) will also result in long BR dominance durations. For this study they used identical sine-wave grating stimuli and the same group of 4 observers for both the dichoptic masking and BR trials (Baker & Graf, 2009). As predicted, dichoptic masking thresholds increased as the orientations of the mask and the target became more similar and, for three observers, BR mean dominance durations increased as the orientation difference between the two eyes' stimuli decreased. These findings further indicate that dichoptic masking and BR result from a shared neural mechanism (Baker & Graf, 2009). Recently, as part of a genome-wide association study (GWAS), Bosten et al. (2015) conducted BR and dichoptic masking experiments on a sample of 1060 observers. They found, like Baker and Graf (2009), that high dichoptic masking thresholds were correlated with long BR mean dominance durations.

Current models for BR and dichoptic masking both include inter-ocular suppression which agrees with findings of Baker and Graf (2009), however the models for the two phenomenon tend to use different types of inter-ocular suppression (divisive for masking and subtractive for rivalry) (Baker & Graf, 2009). Baker and Graf (2009) provide two possible explanations for this discrepancy. There may be a common general suppressive mechanism that is used during both tasks or dichoptic masking may represent an early stage of the suppressive mechanisms used in BR. The latter explanation fits in with the findings of van Boxtel et al. (2007) and Carter and Cavanagh (2007) discussed above. One model that incorporates both BR and masking (cross-orientation supersession) is the ocular opponency model of Said and Heeger (2013) discussed above.

4. Individual Differences:

Many studies have reported considerable inter-individual differences in alternation rate of multistable stimuli (e.g. Fahle, 1981; Pettigrew & Miller, 1998; Miller et al., 2010; Kleinschmidt, Sterzer, & Rees, 2012). These differences can be up to an order of magnitude between individuals but are relatively stable over time for a given subject (Kleinschmidt et al., 2012). Yamashiro et al. (2013) used continuous flash suppression (CFS) to explore individual differences in suppression duration during BR. They found approximately a 130-fold difference in suppression duration between 12 subjects (Yamashiro et al., 2013). Patel et al., (2015) found that stimulus rivalry alternation rate also showed large individual differences. They also found that individuals with fast alternation rates during BR are more likely to experience stimulus rivalry during their flicker/swap rivalry task (Patel et al., 2015). Similarly, individuals with faster BR alternation rates have been found to exhibit greater stereopsis (Halpern, Patterson, & Blake, 1987).

It is possible that these inter-individual differences arise from differences in brain structure. As discussed earlier, Genç et al., (2015) used MRI to determine whether individual differences in the anatomy of the early visual areas (V1, V2, and V3) influenced their perception of the travelling wave. The researchers measured the length of time each individual perceived the travelling wave and correlated that measure with their cortical thickness and surface area of V1, V2, and V3 (Genç et al., 2015). These tests were redone on the same subjects both 6 months and 2 years later to increase reliability (Genç et al., 2015). They found a significant, positive correlation between an individual's travelling wave propagation time and the surface area of their V1 and V2, but not for V3 (Genç et al., 2015). These findings suggest that the temporal dynamics of BR alternation rate is related to the surface area of the subject's primary visual cortex. Also using MRI, Kanai, Bahrami and Rees (2010), investigated whether an individual's alternation rate for a bistable stimulus was related to their cortical thickness, grey matter density or white matter integrity. They found that as cortical thickness of the superior parietal lobule (SPL) and postcentral gyrus (for both the left and right hemisphere) increased, individual's alternation rates became faster (Kanai et al., 2010). Similarly, the authors found an individual's grey matter density and white matter integrity in the bilateral SPL were both correlated with an individual's alternation rate (Kanai et al., 2010). To confirm that these differences in the SPL were causal to bistable switching, Kanai et al. (2010) used TMS. They found that TMS of both the left and right SPL slowed alternation rate compared to TMS of a control area (Kanai et al., 2010). These findings indicate that the SPL plays a causal role in perceptual switching and therefore the individual differences in the brain structure of this area may at least in part account for individual differences in BR alternation rate (Kanai et al., 2010). Kleinschmidt et al. (2012) hypothesized that differences in parietal cortex structure lead to differences in the strength of an individuals' top-down signals from the parietal cortex to the early visual areas. These signals may act to reset the current neural activity and therefore disrupt the rivalry percept, triggering an alternation (Kleinschmidt et al., 2012). Specifically, a greater grey matter density in the superior parietal cortex may lead to stronger top-down signals and this stronger top-down modulation may lead to a faster alternation rate (Kleinschmidt et al., 2012).

These authors also highlight the importance of individual neural connectivity and networks on stimulus perception (Kleinschmidt et al., 2012). Kanai et al., (2011) addressed this aspect of individual differences by using a sibling-descendent cascade-correlation neural network. Using this technique, they found that networks with greater amounts of training had higher alternation rates whereas the networks with less training had lower alternation rates (Kanai et al., 2011). Based on these findings, the authors concluded that individual differences in perceptual alternations may be influenced by that individual's previous training and experience (Kanai et al., 2011).

There is also strong evidence of a genetic component to individual differences in perceptual alternation. Miller et al. (2010) found that BR alternation rate had a higher correlation between monozygotic twins than for dizygotic twins. Overall, their analysis found that genetic factors accounted for 52% of the variance in BR alternation rate (Miller et al., 2010). A recent GWAS also looked into the genetic basis for individual differences in many perceptual phenomenon including BR (Bosten et al., 2015). From their data, the authors confirmed previous findings that rivalry rate significantly decreases with increased age (Bosten et. al, 2015). Another related finding is that of Pettigrew and Miller (1998). They found that individuals with bipolar disorder have slower rates of perceptual switching (Pettigrew & Miller, 1998). Since bipolar disorder is highly heritable, the authors hypothesized that bipolar disorder may be caused by a genetic predisposition for slow interhemispheric switching, that also results in slow BR alternations (Pettigrew & Miller, 1998). Patel et al. (2015) suggest two possible origins for the inter-individual differences in perceptual alternation rate. One of these is individual differences in the strength of adaptation to visual stimuli, the assumption being that the stronger the individual adaptation mechanisms, the faster their alternations will be (Patel et al., 2015). They note that these differences in adaptation strength may be under genetic control (Patel et al., 2015).

The second neural mechanism Patel et al. (2015) suggest for differences in perceptual alternation rate is the strength of neural inhibition. The main inhibitory neurotransmitter in the brain is gamma-amino-butyric acid (GABA) and it is believed to play a role in the inhibitory neural processes thought to underlie alternations in multistable perception (Patel et al., 2015).

van Loon et al. (2013) used a computational model simulation to show that strong cortical inhibition, mediated by $GABA_A$ receptors, likely leads to slower perceptual alternations. When the researchers measured GABA concentrations, they found that subjects with higher GABA did indeed show slower perceptual alternations (van Loon et al., 2013). Additionally, when the researchers stimulated $GABA_A$ receptors with lorazepam this also resulted in the slowing of perceptual alternations (van Loon et al., 2013). Conversely, when they measured glutamate and glutamine (an excitatory neurotransmitter and its metabolite), higher concentrations were associated with shorter dominance durations for structure from motion stimuli (van Loon et al., 2013). Finally, van Loon et al. (2013) used continuous theta burst stimulation (cTBS) on the posterior intraparietal sulcus, since it has been previously shown that cTBS increases GABA concentrations. As expected, the cTBS led to slower perceptual alternations for their structure from motion stimulus.

Fesi and Mendola (2015) recently conducted a study examining the link between individual differences in perceptual rivalry alteration rate and the peak frequency of evoked and induced gamma-band activity (Fesi & Mendola, 2015). It has been previously shown that the peak frequency of induced gamma-band oscillations in response to visual grating stimuli predicts individuals' resting levels of GABA (Edden et al., 2009; Muthukumaraswamy et al., 2009). Since GABA levels have also been found to be predictive of perceptual alterations in BR, Fesi and Mendola (2015) used magnetoencephalography (MEG) to assess whether there was a link between the peak frequency of evoked and induced gamma-band activity in early visual areas and individual differences in BR alternation rate. They found that for both binocular and monocular rivalry, alternation rate was negatively correlated with the peak frequency of late evoked gamma responses in V1 consistent with high GABA leading to slow rivalry (Fesi & Mendola, 2015).

5. Luminance:

So far, we have discussed evidence to suggest a common neural mechanism for binocular rivalry and dichoptic masking, especially that of Baker and Graf (2009). These findings are compelling for the typical dichoptic masking and rivalry stimuli of oriented sine-wave gratings but are these findings applicable to masking and rivalry more generally?

Our lab's interest in luminance-only masking originated with findings by Mendola et al (2006). In subjects with normal vision, a high contrast flickering grating was shown to one eye and a mask of homogenous luminance was shown the other eye (Mendola et al., 2006). In one condition the mask was a mid-level grey (same luminance as the grating background) and in the other condition the mask was black (Mendola et al., 2006). Unsurprisingly, both of these conditions showed more cortical activation than the subject's baseline measure (Mendola et al., 2006). However, when comparing the black condition and the grey condition, Mendola et al. (2006) found that the black mask condition resulted in greater activation than the grey condition. Mendola et al. (2006) then compared these cortical activation patterns with those typically found in rivalry (based on Lumer et al., 1998). Unlike BR, luminance masking showed no activation in the temporal-parietal junction (TPJ) (Mendola et al., 2006). Luminance masking also showed activation of the medial occipital-parietal cortex which is not seen in BR (Mendola et al., 2006). However, similar activation for luminance masking and BR was found in superior parietal, lateral occipital and ventral temporal brain areas (Mendola et al., 2006). Therefore, this data further implies commonality between masking and rivalry in a more universal manner than the findings of Baker and Graf (2009) and this has motivated our lab to systematically investigate if there exists a luminance analogue to their findings.

Binocular combination of stimuli with varying luminance levels has been of interest to psychophysicists because the two luminances in each eye do not simply sum together to create a percept of their combined luminance (Curtis & Rule, 1978; Levelt, 1965). Instead, a phenomenon called Fechner's paradox is observed (Anstis & Ho, 1998; Bourassa & Rule, 1994; Curtis & Rule, 1978, 1980; Levelt, 1965; Pardhan, Gilchrist, Douthwaite, & Yap, 1990). Fechner's paradox refers to the inter-ocular inhibition that takes place during the viewing of targets with different luminance levels, for example if one eye is covered with a neutral density (ND) filter (Bourassa & Rule, 1994; Curtis & Rule, 1978, 1980; Pardhan et al., 1990). In this case, even though the eyes are receiving less total stimulation, monocular viewing of the unfiltered eye results in a greater perceived luminance than binocular viewing (Bourassa & Rule, 1994; Curtis & Rule, 1978, 1980; Pardhan et al., 1990). Fechner's paradox can therefore be considered luminance masking because one monocular input is inhibiting the other. Indeed, Sugie (1982) proposed a brightness model based on Fechner's paradox which had strong excitatory synaptic connections within an eye and weak inhibitory synapses between eyes.

Fechner's paradox does not occur when the luminance levels of the eyes are approximately equal (Bourassa & Rule, 1994; Curtis & Rule, 1978, 1980; Pardhan et al., 1990).

Under these conditions, binocular viewing results in partial brightness summation and therefore binocular luminance is perceived to be greater than monocular luminance (Bourassa & Rule, 1994; Curtis & Rule, 1978, 1980; Pardhan et al., 1990). Similarly, Anstis and Rogers (2012) conducted a study during which they showed one eye dark grey spots on a light grey background and the other eye light grey spots on a dark grey background. They found that detection of monocular luminance information was much worse under these binocular conditions, than for monocular viewing conditions (Anstis & Rogers, 2012). This is because stimuli which have different but similar luminance levels between the eyes will easily fuse (Anstis & Rogers, 2012). But how different is too different to fuse? Formankiewicz and Mollon (2009) investigated the ability to determine inter-ocular differences in luminance and found that Weber's law, which states that the just-noticeable-difference (jnd) between two stimuli is proportional to the magnitude of the stimuli, holds true for judging luminance differences between the eyes. This means that the higher the stimuli's level of luminance, the more different the two eyes' luminance levels must be to notice a difference between them.

There exists a perceptual stage between the undetectable fusing of stimuli with similar luminance levels and binocular rivalry (Ludwig, Pieper, & Lachnit, 2007; Malkoc and Kingdom, 2012). During this stage, although the images are fused, the inter-ocular luminance difference between the stimuli is detectable but no rivalry alternations take place (Ludwig, et al., 2007; Malkoc and Kingdom, 2012). The image instead appears to be shimmering or shiny (Ludwig, et al., 2007; Malkoc and Kingdom, 2012). This perception is called binocular lustre (Ludwig, et al., 2007; Malkoc and Kingdom, 2012). Like stereopsis, although binocular lustre can be achieved in a laboratory setting, is it assumed that we experience lustre in everyday vision when we perceive surface properties, such as shininess or smoothness (Formankiewicz & Mollon, 2009; Ludwig et al., 2007). Since light is reflected from an object's surface in one direction and our eyes are separated spatially, it follows that different amounts of light from the object would enter each eye and this difference results in the perception of a lustrous surface (Formankiewicz & Mollon, 2009).

In terms of luminance based binocular rivalry, according to Brascamp et al. (2015), the study of binocular brightness perception, Fechner's paradox, and how these perceptions were effected by contours (Levelt, 1965) influenced how Levelt characterized BR in his four propositions. Levelt's original propositions can be summarized as: Increasing the stimulus strength in one eye, 1) increases the predominance of that stimulus; 2) decreases the average dominance durations of the other eye's stimulus; 3) increases alternation rate and 4) equally increasing stimulus strength in both eyes, increases alternation rate. Since Levelt described his propositions mostly in terms of changing one eye's stimulus while keeping the other eye's stimulus constant, Brascamp et al. (2015) rephrased propositions 2 and 3 to apply to a broader range of stimulus starting conditions. The revised propositions instead focus on the effects of changing the relative strength between the stimuli as follows: increasing the difference in strength between stimuli, 2) increases the average dominance duration of the stronger stimulus, and 3) decreases alternation rate (Brascamp et al., 2015).

Do Levelt's propositions hold true for BR stimuli for which "stimulus strength" is manipulated by changing luminance levels? Studies by O'Shea, Blake and Wolfe (1994) and Mull, Armstrong, and Telfer (1965) both found that the rate of BR alternations slows down under lower luminance conditions (scotopic luminances versus mesopic and photopic). Similarly, Kaushall (1975) reports that, as predicted Levelt's propositions, as the brightness of stimuli increases, so does BR alternation rate and increasing one eye's luminance increases that eye's predominance during BR. Liu, Tyler, and Schor (1992) investigated the impact of luminance changes on rivalry by manipulating the contrast of orthogonal grating stimuli. They found that as they decreased the contrast of the gratings, rivalry rate slowed and the observers perceived longer periods where the stimuli were fused to form a plaid (Liu et al., 1992). Liu et al. (1992) also reduced the gratings' luminance levels using ND filters. Similarly, they found that decreasing the luminance levels of the stimuli resulted in increased perception of the plaid stimulus (Liu et al., 1992). In line with the discussion above, the fused perception of the two gratings as a plaid was lustrous in appearance (Liu et al., 1992).

When studying luminance perception, it is important to acknowledge that factors other than the absolute luminance of the stimulus effect its perceived brightness. As mentioned earlier, Levelt (1965) identified the importance of contours in brightness perception. He found that when one eye was shown a black target and the other eye was shown a black outline on a white background, this was perceived as brighter than when one eye was shown the same black target and the other eye was shown the white background with no contour (Levelt, 1965). In fact, the second situation resembles seeing the black target in both eyes (Levelt, 1965). Further evidence for the effect on contours on luminance perception stems from findings that the perception of

Fechner’s paradox is reduced when stimuli are presented under ganzfeld conditions, which lack contours (Bourassa & Rule, 1994). Based on the consistent finding that the visual system places more weight on contours or contrast edges (Anstis & Ho, 1998), there is a model of luminance perception called the filling-in model (Pelekanos et al., 2015). This model proposes that the perception of highly salient visual features, such as contrast edges, influence the perception of less salient attributes of the visual scene, such as areas of homogenous luminance. The visual system therefore uses the information from the borders of a stimulus to fill-in the center (Pelekanos et al., 2015). Paradiso and Nakayama (1991) found psychophysical evidence for the filling-in model using backwards masking. As stated above, they found that the perceived luminance of a target stimulus could be disrupted by the subsequent presentation of a mask with a different luminance (Paradiso and Nakayama, 1991). Because they found that this masking effect varied both based on the time interval between the target and the mask and on the relative sizes of the target and the mask, they concluded that the encoding of the target’s luminance began at the edge of the stimulus and then was propagated inwards (Paradiso and Nakayama, 1991). This propagation could however be interrupted by the introduction of another contour, that of the mask (Paradiso and Nakayama, 1991).

Perceiving the luminance of a stimulus also depends on whether the stimulus is lighter than its background (an increment) or darker than its background (a decrement). This has been found to be relevant to the perception of Fechner’s paradox (Anstis and Rogers, 2012; Cohn, Leong and Lasley, 1981; Baker, Wallis, Georgeson and Meese, 2012). As previously described, the typical pattern of luminance perception is as follows: similar luminance levels summate linearly between the eyes, but when one eye’s luminance level is too low, then Fechner’s paradox is observed. However, this classic pattern has been found to apply only when both eyes’ stimuli are increments on a dark background (Anstis & Rogers, 2012; Baker et al., 2012). When the stimuli are decrements, non-linear combination occurs in a winner-take-all fashion (Anstis & Rogers, 2012; Baker et al., 2012). This means that the darker of two stimuli dictates the luminance of the observer’s perception (Baker et al., 2012). Baker et al. (2012) found that this change to non-linear behavior is also seen when the stimuli are increments on mid-grey background, which implies the strength of the increment’s contrast also plays a role. When the researchers tested decrements on a mid-grey background as well as decrements on a half-white, half-black background, they found that in both these situations perceptions resembled winner-take-all combination (Baker et al., 2012).

The complexity of binocular luminance combination had led to many different models of how the visual system interprets luminance, such as the filling-in model discussed above. Another model, called the vector-sum model, represents the luminance input into each eye as a vector (Bourassa & Rule, 1994). The length of the vector corresponds the brightness of the input (Bourassa & Rule, 1994). The two vectors are separated by an angle of α degrees, which represents how the two eyes interact (Bourassa & Rule, 1994). The binocular perception of brightness is the sum of the two vectors (Bourassa & Rule, 1994). The two mechanism theory is a model by Cohn et al. (1981) which proposes that luminance is determined using both a summing and a differencing mechanism. An increment in each eye will lead to a response from the summing mechanism whereas an increment in one eye and a decrement in the other would produce a response in the differencing mechanism (Cohn et al., 1981). Another example is the model by Ding and Sperling (2006) which theorizes that each eye exerts a gain control on the other eye's signal which proportional to its own stimulus energy. This model also includes each eye exerting gain control on the other eye's gain control (Ding and Sperling, 2006).

Experimental Hypotheses:

Based on previous findings related to both BR and masking using both oriented grating and luminance-only stimuli, this study has three main goals. The first is to investigate the relationship between BR and masking. Secondly, for both BR and masking, we wish to explore how the dynamics of these two phenomenon differ depending on whether the two eyes' stimuli are oriented sine-wave gratings or homogenous luminance patches. Lastly, we wish to characterize inter-individual differences for all of our experimental conditions.

1a. ***The length of binocular rivalry dominance durations will increase and alternation rate will decrease as the orientation difference between the two eyes' stimuli decreases*** Previous findings, especially those of Baker and Graf (2009) indicate that binocular rivalry dominance duration length and alternation rate are sensitive to the size of the inter-ocular orientation difference between the two eyes' stimuli. We will attempt to replicate these findings using a large sample of naïve observers.

1b. ***The effects of masking will increase as the difference in orientation between the target and mask stimuli decreases.*** It has been previously found that the strength of masking effects is dependent on the orientations of the stimuli. Baker and Graf (2009) found, using dichoptic masking, decreasing the orientation difference between the mask and target stimuli resulted in stronger masking. We will attempt to replicate these findings using a large sample of naïve observers. To determine whether these findings hold true for all types of masking, we also replicated these experiments using half-binocular masking.

1c. ***The length of binocular rivalry dominance durations will be significantly correlated with the strength of masking effects, suggesting that the two phenomena use a common neural mechanism.*** Due to the similarity of their perceptual effects it has been proposed that these two perceptual phenomena arise from a shared neural mechanism. Using their psychophysical data, Baker and Graf (2009) found those stimulus conditions that resulted high dichoptic masking thresholds also resulted in long BR mean dominance durations and that the correlation between the two was significant. We will attempt to replicate these findings using a large sample of naïve observers and two types of masking.

2a. ***The length of binocular rivalry dominance durations will increase and alternation rate will decrease as the luminance difference between the two eyes' stimuli decreases.*** Baker and Graf (2009) used classic oriented, sine-wave grating stimuli for their binocular rivalry experiments. To determine the applicability of their findings to rivalry in general, we will determine if there is a similar rivalry effect using homogenous luminance rivalry stimuli. We propose that these effects do apply to different types of rivalry stimuli.

2b. ***The perceptual dynamics of homogenous luminance stimuli will agree with the revised Levelt's propositions.*** Levelt's proposition have recently been revised by Brascamp et al (2015). However, they do not consider how these propositions apply to stimuli of homogenous luminance. We propose that perceptual dynamics of luminance-only rivalry (e.g. changes in alternation rate and dominance duration length) will agree with those proposed by the revised Levelt's propositions.

2c. ***The effects of masking will be significant different depending on the luminance of the masking stimulus. The effect of the mask will also depend on whether the stimuli are increments or decrements to the background luminance.*** As with BR, to determine whether the effects of masking reported by Baker and Graf (2009) are applicable to masking of various stimulus types we will investigate the strength of masking for masks with varying luminance levels. Additionally, stimuli that are increments to background luminance have long been found to behave differently than stimuli that are decrements. Therefore, we expect different effects from our increment and decrement masks.

3. ***There will significant inter-individual differences between subjects in binocular rivalry alternation rates and dominance durations and in the size of masking threshold elevation.*** It is well established that individual subjects may differ considerably on binocular rivalry alternation rate. These differences may arise from differences in brain structure, neural inhibition or genetics. Additionally, the findings of Baker and Graf (2009) indicate that slow alternators during binocular rivalry also experience stronger masking. We will the effects of inter-individual differences on both binocular rivalry and masking.

Methods:

1. Subjects:

In total, 25 observers (13 female) participated in these experiments including this MSc candidate (CC). All subjects except CC were naïve to the purpose of these experiments. Subjects were either recruited in person or through an advertisement on Facebook. Six subjects were excluded from analysis because their baseline detection threshold was higher than their threshold elevation on at least one of the masking conditions. Another four subjects were excluded as outliers because their masking thresholds either fell below the threshold set by first quartile – 1.5*IQR (interquartile range, third quartile-first quartile) or fell above the threshold set by third quartile + 1.5*IQR. Our exclusion criteria were based on those used by Baker and Graf (2009). All subjects had normal or corrected-to-normal visual acuity and stereoacuity of at least 30 seconds of arc, as measured by the Titmus stereo test. Subjects provided written informed consent and were remunerated for their time. The experiments were approved by the Research Ethics Board (REB) of McGill University (Protocol NEU-08-03).

2. Display:

All stimuli were presented on a MacBook Pro Laptop (2.3 GHz Intel Core i7) Macintosh computer with 2880 x 1800 resolution, a NVIDIA GeForce GT 750M graphics card, and a 60-Hz refresh rate. Stimuli were generated and presented using Psykinematix software (version 1.5) (KyberVision, Montreal, Canada, psykinematix.com). The screen was calibrated through

Psykinematix using the Spyder 3. The stimuli for each eye were displayed side by side on the screen at a viewing distance of 45 cm. To achieve dichoptic stimulus presentation, the subjects wore prism glasses of 12 diopters. The prism glasses allowed the stimuli presented to each eye to superimpose spatially and fuse. If required, subjects were able to wear the prism glasses on top of their prescription glasses. The screen was divided in half by a cardboard divider, allowing the left image to be presented exclusively to the left eye and the right image to be presented exclusively to the right eye.

3. Stimuli and Procedure:

3.1. General:

For all stimulus conditions, the stimuli presented to each eye were 14.5° apart horizontally, centered 7.25° either side of the screen divider. Dichoptic stimuli presentation using prism glasses depends on the two stimuli spatially superimposing. To achieve this effect, robust cues for fusion must be presented to both eyes. The two cues used in these experiments were borders around the stimuli and fixation points. All the stimuli were presented inside a square border consisting of 2D uniform noise between with a granularity of 8 pixels and size of 8°. The mean luminance contrast of the 2D noise was 50% (similar to background luminance) with individual elements assigned a random luminance. For all stimulus conditions, every pair of stimuli presented to the subject had a different noise pattern making up the border. This was accomplished by randomizing the seed value of the border stimulus. The fixation marks presented to each eye were diamond shaped, sine-wave angular grating stimuli with a spatial frequency of 5 cpd and a hard-edge envelope. The fixation marks' contrast was set to 50% and their size was set at 0.23°. A schematic of the stimuli is shown Figure 1. Before each trial, the subjects were presented with a preview screen that contained images of the stimuli used in the trial and written instructions describing the task. The stimuli and task were then explained verbally to the subject. The subject was then instructed to put on the prism glasses and view the stimuli. This allowed us to verify that the subject had achieved fusion of the two eyes' images before they began the trial. The subject began the trial by pressing the spacebar. For all masking experiments, the mask stimulus and the target stimulus were swapped between the two eyes between trials. Similarly, for all rivalry experiments the stimuli were counterbalanced across the two eyes between trials.

3.2. General Binocular Rivalry:

For all binocular rivalry experiments the stimuli were presented to the observer for trials 90 seconds in duration.

3.3. General Masking:

For all masking experiments and determining subjects' baseline detection threshold, the stimuli were presented for 500 ms in a two interval forced choice (2IFC) design with a 500 ms inter-stimulus interval. The contrast or luminance of all target stimuli were controlled using a 3-down, 1-up staircase.

3.4. Oriented Grating Stimuli:

All oriented grating stimuli were Gabor patches with a spatial frequency of 2 cycles per degree (cpd), in a Gaussian envelope, $\sigma = 1.6$.

3.4.1. Binocular Rivalry: For these binocular rivalry experiments, we used three stimulus conditions: 1) The dichoptic difference in orientation between the stimuli was 30°: one eye's stimulus orientation was 15° and the other eye's stimulus orientation was -15° (relative to horizontal). 2) The dichoptic difference in orientation between the stimuli was 60°: one eye's stimulus orientation was 30° and the other eye's stimulus orientation was -30°. 3) The dichoptic difference in orientation between the mask and the target was 90°: one eye's stimulus orientation was 45° and the other eye's stimulus orientation was -45°. Each experimental condition was run for three trials per subject. Both eyes' stimuli had 32% contrast. During a trial, the subject's perception alternated between the left oriented grating and the right oriented grating. The subjects were instructed to indicate which stimulus dominated their perception. If the perceived stimulus was left oriented, they were instructed to press the keyboard's left arrow key. If the perceived stimulus was right oriented, they were instructed to press the keyboard's right arrow key. Subjects were informed that they should judge a particular stimulus as dominating perception if it covered at least two thirds of the image. From these reports, individuals' mean dominance durations and alternation rates were calculated for the three different conditions. The goal of these experiments was to determine individuals' alternation rates and if they differed between conditions.

3.4.2. Baseline Detection Threshold: To obtain a subject's baseline detection threshold for a target stimulus, one interval contained the target stimulus in one eye, and background luminance, inside a noise border with a fixation mark in the other eye. During the other interval, background luminance was shown to both eyes. The target stimulus had an orientation of 45° from the horizontal. The subject was asked to indicate which interval contained the target stimulus by pressing the keyboard's left arrow key if the target was in the first interval and the keyboard's right arrow key if the target was in the second interval. This task was run three times for each subject.

3.4.3. Dichoptic Masking: For these dichoptic masking experiments, during one interval, one eye was shown the mask while the other eye was shown background luminance. In the other interval the same eye was again shown the mask and the other eye is shown the target stimulus. The same three stimulus conditions, as described above for binocular rivalry (30°, 60°, and 90° difference between the mask and the target), were used. The contrast of the mask stimulus was fixed at 32% and contrast of the target was determined using a staircase. Each experimental condition was run three times for each subject. The goal of this task was to determine how much more contrast, compared to baseline, a subject required to detect the target stimulus when it was occluded by a masking stimulus (the mask and target together were perceived together as a plaid).

3.4.4. Half-Binocular Masking: For these half-binocular masking experiments, the same stimulus conditions, 30°, 60°, and 90° difference between the mask and the target, were used. However, rather than the mask being shown to one eye and the target being shown to the other, in these experiments, the mask in shown to both eyes. The target stimulus was still only shown to one eye, in one of the two intervals, forming a plaid with the mask. Each experimental condition was run three times for each subject. These experiments also determined how much more contrast, compared to baseline, a subject required to detect the target stimulus when it was occluded by a masking stimulus. However, these experiments were added to investigate whether the same trend observed for dichoptic masking could also be found using another type of masking.

3.5. Homogeneous Luminance Stimuli:

For all of the homogeneous luminance experiments the background luminance was set to 50% luminance (mid-level grey). The stimuli were square, 4.5° in size, with uniform luminance.

3.5.1 Binocular Rivalry: For these binocular rivalry experiments, the subject's perception alternated between the two stimuli, either the stimulus with the lighter luminance or the stimulus with the darker luminance. The subjects were instructed to indicate which stimulus dominated their perception. If the perceived stimulus was the darker luminance patch, they were instructed to press the keyboard's left arrow key. If the perceived stimulus was the lighter luminance patch, they were instructed to press the keyboard's right arrow key. Subjects were informed that they should judge a particular stimulus as dominating perception if it covered at least two thirds of the image. From pilot studies, we found that for luminance rivalry, especially for the stimulus conditions with a smaller difference in luminance between the stimuli, perception during the rivalry trials was often a blend between the luminances of the two stimuli. We referred to this stimulus perception as "fusion" and instructed the observers to press the space bar if they experienced a stable and lasting fused percept between the two stimuli luminances. From these reports, individuals mean dominance durations and alternation rates were calculated for the different conditions. Before each luminance-based rivalry trial, during the stimulus preview, the subject was instructed to memorize the luminances of the stimuli to ensure they could accurately identify whether their percept was the lighter stimulus, the darker stimulus, or a blend between the two. The three stimulus conditions for these experiments were as follows: 1) 70% luminance vs. 30% luminance, 2) 80% luminance vs. 20% luminance 3) 90% luminance vs. 10% luminance. For each condition, the stimulus pairs were considered to be of equal stimulus strength (equidominant). Stimulus strength (relative to background) weakest for the 70%vs30% condition and was greatest for the 90%vs10% condition. Each experimental condition was run three times for each subject. The goal of these experiments was to determine individuals' alternation rates for these luminance stimuli and how they differed between conditions in analogy with grating rivalry.

3.5.2. General Luminance Masking: Although default background luminance remained 50%, to ensure that subjects were comparing the perceived luminances of the stimuli rather than comparing each stimuli to the background luminance, between trials the background luminance was changed randomly.

3.5.3. Dichoptic Masking: As with the oriented grating dichoptic masking experiments, for these dichoptic masking experiments, during one interval, one eye was shown the mask while the other eye was shown background luminance. In the other interval the same eye was again shown the mask and the other eye is shown the target stimulus. We had two categories of luminance-based dichoptic masking, both of which contained three conditions. In the first category the **stimuli were decrements to the background**. The three stimulus conditions for this category, based on the luminance of the masking stimulus, are as follows: mask = 10% luminance, mask = 20% luminance, and mask = 30% luminance. On the first trial, the luminance of the target was set to 60% luminance (10% above background luminance). The target stimulus' luminance was controlled using a staircase but it was always lighter than background luminance (increment). Therefore, the interval containing the target had a lighter luminance than the interval only containing the mask. The subjects were instructed to indicate which interval contained the lighter stimulus by pressing the keyboard's left arrow key if the first interval was lighter and the keyboard's right arrow key if the second interval was lighter. Each experimental condition was run three times for each subject. The goal of these experiments was to determine how much luminance above the background a subject required to detect a difference between the target and the mask (**increment detection threshold**). In the second category, the **stimuli were increments to the background.** The three stimulus conditions in this category were: mask = 90% luminance, mask = 80% luminance, and mask = 70% luminance. On the first trial the luminance of the target was set to 40% luminance (10% below background luminance). The target stimulus' luminance was controlled using a staircase but it was always darker than background luminance (decrement). Therefore, the interval containing the target had a darker luminance than the interval only containing the mask. The subjects were instructed to indicate which interval contained the darker stimulus by pressing the keyboard's left arrow key if the first interval was darker and the keyboard's right arrow key if the second interval was darker. Each experimental condition was run three times for each subject. The goal of these experiments was to determine how much luminance below the background a subject required to detect a difference between the target and the mask (**decrement detection threshold**) and whether this changed for different mask luminances.

3.5.4 Half-Binocular Masking: For these half-binocular luminance masking experiments, we used the same mask conditions and tasks that were used for the dichoptic luminance masking experiments. However, in these experiments, the mask was shown to both eyes. The target stimulus was still only shown to one eye.

3.6 Parametric Luminance Rivalry Experiments – Original Luminance Scale:

To obtain a more comprehensive and systematic understanding of luminance-based rivalry we conduced three different experiments. Each experimental condition was run 8 times for each subject. The goal of these experiments to ascertain whether luminance only rivalry dynamics agree with the revised Levelt's propositions

As with the homogeneous luminance experiments, the background luminance was set to 50% luminance (mid-level grey). The stimuli were square, 4.5° in size, with uniform luminance. For these experiments the subjects' task was the same as for the homogenous luminance binocular rivalry described above.

3.6.1. Equidominance: The stimulus pairs in all conditions were of equal strength, meaning that they were the same distance from middle grey. The stimulus conditions for these experiment were as follows: 90% luminance vs 10% luminance; 80% luminance vs 20% luminance; 70% luminance vs 30% luminance; 60% luminance vs 40% luminance; 40% luminance vs. 60% luminance; 30% luminance vs. 70% luminance; 20% luminance vs. 80% luminance; 10% luminance vs. 90% luminance.

3.6.2 One Eye Black: For all conditions, one eye's stimulus was fixed at 0% luminance (black). The other eye's stimulus luminance was varied across conditions as follows: 100% luminance, the condition with the greatest relative stimulus strength and the greatest difference from black; 65% luminance; 50% luminance; 35% luminance, the condition with the weakest relative stimulus strength relative and the smallest difference from black.

3.6.3. One Eye White: For all conditions, one eye's stimulus was fixed at 100% luminance (white). The other eye's stimulus luminance was varied across conditions as follows: 0% luminance, the condition with the greatest relative stimulus strength and the greatest difference from white; 35% luminance; 50% luminance; 65% luminance, the condition with the weakest relative stimulus strength and the smallest difference from white.

3.7 Parametric Luminance Rivalry Experiments – Corrected Luminance Scale:

The luminance scale used for our luminance based binocular rivalry experiments resulted in the stimuli that are decrements to the background having greater perceived contrast than increment stimuli that are an equal distance from mid-level grey. To correct for this imbalance, we calculated Whittle's Contrast (logW, where $W = \Delta L/(L_{min} + k)$), which linearizes the luminance decrement scale and indicates which luminance increments and decrements are perceived as equal in contrast (Kingdom & Whittle, 1996). We tested three subjects on the full set of luminance rivalry tests with this contrast scale using the same experimental design as used for the test above, eight trials per condition with stimuli counterbalanced across eyes. In addition, we added one final test to complete our parametric study of luminance based binocular rivalry. This test maintains a constant interocular difference in luminance so as to be complementary with the other tests. In our equidominance conditions, stimulus strength as well as interocular luminance difference vary simultaneously. Fixing the stimulus in one eye while varying the luminance in the other eye also varies the interocular luminance difference systematically, but also varies the stimulus strength in the second eye.

3.7.1. Equidominance: Using Whittle's contrast, we chose five pairs of luminance stimuli that are perceptually equal. The conditions are as follows (in terms of percent luminance): 50%vs50%; 51%vs49%; 53%vs47%; 58%vs44%; 69%vs36%. For simplicity in comparing these new conditions with the previous luminance scale we labeled the new conditions as follows: 5vs5; 6vs4; 7vs3; 8vs2; 9vs1.

3.7.2. One Eye "Black": Based on Whittle's decrement linearization, our black stimulus is now 25% luminance. Our four conditions, based on keeping one eye constant at 25% luminance, are as follows: 25%vs44%; 25%vs50%; 25%vs58%; and 25%vs99%. For simplicity in comparing these new conditions with the previous luminance scale we labeled the new conditions as follows: 0vs2; 0vs5; 0vs8; 0vs10.

3.7.3. One Eye "White": Since Whittle's calculation acts to equate luminance decrements to luminance increments, our white stimulus value is essentially equal to the one used above, at 99% luminance. Our four conditions, based on keeping one eye constant at 99% luminance, are as follows: 99%vs58%; 99%vs50%; 99%vs44%; and 99%vs25%. For simplicity in comparing these new conditions with the previous luminance scale we labeled the new conditions as follows: 10vs8; 10vs5; 10vs2; 10vs0.

3.7.4. Constant Difference: This test will investigate the dynamics of luminance rivalry when the pairs of stimuli have a constant difference in luminance. Based on Whittle's contrast, we chose four stimulus pairs that are separated by equal differences in perceived luminance. These conditions are as follows: 25%vs49%; 44%vs51%; 49%vs58%; and 51%vs99%. For simplicity in comparing these new conditions with the previous luminance scale we labeled the new conditions as follows: 0vs4; 2vs6; 4vs8; 6vs10.

4. Data Analysis:

4.1 Oriented Grating Stimuli:

For binocular rivalry, average mean dominance duration length and alternation rate was compared between conditions to determine if these characteristics are significantly different based on the size of the orientation difference between the two eyes' stimuli. For dichoptic masking, average threshold elevation was compared between conditions to determine if threshold elevation is significantly different based on the size of the orientation difference between the mask and the target. This analysis was also done for the half-binocular masking experiments to confirm the two types of masking found similar trends. In addition, masking threshold elevation was correlated with binocular rivalry alternation rate to determine whether high masking thresholds correspond to slow rivalry.

4.2 Homogeneous Luminance Stimuli:

For all luminance-based rivalry, as with grating rivalry, average mean dominance duration length and alternation rate was compared between conditions. Unique to luminance-based rivalry is the measure of mean dominance duration length and alternation rate for fusion. These fusion values were also compared between conditions. As with the grating stimuli, the dichoptic masking and half-binocular masking thresholds were compared between conditions and dichoptic masking and half-binocular masking were compared to each other. Additionally, for both types of masking, the results for the increment categories were compared to those for the decrement categories to determine any differences in masking effects between these two categories of stimuli. As above, masking thresholds were correlated with binocular rivalry alternation rate to determine whether high masking thresholds correspond to slow rivalry. These analyses also included fusion as a covariate. We also examine the trends of the results from the Parametric Luminance Rivalry Experiments and compared them to the revised Levelt's propositions.

4.3 Comparison of Oriented Grating Stimuli to Homogeneous Luminance Stimuli:

Lastly, all of the oriented grating stimuli experiments were compared to their corresponding homogenous luminance experiments. The dichoptic and half-binocular grating masking thresholds were compared to the dichoptic and half-binocular luminance masking thresholds. We compared mean values averaged for all subjects as well as individual thresholds across the three experimental conditions. We also compared mean dominance durations and alternation rates for oriented grating rivalry and luminance-only rivalry. We compared mean values across all subjects as well as individual values across all experimental conditions. In the data from both the oriented grating stimuli experiments and the homogenous luminance stimuli experiments this indicates that any trends found are true for masking and binocular rivalry generally rather than specific to certain types of stimuli.

Results:

1. Oriented Grating Stimuli:

1.1. Binocular Rivalry:

Overall, as predicted based on previous findings, we found that binocular rivalry (BR) alternation rate varied with the orientation difference between the two eyes' stimuli. Specifically, BR rate speeds up as the orientation difference between the left and the right eyes' stimulus increases (Figure 2). This means that BR rate was slowest for the 30° difference condition and significantly increases across the two subsequent conditions (60° and 90° difference), $F(2, 30) = 20.90$, $p < .001$. It has been previously found that slow rivalry correlates with physiological markers such high GABA (e.g. van Loon et al., 2013) and high gamma frequency (Fesi & Mendola, 2015), which is thought to indicate high inhibition.

1.2. Dichoptic Masking:

One way to assess the putative link between slow rivalry and high inhibition is to look at dichoptic masking with similar stimuli. Based on the findings of Baker and Graf (2009) we expected to find that dichoptic masking thresholds decrease as the orientation difference between the target and the mask increase. Overall, as shown in Figure 3 (blue bars), we did indeed find a significant decrease in dichoptic masking threshold elevation as the orientation difference between the mask and the target increased, $F(2,30) = 6.082$, $p=.006$. The weakest masking effect was seen for the 90° difference condition, which was also the condition which yielded the fastest rivalry. As the orientation difference decreased across conditions (60° and 30° difference), masking increased, as would putative inhibition levels.

1.3. Half-Binocular Masking:

The overall masking thresholds for all conditions were higher for half-binocular masking than for dichoptic masking (Figure 3, red bars), and a 2x3 repeated measure ANOVA confirmed that there was a significant difference between the overall masking thresholds for the two types of masking (see Figure 3), $F(1,28) = 22.119$, $p < .001$ (see also Meese et al., 2006). Nevertheless, we found the same trend for half-binocular masking as dichoptic masking. The masking effect was strongest for the 30° difference condition and masking thresholds significantly decreased as the orientation difference between the mask and the target increased, $F(2,26) = 98.196$, $p < .001$. These findings indicate that the relationship between BR and masking is not specific to dichoptic masking and can be found using an alternative method of masking.

1.4. Comparisons:

In order to directly compare BR with dichoptic masking for individual subjects, we correlated BR alternation rate with dichoptic masking threshold elevation, across the three orientation conditions (Figure 4). The two were negatively and significantly correlated, $r(46) = -0.38$, $p < .01$. This further indicates that as BR alternations rate slows across conditions (90°, 60°, 30° difference), dichoptic masking thresholds increase. As shown in Figure 5, the same effect occurs when BR alternation rate is correlated with half-binocular masking threshold elevation, $r(37) = -0.48$, $p < .01$. These findings confirm that slow rivalry relates to strong masking and vice versa. This lends evidence to the hypothesis that masking and binocular rivalry share a common underlying mechanism (Baker & Graf, 2009). Finally, to further assess the relationship between our dichoptic masking and half-binocular masking findings at the individual subject level, we compared the thresholds for these two types of masking, and found a positive and significant correlation, $r(37) = 0.49$, $p < .01$ (Figure 6).

2. Homogeneous Luminance Stimuli:

2.1. Binocular Rivalry:

For all three homogeneous luminance binocular rivalry conditions, 70%vs30% luminance, 80%vs20% luminance, 90%vs10% luminance, the light and dark stimuli presented to each eye were approximately equidominant. However, the stimulus strength of the pairs increased across conditions. We found that as stimulus strength increased from 70%vs30% luminance to 90%vs10% luminance, BR alternation rate increased significantly, $F(2,30) = 6.927$, $p = .003$ (Figure 7). Therefore, the weakest stimulus pair (70%vs30% luminance) is associated with the slowest BR rate. Based on the assumptions outlined above, these findings might indicate strong inhibition for the 70%vs30% condition. However, we also found that subjects experienced the longest durations of fusion during the 70%vs30% luminance condition, and hence slow fusion alternation rate. This effect is demonstrated in Figure 8. In Figure 8, luminance BR mean dominance durations are significantly and positively correlated with fusion mean dominance durations *r*(46) = 0.80, *p* < .01. In other words, slow rivalry coincides with long durations of fusion. Based on the premise that fusion indicates a failure to fully suppress either of the two eyes' stimuli, the 70%vs30% condition would have *weak* inhibition indicated.

2.2. Dichoptic Masking:

All luminance based dichoptic masking experiments had three masking conditions differing in stimulus strength. For the **luminance increment detection threshold** conditions (in order of increasing stimulus strength: 30%, 20% and 10% luminance masks), we found that masking thresholds increased significantly as the strength of the mask increased across conditions, *F*(2,26) = 5.623, *p* = .009 (Figure 9, blue bars). This indicates that *unlike* oriented masking, for this luminance masking, the condition that results in the slowest rivalry also results in the weakest masking effects. However, for the **luminance decrement detection threshold** conditions (in order of increasing stimulus strength: 70%, 80% and 90% luminance masks), we did not find a significant mean difference in threshold between conditions, *F*(2,26) = .248, *p* = .782 (Figure 10, blue bars). Nevertheless, we did find that the luminance decrement detection thresholds were significantly and positively correlated with the luminance increment detection thresholds, *r*(40) = 0.36, p < .01. This indicates that individuals who had strong masking thresholds for increment detection also had strong masking thresholds for decrement detection even though the conditions were not significantly different overall.

2.3. Half-Binocular Masking:

As with dichoptic masking, for the **luminance increment detection threshold** conditions (in order of increasing stimulus strength: 30%, 20% and 10% luminance masks), we found that masking thresholds increased significantly as the strength of the mask increased across conditions, *F*(2,30) = 10.463, *p* < .001 (Figure 9, red bars). Consistently, we found that increment dichoptic masking and half-binocular masking thresholds did not differ significantly from each other, *F*(1,28) = 2.321, *p* = .139.

The **luminance decrement detection threshold** conditions (in order of increasing stimulus strength: 70%, 80% and 90% luminance masks) for half-binocular masking also showed significant mean differences (Figure 10, red bars). Again, we found that masking thresholds increased significantly as the strength of the mask increased across conditions, *F*(2,30) = 36.639, *p* < .001. Since dichoptic decrement masking did not show a main effect of condition (above), it makes sense that two types of masking differ significantly, $F(1,28) = 37.615$, $p < .001$. Only half-binocular masking showed the same main effect for both increments and decrements.

2.4. Comparisons:

In contrast to the findings from the oriented stimuli conditions, for homogenous luminance stimuli, we found that there were no significant correlations when we compared luminance BR alternation rate (70%vs30%, 80%vs20%, 90%vs10%) with any of the equivalent luminance masking conditions (neither increment (30%, 20%, 10%) nor decrement (70%, 80%, 90%) detection thresholds for dichoptic or half-binocular masking).

We did however find two surprising significant correlations. As shown in Figures 11 and 12, when the slowest luminance BR condition (70%vs30% luminance) was compared to the strongest half-binocular masking condition for both increment and decrement detection (10% luminance mask and 90% luminance mask respectively), the luminance BR alternation rate data was significantly and negatively correlated with the luminance masking data. Specifically, for luminance increment masking and luminance BR alternation rate $r(46) = -0.40$, $p < .01$ and for luminance decrement masking and luminance BR alternation rate $r(46) = -0.45$, $p < .01$. These findings indicate that those individuals with the slowest luminance BR also exhibit the strongest luminance masking. The correct interpretation of this effect is unclear, but will be examined further in the Discussion section.

3. Parametric Luminance Rivalry Experiments:

3.1. Equidominance:

3.1.1. Original Luminance Scale:

In this third series of experiments, we wanted to explore more fully the properties of rivalry and fusion, for our homogeneous luminance stimuli. As fully presented above, we tested rivalry for an abbreviated set of luminance pairs (70%vs30%, 80%vs20%, 90%vs10%) on a large group of subjects (n=15). This data was previously shown in terms of alternation rate. This data is now shown (Figure 13) in terms of mean dominance durations, with the durations for the light stimulus, dark stimulus and fusion all plotted separately. Fusion is more easily discussed in terms of duration of perception rather than alternation rate, so this series is largely discussed in terms of dominance durations with the understanding that alternation rate will be the inverse. Overall, the mean dominance durations for both the light and dark stimuli decreased slightly across conditions as stimulus strength and interocular difference increased. In addition, the mean dominance duration between the light and dark stimuli were the most unequal for the 70%vs30% condition (4.39 s and 3.17 s respectively), becoming more similar across conditions. For fusion, the mean dominance durations consistently decreased across conditions (from 8.40 s to 3.00 s).

In order to explore a large range of stimulus pairs, we tested two subjects on five conditions: 50%vs50%, 60%vs40%, 70%vs30%, 80%vs20%, and 90%vs10% (Figure 14). The subjects completed eight trials for each experimental condition, with the counterbalanced stimuli for the left and right eye throughout this series. This data shows the same trend observed with the larger cohort. The most striking difference between the full range of conditions is the length of perceived fusion. Since the identical 50%vs50% condition resulted in total perceived fusion, the dominance durations for this condition were 90 s per trial. Mean dominance durations for fusion decreased systematically across conditions as the stimuli increased in strength and difference. In terms of the rivaling stimuli, the **shortest** mean dominance durations were for the 60%vs40% condition (approximately 0.81 s and 2.05 s respectively) because the majority of the trial consisted of perceived fusion. The dominance durations of the light and dark stimuli are similar across the subsequent three conditions. However, in all conditions, the darker stimuli had longer durations, presumably due to greater perceived contrast.

3.1.2. Corrected Luminance Scale:

As shown in Figure 15, like the previous luminance scale, there is total fusion for the 5vs5 condition and the durations of fusion decreased systematically across conditions (from 48.7 s to 6.31s). Another similarity is that light and dark stimuli for the 4vs6 condition show an asymmetry in dominance duration length and this asymmetry decreased across conditions. The main difference for this data is that the **longest** dominance durations for the light and dark stimuli were for the 4vs6 condition. The length of the rivalling stimuli's dominance durations then decreased across conditions and the shortest mean dominance durations were for the 1vs9 condition. Another general difference is that, using the new scale, the dominance durations for the rivalling stimuli were typically longer.

Overall, our findings for our Equidominance conditions indicate that as the difference in luminance between stimulus pairs, as well as stimulus strength increased, the alternation rate of two stimuli increased and the predominance of the fused percept decreases across conditions.

3.2. One Eye Black:

3.2.1. Original Luminance Scale:

For this experiment the luminance in one eye was fixed at 0% luminance (black). In order of increasing difference in luminance between the two stimuli and increasing stimulus strength, the conditions were as follows: 0%vs35%, 0%vs50%, 0%vs65%, and 0%vs100%. As shown in Figure 16, the 0%vs35% condition (with the smallest difference in luminance between the two stimuli) had the largest amount of perceived fusion (26.8 s). The length of perceived fusion decreased across conditions. In terms of the two rivalrous stimuli, the longest mean dominance durations (approximately 25 s), were seen for the black stimulus in the first two conditions (0%vs35% and 0%vs50%). As a result, the other eyes' stimuli for these conditions had very short mean dominance durations of just over 1 s. This imbalance was caused by the much greater perceived contrast of the black stimulus in these conditions. As the stimulus strength became more equal and the difference in luminance between the stimuli increased across conditions, the length of the black stimulus' dominance duration decreased and the length of the other eyes' stimulus' dominance durations increased. For the 0%vs100% condition the stimuli have roughly equal mean dominance durations of approximately 3 s.

3.2.2. Corrected Luminance Scale:

As shown in Figure 17, like the previous luminance scale, the length of perceived fusion decreased across conditions (16.9 s to 4.91 s). Also like the previous data, the longest durations were seen for the "black" stimulus when it was paired with the weakest stimulus (0vs2) and the "black" stimulus had greater predominance than the other eye until the final equidominant condition (0vs10). Unlike the previous data, even though the other eyes' stimulus increased in strength across conditions, for this data we did not see a large change in the other eyes' dominance durations. However, when alternation rate was plotted, it does increase dramatically across conditions indicating increasing stimulus strength. Additionally, the "black" stimulus' dominance durations were noticeably shorter in this data than seen previously. This was because, as intended, the new luminance scale decreased the perceived contrast of decrements.

3.3. One Eye White:

3.3.1. Original Luminance Scale:

For this experiment the luminance in one eye was fixed at 100% luminance (white). In order of increasing difference in luminance between the two stimuli and increasing stimulus strength, the conditions were as follows: 100%vs65%, 100%vs50%, 100%vs35%, and 100%vs0%. As shown in Figure 18, the results for this experiment were consistent with those found in the One Eye Black experiment. The 100%vs65% condition (the weakest stimulus condition with the smallest difference in luminance between the two stimuli) had the largest amount of perceived fusion (42.6 s). The length of perceived fusion decreased across conditions. Note the greater amount of fusion overall compared to the One Eye Black experiment. In terms of the two rivalrous stimuli, the longest mean dominance durations (18.2 s), were seen for the white stimulus in the 100%vs65% condition. As a result, the other eyes' stimulus had very short mean dominance durations of 0.94 s. As stated above, this imbalance was caused by the much greater relative strength of the white stimulus in this condition. However, unlike the One Eye Black experiment, this imbalance was only evident for one condition, perhaps because of the lower perceived contrast of increments. Nevertheless, as above, the length of the white stimulus' dominance durations did decrease across conditions as the other stimulus dominated more. Again, the 0%vs100% condition showed roughly equal mean dominance durations of about 3 s.

3.3.2. Corrected Luminance Scale:

As shown in Figure 19, the length of fusion durations generally decreased from left to right, with the exception of the 10vs8 condition. The smaller amount of fusion seen in this condition was likely caused by the large predominance of the "white" stimulus during this condition. This trend is similar to that seen using the previous luminance scale, however the durations of fusion for this scale are noticeably shorter. The reduced durations of fusion indicate that the perceived contrast of the "white" stimulus was greater for this luminance scale than it was for the previous scale. In terms of the two rivalrous stimuli, as seen previously, the longest mean dominance durations were seen for the "white" stimulus, when paired with the weakest stimulus (10vs8). However, unlike the previous scale, this greater predominance is also evident in subsequent conditions. Also like the previous scale, as the darker other eye's stimulus strength increased, the length of mean dominance durations increased from 1.47s (10vs8) to 2.60 s (10vs0).

Overall, our "One Eye Black" and "One Eye White" conditions yield similar trends. As the luminance difference between the eyes increased and the stimulus strength between eyes became more equal, alternation rate of the two eyes' stimuli increased, the predominance of fusion decreased and the predominance of the two eyes' stimuli became more equal (with the stronger stimulus' predominance decreasing and the weaker stimulus' predominance increasing).

3.4. Constant Difference

In this set of experiments, all of the stimulus pairs had the same perceived interocular luminance difference. This experiment was added because in the previous three luminance rivalry experiments, the stimulus pairs varied in perceived interocular luminance difference between conditions. We wanted to investigate the pattern of results that resulted from having a constant perceived interocular luminance difference for a set of conditions. The stimuli themselves varied in strength relative to the background luminance (mid-level grey). At one extreme of stimulus strength is our "black" stimulus (0). Between stimulus strengths of 0 and 5, stimulus strength (relative to background) decreases and increases between 5 and 10 ("white"). The 0vs4 and 6vs0 conditions both have a large asymmetry in strength between the two stimuli. The other two conditions (2vs6 and 4vs8) have a smaller asymmetry in strength. In the 0vs4 condition, both stimuli are decrements and in the 6vs10 condition, both stimuli are increments. In the remaining two conditions, one stimulus is a decrement and the other is an increment.

As shown in Figure 20, the smaller asymmetry conditions showed the most fusion (21.0 and 24.9 s respectively). These conditions have weaker stimuli so it follows that they would have the longest fusion dominance durations, rather than long periods of exclusive stimulus percepts. The larger asymmetry conditions showed less fusion, which makes sense because these two conditions contained the strongest stimuli. In terms of the two rivalrous stimuli, the two conditions with weaker stimuli showed similar dominance durations between the stimuli in a pair. In the two other conditions, where there was a larger asymmetry between the strength of the two stimuli in a pair, the stronger stimulus showed greater predominance.

In terms of increments and decrements, we found that our conditions where both stimuli were increments or both stimuli were decrements, there was a greater difference in the data between the two stimuli in the pair. In the conditions where one stimulus was an increment and the other was a decrement, the data is more equivalent between stimuli in a pair. This is most likely caused by the nature of stimulus strength for luminance stimuli. The extreme stimuli on either the increment or decrement side will be more predominant and result in faster alternation. When both of stimuli are on one side of background luminance it is likely that one of your stimuli will be very dominant. However, if your stimulus pair is on either side of background luminance it is more likely that your stimuli are equally dominant. The only observable difference between increments and decrements in the data is seen for mean dominance durations. The condition with two decrements (0vs4) shows noticeably longer dominance durations than the condition with two increments (6vs10). However, this difference may disappear if a larger sample is tested.

Discussion:

1. Oriented Grating Stimuli

Overall, we were able to replicate the findings of Baker and Graf (2009). We found that reducing the orientation difference between two dichoptically presented gratings resulted in slower BR and higher masking thresholds for dichoptic masking. We were able to replicate the findings of their study with a relatively small number of trials per observer and using subjects (n=15) who were largely naïve and lacked prior experience performing psychophysical tasks. We also added another masking condition, half-binocular masking. Since we found the same pattern of results for both dichoptic and half-binocular masking, this indicates that increased masking in response to a target and mask of similar orientation is not specific to dichoptic masking but applies instead to masking generally. Additionally, our findings provide further evidence to support the hypothesis that masking and BR may share a common, general suppressive mechanism. Another possible explanation is that dichoptic masking results from an early stage of the suppressive mechanisms used in BR. Two previous findings that provide evidence for this hypothesis are van Boxtel et al.'s (2007) result that dichoptic masking meets the three perceptual conditions for BR and Carter and Cavanagh's (2007) result that the initial rivalry percept shares characteristics with masking.

One model that incorporates both BR and masking (cross-orientation supersession) is the ocular opponency model of Said and Heeger (2013). Ocular opponency neurons respond to differences between the two eyes, and would therefore be active when the eyes are presented with dichoptic gratings (Said and Heeger, 2013). In their model, the response of ocular opponency neurons is increased by competition between the two eyes. Evidence for this model has been found in the recent EEG studies by Roeber (2012) and Katyal, Engel, He, & He (2016) that have found evidence to suggest a cortical mechanism that detects interocular conflict.

Another relevant model is the two stage model of binocular gain control. As explained previously, in the first stage of this model, both monocular inputs are controlled by a divisive suppression (Meese et al., 2006). The second stage involves binocular summation that is also subject to divisive suppression (Meese et al., 2006). Essentially, interocular suppression occurs during both stages (Baker and Meese, 2007). In this model, interocular suppression is made up of the direct effect and the indirect effect (Baker and Meese, 2007; Huang, Zhou, Lu, Zhou, 2011). The direct effect, which occurs during the first stage, is divisive interocular gain control of the signal in the target eye by the mask (Baker and Meese, 2007). The indirect effect occurs in response to the suppression exerted on the target by the mask (Baker and Meese, 2007). The contrast of the target must be set very high to overcome the suppression by the mask. This allows a large amount interocular suppression on the mask by the target. This suppression occurs during the second stage, after binocular summation (Baker and Meese, 2007). Although framed differently, this is essentially mutual inhibition of the two eyes' inputs, very similar to that proposed to underlie BR (as explained in the introduction, e.g. Alais, 2012).

Indeed, Sengpiel and Vorobyov (2005) found that dichoptic masking is weakened when a GABA antagonist was administered, blocking inhibition in the cortex. van Loon et al. (2013) found that administering a GABA agonist slowed perceptual alternations. These two findings are compatible with each other and our findings as well as those of Baker and Graf (2009). If you decrease or block GABA (as did Sengpiel and Vorobyov, 2005), this decreases inhibition which results in weaker masking. As seen in our results and those of Baker and Graf (2009), weaker masking corresponds to fast rivalry. Conversely, if you increase GABA (as did van Loon et al., 2013), this increases inhibition which results in slower rivalry. As seen in our results and those of Baker and Graf (2009), slower rivalry corresponds to stronger masking.

Finally, we found, in accordance with the findings of Baker and Graf (2009), substantial individual differences in BR alternation rate and masking threshold elevation. As mentioned above, we also found a significant correlation between individuals' BR alternation rate and masking threshold elevation. When I examined the characteristics of fast and slow alternators, they were very similar between the two groups. The mean age of the fast alternator group was 21.9 and included five females and three males. The mean age of the slow alternator group was 22.3 and included four females and four males. However, differences may arise between the two groups if a more diverse sample is used in future.

Many studies have investigated the cause of individual differences in BR alternation rate. It is likely that there are multiple factors at play such as genetics, differences in brain structure and, as just discussed, strength of neural inhibition. This topic has not been extensively explored for dichoptic masking, as noted by Baker (2013), because psychophysical masking data is often averaged across observers or involves a small number of observers. To elucidate the question of why contrast sensitivity has such large variation among normal subjects, Baker (2013) investigated which parameters in his masking model had to be altered to fit one subject's masking data to another subject's. He concluded that the differences in contrast sensitivity between subjects arise from individual differences in contrast gain, specifically the degree of its non-linearity. Baker (2013) provides several potential causes for this difference such as genetics and environmental differences during neural development. Additionally, as just discussed, differences in contrast gain may be related to differences in levels GABA.

2. Homogeneous Luminance Stimuli

In analogy with the oriented grating experiments, we developed a set of experiments with stimuli of homogeneous luminance. The purpose of these experiments was to determine if we could obtain the same pattern of results from these simple shape stimuli as for oriented grating stimuli because that would indicate that Baker and Graf's (2009) dichoptic masking and BR findings are applicable to different types of stimuli. At first glance, our homogeneous luminance BR data appears similar to our oriented grating BR data. Specifically, as the two BR stimuli become more different, their alternation rate increases. Our previous findings with orientation differences might indicate that as the luminances of two BR stimuli increase in inter-ocular difference (e.g. 90%vs10% luminance), inhibition between them decreases. However, this premise does not apply here because we found the opposite trend as would be expected for masking. In fact, we found that for both types of masking, these masks resulted in the strongest masking. This trend was present for both increment and decrement detection with the exception of dichoptic masking for luminance decrement detection for which there was no effect. In addition, we did not find any significant correlations for luminance masking threshold and luminance rivalry when comparing equivalent conditions. Therefore, in the case of luminance rivalry and masking, the data suggest that large differences in luminance between stimuli result in greater inhibition, rather than less inhibition as is the case with orientation differences. This finding can be explained by looking more closely at the nature of luminance based rivalry.

As shown in the results section, slow rates of luminance rivalry (as we see for the 30%vs70% luminance condition) are highly correlated with long durations of fusion (mixed perception). Studies on BR and autism spectrum conditions (ASC) have found that, compared to control subjects, observers with ASC exhibit slower rivalry alternations and longer durations of mixed percepts (Freyberg, Robertson, & Baron-Cohen, 2015; Robertson, Ratai, & Kanwisher, 2016). One proposed cause for many ASC symptoms is an atypical balance between cortical excitation and inhibition, referred as the E/I ratio (Freyberg et al., 2015; Robertson et al., 2016; Said, Egan, Minshew, Behrmann, & Heeger, 2013). Specifically, it is believed that individuals with ASC have an elevated E/I ratio, either caused by increased excitatory signaling (associated with glutamate) or decreased inhibitory signaling (associated with GABA) (Freyberg et al., 2015; Robertson et al., 2016; Said et al., 2013). Model simulations by Said et al. (2013) found that either low levels of inhibition or high levels of excitation would result in more mixed percepts during rivalry, as seen in ASC. In addition, there is evidence to suggest that GABA signaling is responsible for the E/I imbalance in ASC. Robertson et al. (2016) recently found that for control subjects, increased GABA concentrations predicted longer rivalry dominance durations. However, this relationship was absent in observers with ASC. On the other hand, glutamate was a good predictor of rivalry dynamics in both groups (Robertson et al., 2016). Based on these findings, Robertson et al (2016) put forth the hypothesis that it is not actually the GABA levels themselves that are disturbed in autism but rather GABA has a reduced effect on behavior, which may involve altered GABA signaling. This hypothesis fits with postmortem tissue analyses that have found that certain GABA receptor subunits are underexpressed in brains of individuals with ASC (Freyberg et al., 2015; Robertson et al., 2016; Said et al., 2013).

Based on this evidence, we can conclude that increased durations of fusion during luminance rivalry (as seen in the 30%vs70% condition) actually indicate reduced suppression for these conditions whereas shorter durations of fusion (as seen in the 10%vs90% condition) indicate increased suppression for these conditions. Operating under this assumption, we can state that in the case of our luminance stimuli, the condition that resulted in the fastest BR and had the biggest difference between the stimuli, 10%vs90%, represents the condition with the most inhibition. This also explains why these masking conditions showed the strongest masking effect.

Although we did not find any significant correlations between corresponding luminance rivalry and luminance masking conditions, we did find one surprising correlation. As stated in the results, we found that individuals who experienced the most suppression for the strongest masking conditions (90% luminance for decrement detection and 10% luminance for increment detection) also experienced the longest dominance durations for the slowest luminance rivalry condition (30%vs70%). In light of our conclusion that strong luminance masking involves high inhibition and slow luminance rivalry involves low inhibition, this finding is anomalous. We have identified two possible explanations for this relationship, one is related to individual differences in eye dominance and the other, individual differences in attention.

A subject's dominant eye is considered to have a stronger input cortical signal. Amblyopia can be thought of as an extreme case of eye dominance, because the signal from the amblyopic eye is suppressed in favor of the fellow eye. It is possible that our subjects with very strong luminance masking and slow rivalry had one very dominant eye. In the case of rivalry, one extremely dominant eye would result in the stimulus in that eye having very long dominance durations and that person would have slow rivalry. In the case of masking, these subjects would be less sensitive to the target in their non-dominant eye and would exhibit more masking when the mask was in their dominant eye. Essentially, this would result in higher masking thresholds for this participant for these trials. This hypothesis is based on the pattern of results obtained for dichoptic masking in amblyopes. For example Baker, Meese and Hess (2008) found that amblyopes and normal observers wearing an ND filter over one eye, both showed an increase in masking threshold in the "bad eye". However, the fellow eye showed a masking pattern similar to that of the "good" eye of a normal observer. In normal observers, Johansson, Seimyr, & Pansell (2015) reviewed the findings of studies that had investigated the impact of eye dominance on binocular viewing. Findings indicate that indeed the dominant eye performs better on dichoptic detection tasks (Johansson, Seimyr, & Pansell, 2015). However, both eyes had the ability to perform equally well under monocular viewing conditions. To investigate our eye dominance hypothesis, we asked our subjects to perform either the Miles or Porta test to determine their dominant eye. We then compared subjects' masking thresholds for the trials where the target was in their dominant eye to the trials where the target was in their non-dominant eye. Of the subjects who provided their eye dominance, a majority did show higher masking thresholds in their non-dominant eye, but this was by no means universal. However, according to the findings of Johansson et al. (2015), the degree of eye dominance is a more important factor during binocular viewing tasks than which eye is dominant. This is likely because most subjects are either ambiocular or have one eye that is only slightly dominant. For example, less than 40% of subjects in a study by Li et al. (2010) were considered to have strong eye dominance. Therefore, more evidence, such as a measure of subjects' degree of eye dominance, is needed to conclude that our surprising correlation was or was not related to eye dominance.

The second possible reason for our surprising correlation is individual differences in attention. The effects of attention on the dynamics of BR have long been debated but it is generally agreed that focusing attention is insufficient to control BR alternations (Alais, 2012). Paffen, Alais, and Verstraten (2006) looked at the effect of removing subjects' attention from the rivaling stimuli on BR alternation rate. Subjects' attention was diverted to another task that was occurring concurrently with BR (Paffen et al., 2006). Although lack of attention could not stop BR alternation, it did result in the slowing of rivalry (Paffen et al., 2006). The degree of slowing was proportional to the difficulty of the task, which implies that the degree of slowing was proportional to the level of attention the subject gave to the BR stimuli (Paffen et al., 2006). Based on these findings, we can hypothesize that those subjects who exhibited exceptionally slow luminance rivalry may not have been focusing their full attention on the stimuli during their BR trials. In terms of masking, Huang and Dobkins (2005) measured the effects of attention vs inattention on contrast discrimination thresholds. They found that inattention caused masking thresholds to increase (Huang and Dobkins, 2005). Based on this finding it is possible to conjecture that the especially high luminance masking thresholds displayed by some subjects may have resulted from compromised attention on the masking task. Taken together, individuals who both exhibited very long luminance rivalry dominance durations and very high luminance masking thresholds may have had compromised attention during testing.

3. Oriented Grating and Homogeneous Luminance Stimuli Comparison

Overall, in light of the differences between our findings for oriented grating and homogeneous luminance stimuli, these two types of stimuli appear to use different mechanisms of inhibition to achieve rivalry and masking. Our finding that dichoptic stimuli with similar orientations result in greater inhibition can be explained in terms of orientation tuned channels in the visual cortex (Hubel and Wiesel, 1974). Using this framework, it makes sense that a small orientation difference between the two eyes' stimuli results in greater interocular inhibition because the two stimuli are using similar orientation channels. This fits with the model proposed by Abadi (1976), discussed in the introduction. He hypothesized that rivalry occurs through lateral inhibition between proximal orientation columns (Abadi, 1976). Since the orientation columns are arranged in the cortex such that more similar orientations are closer together, the most lateral inhibition would occur between similarly oriented stimuli. As we know, more inhibition results in longer dominance durations and a slower BR alternation rate. Large orientation differences result in less lateral inhibition between orientation tuned channels because they are further apart in the cortex. Less interocular inhibition results in short dominance durations and a faster BR alternation rate. The same mechanism can apply for oriented masking, with small orientation differences resulting in strong masking and large orientation differences resulting in weak masking.

To interpret our luminance findings, we can use the Levelt's revised propositions (Brascamp et al., 2015). These propositions characterize BR in terms of the "stimulus strength", usually referring to stimulus contrast, of the two rivalrous stimuli. In the original and revised Levelt's propositions, proposition four states that equally increasing stimulus strength in both eyes, increases alternation rate. This fits with the results found for our three luminance rivalry conditions we tested with our full group of subjects (30%vs70%, 20%vs80% and 10%vs90%). Our results show that BR alternation rate increases across conditions. This indicates that the 30%vs70% condition contained the weakest stimuli and that stimuli increase in strength across conditions. It follows that the 10%vs90% condition has the strongest stimuli, since it has the fastest BR alternation rate. These conclusions make sense intuitively because the in 30%vs70% condition, the stimuli have the smallest interocular difference and are closest in luminance to the background. In contrast, the stimuli in 10%vs90% condition have the largest interocular difference and their luminance levels are far from background luminance. These conclusions also fit with our assumption that the 30%vs70% condition results in the lowest amount of interocular inhibition and the 10%vs90% condition results in the largest amount of interocular inhibition. We can therefore assume that level of inhibition induced by a stimulus is related to that stimulus' strength. Our luminance masking data shows that the masks that induced in the greatest masking effect (90% and 10% luminance masks), were the strongest stimuli. This implies that these strong stimuli induced the most inhibition. Likewise, the masks that resulted in the weakest masking effect, implying the least inhibition, were the weakest stimuli (70% and 30% luminance masks).

Overall, strong luminance masking and fast luminance rivalry seem to be related to high inhibition. High inhibition results from stimuli with high stimulus strength, which in the case of luminance means a stimulus with a luminance level far from both background luminance and the luminances of other stimulus presented alongside it. In this way BR between stimuli with difference luminance levels resembles the BR originally described by Levelt's propositions, BR between stimuli that vary in contrast. Both differences in luminance and in contrast result in stimuli differing in "stimulus strength". Using this terminology, it makes sense that the BR dynamics of oriented grating stimuli do not correspond with those predicted by Levelt's propositions. Since the two eyes' stimuli differ in orientation rather than contrast or luminance, the two eyes' stimuli can be said to have equal "stimulus strength".

Another possible explanation for the discrepancy between orientation and luminance based stimuli arises from our interpretation of fusion. It has been proposed for luminance that when there is no difference between the rivalry stimuli in the two eyes, these stimuli completely fuse and so, inhibition is zero. However, some models of dichoptic orientation differences actually predict that for identical stimuli in the two eyes, inhibition is actually maximal(Meese et al., 2006). The degree to which such models can apply to homogeneous stimuli (sometimes called zero frequency) is still unclear. Also unclear is the neural site of these mechanisms, which could potentially be subcortical as well as cortical. These considerations have implications for interpreting the meaning of fusion for our luminance rivalry stimuli, and it remains possible that fusion is determined by a separate mechanism. To elucidate this mechanism, more investigation, especially physiology, should be done on rivalry conditions where the stimuli tend to fuse.

4. Comparison of Luminance Scales

Overall, the pattern of findings for the new luminance scale using Whittle's Contrast is not dramatically different from that found using the previous luminance scale. In terms of our Equidominance conditions, we still found that as the difference in luminance between paired stimuli as well as their stimulus strength increased, alternation rate increased and dominance durations shortened. However, as expected, alternations rates were more similar between dark and light stimuli in the new data. One unexpected difference, which was true for all except the One Eye "White" dominance durations data, was that for fusion mean dominance durations decreased across all conditions. Also, using the new luminance scale, the trends for fusion were more uniform. This may have been caused by the new luminance values being more similar to each other both within and between stimulus pairs., Similarly, the values obtained for alternation rate and mean dominance durations did not vary as dramatically between conditions. Specifically, for the conditions with the lowest alternation rates and dominance durations, the values were noticeably higher and for the conditions with the highest alternation rates and dominance durations, the values were noticeably lower.

Comparable patterns were also seen for our two luminance scales for both the “One Eye Black” and “One Eye White” experiments. Overall, as the luminance difference between the eyes increased and the asymmetry in stimulus strength between eyes was reduced, the alternation rate of the two eyes’ stimuli increased, the predominance of fusion decreased and the predominance of the two eyes’ stimuli became more equal (with the stronger stimulus’ predominance decreasing and the weaker stimulus’ predominance increasing). Although the pattern remained the same, we did see two desired changes in the new data. Because the new luminance scale linearized the decrement stimuli, the decrements were not perceived to have greater contrast than the increments. Therefore, in our One Eye “Black” experiment there was no longer such a large imbalance in predominance between the “black” stimulus and the lighter other eye stimuli. Correspondingly, in our One Eye “White” experiment, in the new data, the “white” stimulus now shows greater predominance and a faster alternation rate than the dark other eye stimuli. In the data from the previous luminance scale, this imbalance was only evident for one condition. This pattern of results more closely resembles the One Eye “Black” data. This similarity further indicates that the new luminance scale was successful in equating our increment and decrement stimuli.

Finally, in spite of the changed luminance scale, some equidominant conditions still show imbalances between the predominance of the increment and decrement in a stimulus pair. It is possible that these imbalances were not related to the perceived luminance levels of the stimuli but were rather a consequence of our low number of subjects.

5. Revised Levelt’s Propositions

The four revised Levelt’s propositions for BR by Brascamp et al. (2015) are as follows: 1) increasing the stimulus strength in one eye, increases the predominance of that stimulus; increasing the difference in strength between stimuli, 2) increases the average dominance duration of the stronger stimulus, and 3) decreases alternation rate; 4) equally increasing stimulus strength in both eyes, increases alternation rate. For the Equidominance experiments, since stimulus pairs across all conditions are of equal strength, both stimuli in a pair have similar predominance, which agrees with proposition 1). Similarly, as the strength of the pairs increases across trials, alternation rate increases, which is consistent with proposition 4). For the One Eye Black and One Eye White experiments, we see the results of increasing the difference in strength between stimuli (e.g. from the equal 0vs10 to the unequal 0vs2). As predicted by proposition 2), this increased the average dominance durations of the stronger stimulus and as predicted by proposition 3), decreased alternation rate. For our Constant Difference conditions, we see that the stronger stimulus in the pair is more predominant than the other (consistent with proposition 1). Overall our luminance rivalry data fits well with the revised Levelt's propositions.

Finally, we have found that luminance rivalry follows the revised Levelt's propositions, but what does that mean in terms of an underlying mechanism? As noted by Brascamp et al. (2015) the dynamics of the revised Levelt's proposition agree with the rivalry model proposed by Wilson (2007). In many rivalry models, it is proposed that while a stimulus is domination perception, neural adaption accumulates for that stimulus. In Wilson's (2007) model, while the stimulus is suppressed, this neural adaptation decays following a decelerating curve. This means that the level of adaption drops quickly when adaptation is high and decreases more slowly when adaptation is low. Once the adaption reaches a minimal level, then random fluctuations in neural activity can trigger a perceptual alternation. This hypothesis for how adaption leads to a perceptual alternation is referred to as "escape" (Brascamp et al. 2015). Wilson's (2007) model can be applied to the rivalry dynamics described by Brascamp et al. (2015). Proposition 2 and 3 indicate that, increasing the strength of one stimulus relative to the other, results in increasing that stimulus' dominance durations and decreasing alternation rate (Brascamp et al. 2015). Changing stimulus strength can be thought of as changing the length of adaptation decay needed to trigger a perceptual alternation (Brascamp et al. 2015). Increasing a stimulus' strength, increases the amount of adaption associated with that stimulus. The higher the adaption, the faster the adaptation decays to a point of perceptual alternation (Brascamp et al. 2015). This implies that a stronger stimulus will be dominant for longer (builds up high inhibition) and suppressed for a shorter period of time (faster adaptation decay). On the other hand, the weaker stimulus is associated with lower levels of adaptation, which result in slower adaption decay (Brascamp et al. 2015). Therefore, the weak stimulus is suppressed for longer (slower adaptation decay), and has shorter perceptual dominance durations (builds up lower adaptation). Proposition 4 states that, equally increasing stimulus strength in both eyes, increases alternation rate (Brascamp et al. 2015). In this case both stimuli would behave like the strong stimulus discussed above.

6. Future Directions

One problem with our luminance masking experiments was that we did not perform a baseline detection task for our luminance stimuli as we did for our oriented grating stimuli. Because of this difference we were not able to calculate subjects' masking threshold elevation relative to baseline for these luminance masking conditions like we were for the oriented grating masking. This is a significant difference because for luminance masking we don't have a baseline we can use to compare our luminance masking values and therefore can only compare thresholds between conditions. Also, we were unable to identify those individuals who had an elevated luminance threshold merely because they have a higher detection threshold generally. Consequently, before future luminance masking experiments, subjects should be asked to complete a luminance detection task.

Secondly, since it is possible that subjects' eye dominance influenced our results on the luminance masking experiments, in future experiments we should determine subjects' eye dominance during their session in the lab. In this study, we asked subjects to perform the task on themselves after the testing occurred, which may have resulted in some unreliable measurements. Also, we did not receive responses from all of our subjects indicating their eye dominance and we had to exclude these subjects from consideration. Obtaining subjects' eye dominance in the lab during their testing session would eliminate these concerns. Additionally, Johansson et al. (2015) indicated that subjects' degree of eye dominance is often a more relevant measure than which eye is dominant in terms of interpreting results. Therefore, it would also be useful for future experiments where eye dominance may be a factor, to conduct a measure of subjects' degree of eye dominance. This would allow us to identify which subjects exhibit an extreme imbalance in eye dominance.

Thirdly, there are some qualitative differences between the tests we used to explore orientation, luminance, rivalry and masking. For orientation, rivalry was studied based on changing orientation differences whereas our masking tests find contrast change thresholds. In the future we could use. an oriented masking task based on orientation discrimination. This task would measure the degrees of orientation required for the subject to discriminate the target from the mask. It is possible that using this more similar oriented masking task, would result in more coherent masking data for comparison of orientation and luminance. Another related issue in our experimental design arises from using the temporal properties of rivalry as an (indirect) measure of suppression. Based on this difference basic difference from a masking threshold, it is unclear whether we can conclude that the same suppressive processes are at play during the two phenomenon. In the future, we could add a task to measure the depth of suppression during rivalry more directly, rather than inferring suppression based on rivalry rate. For example, during rivalry we could measure probe detection for the suppressed stimulus. Lastly, another design change might aid in our comparison of rivalry between our two types of stimuli. Adding a third button option for oriented rivalry would allow subjects to indicate the duration of mixed percepts for oriented rivalry and this would allow us to compare durations of "fusion" between types of rivalry.

In the future we could also investigate if the behavior exhibited by our "luminance rivalry" really best described by this term. Perhaps a more accurate description could be "low (or zero) spatial frequency rivalry" or "edge-based rivalry". To test this question, we could attempt our luminance rivalry experiments using ganzfield stimuli. These stimuli have no edges, so if we did see similar rivalry dynamics under these conditions, the behavior we have described is truly luminance rivalry. If we do not see similar dynamics with ganzfield stimuli, then indeed one of these other terms may be a more apt description.

One final goal for future experiments is related to our Parametric Luminance Rivalry Experiments. We have already improved these experiments by implementing a new luminance scale that allows increments and decrements to have equal perceived contrast. However, we have only tested an n of 3 on all of the experimental conditions for all four experiments. These experiments should therefore be run on more subjects. This will decrease the variability within conditions and increase the reliability of our findings.

Figures:

Figure 1: Schematic of Stimuli

Figure 2: Oriented Rivalry Alternation Rate, Group Effects

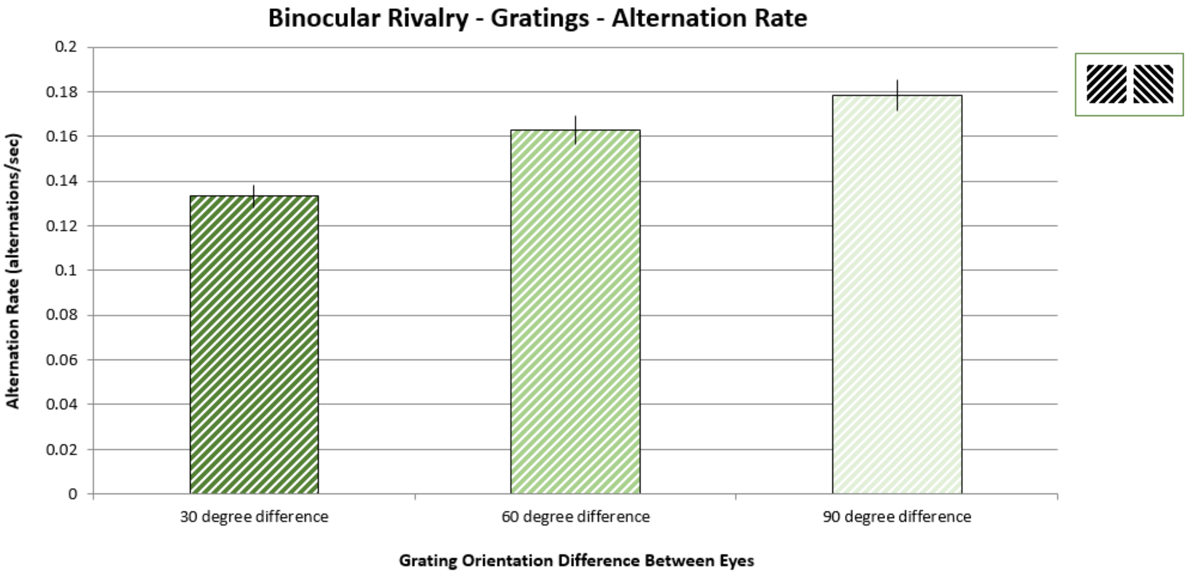

Figure 2: This graph depicts how binocular rivalry alternation rate for our oriented stimuli changed across conditions. As the orientation difference between the two eyes' increased, rivalry rate increased. Based on a repeated measures ANOVA, this finding is statistically significant. Error bars represent standard error of the mean.

Figure 3: Oriented Masking Contrast Increment Detection Threshold Elevation, Group Effects

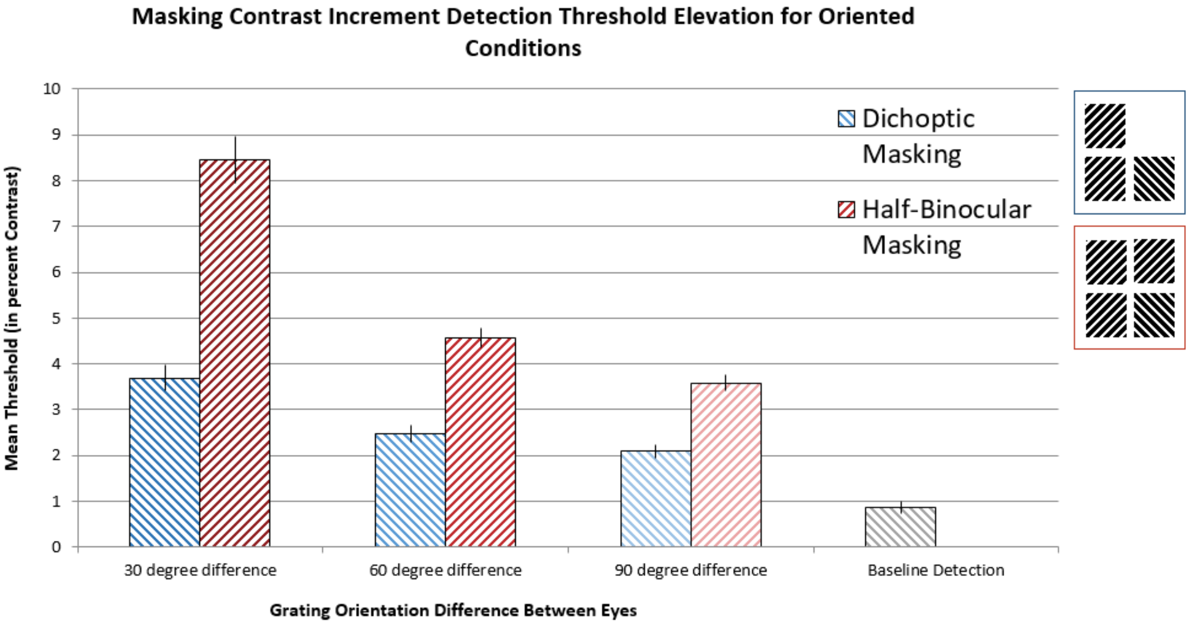

Figure 3: This graph depicts how dichoptic and half-binocular masking thresholds for our oriented stimuli changed across conditions. As the orientation difference increases, strength of masking significantly decreases. Based on a 2 way repeated measures ANOVA, this finding is statistically significant. Also, the thresholds for dichoptic and half-binocular making are significantly different. Error bars represent standard error of the mean.

Figure 4: Oriented Rivalry Alternation Rate Plotted Against Oriented Dichoptic Masking Threshold Elevation, Individual Effects

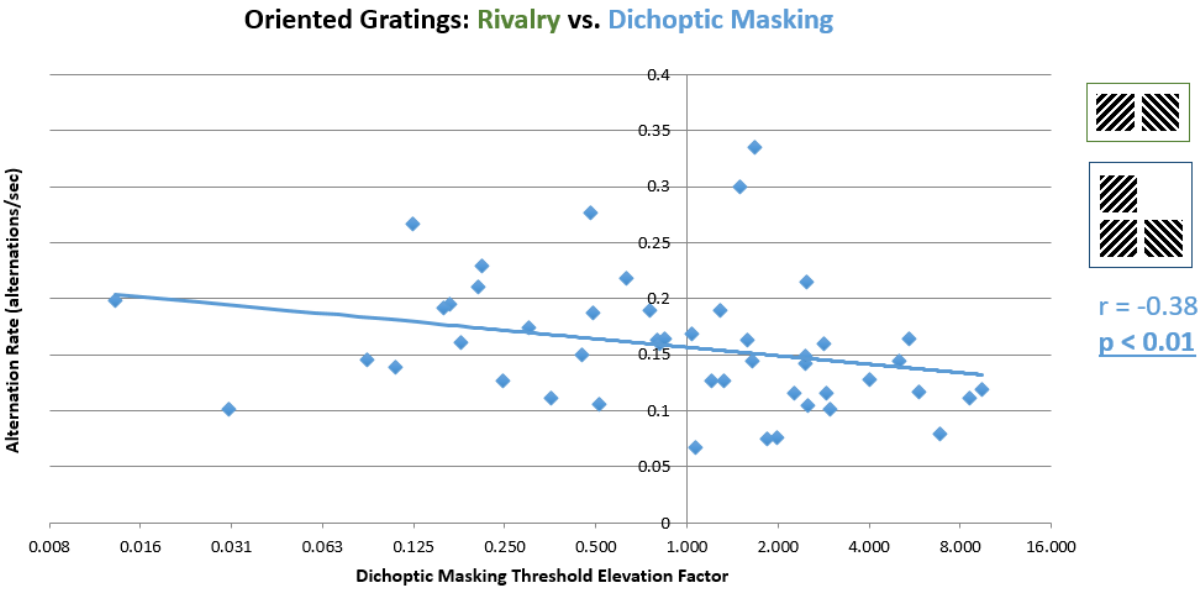

Figure 4: In this graph correlates individuals' oriented rivalry alternation rate with individuals' dichoptic masking threshold elevation. As individuals' rivalry alternation rate decreased, their dichoptic masking threshold elevation increased. This correlation is statistically significant based on Pearson's r.

Figure 5: Oriented Rivalry Alternation Rate Plotted Against Oriented Half-Binocular Masking Threshold, Individual Effects

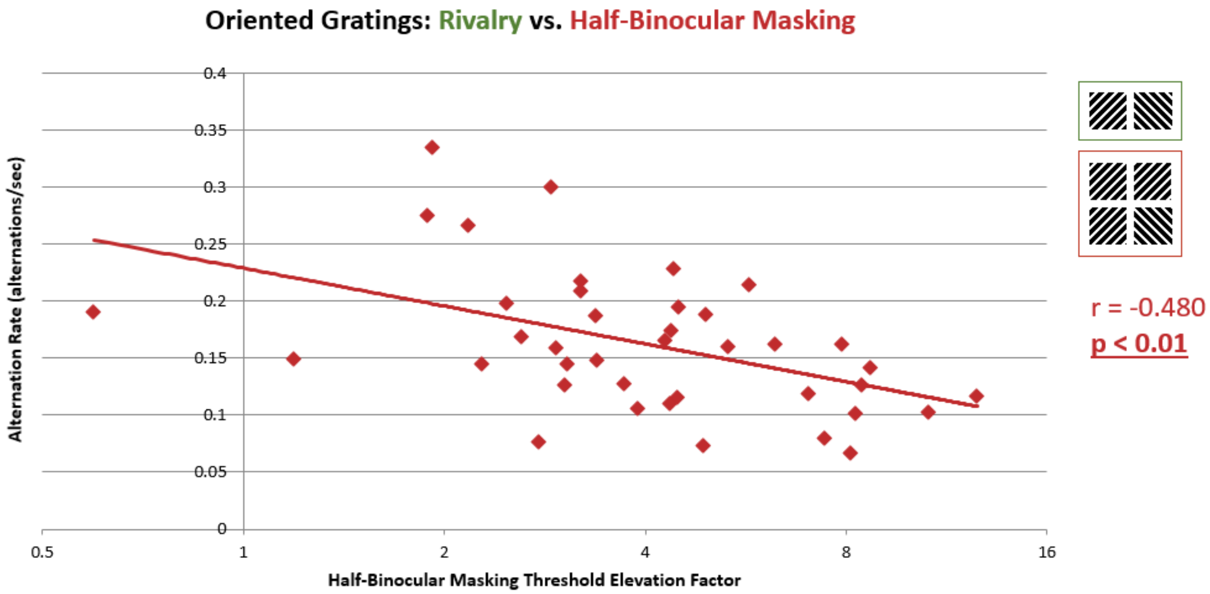

Figure 5: In this graph correlates individuals' oriented rivalry alternation rate with individuals' half-binocular masking threshold. As individuals' rivalry alternation rate decreased, their half-binocular threshold increased. This correlation is statistically significant based on Pearson's r.

Figure 6: Oriented Dichoptic Masking Threshold Elevation Plotted Against Oriented Half-Binocular Masking Threshold, Individual Effects

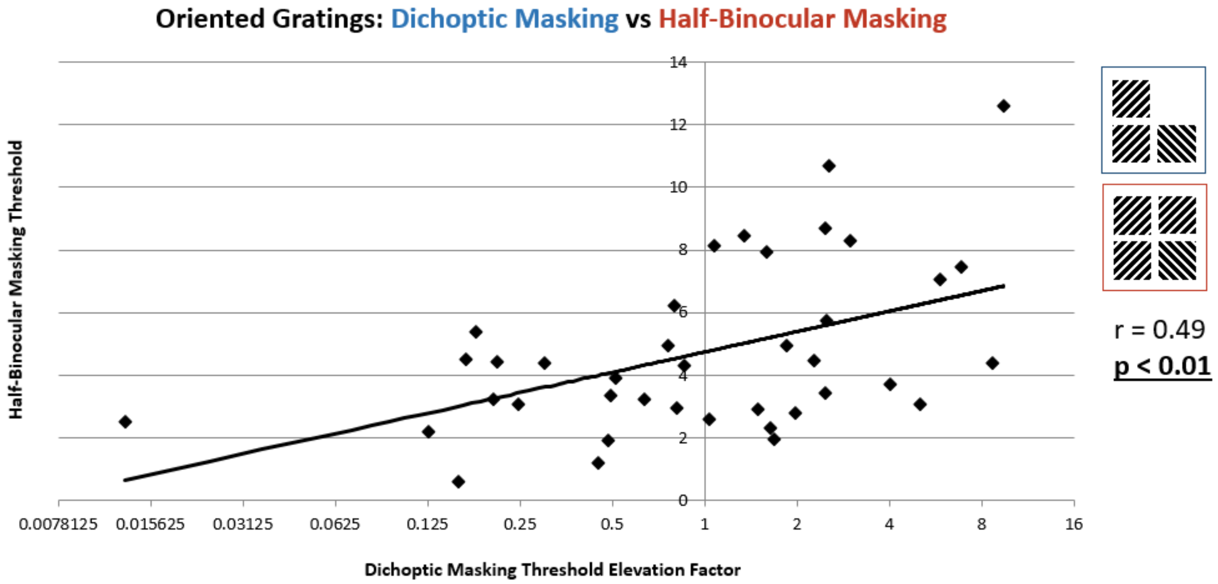

Figure 6: In this graph correlates individuals' oriented dichoptic masking threshold elevation with individuals' half-binocular masking threshold. Individuals' thresholds on these two masking tasks are significantly (Pearson's r) and positively correlated.

Figure 7: Luminance Rivalry Alternation Rate, Group Effects

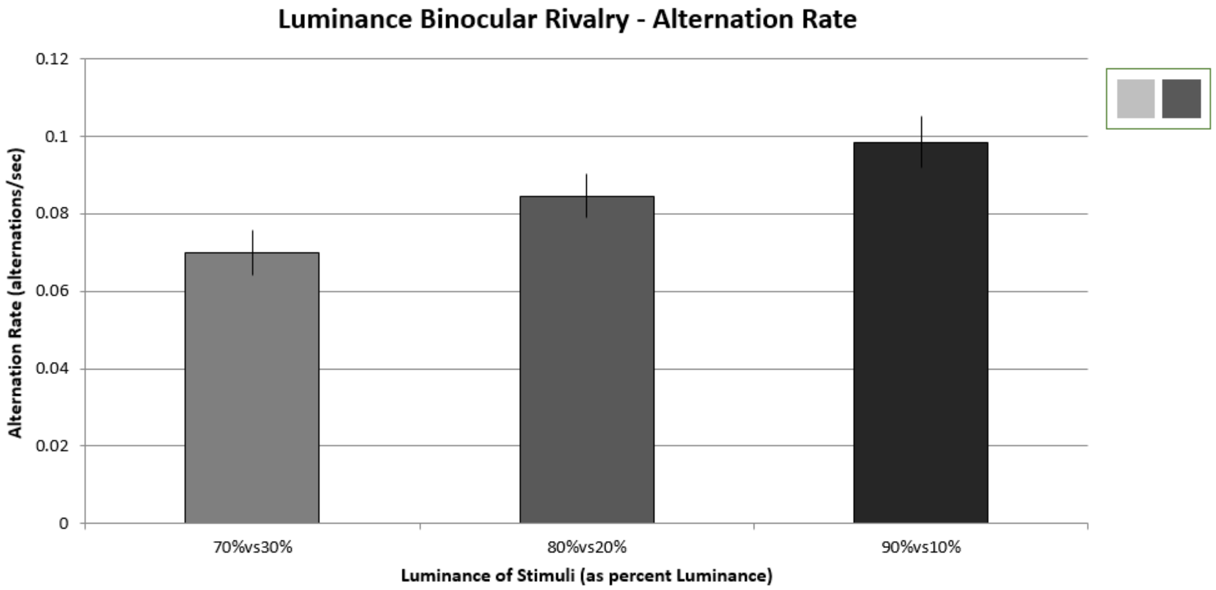

Figure 7: This graph depicts how binocular rivalry alternation rate for our luminance stimuli changed across conditions. As the luminance difference between the two eyes' increased, rivalry rate increased. Based on a repeated measures ANOVA, this finding is statistically significant. Error bars represent standard error of the mean.

Figure 8: Luminance Rivalry Mean Dominance Durations: Light and Dark Stimuli Dominance Durations Plotted Against Fusion Dominance Durations, Individual Effects

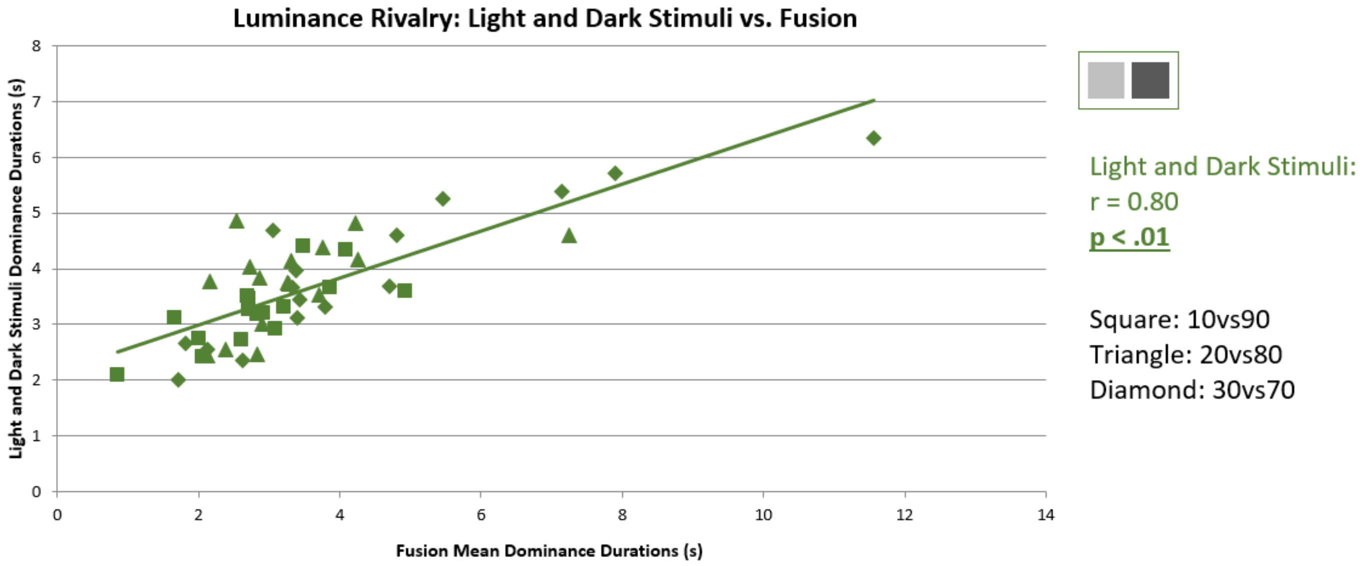

Figure 8: In this graph correlates individuals' mean dominance durations for light and dark stimuli with individuals' mean dominance durations for fusion. Individuals' dominance durations for the rivaling stimuli and fusion are significantly (Pearson's r) and positively correlated.

Figure 9: Luminance Increment Detection Masking Threshold, Group Effects

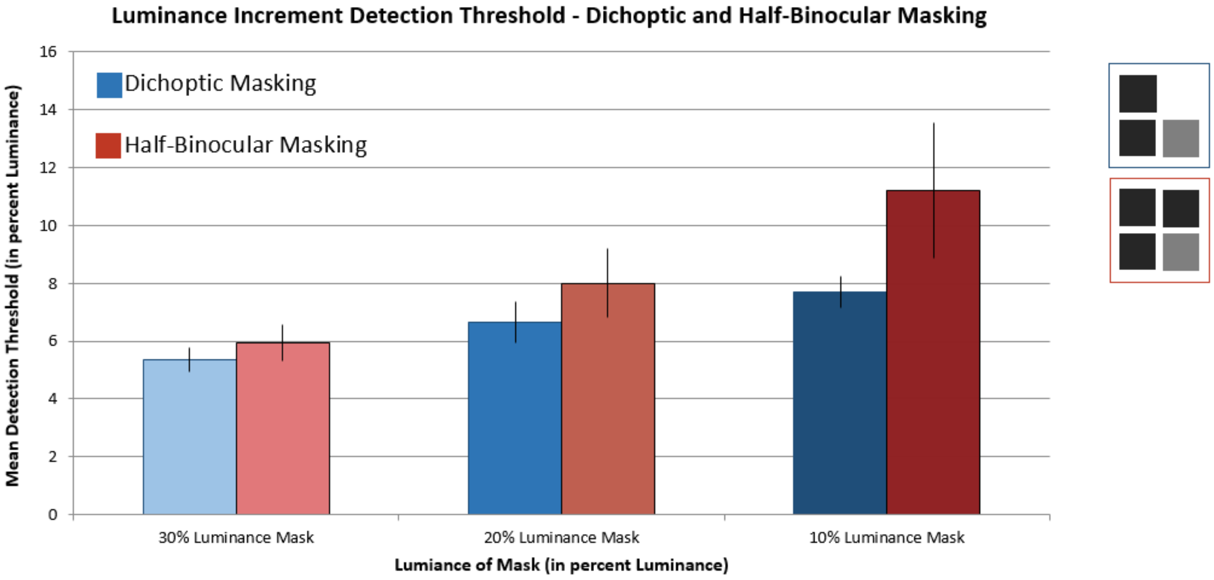

Figure 9: This graph depicts how dichoptic and half-binocular increment detection masking thresholds for our luminance stimuli changed across conditions. As the luminance of the mask decreases, strength of masking significantly increases. Based on a 2 way repeated measures ANOVA, this finding is statistically significant for both types of masking. Error bars represent standard error of the mean.

Figure 10: Luminance Decrement Detection Masking Threshold, Group Effects

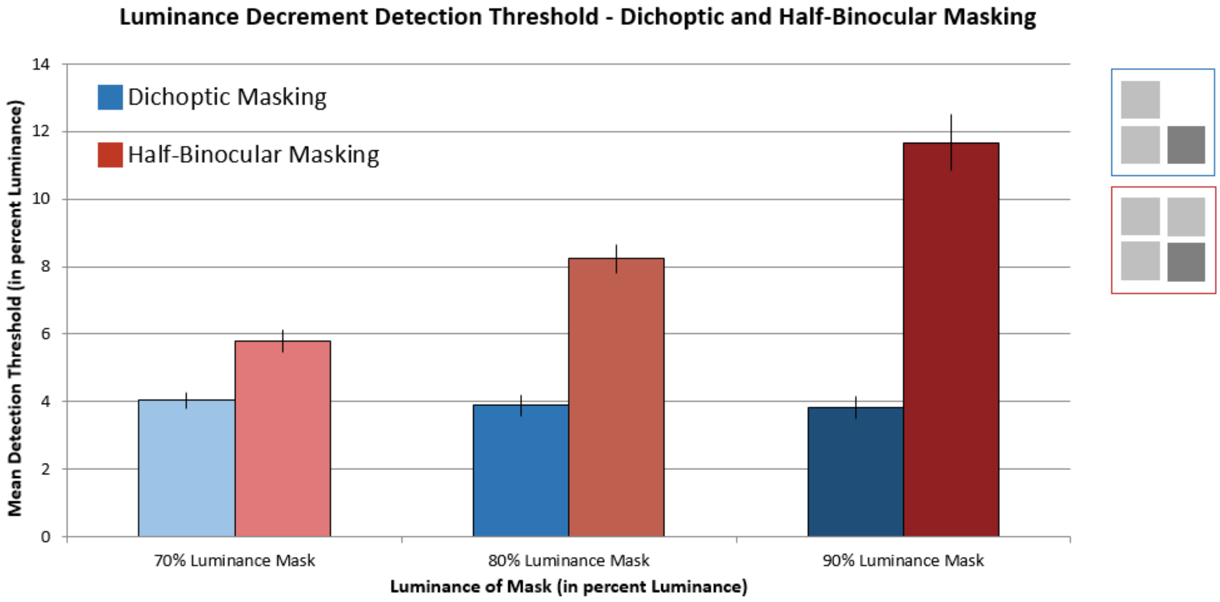

Figure 10: This graph depicts how dichoptic and half-binocular decrements detection masking thresholds for our luminance stimuli changed across conditions. As the luminance of the mask increases, strength of masking significantly increases. Based on a 2 way repeated measures ANOVA, this finding is statistically significant for half-binocular masking. Error bars represent standard error of the mean.

Figure 11: Luminance Rivalry Alternation Rate (Light and Dark Stimuli) Plotted Against Luminance Half-Binocular Masking Threshold (Increment Detection), Individual Effects

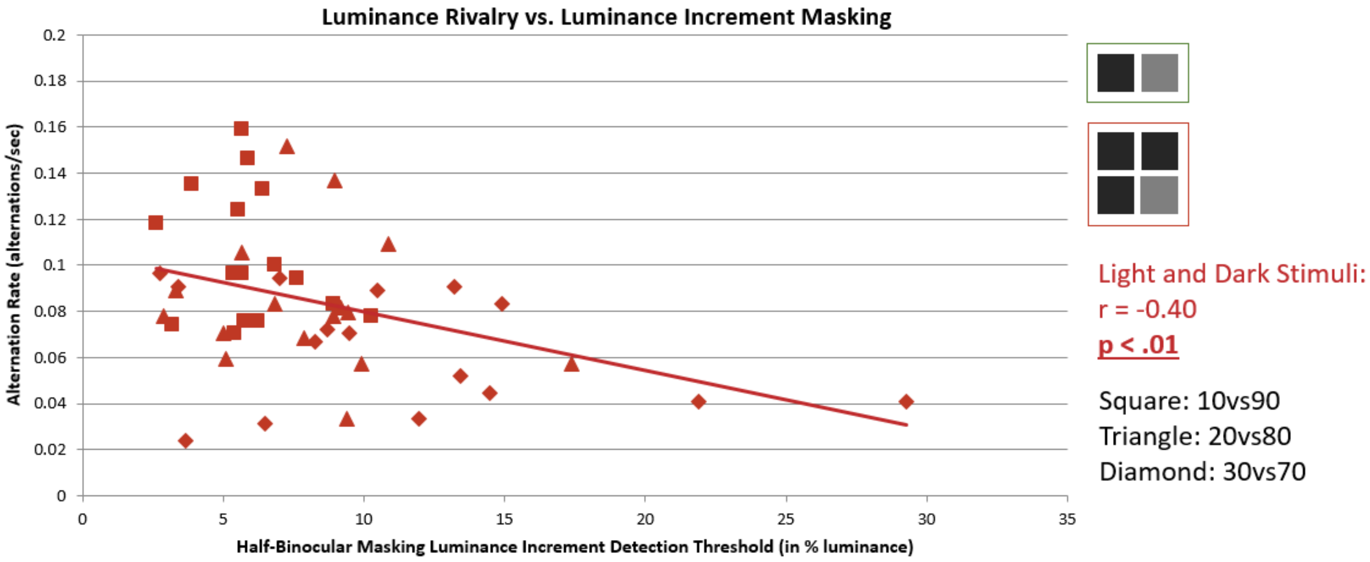

Figure 11: This graph correlates individuals' luminance rivalry alternation rate with individuals' luminance increment detection threshold. This shows that for the slowest rivalry condition (30% vs. 70%) individuals' rivalry alternation rates are significantly (Pearson's r) and negatively correlated with individuals' half-binocular luminance threshold for the strongest masking condition (10% luminance).

Figure 12: Luminance Rivalry Alternation Rate (Light and Dark Stimuli) Plotted Against Luminance Half-Binocular Masking Threshold (Decrement Detection), Individual Effects

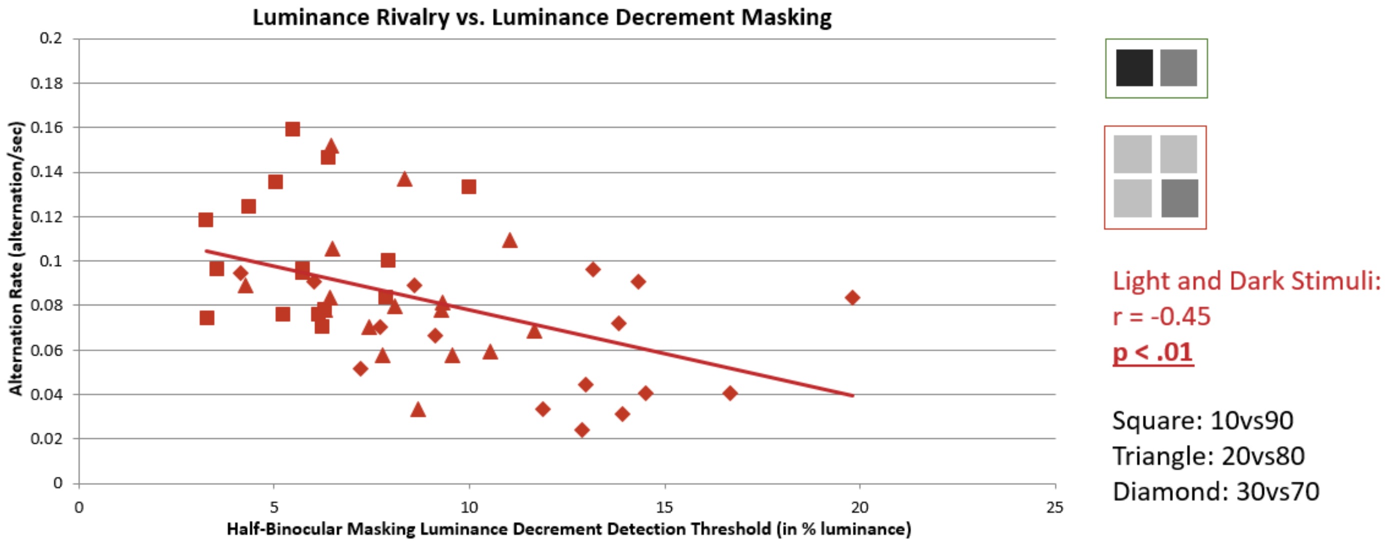

Figure 12: This graph correlates individuals' luminance rivalry alternation rate with individuals' luminance decrement detection threshold. This shows that for the slowest rivalry condition (30% vs. 70%) individuals' rivalry alternation rates are significantly (Pearson's r) and negatively correlated with individuals' half-binocular luminance threshold for the strongest masking condition (90% luminance).

Figure 13: Luminance Rivalry Mean Dominance Duration, Group Effects, n=15

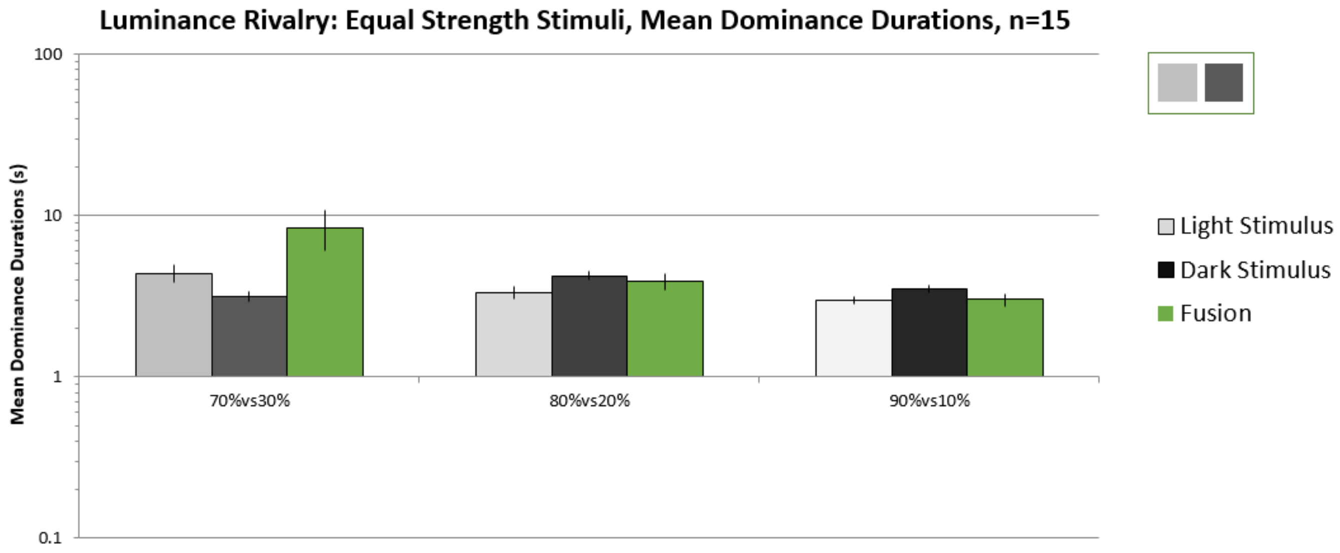

Figure 13: This graph depicts the same data as shown in Figure 6, shown here in terms of mean dominance durations rather than alternation rate. This graph also shows the dominance durations for the light stimulus, the dark stimulus and fusion separately. Dominance durations for both rivaling stimuli and fusion decease across conditions (left to right). Error bars represent standard error of the mean.

Figure 14: Parametric Luminance Rivalry Dominance Durations, Equidominance, n=2

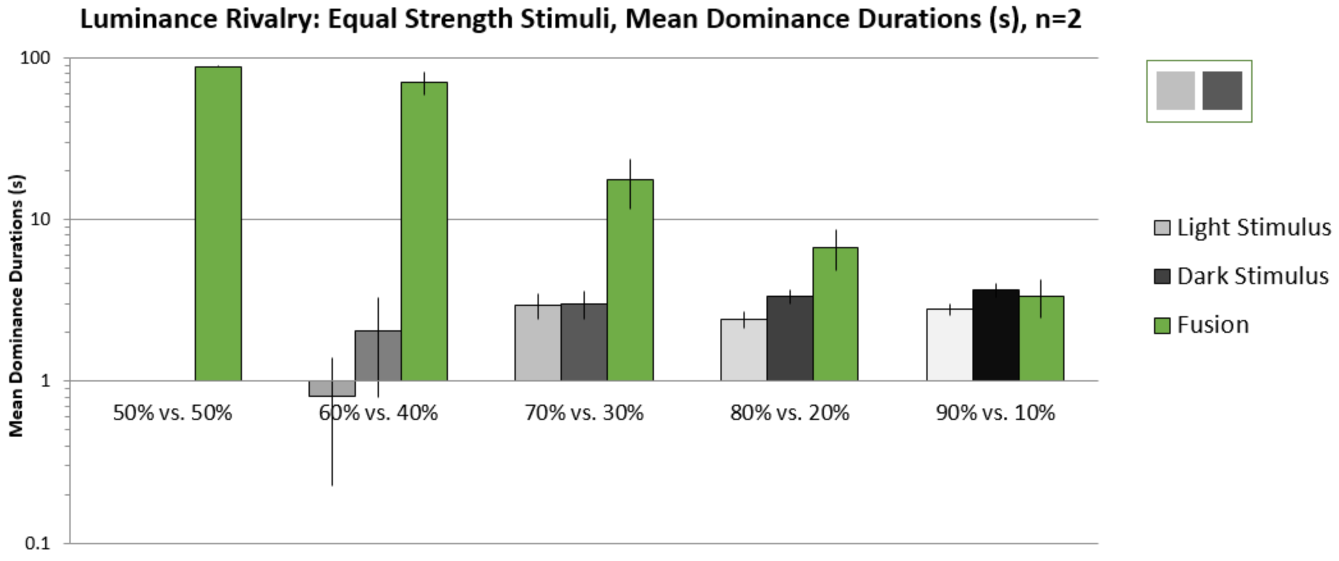

Figure 14: This graph depicts how luminance rivalry dominance durations for our Equidominance experiment changed across conditions. The amount of perceived fusion decreases and length of stimulus dominance durations increases. Error bars represent standard error of the mean. Error bars represent standard error of the mean.

Figure 15: Whittle's Contrast Luminance Rivalry Dominance Durations, Equidominance, n=3

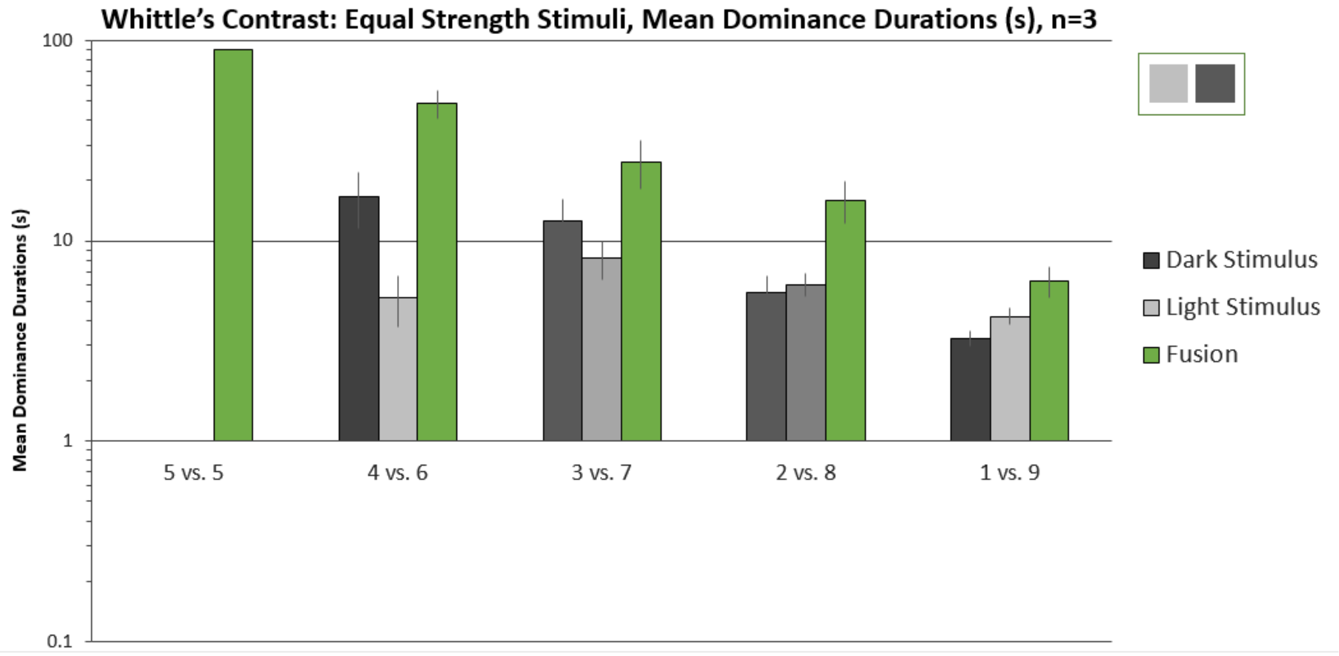

Figure 15: This graph depicts how luminance rivalry dominance durations for our Equidominance experiment changed across conditions, after the stimuli were corrected using Whittle's Contrast. The amount of perceived fusion decreases and length of stimulus dominance durations decreases. Error bars represent standard error of the mean.

Figure 16: Parametric Luminance Rivalry Dominance Durations, One Eye Black, n=2

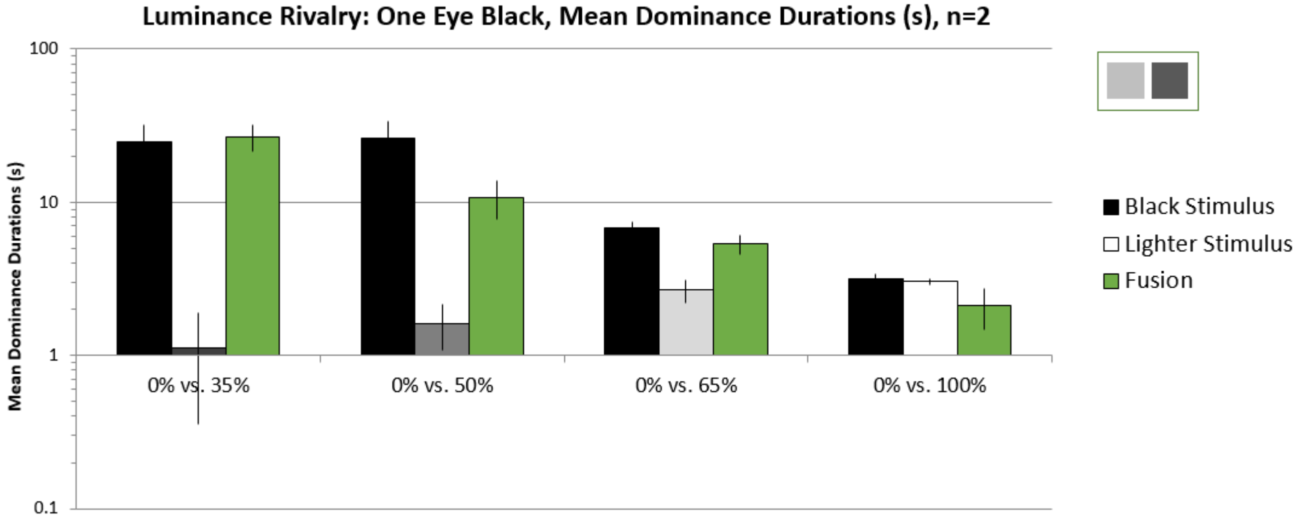

Figure 16: This graph depicts how luminance rivalry dominance durations for our One Eye Black experiment changed across conditions. Across conditions, the amount of perceived fusion decreases, the black stimulus' dominance durations decreased and the other eyes' stimulus dominance durations increased. Error bars represent standard error of the mean.

Figure 17: Whittle's Contrast Luminance Rivalry Dominance Durations, One Eye "Black", n=3

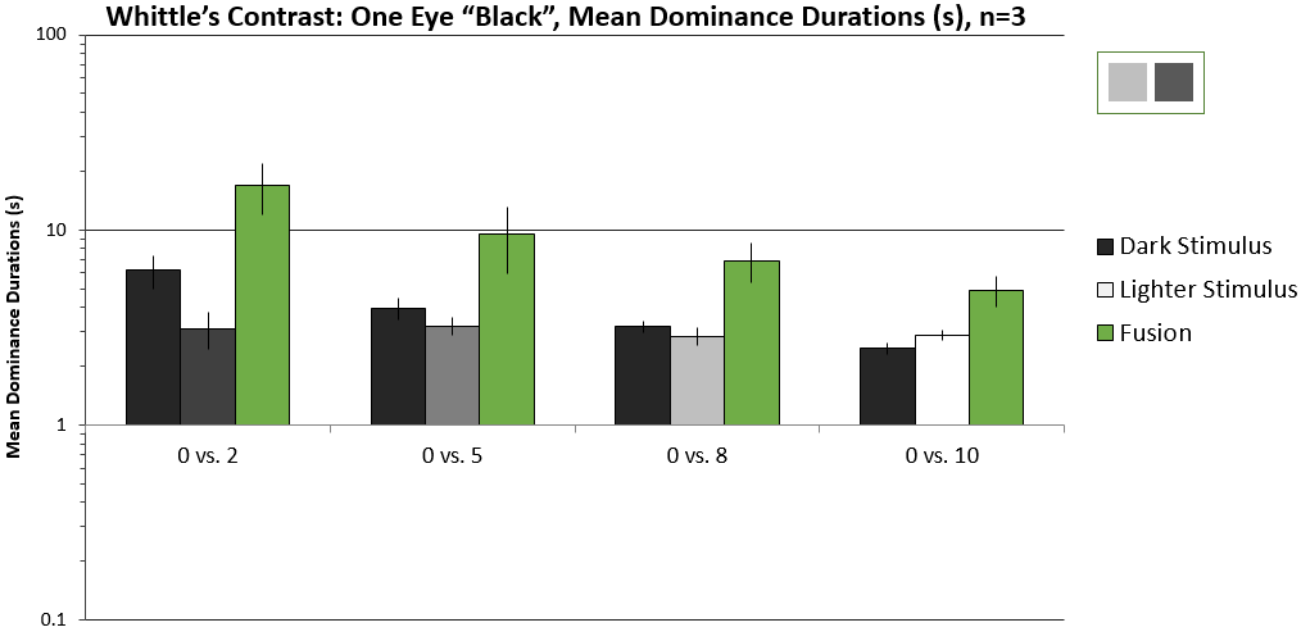

Figure 17: This graph depicts how luminance rivalry dominance durations for our One Eye Black experiment changed across conditions, after the stimuli were corrected using Whittle's Contrast. Across conditions, the amount of perceived fusion decreases and the black stimulus' dominance durations decreased. The dominance durations for the other eyes' stimuli remain similar between conditions. Error bars represent standard error of the mean.

Figure 18: Parametric Luminance Rivalry Dominance Durations, One Eye White, n=2

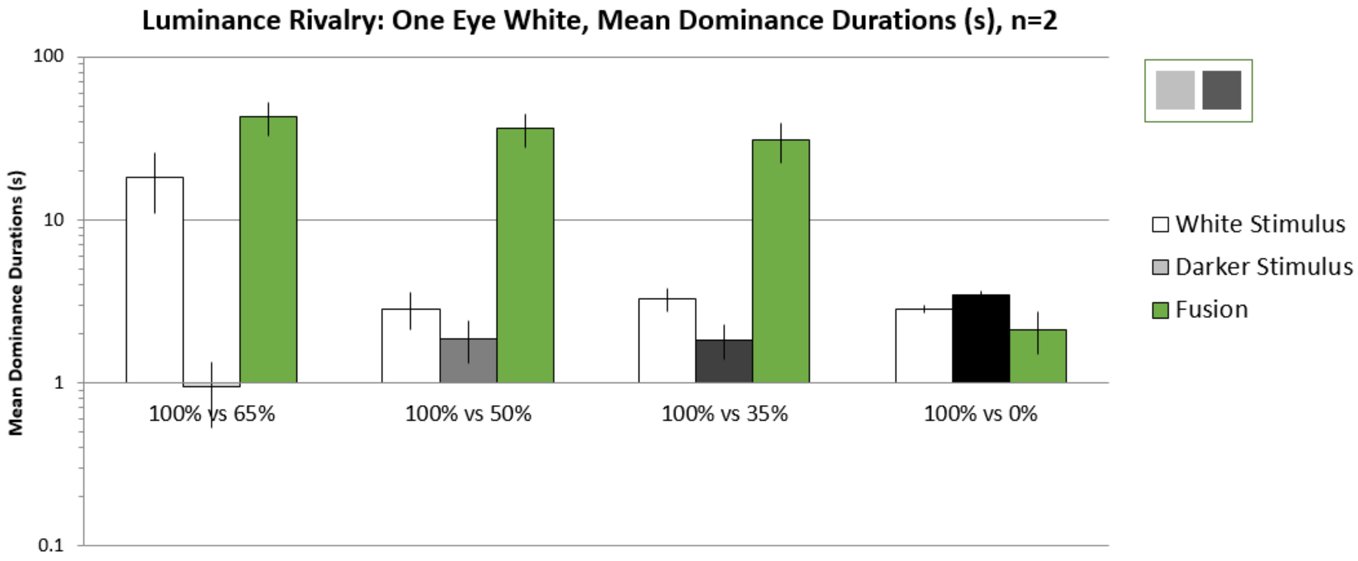

Figure 18: This graph depicts how luminance rivalry dominance durations for our One Eye White experiment changed across conditions. Across conditions, the amount of perceived fusion decreases, the white stimulus' dominance durations decreased and the other eyes' stimulus dominance durations increased. Error bars represent standard error of the mean.

Figure 19: Whittle's Contrast Luminance Rivalry Dominance Durations, One Eye "White", n=3

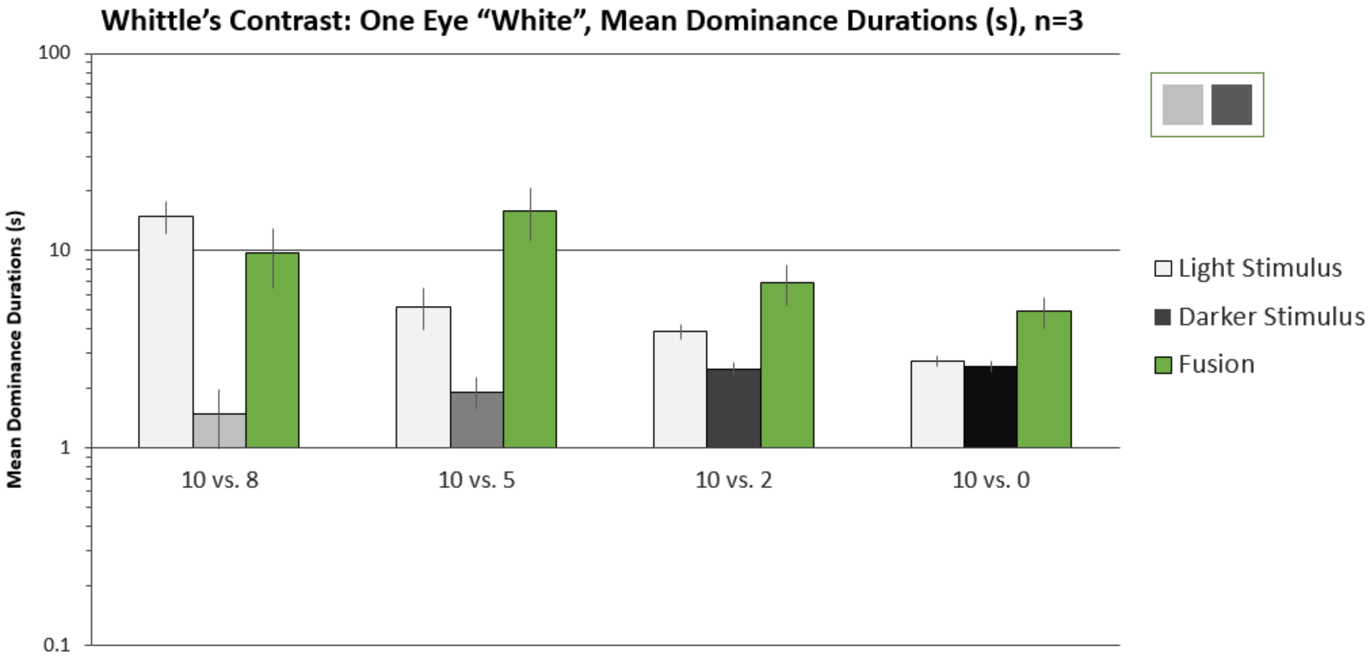

Figure 19: This graph depicts how luminance rivalry dominance durations for our One Eye White experiment changed across conditions, after the stimuli were corrected using Whittle's Contrast. Across conditions, the amount of perceived fusion decreases, the white stimulus' dominance durations decreased, and the other eyes' stimulus dominance durations increased. Error bars represent standard error of the mean.

Figure 20: Whittle's Contrast Luminance Rivalry Dominance Durations, Constant Difference, n=3

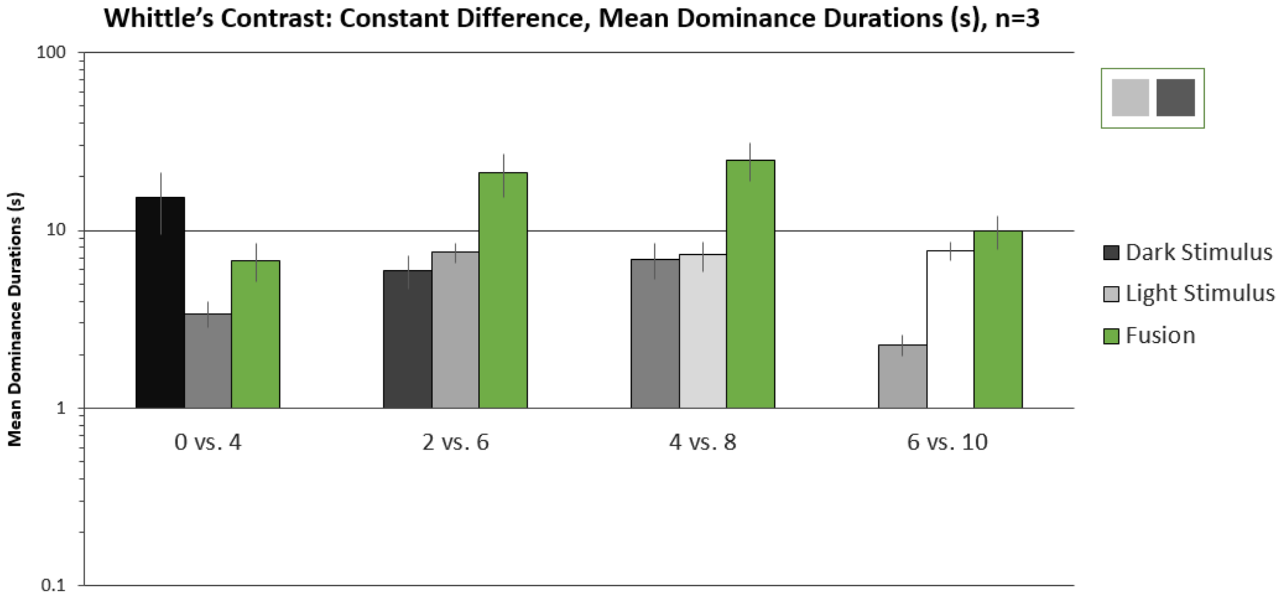

Figure 20: This graph depicts how luminance rivalry dominance durations for our Constant Difference experiment changed across conditions. These stimuli were corrected using Whittle's Contrast. The 0 vs. 4 and 6 vs. 10 stimulus pairs show shorter durations of fusion and more predominance of the stronger stimulus in the pair. The other two conditions (2 vs. 6 and 4 vs. 8) show longer durations of fusion and similar dominance durations between the two rivaling stimuli. Error bars represent standard error of the mean.

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