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Temporal Characteristics of Monoptic, Dichoptic and Half-Binocular Collinear Lateral Masking of Contrast Detection

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ABSTRACT

Purpose. Few prior studies have investigated the temporal properties of inter-ocular (i.e. dichoptic) contrast integration across space in primary visual cortex. My pilot study used collinear flanks to investigate the effect of varying the interstimulus interval (ISI) and flank duration on contrast detection threshold (CDT). As expected, the results revealed CDT facilitation at shorter stimulus onset asynchronies (SOA = ISI + flank duration) and reduced inter-ocular contrast integration relative to intra-ocular (i.e. monoptic) integration. It also showed unexpected, inter-ocular CDT suppression at longer SOAs. To better understand that surprising finding, I conducted additional experiments that added more subjects, longer SOAs, an additional viewing condition (half-binocular), and orthogonal flanks.

Methods. Eleven subjects with normal vision participated. Nine were naive to the purpose and participated for a mean of 25 hours each. The primary investigator (WK) and a summer research fellow (MM) participated for approximately 240 and 100 hours, respectively. In the main experiment, target and flanks were three cpd vertical sinusoids separated by six lambda (sigma=1.5 lambda) center-to-center vertical separation. Flank contrast was normalized to 3X flank CDT. Flanks were presented at four durations (67-500ms) and ISIs at

seven durations (0-2500ms) resulting in SOAs from 0-3000ms. Target presentations were 250ms to the dominant eye via mirror haploscope and septum. Flanks were presented to dominant (monoptic and half-binocular viewing) and non-dominant eyes (dichoptic and half-binocular viewing). Forward masking was used with a 1-FC detection paradigm and 7-level MOCS. Each threshold was calculated from approximately 700 trials (approximately 10 runs over 2-3 days). A supplemental, orthogonal flank experiment resembled the main experiment with the exception of flank orientation and SOA range (0-1000ms).

Results. As expected, simultaneous presentation of collinear flanks resulted in mean CDT facilitation (monoptic 18.9% ± 3.9% (SE); dichoptic 13.9% ± 4.0%; half-binocular 18.0% ± 4.2%). For all viewing conditions, relative facilitation decreased as SOA increased up to 1000ms. Surprisingly, dichoptic and half-binocular viewing showed CDT suppression at long SOAs beginning at 500ms (dichoptic) and 750ms (half-binocular), with maximal suppression (9.9% ± 5.1% and 5.3% ± 4.7%, respectively) occurring at 1000ms. For dichoptic viewing, the CDT suppression was statistically significant ($p < 0.05$) at all 5 SOAs from 500-1000ms. All viewing conditions approached no effect at the longest SOAs (1500-3000ms). Flank duration had a significantly greater contribution to the overall effect than ISI for monoptic and half-binocular viewing. There was no significant difference in contribution under dichoptic viewing. Both monoptic orthogonal and dichoptic orthogonal flanks produced CDT facilitation at shorter SOAs that decreased with increasing SOA. Importantly, neither orthogonal flank condition produced CDT suppression.

Discussion. The collinear CDT facilitation produced by intra-ocular and inter-ocular flanks at shorter SOAs is consistent with the properties of long-range, lateral connections in primary visual cortex. This facilitation persists well beyond the maximal temporal integration limit (approximately 200ms) of the transducer model of contrast integration and therefore appears inconsistent with that model. The reduced degree of dichoptic CDT facilitation at shorter SOAs (compared with monoptic viewing) is evidence of decreased inter-ocular contrast integration. In general, the results are in agreement with existing models of intra- and inter-ocular contrast gain control. The temporal aspects of long SOA inter-ocular CDT suppression observed in the present study are consistent with the temporal properties of illusory contour perception reported in prior studies.

Conclusions. I propose the novel hypothesis that the CDT suppression produced by collinear flanks at longer SOAs under dichoptic and half-binocular viewing is due to one-way, contrast adaptation from lateral propagation that produced the effect of a collinear, illusory contour. This hypothesis is supported by the dichoptic, orthogonal flank experiment that showed no CDT suppression at the same longer SOAs.

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Chapter 1

Visual system overview through primary visual cortex

The ability to detect and extract useful information from differences in luminance across space (i.e. contrast) is known as spatial vision. Given spatial vision's importance as a building block for visual, motor and cognitive functions, it shouldn't be surprising that this area has been extensively studied over the past three decades. One aspect of this research investigates the integration of surround (spatially adjacent) contrast. Studies using psychophysics, physiology, and electrophysiology have contributed to our understanding of cortical neural networks and the mechanisms underlying contrast integration across space under monoptic (intra-ocular) and binocular viewing.

Current models of contrast integration incorporate physiologic knowledge of horizontal (lateral) cortical connections in V1 and feedback/forward connections between and within cortical (V1-V5) and sub-cortical (LGN and superior colliculus) areas. This study was designed to further elucidate these cortical networks as well as contribute novel findings about the mechanisms of inter-ocular contrast integration across space. Specifically, I was interested in how varying the temporal separation (i.e. flank duration and ISI) between suprathreshold flanking contrast and a foveal target affects the contrast detection threshold of the target.

1.1 Central visual pathway

The target and flanks utilized in this study stimulate the retinal fovea almost exclusively. Since each individual stimulus had a diameter of two visual degrees and the stimuli were basically abutting, the total visual space from the upper limit of the top flank to the lower limit of the lower flank was about six degrees. Hence, the distance from the center of the target to the edge of either flank (the radius of the total stimulus area) was approximately three degrees. This slightly exceeds the commonly cited foveal radius size of 2.5 degrees (Schwartz, 1998; Snell and Lemp, 1997). The presentation of stimuli in visual space corresponding to the fovea is significant due to the asymmetric distribution of retinal ganglion cells (RGCs) carrying information to cortex from the central retina. Approximately 50% of ganglion cells lie within five mm (approximately 15 degrees) of the fovea's center, an area making up only about 7% of the retina's total area. This asymmetric distribution is also reflected in the relatively high percentage of primary visual cortex representing the fovea.

After photons strike foveal photoreceptors cells (mainly cones in this study since it deals with the fovea under photopic viewing conditions), a graded potential is generated. This signal then travels to retinal ganglion cells via bipolar cells. Along the way it is heavily modified by laterally-expansive, inhibitory horizontal and amacrine cells. RGCs produce the first action potential of the visual pathway. Their output is organized into receptive fields of varying size with center/surround organization.

RGCs are bundled together and exit the posterior eye via the optic nerve. Three types of RGCs constitute a substantial majority (approximately 80%) of the entire RGC population (Field and Chichilnisky, 2007). These are the midget, parasol, and small bistratified RGCs. Midget RGCs exhibit sustained responses and project to the parvocellular layers of the lateral geniculate nucleus (LGN). Traditionally, they are thought to show relatively high spatial resolution and slow action potential propagation. Parasol RGCs exhibit transient responses and project to the magnocellular layers of the LGN. They are traditionally thought to demonstrate relatively low spatial resolution and rapid action potential propagation. Bistratified RGCs are a relatively recent discovery that carry a distinctive blue-on/yellow-off chromatic signal and project to koniocellular LGN layers. As mentioned above, these three RGC types constitute about 80% of RGC projections. For a complete review of RGC types see Field and Chichilnisky (2007). The stimuli in this study are achromatic, stationary and primarily stimulate midget RGCs and the parvocellular pathway.

The right and left optic nerves travel to the optic chiasm where approximately 50% of optic nerve fibers decussate. Fibers originating in temporal retina stay ipsilateral and nasal fibers crossover to the contralateral side. As a result, distal to the optic chiasm information from the right hemifield is carried to the left side of primary visual cortex and vice versa. Beyond the optic chiasm, the optic nerve fibers are formed into right and left optic tracts. The optic tracts synapse (the first post ganglion cell synapse) at the thalamus. These synapses form the right and left LGN.

The LGN is arranged into six distinct layers of cells. Each layer contains projections from a single eye. Layers 2, 3 and 5 receive projections from the ipsilateral eye and layers 1, 4 and 6 receive projections from the contralateral eye. Hence, at the level of the LGN incoming information from earlier in the visual pathway is still segregated by eye (i.e. monocular). The receptive fields of LGN neurons closely resemble the center/surround organization of ganglion cell receptive fields.

In addition to projections originating from the retina, approximately 80% of excitatory LGN input originates in primary visual cortex (Bear *et al.*, 2007). The corticogeniculate neurons that constitute this feedback pathway are located in layer 6 of primary visual cortex (V1). Corticogeniculate feedback appears to be segregated into parallel streams analogous to the forward processing pathways (see below). Corticogeniculate neurons in the upper portion of V1's layer 6 project axons that target parvocellular layers in the LGN and corticogeniculate neurons in the lower portion of V1's layer 6 target the magnocellular layers of LGN. Also, a small percentage of corticogeniculate neurons in the lower portion of layer 6 appear to provide input to the koniocellular layers of LGN. For a complete review of corticogeniculate feedback in primate see Briggs and Usrey (2011).

One implication of this corticogeniculate feedback is that LGN neurons may receive information from both eyes. Hence, it is possible that binocular interactions occur at the level of the LGN. However, the similarity of LGN neuron properties to the properties of upstream neurons (e.g. the same center/surround organization as retinal gangion cells) suggests that the corticogeniculate pathway is modulatory rather than driving (Sherman and Guillery, 1998). The implication of this is that the LGN is more than simply a relay station on the way to cortex.

Projections from the LGN travel along the geniculo-calcarine tract and synapse in V1. Like the rest of cortex, V1 (also known as striate cortex) is organized into six layers. Although there are technically six layers, layer four is considered to have three distinct layers (layers 4A, 4B, and 4C) creating eight functional layers. Magnocellular and parvocellular pathway axons primarily project to layers 4Cα and 4Cβ of striate cortex, respectively. However, both magnocellular and parvocellular pathways also provide input to layer 6 of V1. Koniocellular pathway axons target cytochrome-oxidase rich blobs, layer 1, and layer 4A in some species, including macaque monkeys (Sherman and Guillery, 1998).

Neurons in layer 4 tend to have center surround organization (similar to retinal ganglion cells and LGN neurons) and monocular receptive fields. After the second cortical synapse (layer 3 of V1 for most projections) neurons have more complex receptive fields and most receive input from both eyes. Importantly, this is thought to be the first synapse to receive binocular input and approximately 50% of V1 neurons are binocular. Prior to this step in the visual pathway information is monocular. Downstream from primary cortex, at visual area two (V2) and beyond, neurons receive almost exclusively binocular input and visual fields become much more complex. For a review of V1 neuro-physiology literature see Sincich and Horton (2005).

The windowed sinusoid stimuli used in this study were designed to primarily stimulate a single population of neurons in early visual cortex. Unlike square waves that contain multiple odd integer harmonic frequencies (Fourier components) and real world scenes that contain all integer harmonics, sinusoids only contain a single spatial frequency and stimulate a single spatial frequency channel (population of neurons). Using a Gaussian window also helps to limit the stimulation of neurons outside the target population. For sinusoid with a hard edge window, the edge contains multiple spatial frequencies and stimulates a wide range of neurons in V1/V2. Using a single spatial frequency (3 cpd), windowed sinusoid avoided this and primarily stimulated a single spatial frequency channel in early visual cortex.

Dichoptic flank presentation effects (CDT facilitation or suppression) require the inter-ocular transfer of contrast information. Therefore, given what is known about the visual pathway, it is reasonable to assume that when a dichoptic effect is observed it is initially generated by a neuron at or beyond layer 2/3 of V1. Also, since the windowed sinusoids utilized in this study target a single population of V1 neurons, the effect likely occurs prior to V2. Hence the dichoptic effects observed in this study probably occur at or beyond layer three of V1, but prior to V2.

1.2 Lateral connections in primary visual cortex

In addition to the sequential flow of visual information from retina to higher cortical areas and feedback connections (e.g. cortex to LGN), the visual system also extensively utilizes lateral connections to integrate visual information from areas larger than the classical receptive field (CRF). Using intracelluar injections of horseradish peroxidase in cat, Gilbert and Wiesel (1979; 1983) showed that individual neurons are able to communicate over long distances (two mm or more) horizontally, parallel to the cortical surface. Gilbert and Wiesel also reported intra-layer and inter-layer lateral connections in layers 2+3, 3, 4, 5, and 6 of cat primary visual cortex. Subsequent studies in primate have found lateral connections as great as seven mm in length corresponding to four degrees of object space (Kapadia *et al.*, 1995 and 2000). These values correlate well with the spatial interactions demonstrated in psychophysical studies (Li and Gilbert, 2002).

The existence of correlated excitation patterns between cortical neurons with similar orientation field preferences (Ts'o *et al.*, 1986; Ts'o and Gilbert, 1988) suggests that cells connect mainly to other cells with similar orientation preferences (intra-channel connections). However, these correlated excitation patterns are not yet supported by primate experimental results (LeVay, S., 1988). For a recent review of lateral connection studies, see Voges *et al.* (2010). For a discussion of lateral connections as they relate to the present study see section 2.6 (Linking hypotheses: psychophysics with neuro-physiology).

Chapter 2

Introduction

2.1 Psychophysical studies of contrast integration across space from collinear flanks under monocular and binocular viewing

It has been demonstrated in a number of studies that the detection of foveal targets may be facilitated by the concurrent presentation of collinear, higher contrast flanks of the same spatial frequency (Polat and Sagi, 1993, 1994; Solomon *et al*., 1999; Solomon and Morgan, 2000; Woods *et al*., 2002; Huang *et al*., 2012). In their seminal psychophysics paper, Polat and Sagi (1993) used a central Gabor target flanked vertically by 40% contrast, collinear Gabors in an experiment that demonstrated both suppression and facilitation of target detection. The effect (suppression vs. facilitation) was shown to be dependent on the separation of flanks from the target. Less than two wavelength (λ = one cycle) separations produced suppression and two or greater λ separations produced facilitation of target detection. The amount of facilitation decreased gradually to approximately 12λ separation where it approached the baseline (target alone) threshold. Subsequent studies have confirmed many of these general findings for separation (Polat and Sagi, 1994; Solomon *et al*., 1999; Cass and Spehar 2005; Polat and Sagi, 2006; Tanaka *et al*., 2007). This effect was evaluated at several target/flank wavelengths and found to be largely spatial scale invariant with respect to spatial frequency. The center-to-center separation between target and flankers relative to their spatial frequencies contributes more to determining the effect than the visual angle subtended by the separation.

Here, it is useful to examine the effect of flank contrast on target contrast detection threshold (CDT). Woods *et al.* (2002) found that, in general, as flank contrast increased the target CDT decreased. At the highest flank contrasts they evaluated (20-40% Michelson contrast) the effect tended to asymptote at the maximum effect. Even sub-threshold flanks were associated with a relatively low degree of facilitation. Yu *et al.* (2002) also studied the effect of surround contrast on target CDT, but used orthogonal flank and annulus surrounds. They included a wider range of surround contrasts (2.5-80% Michelson contrast) and found facilitation that peaked around 10% contrast and gradually transitioned to no effect at the highest and lowest surround contrasts. Because of differences in other parameters (spatial frequency, sigma, etc.) it is difficult to directly translate these findings to other studies. However, the findings are still useful for establishing broad hypotheses.

An area of recent interest is the effect of collinear facilitation across depth. Huang *et al*. (2012) used Gabor flankers and targets presented to both eyes to study the effect of differences in surface assignment and differences in disparity on collinear facilitation. The flankers in their study were high contrast (50%) with center-to-center three λ separation between flanks and targets. All stimuli had a spatial frequency of 1.6 cpd and a Gaussian envelope (σ) of 0.47 degree. The paradigm was a 2-AFC staircase used to measure detection threshold of the target. In the frontal-collinear condition (essentially binocular, collinear flanks and targets), the flank effect was an approximate 88% increase in sensitivity (i.e. facilitation). Manipulations of perceived depth and slant suggested that differences in surface assignment cause more disruption of collinear facilitation than differences in disparity. This contradicts Huang *et al*. (2006) who reported that differences in depth produced disruption of collinear facilitation. One implication of Huang *et al*. (2012) for the present study is that in the unlikely event a subject did not maintain complete fusion and perceived the target and flanks at slightly different depths, the disruption of collinear facilitation would not be expected.

Petrov *et al*. (2006) hypothesized that the facilitation of CDTs observed in collinear, flanking experiments derived mainly from a reduction in uncertainty about the stimulus location. To test this hypothesis, they added two conditions to a Gabor flanking experiment: 1) a thin (1.2 arc min) circle surround and 2) four thin, surrounding lines with the same orientation as the target. All Gabor stimuli (target and flanks) were three cpd with 2.5λ separation between the target-center and the flank-center. Flanks were always 30% Michelson contrast. Unlike most other collinear flanking paradigms in which the stimuli are vertical, Petrov *et al.*'s (2006) stimuli were oriented 45 degrees from vertical. In the circle surround experiment, the 15% contrast circle was 2.5λ in diameter and 1.2 arcmin wide. The line surrounds were two λ long and their center was 2.5λ from the center of the target.

Petrov *et al*. (2006) found similar levels of CDT facilitation for the circle surround (28%) and the line surround (27%) when Gabor surrounds were not included. When Gabor surrounds were included the level of facilitation increased to 46% and 40% for the circle and line surrounds, respectively. While all four of these conditions demonstrate significant facilitation compared with the target alone CDT, none of the four are significantly different from one another. Based on these results, the authors conclude that a reduction in uncertainty accounts for most of the contrast detection facilitation. However, the lack of a condition with only Gabor flanks (not including circle or line surrounds) makes the interpretation of these findings more difficult.

Most flanking experiments have used the same high contrast, supra-threshold flanks for all subjects participating in the experiment (Polat and Sagi, 1993, 1994; Cass and Spehar, 2005; Meese and Hess, 2005; Shani and Sagi, 2006). In this experiment, we instead scaled flank contrast based on individual flank CDTs. The time intensive nature of this experiment makes it difficult for subjects to complete the entire experiment. Hence, the ability to make valid intra-subject comparisons takes on added importance and the use of scaled flank contrast in the present study adds to the validity of intra-subject comparisons. It has also been shown in animal, single-cell studies that modulations of cell response by a stimulus outside the cell's classic receptive field depends on the contrast level relative to the cell's response threshold and not simply the absolute contrast of the flanking stimulus (Mizobe *et al*., 2001).

Another frequently utilized stimulus for examining the effect of adjacent contrast on a foveal target is an annular surround. Unlike flanks that only occupy a portion of the visual space adjacent to a target, an annular surround, as the name suggests, completely surrounds the target. Yu *et al*. (2003) used monocular annular surrounds to study threshold-versus-contrast functions over a wide range of pedestal and surround contrasts. They found that an orthogonal surround (a surround oriented 90 degrees from the target) lowered contrast thresholds (i.e. produced CDT facilitation) over the entire range of pedestal and surround contrasts. They also found that the effect of collinear surrounds was dependent on the contrast of the surround. The effect was facilitative when the surround/pedestal contrast ratio was less than one and suppressive when the same ratio was greater than one. This suggests that cross- and iso-oriented surrounds are mediated by different mechanisms.

With binocular viewing of collinear, annular surrounds and a contrast matching paradigm, Nurminen *et al.* (2010) found facilitation of contrast perception that extended out as far as 19.8 cycles (λ). This facilitation decreased as the surround-to-center contrast ratio increased and eventually became suppression at their highest surround-to-center ratio (3:1).

2.2 Neuro-physiology studies of contrast integration across space

The classical receptive field (CRF) is usually defined as the region of visual space that is responsive to the presentation of light or dark stimuli (Hartline, 1938). At the level of primary visual cortex (V1), most neurons have well defined receptive fields (Hubel and Wiesel, 1958). Many of the findings reported in psychophysical experiments have also been demonstrated in animal experiments that examined the response of individual cells in striate visual cortex. In these studies, a stimulus is projected onto the retina and the spiking responses from a single visual cortex cell are recorded. Stimuli presented outside the CRF's visual space have also been shown to influence the firing rate of visual neurons. The presentation of these "surround" stimuli is analogous to the presentation of flanking stimuli in psychophysical paradigms.

Both inhibitory and facilitatory surround interactions have been reported in single cell studies, although inhibition is more frequently described. In cat, Hubel and Wiesel (1963) recorded receptive fields in which firing rates drop off sharply if a bar-shaped stimulus extended beyond a critical length. Other studies have confirmed the presence of these "end-stopped" cells cat area 17 (Sengpiel *et al.*, 1997, 1998; Walker *et al.*, 1999, 2000) and primate V1 (Jones *et al.*, 2001).

The diameter of the inhibitory surround has been approximated to be 2-5 times the CRF diameter (Li and Li, 1994; Maffei and Fiorentini, 1976). Orientation (Levitt and Lund, 1997; Li and Li, 1994), spatial frequency (Levitt and Lund, 1997; Walker *et al.*, 1999) and relative phase (Levitt and Lund, 1997; DeAngelis *et al.*, 1994) have all been shown to be important in determining the level of suppression. In general, the greater the difference between the target and surround the less suppression is demonstrated. Dichoptic presentation of the center and surround stimuli has been shown to decrease (but not eliminate) the suppressive effects of the surround in cat (DeAngelis *et al.*, 1994). This suggests that at least a portion of the integration of surround contrast occurs after binocular integration.

A smaller number of studies have reported the facilitation of cell firing by stimuli outside the CRF. Maffei and Fiorentini (1976) identified orientative selective, facilitory regions in cat. Nelson and Frost (1985) reported facilitation of the neuron firing rate by stimuli that were of a similar orientation and aligned with the long axis of the neuron's receptive field. Kasamatsu *et al*. (2010) used flanking, Gabor patches to investigate a possible relationship between collinear facilitation and the expansion of receptive fields in cat neurons.

Previous studies had shown that low target contrast neuronal receptive fields are up to 3x's larger than high contrast, target receptive fields (Kapadia *et al*., 1999; Sceniak *et al*., 1999; Cavanaugh *et al*., 2002). The contrast dependent nature of the receptive fields described in these studies suggested that effect modulation by flanks might be due to variable receptive field size. However, when Kasamatsu *et al*. (2010) directly compared receptive field size changes associated with decreased target contrast with changes produced by altering target to collinear flank separation, they found that the spatial extent of receptive field expansion (when it existed) was smaller than the spatial extent modulated by collinear flanks. Kasamatsu *et al*. (2010) conclude that receptive field size changes associated with decreased contrast and effect modulation by collinear flanks are separate processes that function independently from one another. This supports the hypothesis that collinear flank effects are caused by long-range, lateral connections in area V1 of primate visual cortex.

The sign of the surround's modulation (inhibition or facilitation) is dependant on the contrast of the center stimulus relative to the cell's contrast threshold (Mizobe *et al*., 2001; Polat *et al*., 1998; Sengpiel *et al*., 1997; Toth *et al*., 1996). Close to the threshold, the presentation of surround stimuli is associated with a relative facilitation of the neuron's firing rate. As target contrast increases and moves further from threshold, the presentation of surround stimuli is associated with relative suppressive of the firing rate. These findings are consistent with the surround contrast adding to center contrast and affecting the contrast gain (i.e. contrast response function) of the neuron.

Mizobe *et al.* (2001) attempted a systematic study of the conditions that promote CDT facilitation. They found that facilitation and suppression frequently occurred in the same cell and that the effect was dependent on the contrast of the central target. Facilitation with collinear flankers occurred most frequently near the neuron's contrast threshold and suppression became more frequent at high target contrasts. They also reported that cross-oriented flankers (rotated 90 degrees relative to the target) did not facilitate target detection.

In summary, neuro-physiology studies in cat and primate have demonstrated that surround stimuli outside the CRF can have inhibitory or facilitatory effects on cortical neuron firing rates. In general, the greater the difference between center and surround in orientation, spatial frequency, and relative phase the less the surround effect. The sign of the effect (inhibition or facilitation) may be dependant on the relative contrast of the center and surround.

At relatively low target contrast levels surrounds tend to produce firing rate facilitation and at relatively high target contrast levels surrounds tend to produce firing rate inhibition.

Dichoptic presentation of center and surround has been shown to produce surround effects suggesting that surround contrast integrates beyond the first cortical synapse. Receptive field size has been shown to increase at low contrast levels. At first this seems to suggest that facilitatory surround effects may simply be due to receptive field expansion. However, there is experimental evidence that contrast dependant field size changes and collinear flank effects are independent (Kasamatsu *et al*., 2010). This supports the hypothesis that collinear flank effects are dependant on lateral, cortical connections.

2.3 Psychophysical and neuro-physiology studies of contrast integration across space from orthogonal flanks

Polat and Sagi (1994) used a flanking paradigm to explore the interaction between the local and global orientations of 13.3 cpd Gabor stimuli ($\sigma=\lambda$). A 2-AFC method was used to determine the CDT of a foveal target presented to both eyes (binocular viewing) simultaneously with two high contrast flanks. They reported CDT facilitation at 2-8λ center-to-center separations for both collinear and orthogonal flanks. Facilitation was maximal with vertical (collinear) orientations, but smaller facilitatory effects were also observed with orthogonal orientations. Diagonal (45 degree) local orientations had minimal effect on detection thresholds.

Polat *et al*. (1997) used both psychophysical and visual evoked potential (VEP) measures to evaluate the neural interactions between foveal Gabor targets and Gabor flankers in normal and amblyopic subjects. At three λ center-to-center target/flank separation and a flank contrast of 40%, they found that orthogonal flanks produced significant CDT facilitation in normal subjects. However, the degree of facilitation was approximately 1/3 less than the facilitation observed with collinear flanks. In the same experiment, amblyopic subjects also showed facilitation with collinear flanks, although the degree of facilitation was about 1/3 the amount seen with normal subjects. Orthogonal flanks produced minimal effects in the amblyopic subjects.

In Polat *et al*.'s (2007) VEP experiment, the test/flank separation was 6λ and the flank contrast was set at 50%. Test contrast was 8%, 16%, or 32%. It is worth noting that all three of these values are well above typical CDT levels. Test-alone and flank-alone VEPs were summed and compared to the response seen when test and flanks were displayed simultaneously. This was termed the interaction index. When test and flanks were collinear, normal subjects showed a significant, positive interaction index (analogous to facilitation) at 8% target contrast and minimal facilitation with 16% and 32% test contrasts. When test and flanks were orthogonal, normal subjects showed minimal effect with 8% test contrast. Mildly negative interaction index values (analogous to inhibition) were observed at 16% and 32% test contrasts.

Compared with the number of collinear flanking studies, relatively few studies have evaluated the effect of orthogonal flanks. Those that have included orthogonal flanks show mixed results. In both studies described above (Polat and Sagi, 1994; Polat *et al*., 1997) psychophysical experiments indicate that orthogonal flanks produce CDT facilitation, but less than collinear flanks. The VEP experiment in Polat *et al*. (1997) showed signal inhibition by orthogonal flanks at test contrasts of 16% and 32%. However, those contrasts are well above detection threshold levels. As a result, they are probably located in a different (decelerating) portion of the contrast gain control curve (see section 6.2).

Orthogonal surrounds have also been included in neuro-physiology studies. In paradigms where collinear flanks produce neuron firing rate suppression, orthogonal flanks tend to produce less effect (suppression in this case) than collinear surrounds. It has also been reported that orthogonal surrounds can produce a net facilitation of the firing rate (Jones *et al*., 2001; Sillito *et al*., 1995). In such cases, the firing rate is greater for the surround and optimal target together than the optimal target alone firing rate. Interestingly, some of the cells examined in Sillito *et al*. (1995) responded strongly even if the orientation of the target and surround were switched. The authors propose that the observed neuron firing rate facilitation has two components: 1) an active facilitatory mechanism produced by the target and 2) a disinhibitory mechanism that reduces inhibitory input from the surround. Together these components produce a supra-optimal response.

2.4 Psychophysical studies of contrast integration across space from collinear flanks under dichoptic viewing

Tanaka and Sagi (1998) used Gabor flanking experiments to evaluate the effect of briefly presented vertical flanks on contrast detection thresholds. Forward masking was utilized throughout. The 90ms flank presentation preceded a very brief (36ms) target presentation. Stimulus onset asynchrony (SOA) varied between 0ms (simultaneous) and 16290ms. Center-to-center target/flank separation ranged from zero λ (shared visual space) to 12λ. In contrast to the 1-AFC (yes/no) paradigm used in this study, Tanaka and Sagi (1998) used a 2-AFC paradigm with randomly determined delay periods inserted between presentation intervals. This 2-AFC paradigm resulted in very lengthy trials up to 55,332ms.

Under monoptic viewing, Tanaka and Sagi (1998) found maximal CDT facilitation when flanks and target were collinear. They also found mild CDT facilitation for both three λ and 12λ separations of collinear flanks that continued out to the maximum SOA included in the experiment (16290ms). However, this SOA was only evaluated for a single subject. Two other subjects showed similar levels of mild facilitation up to a 2700ms SOA (the maximum SOA they were evaluated at). The authors also report that the effect was dependent on spatial frequency and relative phase.

Tanaka and Sagi (1998) also evaluated the effect of dichoptic viewing for two subjects at three SOAs (167ms, 336ms and 867ms), but did not include a simultaneous presentation. They found significant CDT facilitation under monoptic viewing at the 336 and 867ms SOAs, but did not find significant facilitation at any SOA under dichoptic viewing. Based on these results, they conclude that the masking effect is strictly monocular.

Huang *et al*. (2006) used a 2-AFC paradigm to examine the effect of flank presentation on target CDTs. Their stimuli (flanks and targets) were 0.75 cycle/deg vertically oriented, collinear Gabor patches. High contrast (40%) flanks were used throughout and the center-flank to center-target separation was always three λ. Both presentations (flanks alone and target with simultaneous flanks) had 1000ms durations with a 1000ms inter-stimulus interval (ISI) between the presentations. They found significant CDT facilitation under monoptic and binocular flank conditions for all three subjects. For dichoptic viewing, the outcome was mixed. Two subjects exhibited CDT suppression and one subject showed CDT facilitation. The mean effect for the dichoptic condition was not statistically significant. Based on this somewhat limited data set, the authors conclude that flank-facilitated detection is a purely monocular phenomenon.

Using annular surrounds, Meese and Hess (2004) evaluated the effect of spatial scale, orientation, field position and eye of origin on both contrast detection and contrast matching. They used monoptic and dichoptic presentations. In the contrast detection experiment, a temporal 2-AFC paradigm was used to estimate thresholds. Both stimulus presentations (annular surround alone and annulus+target) had 200ms durations and were separated by a 500ms interval. In the contrast matching experiment, the contrast of the test stimulus was adjusted in a staircase procedure to match the perceived contrast of a reference stimulus over a range of reference contrasts. Stimulus duration was 200ms and the interval between stimuli was 500ms.

Meese and Hess (2004) found the greatest degree of suppression when the spatial frequency, stimulus orientation and field position were different for mask and target stimuli. In their contrast detection experiment, both subjects showed suppression in the monoptic and dichoptic presentations. One subject showed greater suppression in dichoptic than monoptic presentation. The authors note that the finding of dichoptic (inter-eye) suppression contradicts prior work that concluded that surround suppression was strictly monocular (Chubb *et al.*, 1989).

As mentioned above, evidence has been reported that both contradicts (Tanaka and Sagi, 1998; Huang *et al.*, 2006) and supports (Meese and Hess, 2004) inter-ocular (dichoptic) contrast integration across space. However, in the present study the simultaneous presentation of dichoptic flanks was expected to facilitate the detection of a foveal target. This expectation was based on several sources including annular surround studies that reported inter-ocular contrast integration (Yu et al., 2003; Meese and Hess, 2004), a neuro-physiology study that demonstrated inter-ocular contrast integration (DeAngelis *et al.* (1994) and prior experiments in our lab that used a collinear flanking paradigm and produced CDT facilitation (unpublished data). The long-range lateral connections known to provide excitatory input between V1 neurons (Gilbert and Wiesel, 1979, 1989) also provide an anatomic basis for the expectation of inter-ocular contrast integration.

2.5 Phase effects in psychophysical studies of contrast integration across space from collinear flanks

The effect of phase differences between targets and non-overlapping masks is another parameter that has been investigated in prior studies. The experimental results are mixed. Zenger and Sagi (1996) reported that flanking Gabors of opposite phase facilitated target detection. However, facilitation only occurred at relatively large differences in target/flank orientation and spatial location. At smaller orientation and spatial location differences target thresholds were suppressed. Yu and Levi (1997) found facilitation using inducers of opposite polarity that flanked a line target. As mentioned above, Tanaka and Sagi (1998) also reported that opposite phase flanks facilitated target detection when presented simultaneously. At SOAs greater than 144ms up to and including 1800ms (the maximum SOA evaluated) Tanaka and Sagi observed suppression.

Solomon *et al*. (1999) examined the effect of phase using a paradigm of horizontal, flanking Gabors. They reported that opposite sign flanks resulted in target detection facilitation, but the degree of facilitation was reduced compared with the effect of same-sign flanks. They used their results to argue that the transducer model can explain facilitation from non-overlapping stimuli. In the transducer model, CDT suppression and facilitation are thought to be the product of a nonlinear response of neurons sensitive to local (similar visual space) contrast. Subjects detect a target when its presence causes a criterion change in neuronal response. At low contrasts, the response is accelerating and at high contrasts it is decelerating. Hence, near detection threshold, adding small amounts of contrast facilitates target detection. Williams and Hess (1998) also reported that facilitation by flanking patterns was phase dependent.

The effect of phase difference on perceived contrast has also been evaluated. Huang *et al.* (2010) conducted a binocular contrast matching experiment that varied inter-ocular phase differences. Using relatively high contrast (16%, 32%, and 64%) sinusoid stimuli, they found that binocular perceived contrast was independent of the relative phase in the respective eyes. However, the perceived phase of the binocular image did depend on the relative phase and contrast ratio of the monocular images. In a recent study, Baker *et al.* (2012) utilized lower contrast sinusoid stimuli (2-32%) and report a more complex interaction than Huang *et al.* (2010). Baker *et al.* (2012) found that, at low contrast levels, perceived contrast reduced monotonically as the inter-ocular phase difference increased. At higher contrast levels, perceived contrast was unaffected by the inter-ocular phase difference for in-phase and antiphase conditions, but increased slightly at intermediate phases. In the present study, unintended phase dependent effects were avoided by presenting all targets and flanks in phase.

2.6 Linking hypotheses: psychophysics with neuro-physiology

Psychophysical contrast integration experiments have the potential to reveal many underlying visual neural mechanisms. Several models have been put forward in an attempt to link neuro-physiology with these psychophysical findings. These models are generally based on a few underlying assumptions. These assumptions generally include the following. 1) The average (mean) firing rate of V1 neurons is somehow correlated with a subject's ability to detect or discriminate between stimuli (Li, 2002; Adini *et al.*, 1997). 2) A change in the perception of an original stimulus caused by the presentation of another stimulus or set of stimuli is due to the modulation of the firing rate of neurons sensitive to the original stimulus. In their review of V1 receptive field surrounds, Series *et al.* (2003) pose two questions related to these assumptions. First, when V1 neuron responses increase or decrease due to surround influences, which aspect of visual representation is modulated? Second, what is the implication of V1 neuron activity in perceptual judgment?

Presently, there are two main mechanisms used to explain collinear facilitation. In the first, facilitation is caused by interactions within a single neuron or localized group of neurons (Georgeson and Georgeson, 1987). This effect is believed to arise from the non-linear response of neurons tuned to local contrast. In these transducer type models, the detection threshold of a target is adjusted by a criterion change in neuronal response. At low contrast, the response is accelerating and detection thresholds are lowered. At high contrast, the response is decelerating and detection thresholds are elevated (Solomon *et al.*, 1999). While the transducer model was originally applied to masks and targets presented in the same spatial location (Legge and Foley, 1980), it has also been adapted in an attempt to explain detection facilitation when the mask (flanks) are spatially separated from the target (Solomon *et al.*, 1999).

In the transducer model, flank interactions are expected to be rapid and have maximal effect within close temporal proximity to the target (Huang and Hess, 2008). Estimates of the integration time of target response have been obtained from physiological experiments (Mizobe *et al.*, 2001; Polat *et al.*, 1998) and psychophysical experiments (Watson *et al.*, 1983). These studies suggest an upper limit of 200ms for contrast detection at threshold. This implies that under the transducer model, temporal separations greater 200ms contrast would have no effect. Given the rapid speed of intra-neuron communication, spatial separation between the target and flanks should have very little effect on this integration time. In our experimental paradigm, the transducer model predicts that inter-stimulus intervals (ISI) greater than 200ms (250ms and 500ms ISIs) should have little or no effect on target detection threshold.

The second mechanism that is frequently cited to explain collinear facilitation is the interaction of two or more neuron groups acting via long-range, lateral connections in V1 (Polat and Sagi, 1993; Cass and Spehar, 2005; Polat and Sagi, 2006). In this mechanism, one of the neuron populations is responding to the target and the others are responding to flank contrast. The long-range, lateral connections are understood to have relatively slow propagation speeds. Hence, the effect should be delayed in a manner that co-varies with spatial separation between target and flanks. As separation between target and flank increases, the integration time required to reach maximal facilitation should also increase.

Several experiments have obtained cortical propagation speed estimates in this manner. These estimates vary by cortical location and spatial frequency, but range from approximately 0.10m/s to 0.23m/s (Davey *et al.*, 1998; Cass and Spehar, 2005). Using the slower of these estimates (0.10m/s) and the human cortical magnification factor reported by Horton and Hoyt (1991), only the shortest of the stimulus onset asynchronies (SOA) used in our experiment (67ms flank time+67ms ISI=134ms) should not allow full contrast integration.

Referring back to the transducer model, it has been suggested that the expansion of cell receptive fields in the presence of low contrast stimuli is the underlying cause of effects attributed to modulation by flankers. In cat striate cortex, Kasamatsu *et al.* (2010) directly compared receptive field size changes when stimulus contrast decreased with receptive field changes associated with changing target to collinear, flanker separation. They found receptive field expansion at low contrast in some, but not all of the cells they measured. Importantly, when receptive field expansion was recorded, it was smaller than the area of collinear, flanker modulation. This suggests than collinear, flanker facilitation is a separate process from receptive field expansion at low stimulus contrast.

To summarize, linking psychophysical results with neuro-physiology findings allows us explore the anatomical basis of perception. The transducer model of contrast integration was originally applied to pedestal-type, same object space experiments, but has been adapted to explain spatially separated flank effects on target visibility. It predicts rapid contrast integration driven by feedback/feed-forward connections and maximal effect in close temporal proximity to the target with little temporal dependence on spatial separation. The long-range lateral connection model predicts relatively slow contrast integration that is dependent on the spatial separation between target and flanks. Prior studies that examined the effect of spatial separation on integration time have supported the lateral connection model (Polat and Sagi, 1993; Cass and Spehar, 2005; Polat and Sagi, 2006).

2.7 Psychophysical studies of the temporal properties of contrast integration across space

Most lateral integration experiments have simultaneously presented flanks with a target. Thus, the temporal aspects of flanking contrast integration are not as well understood (Cass and Spehar, 2005; Polat and Sagi, 2006; Huang and Hess, 2008). The present study is intended to fill this gap in knowledge. A better understanding of the temporal integration of peripheral contrast will expand our current understanding of the underlying neural processes. A comparison of the monoptic and dichoptic conditions, in particular, may be beneficial because the intra-ocular and inter-ocular integration of contrast occur at different locations in the visual pathway.

The temporal aspects of masking under conditions in which the target and mask appear in the same object space (i.e. pedestal experiments) have been well studied and serve as a foundation for studying the temporal aspects of flank contrast integration. In general, when a mask is presented a short time before (forward masking) or after (backward masking) a target the visual system's ability to detect the target is reduced. The existence of backward masking can seem counterintuitive. How does a mask that is presented after a target affect the target's visibility? The answer lies in the relative contrast of the mask and target. If the mask is high contrast and the target is near threshold, the mask information is transmitted faster along the neural pathway and reaches cortex before the slower (low contrast) target information. The temporal separation between mask and target is usually limited to 100ms or less. Beyond that, the effect of the mask approaches zero. For a review see Breitmeyer (2007).

Studies that have investigated the temporal separation between flanks and target typically vary the time lag between target and flanks (ISI), but not the duration of the flanks. Huang and Hess (2008) varied the ISI between vertical, collinear flanks and target of multiple spatial separations (three λ, 4.5λ, and six λ). The flanks and target each had brief (50ms) presentation times. Flank contrast was set at 50%. Using a binocular presentation and temporal 2-AFC paradigm, they found facilitation near the simultaneous presentation of target and flanks for all spatial separations. Facilitation was greatest for the three λ spatial separation. This facilitation peaked when the target preceded the flanks (backward masking) by 50ms. The maximum temporal separation that they examined was a 200ms SOA. At this temporal separation, the effect of the flanks approached zero for both backward and forward masking.

Using binocular presentation of a novel, rotating flank paradigm Cass and Alais (2006) also reported finding facilitation when the target onset preceded physical collinearity with the flanks (analogous to backward masking). However, they found that peak facilitation occurred when target onset succeeded physical collinearity (analogous to the forward masking paradigm used in this study). Flanks and target were horizontally arranged 0.67 cpd Gabors. Center-to-center separation was set at three λ, 4.5λ, and six λ. For all three subjects, the temporal separation between physical collinearity and the facilitative peak increased as the spatial separation between flanks and target increased. At the six λ separation, this facilitative peak occurred between 80ms and 140ms after collinearity and faded toward no effect as the target onset latency approached 200ms.

In summary, temporal experiments with mask and target presented in the same object space (i.e. pedestal studies) have shown that beyond approximately 100ms of SOA the effect of a collinear mask approaches zero. Relatively few temporal studies have examined the effect of collinear flanks on target detection. Of those, the findings are mixed regarding when peak facilitation occurs. However, both Cass and Alais (2006) and Huang and Hess (2008) found that with forward masking the flank effect (CDT facilitation) approached zero at an SOA of approximately 200ms. Cass and Alais (2006) found the temporal location of peak facilitation was dependant on the spatial separation between target and flanks. This finding is consistent with flank effect mediation by lateral cortical connections.

2.8 Potential effect of binocular rivalry on the temporal properties of contrast integration across space

Binocular rivalry results from the introduction of markedly dissimilar images to each eye in the same object space. In this condition, the images alternate dominance with the dominant image being consciously perceived and the non-dominant image being suppressed. The period of suppression can be affected by several factors including differences in luminance (Fox and Rasche, 1969), image contrast (Meuller and Blake, 1989), contour context (Sobel and Blake, 2002), spatial frequency (Fahle, 1982), orientation (Stuit *et al*., 2009) and color (Kovas *et al*., 1996). This is an area that has received considerable attention from researchers due to its potential contribution to identification of neural pathways and understanding visual awareness.

In one model of binocular rivalry, information from monocular stimuli travels neural pathways connecting the primary visual cortex to higher cortical areas. During rivalry, information is suppressed along the entire length of one pathway allowing the other to dominate. The depth of suppression is thought to increase as information moves from lower to higher cortex (Freeman *et al.*, 2005). Although the relatively brief presentation times of the stimuli in this experiment are not long enough in duration to be considered truly rivalrous, the concept of increased suppression depth accompanying transitions to higher cortex has potential application to the experiments in this study.

The model for increasing depth of suppression at higher cortical levels has received support from physiological findings. Leopold and Logothetis (1996) recorded from individual monkey neurons in V1, V2, and V4 while presenting a stimulus that evoked binocular rivalry. They found cells, especially in V4, that demonstrated patterns of activity correlated with the monkeys' perceptual state (dominance or suppression). In a subsequent study, Sheinberg and Logothetis (1997) found that the activity of a very large percentage of monkey neurons in inferior temporal cortex and the visual areas of the superior temporal sulcus (much further downstream than V1, V2, or V4) depended on the perceptual dominance of the stimulus. Together these findings provide evidence for the model and suggest that the depth of binocular rivalry suppression increases at higher cortical levels.

In a functional magnetic resonance imaging (fMRI) study Polonsky *et al.* (2000) reported consistent V1 response modulation during binocular rivalry. Polonsky *et al.* and another fMRI study (Lee and Blake, 2002) both reported that the response modulations in V1 were approximately one-half those evoked by physical alternations of the stimuli. Also, the relative degree of fMRI response was fairly constant across visual areas. These findings do not appear to support the model of increasing binocular rivalry depth at higher cortical levels. However, since approximately 50% of V1 neurons are driven by binocular input and Polonsky *et al*. (2000) did not isolate monocular V1 cell activity, there was not a direct assessment of whether rivalry is produced by monocular neuron competition or binocular pattern-selective neurons.

In another fMRI study, Tong and Engel (2001) used the large monocular region in V1 corresponding to the cortical representation of the physiologic blind spot to isolate monocular responses. They found that V1 blind-spot representation was highly correlated with rivalry perception in all four of their subjects. The presumably monocular blind-spot representation showed a large increase in activity following the perceptual dominance of an ipsilateral grating spanning the blind spot. Activity decreased when a stimulus presented to contralateral (competing) eye became perceptually dominant. These results support the inter-ocular competition theory which states that inter-ocular competition leads to the early selection of a single monocular stimulus for perception that is processed further by subsequent visual areas (Tong, 2005).

In the present experiment, the monoptic condition is defined by a target stimulus flanked vertically by two similar stimuli presented to the same eye. Each stimulus occupies approximately two degrees of visual space. Since the target and flanks are nearly abutting, they occupy about six degrees of vertical visual space. Thus, while target and flanks are not overlapping, they are relatively close in terms of visual space and nearly within the approximate five degree diameter of the fovea.

In the dichoptic condition, the target is presented to the dominant eye while flanks are presented to the fellow (non-dominant) eye. The final condition involves the presentation of a target to the dominant eye and flanks to both dominant and non-dominant eyes. Following the increasing suppression depth model described above, we would expect the "baseline" level of suppression to be deeper in dichoptic than monoptic conditions since dichoptic integration occurs further along the neural pathway. This could be manifest as an overall shift toward suppression (or reduced facilitation).

Determining the model's expectation for a half-binocular condition is more complicated. The most straightforward interpretation involves summation of the dominant and non-dominant eye flank effects. In this interpretation half-binocular suppression (or reduction in facilitation) should be greater than for the dichoptic condition. However, this interpretation does not include the potential for between eye flank effects. The dominant and non-dominant eye flanks occupy the same object space and may not be perceived as rivalrous stimuli. If the flanks are not rivalrous, the shift toward suppression caused by non-dominant eye flanks in the dichoptic condition will not be seen when the same flanks are presented in a half-binocular setting. In this case, expectations for the half-binocular condition may be similar to the monoptic findings.

2.9 Potential effect of flank induced illusory contours on dichoptic contrast integration across space

When two low-contrast, collinear gratings are separated by a blank gap, a fill-in effect may be perceived (Tynan and Sekuler, 1975). These illusory contours bridge the gap between the physical gratings and appear to match their pattern, motion, color and texture and can mimic the perceptual effect of physical stimuli (Meng *et al.*, 2005). Moving inducing gratings produce especially vivid illusory contours and can lead to motion aftereffects in the blank gap. This suggests that illusory contours are actively represented in visual cortex (Weisstein *et al.*, 1977).

While collinear CDT facilitation has been documented in both psychophysical (Polat and Sagi, 1993, 1994; Solomon *et al.*, 1999; Solomon and Morgan, 2000; Woods *et al.*, 2002; Huang *et al.*, 2012) and neuro-physiology (Mizobe *et al.*, 2001; Polat *et al.*, 1998; Sengpiel *et al.*, 1997; Toth *et al.*, 1996) studies, its real world visual significance is not well understood. Studies of contour integration have shown that suprathreshold stimuli aligned to form a virtual curve are perceived to stand-out against a background of a randomly oriented lines or Gabors (Field *et al*., 1993; Hess *et al*., 2001; Huang *et al*. 2006). The apparent arithmetic similarities between collinear facilitation and contour integration prompted Polat and Bonneh (2000) to suggest that the two might be regulated by the same mechanism(s). However, this link is still being debated (Hess *et al*., 1998).

Contrast adaptation to an illusory contour may have produced the CDT suppression observed in the present study at long SOAs under dichoptic and half-binocular viewing. Hence, the results of prior illusory contour experiments are explored here and related to the present study's findings in the Discussion (Chapter 6).

Site of illusory contour representation in the visual pathway

The site of illusory contour representation has been the subject of several studies. Tynan and Sekuler (1975) investigated this by arranging oppositely oriented Polaroid analyzers over an oscilloscope display to produce dichoptic, viewing conditions. In their study, vertical sinusoidal gratings were displayed on an oscilloscope. The spatial frequency of the gratings was 0.75 cycle/deg, contrast was 25%, mean luminance was 60 cd/m^2 and they drifted horizontally at one hertz. The upper inducing grating was visible only to the right eye and the lower inducing grating was only visible to the left eye. The illusory contours (referred to as "visual phantoms" in Tynan and Sekuler) observed with dichoptic viewing were of "normal vividness" compared with contours observed with binocular viewing. However, when both upper and lower inducers were viewed with the same eye (monoptic viewing), illusory contours were not seen. Meng *et al.* (2007) also reported the intact dichoptic perception of illusory contours. These findings are consistent with the site of illusory contour generation being cortical and beyond the point of binocular combination (layer three of V1 for most projections).

Meng *et al*. (2005) reported evidence that illusory contours (again referred to as "visual phantoms") lead to enhanced fMRI activity in cortical visual areas representing the blank gap region. They presented 15% contrast, 0.286 cycle/deg sinusoid gratings above and below fixation with the center of the blank gap between the inducing gratings and eight degrees to the left of fixation. Thus, they evaluated the formation of illusory contours peripheral to the macula. Their experiment assumed the perception of illusory contours whenever upper and lower inducers were both vertical (collinear). This assumption was confirmed in a separate experiment performed after the fMRI study. During that experiment, subjects performed a task that required either attention at fixation or attention at the inducing gratings. They found that significant neural filling-in effects corresponding with the blank gap region occurred in visual cortex areas V1 and V2, regardless of where the subject attended. However, the neural effect was greater when subjects attended to the physical gratings.

A second experiment in the same article (Meng *et al*., 2005) examined the neural correlates of conscious perception. Here, a binocular rivalry paradigm was utilized to create spontaneous alternations between perceptual dominance and suppression of illusory contours. With a button push, subjects indicated the perception of: 1) an illusory contour between two vertical inducing gratings, 2) no illusory contour between two horizontal gratings, or 3) mixed dominance and no illusory contour. Thus, attention was held constant (on the blank gap between gratings) and perception was allowed to fluctuate. The authors found that changes in perception of the illusory contour without changes in the physical stimuli led to neural effects similar to those seen with changes to the physical stimuli. This was interpreted as a tight coupling between neural activity in early visual cortical areas representing the gap region between inducers and alternations in conscious perception of the illusory contours.

Meng *et al*. (2007) utilized the relationship between illusory contour perception (termed "perceptual filling-in" by Meng *et al*.) and dominance state during a binocular rivalry task to examine the temporal dynamics of illusory contour perception. In experiment one, subjects viewed peripheral, dichoptic rivalry stimuli through a mirror stereoscope. Vertical, collinear sinusoid gratings (15% contrast, 0.5 cpd, 16 cd/m^2) were presented to the left eye and paired against horizontal gratings of the same contrast, spatial frequency, and luminance presented to the right eye. Both grating pairs drifted within a stationary window at a rate of 0.5 cycle/s and reversed every two seconds. Each stimulus center was six degrees to the left of fixation and 4.5 degrees above/below fixation. This resulted in a blank gap size of approximately three degrees. During the 120s viewing period, subjects reported: 1) transitions in rivalry perception via button push with the right hand and 2) illusory contour (termed "visual phantoms") perception via button push with the left hand.

They found that illusory contour perception was strongly tied to rivalry state. Immediately after the vertical gratings (left eye) became dominant, an illusory contour was perceived in greater than 80% of trials for all three observers. Conversely, after the horizontal gratings (right eye) became dominant, illusory contour perception approached (but did not reach) zero for all observers. After the high initial rate of illusory contour perception following vertical grating dominance, the perception rate decreased as time elapsed. Following a switch to horizontal grating dominance, the illusory contour perception rate increased with time. For two out of three observers, the illusory contour perception rate began to decrease beyond 400ms and converged at around 50% perception approximately 1000ms after the rivalry switch. The third observer's illusory contour perception did not converge until approximately 2500ms after the rivalry switch. These findings imply that illusory contours began to fade after about 400ms and persisted for up to 1000-2500ms. The authors suggest that these results support the hypothesis that rivalry suppression occurs prior to or at a common stage of visual processing relative to the site of illusory contour processing.

To summarize, the perception of illusory contours with dichoptic viewing of the upper and lower inducing stimuli suggests that illusory contours form beyond the point of binocular combination (Tynan and Sekuler, 1975; Meng *et al.*, 2007). Neuroimaging (fMRI) has shown activity in areas V1/V2 corresponding to the blank gap region is correlated with the presentation of inducing stimuli (Meng *et al.*, 2005). Neuroimaging has also shown that changes in illusory contour perception produced similar V1/V2 neural effects as adding a physical grating stimulus to the blank gap region (Meng *et al.*, 2005). This suggests that illusory contours could produce similar neural effects as a physical grating (e.g. contrast adaptation). It has also been demonstrated that illusory contour perception is strongly tied to the rivalry state (Meng *et al*., 2007). This suggests that illusory contour formation occurs either at a common stage as, or after binocular rivalry.

Temporal aspects of illusory contour appearance and disappearance

In other experiments, Meng *et al*. (2007) used flash suppression to characterize the temporal aspects of the effect of rivalry on illusory contour formation for both experienced and inexperienced observers. For four experienced observers, low contrast (15%), vertical, drifting sinusoid gratings (0.5 cpd, 1.71 cycle/s) were presented to the left eye for 5-6s prior to the introduction of otherwise identical high contrast (75%), horizontal gratings presented to corresponding locations in the right eye. The vertical, left eye grating presentation continued throughout the trial. The introduction of high contrast, horizontal gratings produced suppression of the illusory contour inducing, vertical grating in almost every trial for all observers. Trials in which flash suppression was not reported were discarded. The observer's task was to report when the phantom disappeared. In another condition, low contrast horizontal (non-illusory contour inducing) gratings were presented to the right eye for 5-6s and then high contrast, vertical gratings were added to the left eye. Here, the observer's task was to report when the phantom appeared. Both conditions (vertical gratings presented first and horizontal gratings presented first) were completed for two, three, four, and five degree gap sizes.

The experienced observers reported very similar intra-observer illusory contour appearance and disappearance times for the two degree gap size (approximately 0.6-1.5s range for all experienced observers). Illusory contour disappearance time stayed about the same for all observers as gap size increased. However, the time for an illusory contour to appear increased as gap size increased up to approximately 1-3s for a five degree gap.

Data for the 12 inexperienced observers were reported as means. The inexperienced paradigm was similar to the experienced observer paradigm described above with a few exceptions. The initial stimuli (subsequently flash suppressed) were only presented for 2-3s before mask onset. Vertical, illusory contour inducing gratings were presented at 8% and 16% contrast and masked 2% contrast horizontal gratings. Horizontal gratings presented at 80% contrast masked 8% and 16% vertical gratings. Also, unlike the experienced observer paradigm, eye assignment of stimulus displays was randomly assigned to each subject. Inexperienced observer results were very similar to those reported for experienced observers. For both 8% and 16% contrast vertical inducers, the time required for illusory contour formation increased as the gap size between the inducers increased. However, the time required for illusory contours to disappear after being masked by horizontal gratings did not vary as a function of gap size.

For all subjects (experienced and inexperienced combined) the average response time for illusory contour formation time ranged from 1163ms for a two degree gap to 1612ms for a five degree gap. Of course, the response time includes not only the time required for illusory contour formation, but also the time required for a button push after the contour forms. If button push response time is subtracted from the total response time, the time required for formation of illusory contours would be significantly less than the total response times (1163-1612ms). The authors interpreted the dependence of time required for the formation of illusory contours on gap size as suggestive that illusory contours require more time to propagate across larger gaps. This is consistent with theories of active filling-in in which signals are propagated by horizontal connections in early visual cortex. A specific prediction of active filling-in theories is that because of the relatively slow transmission speed of horizontal connections, larger blank gaps will result in delayed illusory contour perception.

Using the same flash suppression paradigm described above, Meng *et al.* (2007) also evaluated the time required for an illusory contour to disappear after initial formation. For the 12 inexperienced subjects, mean disappearance times fell into the 800-900ms range for all four of the evaluated gap sizes (two, three, four, and five degrees of separation) with both 8% and 16% contrast inducing stimuli. This strongly suggests that illusory contour disappearance time is independent of gap size for this paradigm.

Ringach and Shapley (1996) investigated the temporal properties of illusory contours and amodal completion using a shape discrimination task. They used Kanizsa-like squares and squares with small deformations that produced the perception of illusory contours and found that shape discrimination performance depended on boundary completion. Based on this finding, they investigated the relationship between illusory contour completion and spatial scale of the figures. The relationship was reported as approximately scale-invariant (the relative separation between inducing stimuli was more important than the absolute separation) and subjects were able to integrate information from inducing stimuli separated by gaps as large as 13 degrees. This finding is reminiscent of the scale invariance previously described in collinear, facilitation experiments (Polat and Sagi, 1993; Polat and Sagi, 1994). Ringach and Shapely (1996) also performed an experiment that compared shape recognition for illusory contour completion and amodally completed contours. They reported similar accuracy for both.

Ringach and Shapely's (1996) final experiment explored the temporal dynamics of boundary completion using a backward masking paradigm. This experiment has particular relevance to this dissertation because it specifically asked how long the process of contour formation takes to occur. Previous estimates of the time required for contour formation were inconsistent with estimates ranging from 30ms (Spillman *et al*., 1976) to approximately 1000ms (Gellatly, 1980). Two non-naive subjects (both authors) participated in Ringach and Shapely's (1996) temporal experiment. The inducing stimuli were separated by a 9.5 degree gap. Kanizsa-like square stimuli were presented for variable times, followed by a 50ms presentation of pinwheel-like masks. The relationship between detection threshold (in degrees of stimuli rotation) and presentation time of the stimuli was examined. For both subjects, detection thresholds asymptoted 100-117ms after initial stimulus presentation. This suggests that, for this paradigm, the inducing stimuli must be present for about 100-117ms to cause their maximal inducing effect.

Gold *et al*. (2000) used a Kanizsa-like square stimuli paradigm similar to Ringach and Shapely (1996), but added a response classification technique that provided pictorial representations of the stimulus parts observers used to make perceptual decisions. Where previous studies showed indirect evidence that illusory contours are used to perform perceptual tasks, response classification provided a more direct link. Two signals (either "thin" or "fat" Kanizsa-like squares in this case) are presented in luminance noise on subsequent trials. The subject's task is to determine which of the two signals is presented in a given trial. Signal contrast is adjusted across trials until the subject maintains a criterion performance level (75% correct here). A statistical test then correlates the contrast at each pixel (after the incorporation of luminance noise) with the subject's responses across all trials. A map showing the degree to which noise affects the subject's response can then be constructed. In the Gold *et al*. (2000) a gray-scale map was produced with darker areas representing a negative correlation between noise and the subject's response. Lighter areas represented a positive correlation between noise and the subject's response. Thus, if the classification map showed that subject responses were affected by noise in locations where illusory contours were perceived it could be interpreted as direct evidence that subjects were basing their decisions on a perceptually completed representation of the stimulus. The location of the illusory contours should be specified on the classification map as dark (negative correlation) areas.

Gold *et al*. (2000) found nearly identical classification images for the Real condition in which thin parabolic contours physically connected the inducing stimuli and the Virtual condition where only the inducers were present. This provides strong evidence that subjects used illusory contours in the Illusory condition to perform a discrimination task ("fat" vs. "thin" squares in this case) in the same way they used physical contours present in the Real condition. In addition to the Real and Illusory conditions, the authors included an Occluded condition in which a thin ring surrounded the perimeter of each inducing stimuli. This created the appearance of a thin or fat square viewed through four holes in an occluding surface. As in the Illusory condition, classification response images for the Occluded condition closely resembled the Real classification response images for all subjects. Again, this provides robust evidence that for this discrimination task subjects used illusory contours in a similar manner as physical contours.

Gold and Shubel (2006) used the response classification technique to examine the spatiotemporal properties of visual completion. Three subjects (two naïve) were presented with “fat” or “thin” stimuli created by rotating the corners of Kanizsa-like squares by ± 1.75 degrees. Each stimulus occupied 0.34 degrees of visual angle and the center of each was 1.36 degrees from the center of adjacent inducers. This resulted in a support ratio (the ratio of a single inducer's diameter to the distance between the centers of adjacent inducers) of 0.25. A 1000ms fixation point was presented before each trial followed by a thin or fat Kanizsa square (2-AFC task) viewed binocularly for approximately 500ms. Luminance noise (43 frames totaling approximately 500ms) was presented at the same time as the stimuli in the same visual space. The final stimuli + noise frame was followed by a 36ms blank screen and then the subject responded as to whether the stimuli was thin or fat. A Weibull function was fit to the resulting data to estimate the stimulus contrast level that yielded 71% correct performance.

To explore the temporal properties of visual completion, Gold and Shubel (2006) then created classification movies showing the correlation between pixel contrast at each stimulus location and subject response over the course of the 43 stimulus frames. If visual completion (illusory contour formation) is temporally dependent such a movie should show the gradual formation of illusory contours between the inducing stimuli. Classification movies created using real contours (physical lines connecting the inducing stimuli) served as controls for this experiment, ensuring that changes seen in the illusory contour condition do not simply reflect the time course of normal visual information processing between the inducers. Of the three subjects, one did not show any influence of noise in the area between the inducing stimuli. The other two subjects showed a gradual increase over time in the influence of noise in the area between inducing stimuli where illusory contours are thought to form. A graphical representation of the cross-correlation between actual subject performance and the ideal observer standard over time (0-500ms) showed that the gradual increase in noise influence peaked around 130-180ms. The authors interpret this result as consistent with the idea that there is a time course to illusory contour completion on the order of approximately 175ms.

Measurements of illusory contour formation time have produced a variety of estimates ranging from 30ms (Spillman *et al.*, 1976) to 1000ms (Gellatly, 1980). More recent estimates have reported illusory contour completion times of 100-117ms (Ringach and Shapley, 1996) and 175ms (Gold and Shubel, 2006). However, the comparison of completion time estimates is complicated by differences in experimental paradigms and the inclusion of subject reaction times in some estimates. When Meng *et al*. (2007) compensated for reaction time by varying the gap size and measuring the difference in fill-in time, they found that it that took approximately 150ms for an illusory contour to complete each additional degree of gap. For the present study's two degree gap between inducing stimuli, this suggests that illusory contour completion should take approximately 300ms.

Signal Detection Theory applied to illusory contour formation

Polat and Sagi (2007) examined the relationship between subjective and objective aspects of illusory contours (termed "visual filling-in" in their study) using a 1-FC (yes/no) detection task. Utilizing a paradigm very similar to the present study's paradigm, Polat and Sagi's results show that illusory contours formed between collinear flanks and that those illusory contours affected perception of the target. They used Signal Detection Theory (Green and Swets, 1966) (SDT) to measure both the objective (d') and subjective (criterion) descriptors of SDT for a low contrast Gabor target with variable target-flanker (inducer) separation. Flanker contrast was set at 60% throughout and target-flanker separation varied from 1-15λ. Illusory contours can be thought of arising from an increase in the firing rate of neurons sensitive to the detection stimulus (vertically oriented, nine cpd Gabors in Polat and Sagi (2007)). If the visual field of the stimulated neurons falls within the visual space between the inducing flankers, such an increase in activity would be expected to produce a higher rate of false-positives (and true-positives) if the subject's absolute response criterion were not adjusted upward as well. Under most settings, subjects are able to adjust their own response criteria to minimize false alarm rates by requiring a higher neuronal activity level to produce a Yes response. However, multiple detection tasks make it more difficult to adjust the absolute response criterion for individual tasks and subjects have been shown to apply the same absolute response criterion to all tasks (Gorea and Sagi, 2000; Gorea *et al.*, 2005).

If increased neuronal activity produces illusory contours and the response criterion is not adjustable, then the expected outcome of inducing flankers is an increase in the false-positive rate. Polat and Sagi (2007) created a multiple detection task environment by interleaving multiple target-flanker separations (termed the "Mix" condition) within an experimental session. They compared the Mix condition with sessions that were blocked into a single target-flanker separation (termed the "Fix" condition). Under the Fix condition they found that subjects had a moderate criterion bias that was weakly dependent on separation. In the Mix condition, subjects showed a large increase in the false positive rate at small target/flanker separations that gradually decreased as the distance between target and flanker increased. At the largest separations (approximately 9-15λ) the Mix false-positive rate closely resembled the Fix false-positive rate. In other words, when subject response criterion was allowed to vary, the false-positive rate was close to constant. However, when subject response criterion was held constant, the false-positive rate was elevated at target/flank separations where flanks are know to have their greatest effect on detection thresholds. This result is consistent with the perception of illusory contours being the result of a filling-in process caused by lateral excitation.

2.10 Summary of introduction

Prior psychophysical studies have shown that the simultaneous presentation of monocular or binocular collinear flanks can facilitate the detection of a foveal target of the same spatial frequency (Polat and Sagi, 1993, 1994; Solomon *et al.*, 1999; Solomon and Morgan, 2000; Woods *et al.*, 2002; Huang *et al.*, 2012). Relatively few psychophysical studies have examined the effect of dichoptic, collinear flank presentations. Tanaka and Sagi (1998) showed no mean effect with dichoptic, collinear flanks and Huang *et al.* (2006) reported mixed results (one subject showed facilitation and two showed suppression).

Studies with dichoptic presentations of collinear, annular surrounds have reported both no effect (Chubb *et al*., 1989) and inter-ocular contrast integration (Yu et al., 2003; Meese and Hess, 2004). In cat, a neuro-physiology study has also demonstrated the existence of dichoptic contrast integration (DeAngelis *et al*., 1994).

Under monocular and binocular viewing conditions several variables including flank spatial separation, temporal separation between flank and target, and spatial phase have been shown to affect the degree of collinear flank facilitation. Facilitation was maximal at approximately 3λ center-to-center flank separation (abutting the target) and decreased as spatial separation increased (Polat and Sagi, 1993; Polat and Sagi, 1994; Solomon *et al*., 1999; Cass and Spehar 2005; Polat and Sagi, 2006; Tanaka *et al*., 2007). The results of studies investigating the effect of spatial phase differences between a target and non-overlapping flanks are mixed. In some studies, phase differences did modulate the flank effect (Solomon *et al*., 1999; Williams and Hess, 1998). In other studies, phase differences did not modulate the flank effect (Zender and Sagi, 1996; Yu and Levi, 1997; Tanaka and Sagi, 1998).

Relatively few studies have examined the effect of temporal separation between collinear flanks and target. Under binocular viewing, peak contrast detection facilitation has been reported for both backward (Huang and Hess,

2008) and forward (Cass and Alais, 2006) masking. However, both of these studies returned facilitation for both forward and backward masking that approached zero at a 200ms SOA.

When two low-contrast collinear gratings are separated by a blank gap (as in the present study), a fill-in perception in which the gratings appear to continue across the gap may be perceived (Tynan and Sekuler, 1975). This perception is frequently referred to as an illusory contour. The intact perception of illusory contour formation under dichoptic viewing suggests that illusory contour perception is cortical and occurs beyond the point of binocular combination (Tynan and Sekuler, 1975; Meng *et al.*, 2005). Neuroimaging studies have shown that illusory contour perception produces similar V1/V2 neural effects as a physical grating presented to the blank gap region (Meng *et al.*, 2005).

Relatively few studies have examined the temporal aspects of illusory contour formation and disappearance. Estimates of the time between inducing flank presentation and the perception of an illusory contour vary widely ranging from 30ms (Spillman *et al.*, 1976) to 1000ms (Gellatly, 1980). However, a more recent experiment that compensated for subject reaction time (Meng *et al.*, 2007) reported that each degree of blank gap took approximately 150ms for illusory contour completion. Hence, the two degree gap in the present study should require approximately 300ms for illusory contour perception. In the same study, Meng *et al*. (2007) found that the time required for an illusory contour to disappear was not dependant on the blank gap size and occurred approximately 800-900ms after initial illusory contour formation.

Both Meng *et al*.'s estimate of illusory contour formation time and the estimate of time to disappearance compare favorably with the temporal aspects of the longer SOA threshold suppression produced by inter-ocular flanks in the present study (see section 6.4 for a more detailed explanation). This supports the hypothesis that a potential mechanism behind the unexpected suppression produced by inter-ocular flanks at longer SOAs is contrast adaptation to an inter-ocular illusory contour. More direct support for this hypothesis is provided by a supplemental, orthogonal flank experiment (see section 5.7) which demonstrates that flank/target collinearity is necessary for the suppression to occur.

Chapter 3

Methods

3.1 Subjects

A total of 11 subjects participated in the study. Of these, nine were naïve to the purpose of the experiments and the other two knew about the purpose (primary investigator WK and UMSL College of Optometry summer 2011 research fellow MM). They ranged from 20 to 36 years of age. Six were male and five were female. Eight subjects were right eye dominant (AW, CL, WK, MBM, JS, TP, ND, and MM) and three were left eye dominant (AM, CP, and TH). One subject was left hand dominant (WK) and 10 were right hand dominant.

All subjects were examined by a licensed optometrist and shown to have normal or corrected to normal visual acuity in both eyes, normal binocular vision (including local and global stereopsis), and were free from active ocular disease. Subjects requiring visual correction wore the same spectacle prescription throughout the experiment. Contact lenses were not worn during experimental sessions due to the increased variability in vision associated with their wear, especially at low contrast levels (Timberlake *et al.*, 1992).

One subject (WK) completed all the experiments in the study. Due to the time intensive nature of the experiments (see below), the other 10 subjects participated in portions of study and their data was combined to form complete data sets. Within the main experiment, sessions were blocked by ISI with each ISI set containing four flank durations. All subjects completed a minimum of one ISI set. Prior to participating in the study, informed consent was obtained and subjects were given a copy of the informed consent form. Subjects were compensated for their participation at a rate of 12 dollars per hour. All procedures were conducted in accordance with the guidelines of the University of Missouri-St. Louis Human Subjects Committee (protocol number 100506K).

3.2 Time requirements

Subject WK took approximately 240 observation hours to complete all the experimental conditions in the study. The other investigator (MM) participated for approximately 100 hours. The nine naïve subjects participated for an average of approximately 25 hours with a minimum of eight hours (subject CP). These hours were split into sessions lasting an average of 1.5 hours. Each session included multiple subject initiated breaks. Since most subjects attended 2-3 sessions per week it took approximately 5-8 weeks for them to complete their portion of the study.

3.3 Apparatus

Two nearly identical experimental apparatus were used. Stimuli were displayed on 19” CRT monitors (NEC model FE992 and Viewsonic G90fB). Screen resolution was set at 1280x1024 pixels with a 75Hz refresh rate throughout the experiment. This resulted in an approximate pixel diameter of 0.25mm or 0.91 seconds of arc. Subjects observed the monitor at a 95cm viewing distance resulting in a 19.12x15.35 degree field of view. The mean luminance of the monitors was 73.2 cd/m^2. A PR-650 SpectraScan Spectra Colorimeter (Photo Research, Inc.) was used to linearize gamma output from the individual guns and their combined output.

A fixed chin and headrest were used to control the viewing distance and keep the subject’s head stable. A full-length, black, foam-board septum running from the screen to the chin rest assured independent visual input to each eye, and a two mirror haploscope system allowed comfortable fusion of the images (Figure 1). The septum created a corridor-like visual effect when properly fused and served as a suppression check prior to and during sessions. The right side of the corridor was formed by the image of the septum on the left eye’s temporal retina and vice versa. Hence, if one side of the corridor was not perceived it was possible to ascertain which eye was suppressed.

Before each session, subjects made vertical and horizontal adjustments to the haploscope mirrors while viewing fixation stimuli. These adjustments allowed comfortable, fused vision. Subjects also had the opportunity to adjust the mirrors between trials if they experienced eyestrain or diplopia. Maintaining fused vision was essential during dichoptic and half-binocular presentations because it ensured that the stimuli were presented in corresponding visual space. All experimental runs were conducted in a consistent, dimly lit room with a luminance of approximately 28 cd/m^2. A hood attached to the monitor and blinders affixed to the chin rest apparatus minimized outside sources of light. The blinders also ensured that extraneous images from the room were not imaged onto the peripheral retina. Peripheral images would have added noise to the system and made the contrast detection task more difficult.

Stimuli were created with Psykinematix (version 1.2.3). Two 13.3" MacBook Pro computers (one for each experimental apparatus) were used to generate the stimuli. Both ran Macintosh OS X. The MacBook Pro 7,1 had a 2.4 GHz Intel Core 2 Duo processor and a NVIDIA GeForce 320M video card. The MacBook Pro 8,1 had a 2.3 GHz Intel Core i5 processor and an integrated Intel HD Graphics 3000 video card. Output from each graphics card was increased to 1,786 gray levels using a 10.8 bit-stealing algorithm (Tyler, 1997) integrated into Psykinematix.

Figure 1. Experimental apparatus. A second, very similar apparatus differed in the brand of the monitor and the video card.

3.4 Viewing conditions

Thresholds were obtained under monoptic, dichoptic, and half-binocular viewing conditions. In the monoptic condition, the dominant eye viewed both the target and flanks. Under dichoptic conditions, a target was shown to the dominant eye and flanks were presented to the non-dominant eye. The half-binocular condition was essentially a combination of monoptic and dichoptic conditions. A target was presented to the dominant eye and flanks were presented to both dominant and non-dominant eyes. Eye dominance was established during an initial patient history and confirmed using a variant of the Miles test (fixating a distance target through a hole formed between the hands).

3.5 Stimuli

All stimuli (targets and flanks) were sine wave gratings with a spatial frequency of three cycles per degree (cpd). This spatial frequency was chosen for two reasons. First, it is near the peak of the human contrast sensitivity function (Regan, 2000). Second, it matches the stimuli used in previous lateral integration experiments performed in our lab and makes direct comparison with those studies possible. An approximate pixel diameter of 0.25mm (see section 3.3) and spatial frequency of three cpd resulted in about 100 pixels per cycle (or 50 pixels per bar). A Gaussian window was applied and the standard deviation of

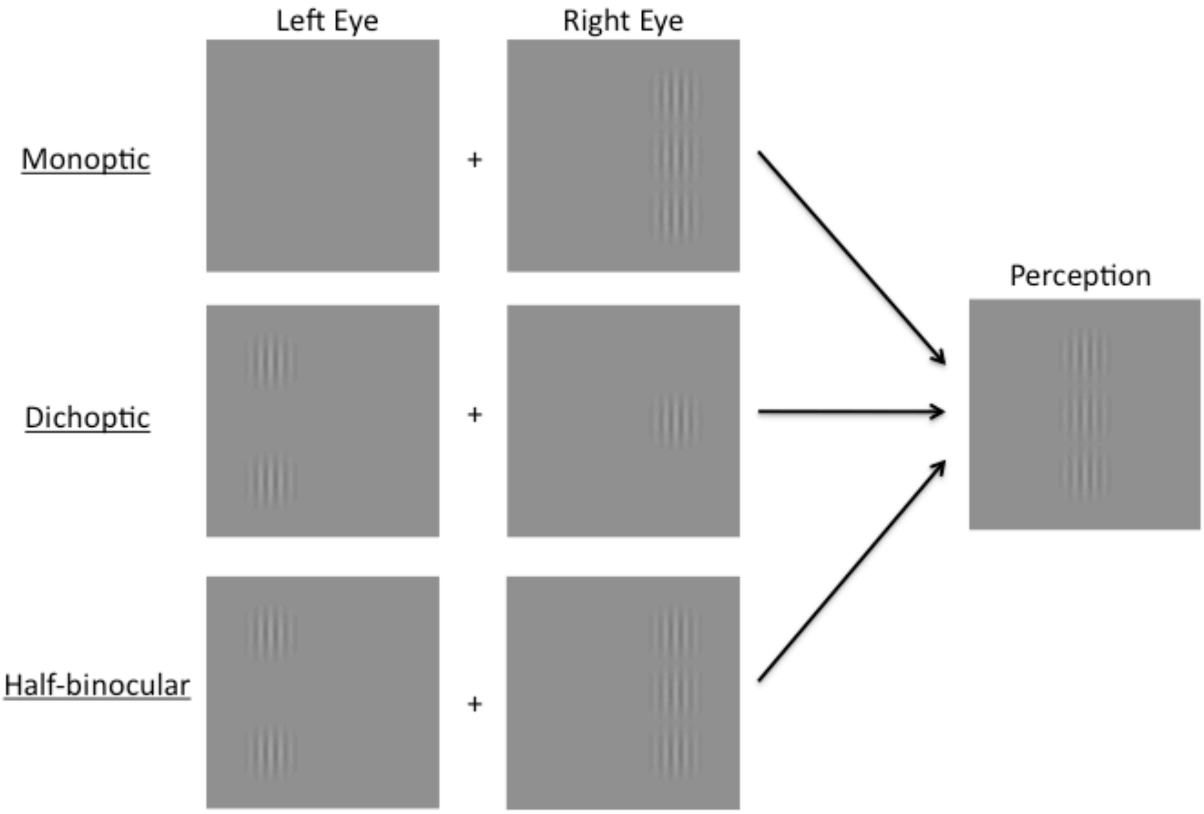


Figure 2. Summary of viewing conditions. In the monoptic viewing condition, all stimuli (target and flanks) were presented to the dominant eye (right eye in this example). Under dichoptic viewing, the target was presented to the dominant eye and flanks were presented to the non-dominant eye. With half-binocular viewing, the target was again presented to the dominant eye and flank sets were presented to both dominant and non-dominant eyes. The stimulus eye of origin was lost in the final perception (i.e. perception did not vary with the viewing condition).

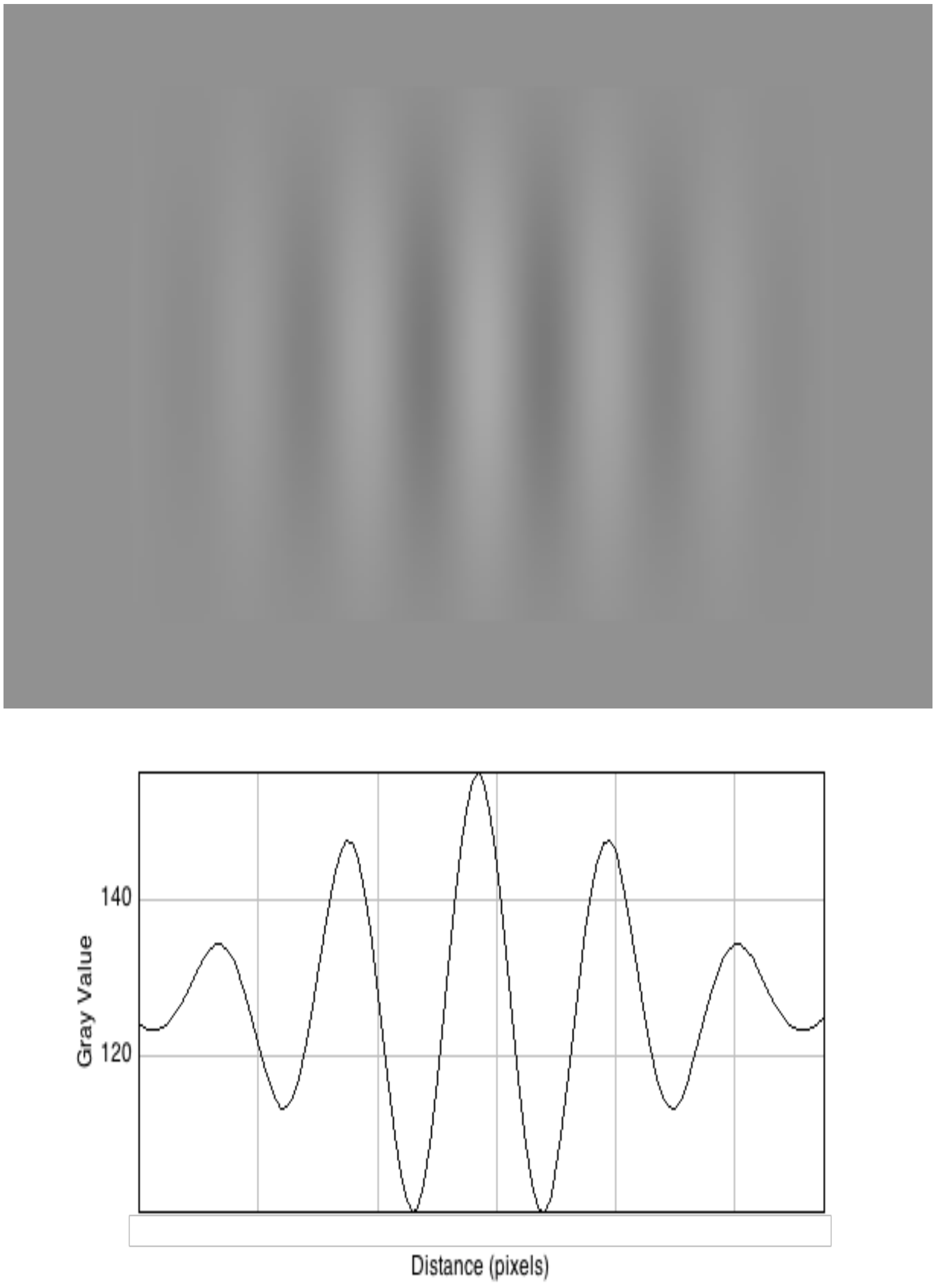


Figure 3. Windowed sinusoid stimuli (top) and luminance profile (bottom). Stimuli had approximately five visible cycles in all experiments.

the window (sigma) was set at 0.5 degrees. Using a Gaussian window eliminates the sharp cutoff seen at the edge of non-windowed stimuli, and helped to ensure that only the targeted cortical neurons were stimulated. Stimuli were defined by the following sinusoid equation:

$$L(x,y) = L_{mean}\,[1 + C\sin(2\pi Fx + \Phi)^{*}\ \exp(-(x^2+y^2)/2\sigma^2)]$$

where L_{mean} is mean luminance of the background, C is contrast, F is spatial frequency, Φ is spatial phase, x and y are horizontal and vertical distances from the peak of the contrast envelope, and σ is the standard deviation of the windowed envelope.

All stimuli (target and flanks) in the main experiment were vertically oriented and collinear. Previous studies have shown that flank separations from 3-10 lambda demonstrate facilitation with a collinear orientation (Polat and Sagi, 1993; Solomon *et al.*, 1999; Cass and Spehar, 2005; Shani and Sagi, 2006). Facilitation peaked around three lambda, and tended to cause suppression of the target contrast detection threshold (CDT) at separations less than three lambda. Since the goal of this project was to examine the temporal effect of ISI and flank durations, we choose a separation designed to promote maximal facilitation.

In most collinear flanking experiments the stimuli have been Gabors (Graham, 1989) with approximately 2.5 visible cycles. In these experiments, a three lambda separation between target and flanks results in stimulus edges that are approximately abutting. We chose to use a windowed sinusoid that produced about five visible cycles (the exact number of visible cycles being dependant on the stimulus contrast) to promote spatial interactions. As a result, we used a six lambda target/flank separation in this pilot project to make it comparable to a three lambda separation using Gabor stimuli.

3.6 Flank contrast

Flank contrast detection thresholds were obtained by presenting near threshold flank stimuli two degrees above and below fixation while the subject maintained central fixation. Using a yes/no, seven-level MOCS paradigm described below, the subject reported when the flanks were or were not visible. The results of the flanks alone contrast detection thresholds were used to scale each individual subject's flank contrast level for all subsequent experiments. The flank contrasts were set at 3X the flank detection threshold for all subjects and conditions except for subject AW who completed the monoptic condition at 4.5X his flank detection threshold during a pilot experiment. The use of 3X threshold flanks resulted in a dominant eye flank contrast range of 4.2% to 5.94% and a non-dominant eye flank contrast range of 4.98% to 6.93% (Figure 6).

3.7 Paradigm

A single alternative (yes/no), forced choice contrast detection paradigm was used throughout the study. All programs were based on native Psykinematix programs. Fixation circles (0.04 deg radius, 43% contrast) were presented to each eye for 500ms prior to the presentation of the flank stimuli. Subjects were instructed to maintain fixation and avoid eye movements within each trial. Two flanks were presented above and below fixation with two degrees of center-to-center separation between each flank and fixation. At a spatial frequency of three cpd, two degrees of separation created six wavelength (λ) spacing between the stimuli.

3.8 Collinear flanking experiment

Ten subjects participated in the main, collinear flank experiment. The flanks were presented at four durations (67ms, 117ms, 250ms, and 500ms) and were followed by an inter-stimulus interval (ISI) presented at seven durations (67ms, 117ms, 250ms, 500ms, 1000ms, 1500ms, and 2500ms). A simultaneous presentation with flanks and target in the same visual space for 250ms was also included. This created total stimulus onset asynchronies (SOA = flank duration + ISI) ranging from zero to 3000ms. A central target stimulus followed the ISI and was presented for the same duration (250ms) in every condition.

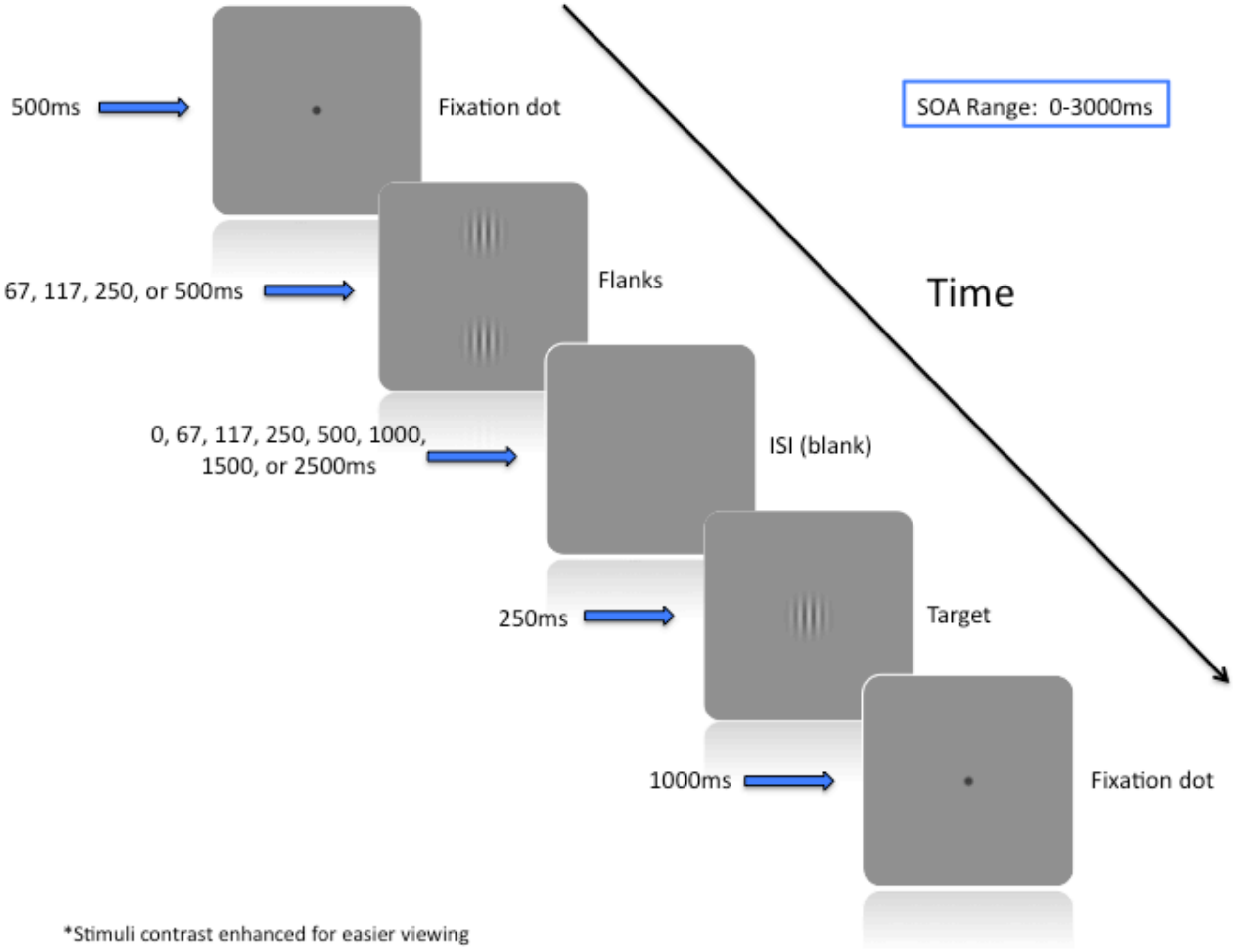


Figure 4. Timing diagram for the main (collinear flank) experiment. Slides represent subject perception for all viewing conditions. The 14 SOAs ranged from 0-3000ms.

A 250ms target presentation was chosen because it exceeds prior psychophysical study integration time estimates of 160-200ms (Watson *et al.*, 1983) and 120ms (Polat *et al.*, 2007). A relatively longer duration target presentation was also chosen in anticipation of including people with amblyopia in future variations of this experimental setup. Since people with amblyopia are known to have longer integration times (Levi and Harwerth, 1980), 250ms would allow sufficient time for people with mild to moderate amblyopia to process the target and allow direct comparison to the present study. A second set of fixation circles identical to the first followed the target and remained on screen until the subject responded. The subject's task was to indicate whether or not the target was visible by pressing one of two buttons on a keyboard. No feedback was given within runs. Subjects were unable to respond until 1000ms after the second set of fixation circles appeared. Responses entered prior to this, were not recorded and the next trial was not triggered. This ensured that the aftereffects of one trial did not carry over into the next. A final condition consisted of simultaneous presentation of the flanks with the target (test) stimulus.

A 1-FC detection design was chosen over a two alternative, forced choice (2-AFC) design because of the importance of the temporal aspect to our hypothesis. A 2-AFC design would have resulted in very long trials within which order effects would have been difficult to account for and confounded our ability to extract useful information about how varying the ISI and flank presentation time affected thresholds.

For SOAs up to 1000ms, subjects completed all four flank durations within a single ISI. Runs were counterbalanced within each ISI. Each subject did 2-3 runs per flank duration before moving on to another flank duration. This allowed flank durations to be completed in a parallel manner that minimized the influence of learning effects. Dominant eye, target alone runs were also conducted at the beginning or end (alternating) of each session. This allowed us to monitor subjects for threshold changes over time.

To allow for easy comparison between subjects, thresholds were adjusted for each condition by dividing the threshold of the target with flanks by the subject's target alone threshold. This ratio was then subtracted from one. In the resultant quantity, positive values indicate facilitation of detection and negative values indicate suppression.

3.9 Orthogonal flanking experiment

A supplemental experiment designed to investigate the unexpected CDT suppression seen with dichoptic and half-binocular flanks utilized orthogonal flanks in a paradigm that was otherwise very similar to main (collinear) experiment. The orthogonal flanks were identical to the previously described collinear flanks except their orientation was rotated 90 degrees relative to the vertical target. The same forward masking, 1-FC detection paradigm, and 7-level MOCS used in the main experiment were utilized for the supplemental experiment. Five subjects participated in the orthogonal flanking experiment.

The temporal aspects of flank presentation did differ slightly from the main experiment. As in the main experiment, fixation circles (0.04 deg radius, 43% contrast) were presented to each eye for 500ms prior to each trial. However, since understanding the relative contributions of flank duration and ISI to the overall effect was not experiment's intent, the number of SOAs was limited to six. These SOAs were created by pairing 67ms flank duration with 67ms ISI, 117ms flank duration with 117ms ISI, 250ms flank duration with 250ms ISI, 500ms flank duration with 250ms ISI, and 500ms flank duration with 500ms ISI. As a result of these pairings, the SOAs ranged from zero to 1000ms.

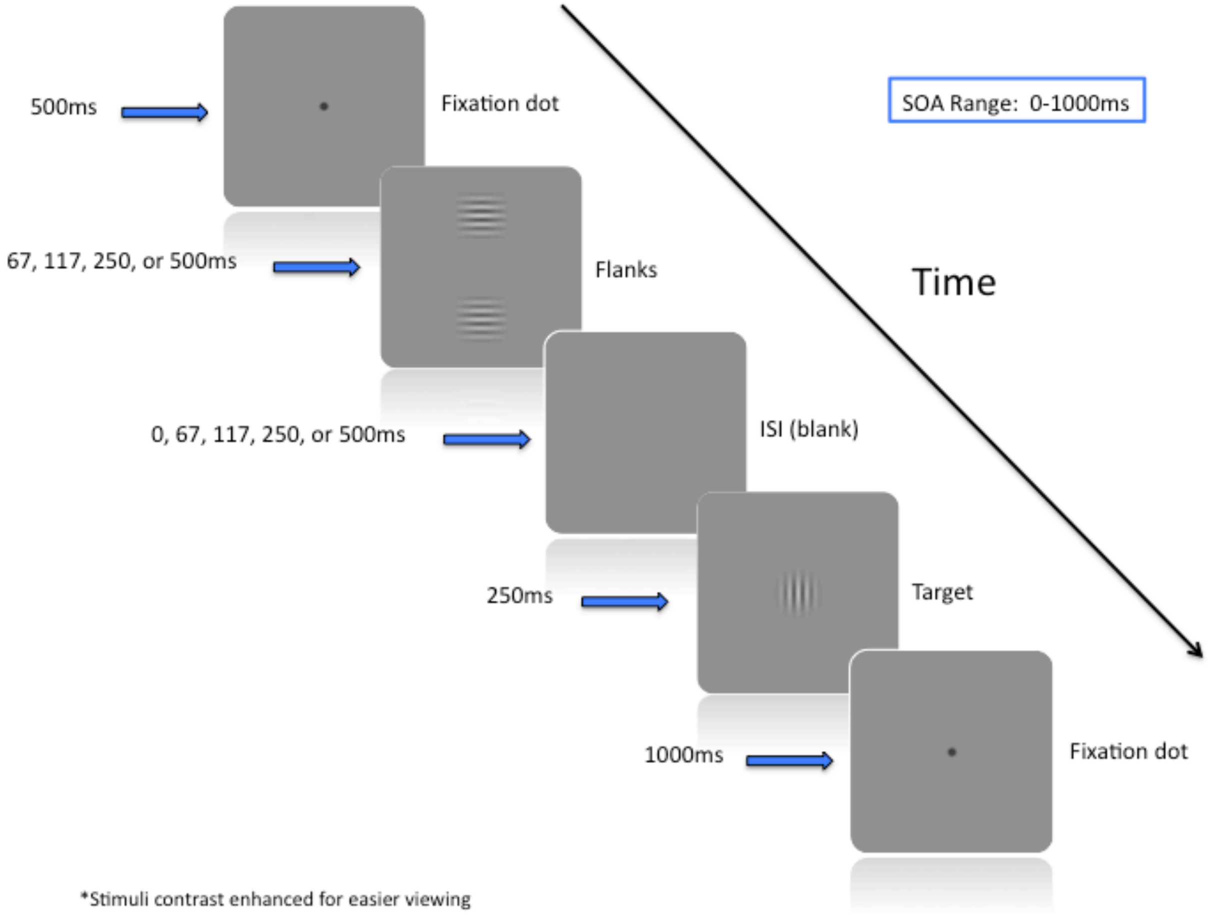


Figure 5. Timing diagram for the supplemental, orthogonal flank experiment. Slides represent subject perception for all viewing conditions. The six SOAs ranged from 0-1000ms.

3.10 Analysis

A seven level method of constant stimuli (MOCS) with 10 trials per level was used to obtain psychometric functions with a Weibull fit. The threshold criterion was set at 50%. The contrast difference between MOCS levels was created using 0.05 log steps. Contrast levels were established by dividing the maximum and each subsequent value by 1.122 (the antilog of 0.05). This normalized contrast levels despite differences in individual sensitivity and increased the validity of intra-subject comparisons. Maximum contrast levels were carefully chosen so that the range of contrasts presented to a subject included a maximum value that approached 100% visibility and a minimum value that approached 0% visibility (i.e. values that spanned the psychometric function). Since a 1-FC procedure was used, contrast levels one and seven provided an effect similar to catch trials. For most subjects, several runs were needed to establish the optimal maximum contrast level and this process had to be repeated for each condition. This process was time consuming but necessary due to the importance of selecting the appropriate maximum contrast levels.

The Psykinematix “Plotter” module allowed for easy evaluation of each individual run’s psychometric function both within and between sessions (Figure 6). This instant feedback assisted in the selection of optimal contrast levels and allowed subjects to maintain a more consistent decision criterion. Each threshold was estimated 10-12 times over 2-3 sessions and pooled to obtain the final threshold values. Since each experimental run consisted of 70 trials (7 MOCS levels shown 10 times each), the final threshold for each condition was the product of approximately 700-840 trials.

The Weibull functions producing contrast detection thresholds, variance, and exponents (slopes) were obtained using an Apple PowerBook computer running Matlab®. The Weibull function has the general form: $F(x) = 1 - \exp^{-(x/\alpha)^{\beta}}$ where x, α, β are greater than zero. α is the scale parameter (threshold), and β is the form parameter (slope). Standards errors and 95% confidence intervals were calculated using the macro capabilities of Microsoft Excel software. Paired T-tests, regressions, and correlations were calculated using SPSS software (version 19). Figures were produced using Microsoft Excel, Microsoft PowerPoint, SPSS, and Igor Pro (version 5.03) software.

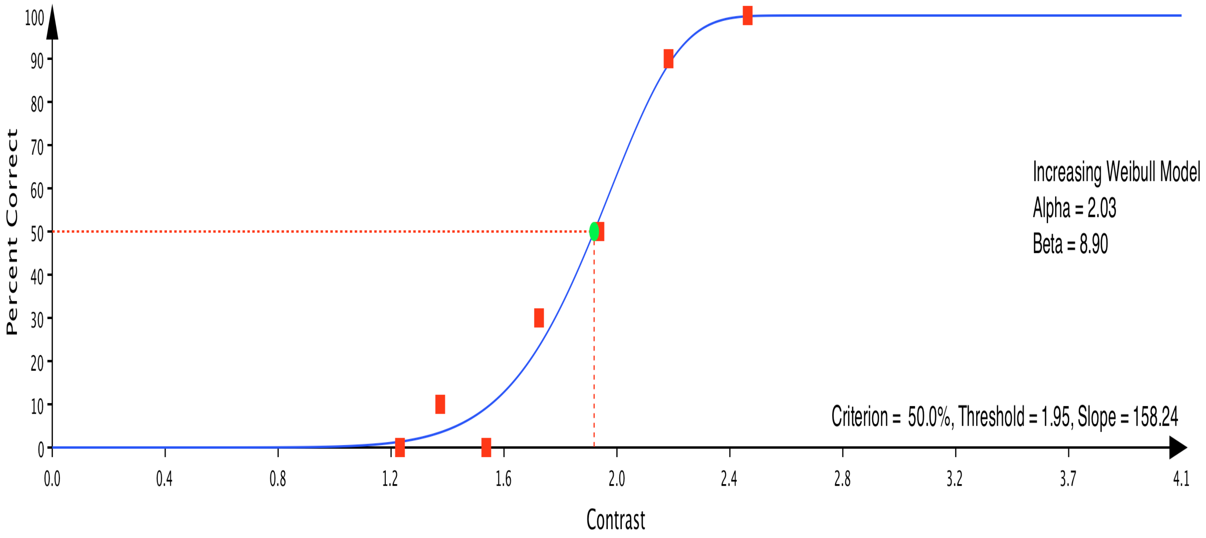


Figure 6. Cumulative Weibull distribution over a linear x-axis as displayed by the Psykinematix Plotter module. The Plotter module provided feedback within and between experimental sessions assisting in the selection of optimal contrast levels and allowing subject to maintain a more consistent decision criteria. MOCS contrast levels 1 and 7 anchor the distribution at 0% and 100% visibility, respectively and perform a function similar to catch trials.

3.11 Summary of variables

Collinear flank experiment

Viewing conditions: monoptic, dichoptic, and half-binocular

Center-to-center target/flank separation: 3λ (2 degrees)

Target and flank spatial frequency: 3cpd

Flank contrasts: 3 times individual flank detection threshold (3X)

Flank durations: 67ms, 117ms, 250ms and 500ms

Inter-stimulus intervals: 0ms, 67ms, 117ms, 250ms, 500ms, 1000ms, 1500ms, and 2500ms

Stimulus Onset Asynchronies: 14 ranging from 0-3000ms

Supplemental orthogonal flank experiment

Viewing conditions: monoptic and dichoptic

Center-to-center target/flank separation: 3λ (2 degrees)

Target and flank spatial frequency: 3cpd

Flank contrasts: 3 times individual flank detection threshold (3X)

Flank durations: 67ms, 117ms, 250ms and 500ms

Inter-stimulus intervals: 0ms, 67ms, 117ms, 250ms, and 500ms

Stimulus Onset Asynchrony: 6 ranging from 0-1000ms

Chapter 4

Hypotheses

In general, collinear flanks were expected to produce facilitation at the six wavelength (λ) center-to-center separation used in this study. With collinear, vertical Gabor stimuli, Polat and Sagi (1993) found suppression of contrast detection at target/flank separations from approximately 0-2λ and a zone of contrast detection facilitation from greater than 2λ out to 10λ separation. They also found facilitation to be greatest in the 3-4λ separation zone. Another, more recent Polat and Sagi (2006) article also reported maximal facilitation for collinear flanks around 3λ separation.

While these findings were useful in shaping the expectations for this study, there are a few significant differences between those paradigms and this study. First, the flanks used by Polat and Sagi (1993) are higher contrast (40%) than the individually scaled flanks in the present study (averaging approximately 5.4% contrast). Second, the Gabor stimuli from Polat and Sagi's papers (1993, 2006) have fewer visible cycles (2-2.5) than the windowed sinusoids used in this study (approximately 5 cycles). Finally, the spatial frequency of their stimuli was nine cpd (compared to three cpd). A more direct comparison can be made to recent experiments conducted in our lab. Utilizing very similar stimuli, we found that individually scaled 3X contrast, collinear flanks produced similar amounts of facilitation at 4.5λ and 6λ separation with less inter-subject variation at 6λ (unpublished results). Hence, the 6λ separation was selected.

Given that our general expectation was for facilitation, we anticipated the independent variables (ISI and flank presentation duration) to affect the degree of facilitation, but did not expect to find suppression of the detection threshold under any of the evaluated conditions.

Because the flanks and ISI are presented in succession immediately prior to the target, the addition of these two variables yields the SOA. Given that the shortest flank duration was 67ms and the shortest ISI was 67ms, the briefest SOA (flank duration + ISI) in this study was 134ms. Assuming a cortical propagation speed in the approximate range of 0.10-0.23 m/s (Cass and Spehar, 2005) even the briefest SOA of the flanks presentation time/ISI conditions (134ms) should be sufficient to allow near complete lateral integration of three cpd stimuli at a 6λ separation.

Since CDT suppression was not expected at any SOA under any viewing condition, the long SOA suppression observed under dichoptic and half-binocular viewing was surprising. The supplemental, orthogonal flanks experiment was designed to test the hypothesis that the long SOA inter-ocular suppression produced by collinear flanks was the result of inter-ocular contrast adaptation to an illusory contour. Previous experiments have shown that inter-ocular flanks can produce illusory contours (Tynan and Sekuler, 1975; Meng *et al.*, 2007). An illusory contour formed between the upper and lower flanks presented to the non-dominant eye would be in the same visual space as a target presented to the dominant eye.

All 11 subjects in the present study described the formation of such an illusory contour during the simultaneous presentation of target and flanks. The sustained presence of same visual space contrast (in the form of an illusory contour) might produce contrast adaptation of cortical neurons with receptive fields corresponding to the physical target. Adaptation would decrease neuronal sensitivity and result in a suppression of detection threshold relative to the target alone threshold.

If inter-ocular contrast adaptation to an illusory contour were occurring, utilizing orthogonal flanks (instead of collinear flanks) should eliminate the inter-ocular, long SOA suppression. Hence, the expectation for the orthogonal flanks experiment was CDT facilitation at shorter SOAs that decreased as SOA increased and approached no effect at the longest SOA studied (1000ms). Relative to collinear flanks, orthogonal flanks were generally expected to produce less facilitation. The absence of CDT suppression under dichoptic and half-binocular viewing would indicate that the collinear orientation of flanks and target was required to produce inter-ocular CDT suppression at longer SOAs. This would support the hypothesis that contrast adaptation to an illusory contour was a primary contributor to the long SOA suppression seen under dichoptic and half-binocular viewing with collinear flanks.

Chapter 5

Results

5.1 Target alone and flanks alone CDTs

Contrast detection thresholds were obtained for a dominant eye foveal target, dominant eye flank stimuli, and non-dominant eye flank stimuli. Flank thresholds were used to scale flank contrast for monoptic, dichoptic, and half-binocular conditions and were obtained prior to beginning the main experiment. Dominant eye target CDTs were based on runs conducted throughout the course of the experiment. This allowed for monitoring of changes in decision criteria. Thresholds were based on runs completed after decision criteria stabilization. Target CDTs ranged from 1.33% to 2.07% with an arithmetic mean of 1.72% ± 0.25% (SE) (Figure 7). All 11 subject's target CDT fell within the 95% confidence interval of the mean. Six of the 11 subject's (MM, ND, MBM, CL, AW, and WK) target CDTs were tightly clustered ranging from 1.62% to 1.88% contrast (Figure 7). Dominant eye flank CDTs ranged from 1.39% (ND) to 2.06% (CP) with a arithmetic mean of 1.77% ± 0.20%. Non-dominant eye flank CDTs were slightly less sensitive on average, ranging from 1.67% (TP) to 2.31% (AW) with an arithmetic mean of 1.87% ± 0.19%.

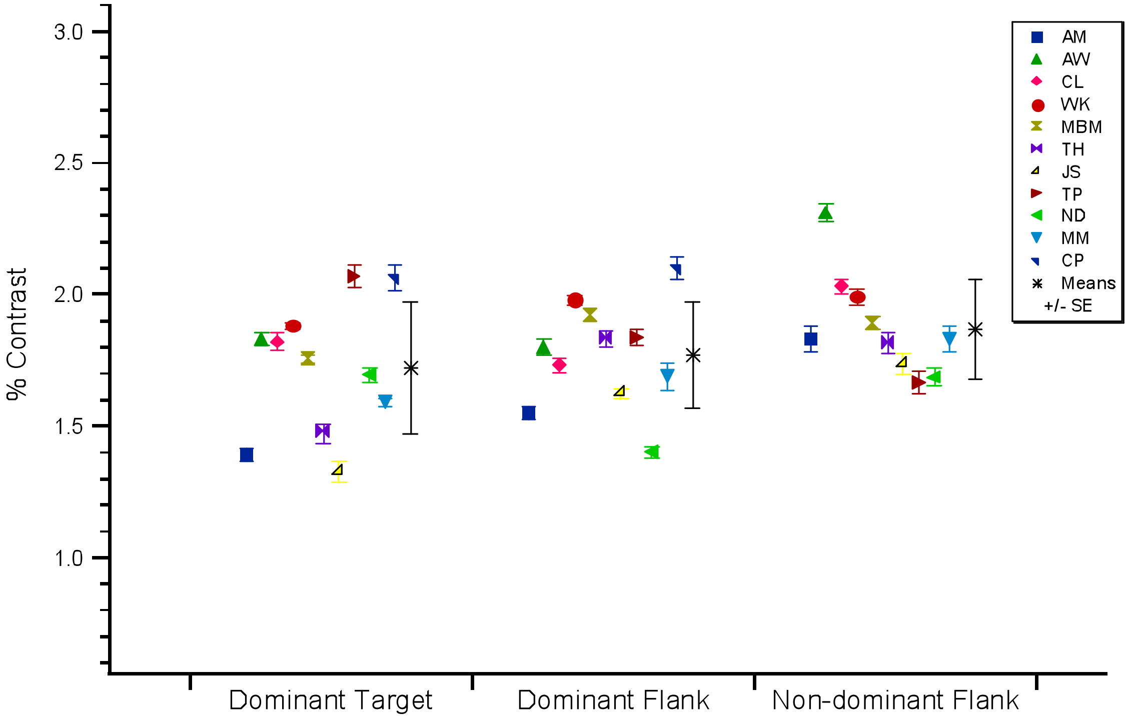


Figure 7. Individual subject contrast detection thresholds (CDT) for dominant eye target alone, dominant eye flanks alone, and non-dominant eye flanks alone. Error bars represent standard errors for individual thresholds and the standard error of the mean for mean thresholds. Individual thresholds show approximately normal distributions for all three conditions and minimal difference in mean CDT among the conditions.

5.2 Monoptic, collinear flank results

As expected, the presence of monoptic, collinear flanks generally resulted in lower CDTs than when the target was viewed alone. Facilitation was maximal for all subjects in the simultaneous presentation. Simultaneous presentation resulted in CDT facilitation ranging from 13.8-22.2% with a mean of 19% ± 3.9% (SE).

In general, as the SOA (the combination of ISI and flank duration) increased, the effect was diminished (the amount of facilitation decreased). If we consider the effect of flank duration within each ISI a slightly more complicated mechanism emerges. Because one subject (author WK) completed all conditions and each of the other four subjects completed all the flank durations within a single ISI duration, there are at least two data points available for comparison at each combination of flank duration/ISI duration. Subject WK completed all the conditions, thus it is possible to make comparisons both within and between ISIs. However, for the other subjects who only completed the flank durations within a single ISI it is impossible to compare between ISI within subjects and very difficult to interpret comparisons between ISIs completed by different subjects.

At the 67ms ISI duration, the effect generally decreased as flank duration increased. For subject WK (Figure 8), the 67ms flank was an exception, showing less facilitation than the 117ms flank, but more than the 250ms flank. It seems unlikely that the 67ms ISI/67ms flank (SOA = 134ms) was not long enough to allow complete integration of the flank contrast. Using the slower of two cortical propagation speeds calculated by Cass and Spehar (2005, 0.1m/s) as a reference, a signal should travel approximately 13.4mm in 134ms. Applying the two degree center-to-center separation to Horton and Hoyt's (1991) cortical magnification factor formula ($y = 17.3\ln(E+0.75)$) (where E = eccentricity in degrees) yields 17.5mm as the distance a signal would need to travel to link stimuli separated by two degrees.

While 17.5mm is greater than the estimated 13.4mm that a signal could travel in 134ms, it is also necessary to consider that the spatial frequency used in this experiment (3 cpd) is 0.5 to 1.5 octaves below the spatial frequencies Cass and Spehar (2005) used to calculate the 0.1m/s propagation speed (4.65 and 9.3 cpd). Using a 2.32 cpd stimulus in the same paper Cass and Spehar estimated a cortical propagation speed of 0.23m/s. At that speed, a signal

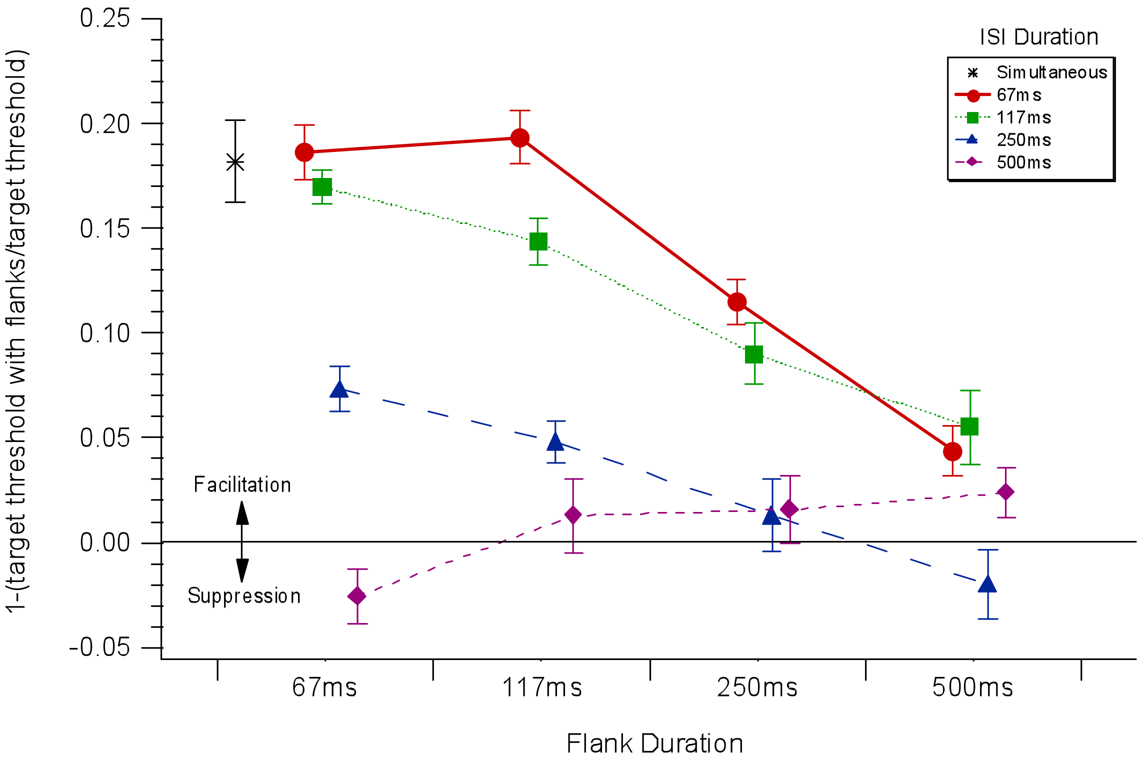


Figure 8. Monoptic viewing CDT by flank duration and ISI for subject WK. Detection thresholds are depicted relative to the target alone detection threshold. As a result, values greater than zero indicate CDT facilitation and values less that zero indicate CDT suppression. Error bars indicate ± one standard error.

would travel approximately 30.82mm and easily reach a point 17.5mm away. Given this, it seems unlikely that CDT facilitation being slightly less at 67ms ISI/67ms flank duration than 67ms ISI/117ms flank duration is due to a lack of integration time.

At the 117ms ISI, subject WK degree of facilitation decreased with increasing flank duration until the 500ms flank approached no effect. Subject AM (Figure 9), also completed the 117 ISI and showed less difference between the effect of flank durations than subject WK although the 67ms and 117ms flanks did show more facilitation than the 250ms and 500ms duration flanks. At the 250ms ISI, subject WK showed facilitation at the 67ms and 117ms flank durations and minimal effect at the 250ms and 500ms flank durations. Subject AW (Figure 10) showed a similar degree of facilitation for 67ms, 117ms and 250ms flanks. Slightly less facilitation was shown at the 500ms flank duration.

At the 500ms ISI, subject WK showed mild facilitation for the 67ms, 117ms, and 500ms flank durations. The CDT was mildly suppressed at the 250ms flank duration. Interestingly, subject CL (Figure 11) showed a very similar pattern with the 250ms flank duration again showing mild suppression. While only demonstrated in two subjects, the repeatability of this finding indicates that it may be significant and warrants further study (i.e. additional subjects).

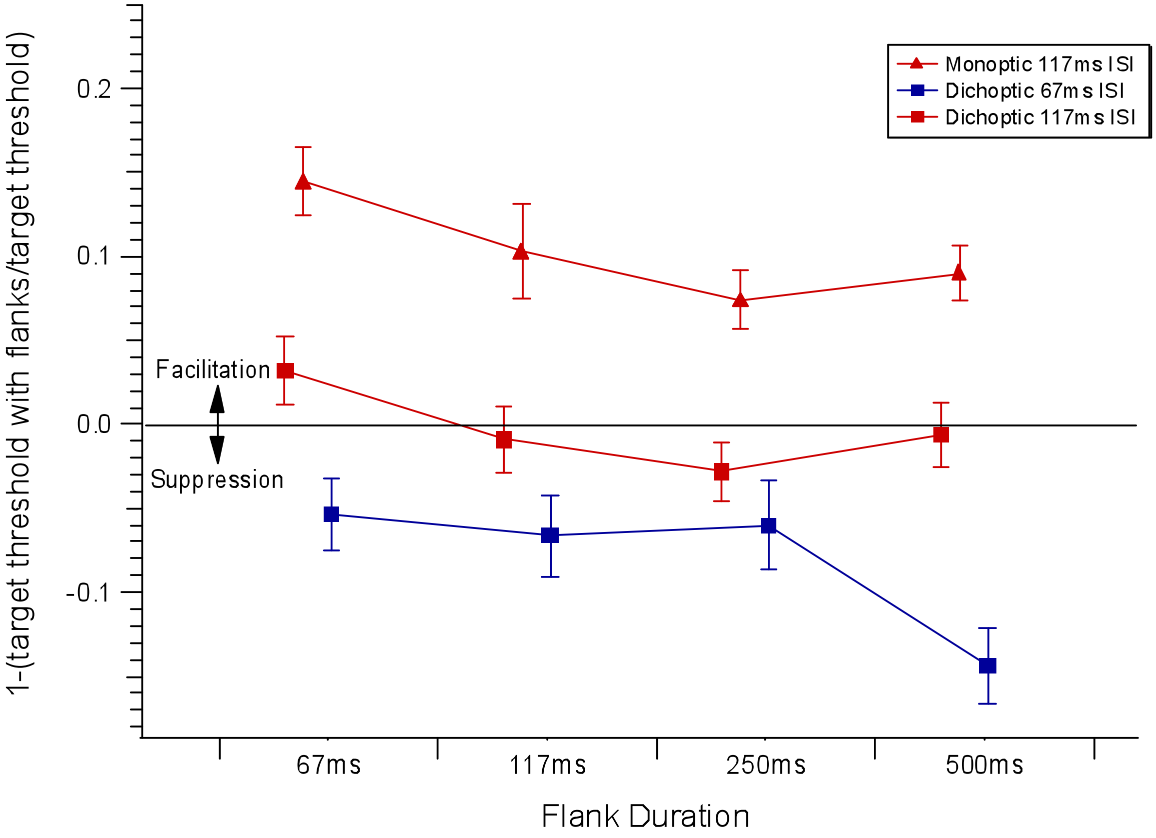


Figure 9. Individual data for subject AM. Detection thresholds are depicted relative to the target alone detection threshold. As a result, values greater than zero indicate CDT facilitation and values less that zero indicate CDT suppression. Error bars indicate ± one standard error.

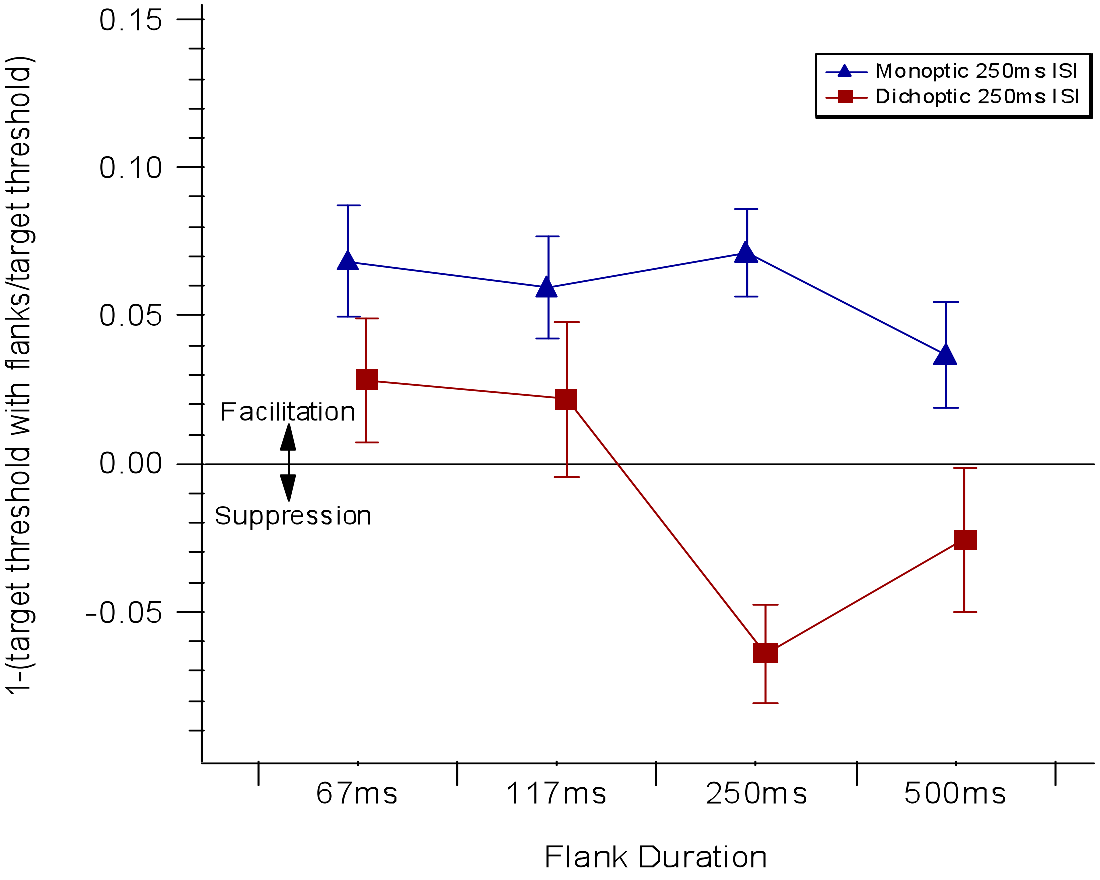


Figure 10. Individual data for subject AW. Detection thresholds are depicted relative to the target alone detection threshold. As a result, values greater than zero indicate CDT facilitation and values less that zero indicate CDT suppression. Error bars indicate ± one standard error.

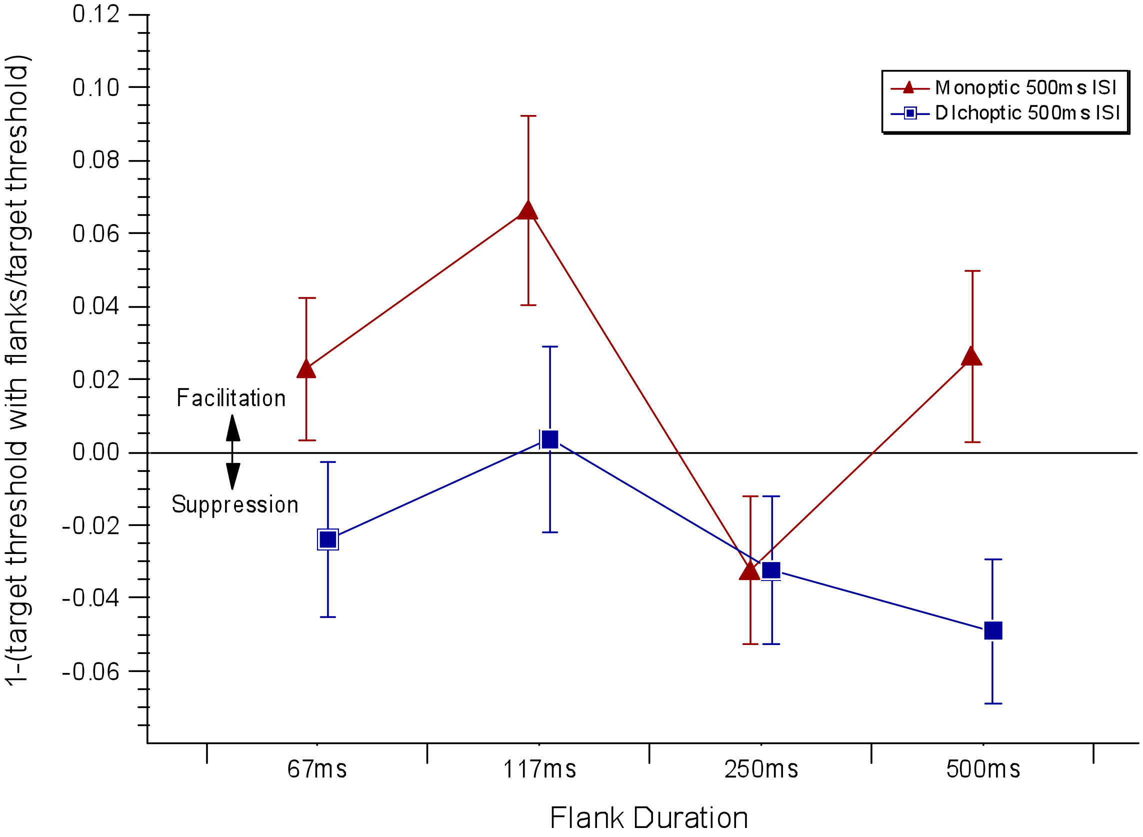


Figure 11. Individual data for subject CL. Detection thresholds are depicted relative to the target alone detection threshold. As a result, values greater than zero indicate CDT facilitation and values less that zero indicate CDT suppression. Error bars indicate ± one standard error.

In Figure 12 the monoptic adjusted ratio of CDT with flanks to target alone CDT is plotted against the log scale of SOA in milliseconds. Also in this figure, a curve is plotted using an exponential function to fit the arithmetic means of data points at each of the SOAs recorded in this experiment (simultaneous presentation, 134ms, 184ms, 234ms, 317ms, 367ms, 500ms, 567ms, 617ms, 750ms, and 1000ms). At the longest SOA (1000ms), the effect of the flanks approached zero. The exponential function $Y = y_0+A\exp[-(x-x_0)/\tau]$ (Igor Pro v5.0) provided a good fit to the data. Table 1 provides the exponential function variables for all viewing and flank conditions.

As mentioned previously, there was a strong overall tendency for the degree of facilitation to decrease as SOA increased. Up to the 184ms SOA, the amount of facilitation remains fairly steady with only a mild decrease. From 184ms up to approximately 500ms the absolute value of the slope increases and resembles a linear function. Beyond 500ms, the slope levels off and approaches zero. The correlation between degree of facilitation and SOA suggests that the duration between initial presentation of flanks and presentation of the target is an important factor in determining how lateral contrast is integrated to affect the CDT of a foveal target.

Table 1. Exponential function variables for 0-1000ms SOA functions. In this exponential function (exp Xoffset from Igor Pro), x_0 and y_0 are the offset constants. Multiple fits were attempted and the exp Xoffset equation provided the best fit (see section 6.1 for a line fit figure). *A* represents the initial amount constant and t is the decay constant. Y and x represent the vertical and horizontal co-ordinate positioning, respectively. Errors represent ± one standard deviation.

$Y= y_0+A\exp[-(x-x_0)/t]$		y_0	A	t
Collinear Flanks	Monoptic	0.0044 ± 0.0174	0.2009 ± 0.0182	250.7 ± 64.6
	Dichoptic	-0.0965 ± 0.0276	0.2051 ± 0.026	324 ± 110
	Half-binocular	-0.0747 ± 0.0501	0.2852 ± 0.0459	377.2 ± 153
Orthogonal Flanks	Monoptic	-0.0914 ± 0.218	0.2135 ± 0.213	1194 ± 1720
	Dichoptic	-0.0148 ± 0.0615	0.1507 ± 0.0579	580 ± 466

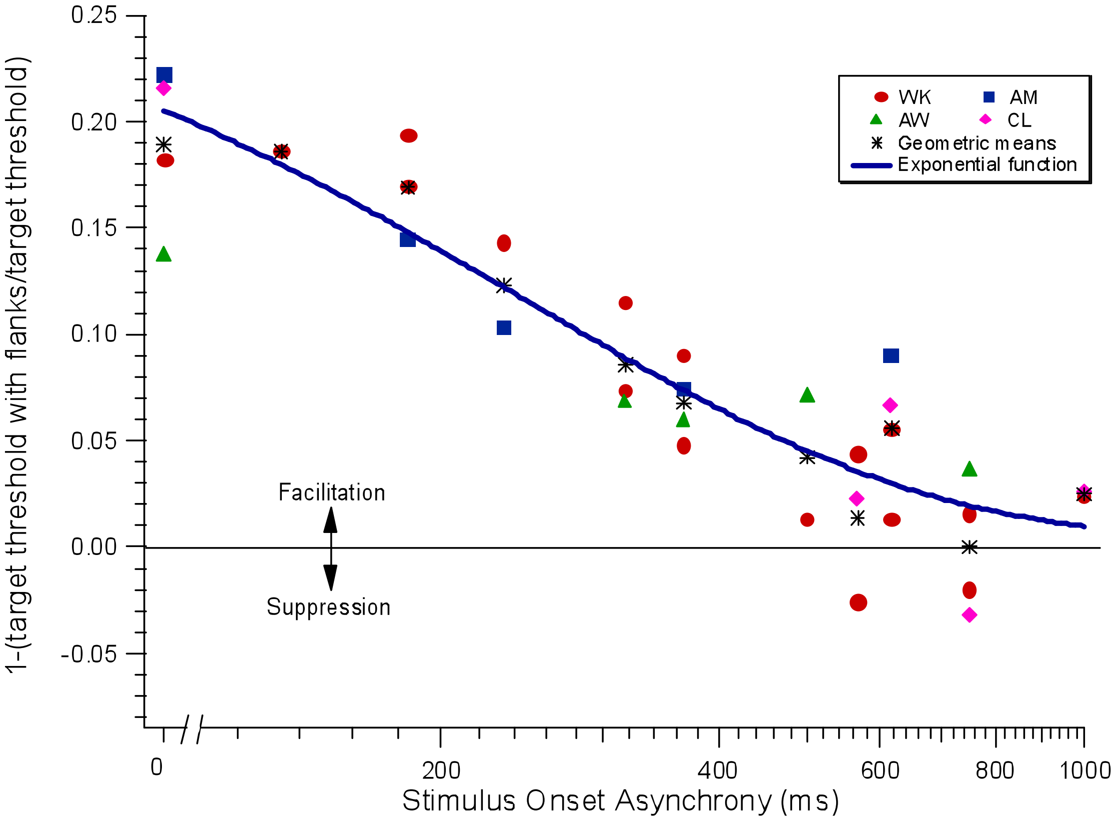


Figure 12. The effect of monoptic flanks on CDT up to a 1000ms SOA (flank duration and ISI combined). As mentioned in the Methods, subject AW used 4.5X contrast flanks and all other subjects used 3X contrast flanks. Error bars are omitted for clarity. Each individual data point is the product of approximately 700 trials. An exponential function was fit to the arithmetic means. CDT facilitation is maximal when target and flanks are displayed simultaneously. The degree of facilitation decreases gradually as SOA increases until it approaches no effect at

800-1000ms. At no point do monoptically viewed flanks produce CDT suppression.

5.3 Dichoptic, collinear flank results

The dichoptic introduction of collinear flanks generally resulted in CDT facilitation at short SOAs, CDT suppression at long SOAs (from approximately 500ms-1000ms) and a return to approximately no effect at the longest SOAs evaluated (1500-3000ms). The data is best fit by an exponential function and generally mirrors the monoptic function shape, but is shifted vertically (Figure 13). Where the monoptic function's slope decreases and appears to asymptote near no effect, the dichoptic function crosses over into suppression before it returns to no effect. The dichoptic suppression of CDT at long SOAs was unexpected. The study's original hypothesis was that both monoptic and dichoptic conditions would show CDT facilitation at short SOAs that would decrease as SOA increased until they approached no effect at long SOAs. The longest SOAs in this study (1500ms, 2000ms, and 3000ms) were added to evaluate the duration of inter-ocular CDT suppression (Figure 14). For efficiency, only two subjects were evaluated at these longest SOAs.

Mean dichoptic, collinear flank effect sizes ranged from maximal facilitation of 13.9% ± 4.00% at the 0ms SOA (simultaneous presentation) to maximal suppression of -9.90% ± 5.10% at the 1000ms SOA. Suppression was observed from the 500-1000ms SOAs. T-tests (SPSS version 19, Table 2) showed that the suppression at 500ms, 567ms, 617ms, 750ms, and 1000ms SOAs were statistically significantly ($p = 0.036, 0.019, 0.034, 0.002, 0.030$ respectively, 2-tailed). This suppression was consistent across all six subjects who completed the two longest SOAs (750 and 1000ms). This suggests that these suppressive effects could be generalized to the rest of the normal population.

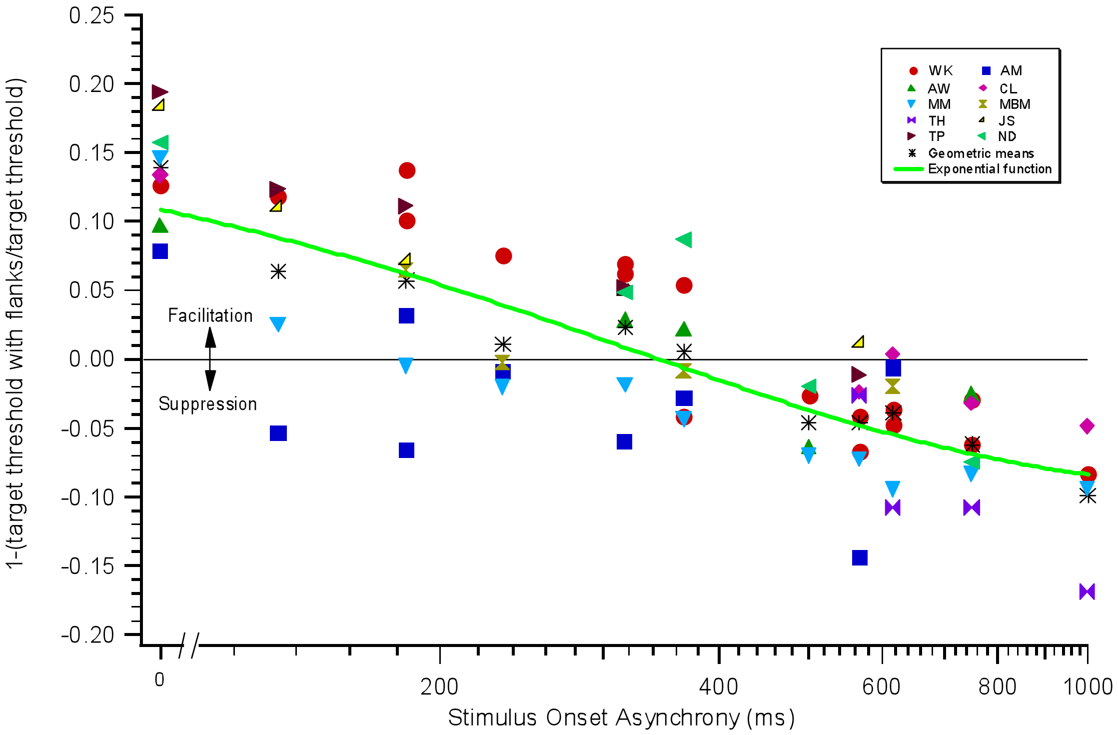


Figure 13. The effect of dichoptic flanks on CDT up to a 1000ms SOA for 10 subjects. Each individual data point is the product of approximately 700 trials. Error bars are omitted for clarity. An exponential function was fit to the arithmetic means. Dichoptic flanks produced maximal CDT facilitation with simultaneous target presentation. The degree of facilitation decreases as SOA increases until there is minimal effect around 360ms SOA. Beyond approximately 400ms, dichoptic flanks produced CDT suppression that was maximal at a 1000ms SOA.

Table 2. Statistical analysis of longer SOA threshold suppression produced by collinear, dichoptic flanks. T-tests show statistically significant threshold suppression at 500-1000ms SOAs.

Dichoptic SOA	Mean Difference from zero	t	df	Sig (2-tailed)
500ms	-0.0457	-3.645	3	0.036
567ms	-0.0445	-2.929	8	0.019
617ms	-0.0442	-2.738	6	0.034
750ms	-0.0595	-4.997	6	0.002
1000ms	-0.0989	-3.908	3	0.030

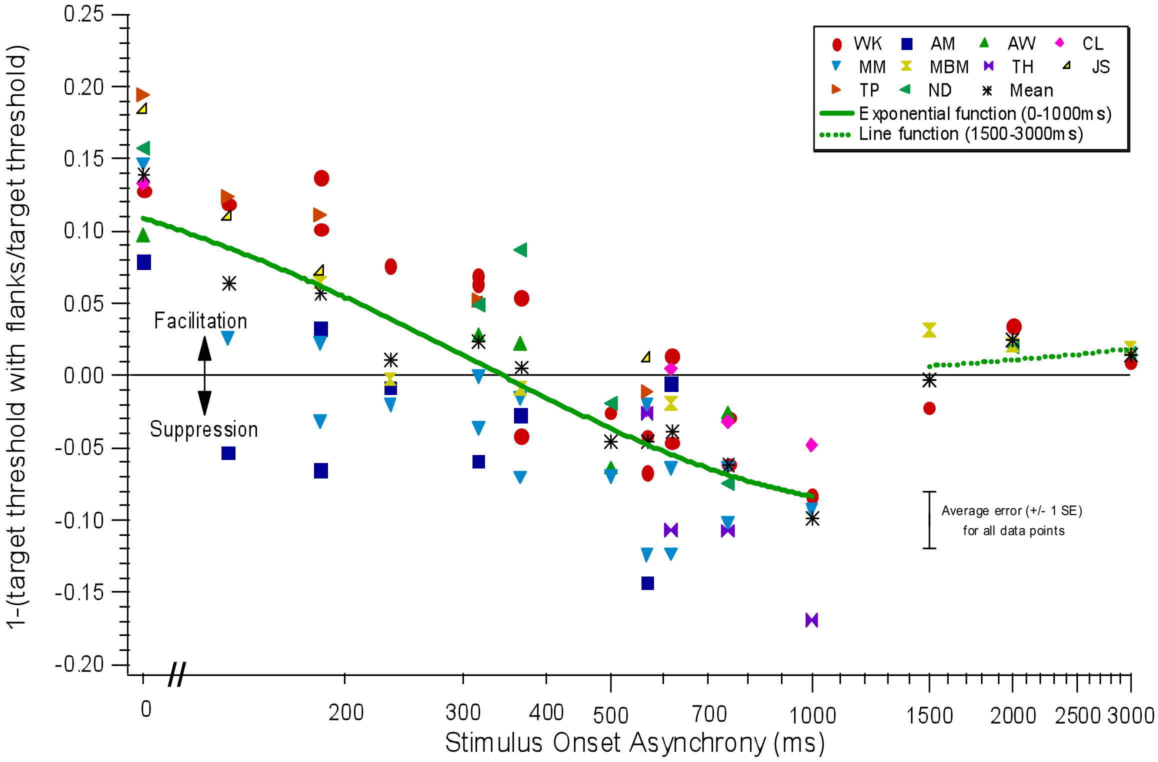


Figure 14. The effect of dichoptic flanks on CDT up to a 3000ms SOA. Individual error bars are omitted for clarity. The longest SOAs (1500ms, 2000ms, and 3000ms) show minimal flank effect for the two subjects evaluated at those SOAs.

As with the monoptic results above, it is appropriate to review the effect of flank duration within each ISI. Again, subject WK completed all ISI/flank duration combinations and the other three subjects completed all flank durations within a single ISI. For WK's dichoptic 67ms ISI condition (Figure 15), the degree of facilitation was nearly flat between the 67ms and 117ms flank durations. Facilitation decreased sharply at the 250ms flank and crossed over into suppression at 500ms. Subject AM also completed the dichoptic 67ms ISI condition (Figure 9). AM's thresholds followed a similar pattern as subject WK's (plateau followed by a sharp downward vertical shift) with two major differences. First, for subject AM, dichoptic flanks caused suppression throughout the 67ms ISI. Second, subject AM's downward vertical shift occurred at the 500ms flank duration as opposed to subject WK's downward shift beginning at the 250ms flank. Subject AM generally showed less dichoptic integration than the other three participants.

Subject WK's 117ms ISI block (Figure 15) followed a pattern similar to his 67ms ISI, but crossed over into suppression at the 250ms flank duration, earlier than the 67ms ISI. This is not altogether unexpected since the total SOA at these points are roughly comparable. Subject AM also completed the 117ms ISI under

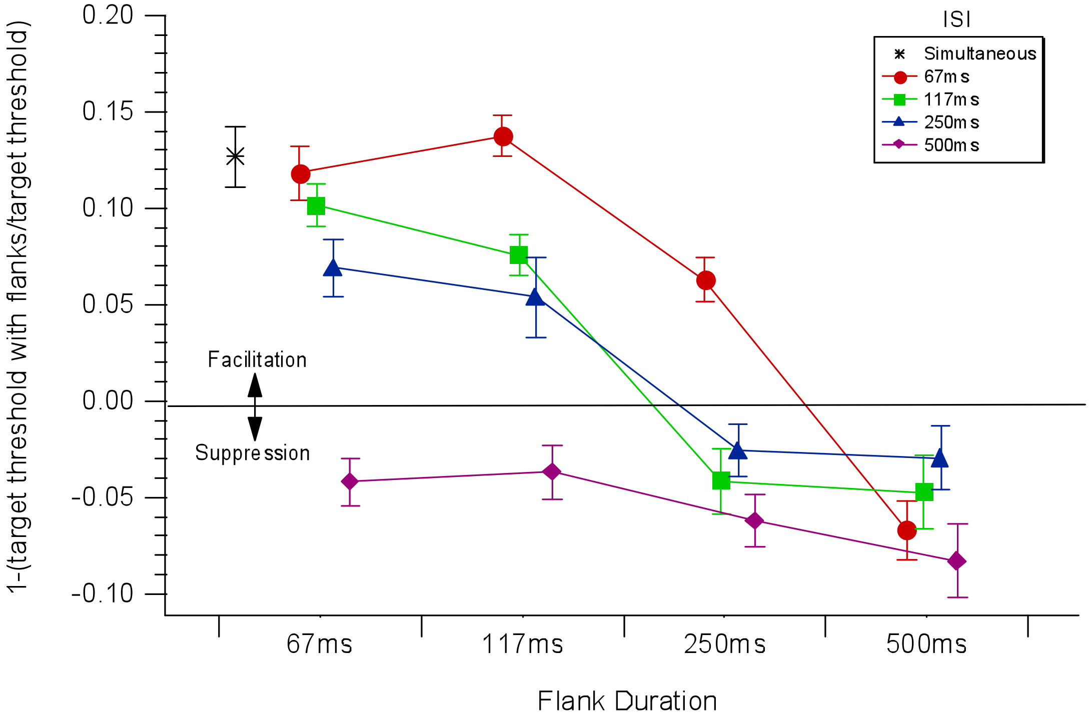


Figure 15. Dichoptic viewing CDT by flank duration and ISI for subject WK. Detection thresholds are depicted relative to the target alone detection threshold. As a result, values greater than zero indicate CDT facilitation and values less that zero indicate CDT suppression. Error bars indicate ±1 standard error.

dichoptic conditions (Figure 9). AM’s thresholds showed a pattern similar to subject WK although, as mentioned previously, the dichoptic flanks affected AM's thresholds much less than they did under monoptic conditions. The most apparent pattern in Figure 9 is the similarity of subject AM's 117ms ISI monoptic and dichoptic curves. The curve shapes are nearly identical with the dichoptic curve shifted vertically downward. At least for AM, this argues in favor of a similar method of intra and inter-ocular contrast integration.

Subject WK's 250ms ISI pattern closely resembles the 117ms ISI pattern, but with slightly less facilitation at the 67ms and 117ms flank durations and slightly less suppression at the 250ms and 500ms flank durations. Closely resembling WK's results, subject AW showed slight facilitation at the 67ms and 117ms flank durations and mild suppression at the 250ms and 500ms flank durations. Although not a striking as AM's 117ms ISI blocks, subject AW's monoptic and dichoptic 250ms ISI conditions (Figure 10) closely resemble one another, but with the dichoptic condition shifted vertically downward.

At the 500ms ISI WK's results show suppression of the detection threshold throughout that increases slightly as SOA increases. Subject CL also completed the 500ms ISI dichoptic condition (Figure 11). This subject showed close to zero effect at the shorter ISIs, which transitioned to slight suppression at the longer SOAs.

Figure 16 shows the mean flank effect by flank duration and ISI for all 10 subjects that participated in the dichoptic viewing condition. Within every ISI (67ms, 117ms, 250ms, and 500ms) the CDT decreases as flank duration increases. With the exception of the 117ms and 250ms ISIs, the ISI sets resemble one another in shape, but are vertically shifted with the longer ISIs having lower overall CDTs. The 117ms and 250ms ISI sets have approximately the same shape and vertical positioning.

In Figure 13 the dichoptic adjusted CDT ratio is plotted against the log of the stimulus onset ratio. An exponential function provides a good fit to arithmetic means of the data points at each SOA. This function's curve is plotted on the figure in solid red. The curve starts with approximately 11% facilitation when the flanks are presented simultaneously. The degree of facilitation decreases gradually as SOA increases until approximately 400-500ms SOA when the flank effect transitions to CDT suppression. The suppressive effect persists up to the 1000ms SOA. Beyond that (1500-3000ms), the flank effect is minimal (Figure 14).

Compared to the monoptic function shown in Figure 12, there are two obvious differences. First, the dichoptic individual data shows more variability than the individual monoptic data, especially at shorter SOAs. The dichoptic exponential function fits the dichoptic data well. Previous experiments in this lab

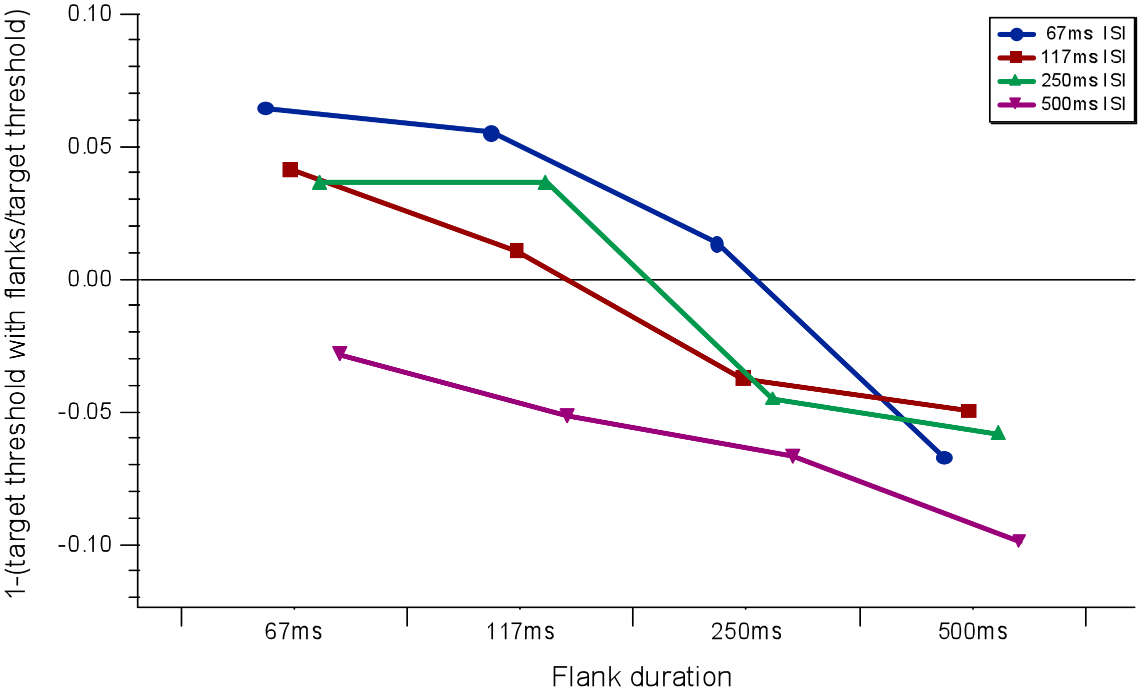


Figure 16. The mean effect of dichoptic flanks on CDT by flank duration and ISI. Each data point represents the mean for all subjects that contributed to that flank duration/ISI combination. For each ISI, CDT decreases as flank duration increases.

that utilized monoptic and dichoptic conditions have also reported more dichoptic inter-subject variability. As mentioned previously, subject AM in particular added to the variability. AM showed mild CDT facilitation with simultaneous flank presentation, but beyond that showed either suppression or approximately no effect at each SOA. Subject MM (Figure 13) also appeared to show minimal inter-ocular contrast integration at short SOAs. The second difference is a vertical shift of the dichoptic function compared with the monoptic function. This shift is remarkably consistent across the entire range of SOAs.

To review, dichoptic flank presentation produced CDT facilitation at shorter SOAs (up to 500ms) and unexpected CDT suppression at longer SOAs (500-1000ms). At the longest SOAs (1500-3000ms), dichoptic flank effects were minimal. Compared to the monoptic flank findings, inter-subject variability was greater with dichoptic flank presentations. The unanticipated dichoptic CDT suppression at longer SOAs prompted the inclusion of a half-binocular (Meese and Hess, 2005) viewing condition (discussed below in section 5.4).

5.4 Half-binocular, collinear flank results

In addition to the previously described monoptic and dichoptic viewing conditions, four subjects completed at least a single ISI block of the half-binocular condition. Two of those four subjects (WK and MM) completed the entire half-

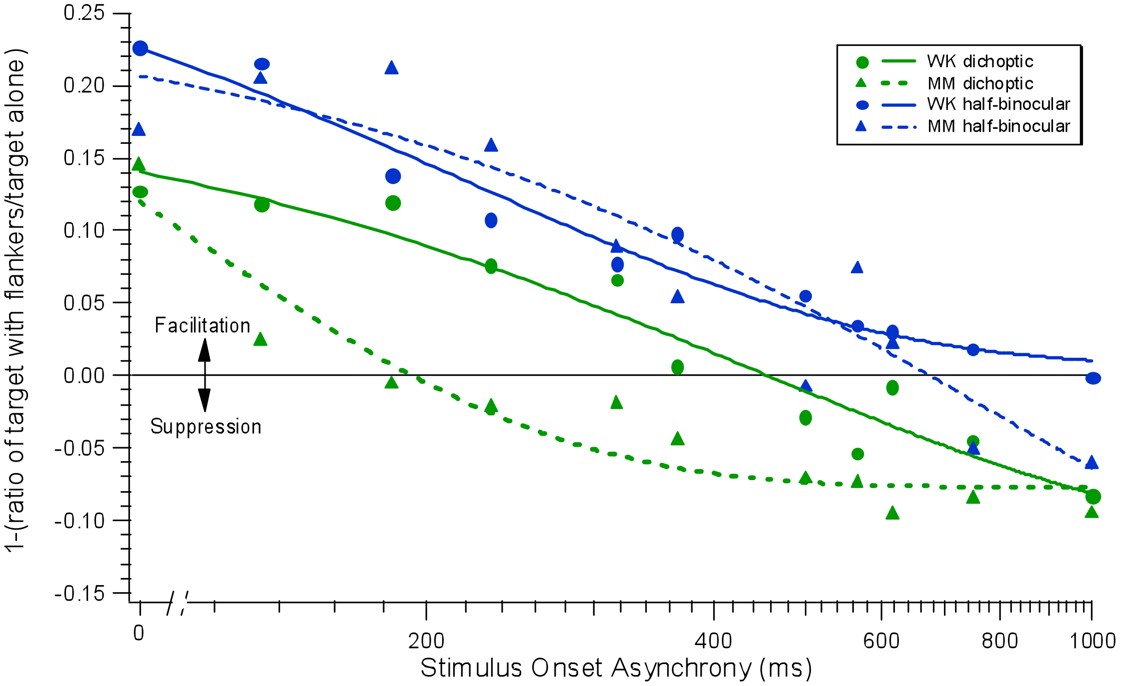


Figure 17. Half-binocular and dichoptic flank effects for subjects WK and MM (the only two subjects to complete the entire half-binocular and dichoptic viewing conditions). With half-binocular viewing, WK and MM show similar degrees of CDT facilitation at shorter SOAs. At longer SOAs (750ms and 1000ms), half-binocular flanks showed minimal effect on WK's thresholds and suppressed MM's thresholds. For both subjects, simultaneous dichoptic viewing produced CDT facilitation that decreased with increasing SOA and became CDT suppression at longer SOAs. However, for subject MM, CDT suppression began at shorter SOAs than it did for subject WK.

binocular condition. Their half-binocular results (along with their dichoptic results) are shown in Figure 17. For half-binocular viewing, the flanking stimuli were presented to both eyes, but the target was only presented to the dominant eye. In essence, the half-binocular condition is a combination of the monoptic and binocular flanks. The effect produced by half-binocular flanks might

From Figure 18, the simultaneous presentation of half-binocular flanks resulted in mean CDT facilitation of 18.0% ± 4.2%. Maximal facilitation occurred at the 134ms SOA (21.0% ± 0.7%). The degree of CDT facilitation generally decreased as SOA increased until the mean effect crossed over to suppression at the 750ms and 1000ms SOAs with maximal CDT suppression occurring at 1000ms (-5.3% ± 4.7%). However, t-tests (SPSS version 19) showed that the suppression was not statistically significant at the 750ms ($p = 0.201$, 2-tailed) and 1000ms ($p = 0.194$, 2-tailed) SOAs.

An exponential function fit to the half-binocular means provides a good fit (Figure 18). It resembles the monoptic and dichoptic functions in shape, but some differences are apparent. At shorter SOAs (0-500ms) the half-binocular function nearly overlays the monoptic function. However, from the 500-1000ms SOAs the half-binocular function diverges from the monoptic function and lies midway between the monoptic and dichoptic functions in terms of relative facilitation. At the longest SOAs (1500-3000ms) the effect of half-binocular flanks approaches no effect (Figure 19).

To review, half-binocular flanks produced CDT facilitation at shorter SOAs (up to 750ms), mild suppression at longer SOAs (750-1000ms), and minimal effect at the longest SOA (1500-3000ms). This pattern closely resembles the monoptic flank effect at shorter SOAs and appears to be a combination of monoptic and dichoptic flank effects at longer SOAs (Figure 31 in the Discussion shows all three viewing condition functions on the same graph).

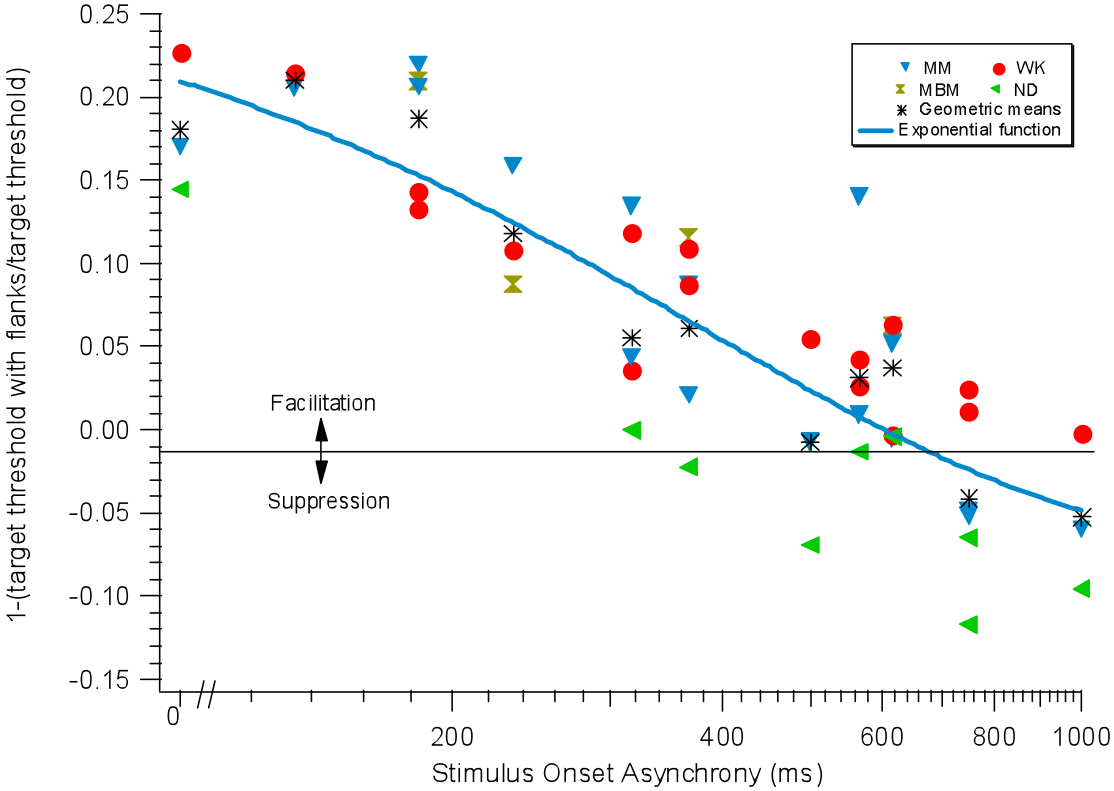


Figure 18. The effect of half-binocular flanks on CDT up to a 1000ms SOA. Each individual data point is the product of approximately 700 trials. An exponential function was fit to the arithmetic means. Error bars are omitted for clarity. Half-binocular flanks produced CDT facilitation at shorter SOAs with maximum facilitation at the 134ms SOA. The degree of facilitation gradually decreased to approximately 600ms. Beyond 600ms, half-binocular flanks produced mild CDT suppression.

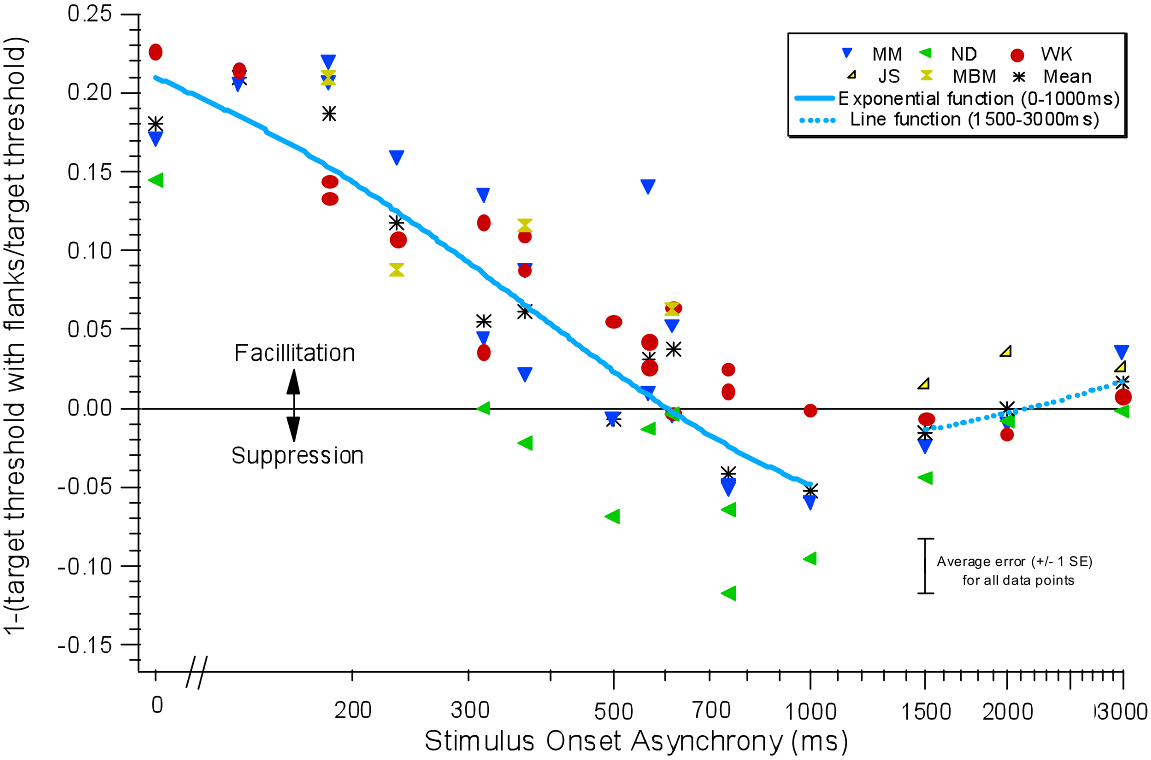


Figure 19. The effect of half-binocular flanks on CDT up to a 3000ms SOA. Individual error bars are omitted for clarity. The longest SOAs (1500ms, 2000ms, and 3000ms) show minimal flank effect for the four subjects evaluated at those SOAs.

5.5 Effect of flank contrast

In my pilot experiment, flanker contrast was increased to 9X the flank contrast detection threshold and the collinear flank experiment was repeated for one subject (WK) under monoptic conditions for all flank durations within the 117ms ISI duration. This resulted in the generation of five thresholds (simultaneous, 67ms, 117ms, 250ms and 500ms flank durations) for the 9X flanks. These are plotted in Figure 20 along with the comparable 3X flanks contrast values for subject WK. While it is difficult to draw conclusions from a limited data set, the available data suggest that thresholds may be mildly depressed relative to the 3X flanks for simultaneous, 67ms and 117ms flank durations. The 250ms and 500ms 9X flank thresholds are very similar to thresholds for the 3X flanks.

Another point relevant to the flank contrast effect is that subject AW completed the 250ms ISI block of the monoptic, collinear flank experiment using 4.5X contrast flanks instead of the 3X flanks used in the rest of the study (see Methods section). In Figure 12, AW's 4.5X flank thresholds are very similar to the other subject's 3X flank thresholds. Again, this is a limited dataset, but it suggests that the difference between 3X and 4.5X contrast flanks is minimal.

To summarize, relative to the 3X flank thresholds used in the main experiment, there is mild threshold suppression with 9X contrast flanks at the shorter flank durations that decreases until it converges with the 3X thresholds at longer flank durations. This finding is important because it suggests that the 3X flanks used in the main experiment were consistent with the goal of obtaining maximal facilitation.

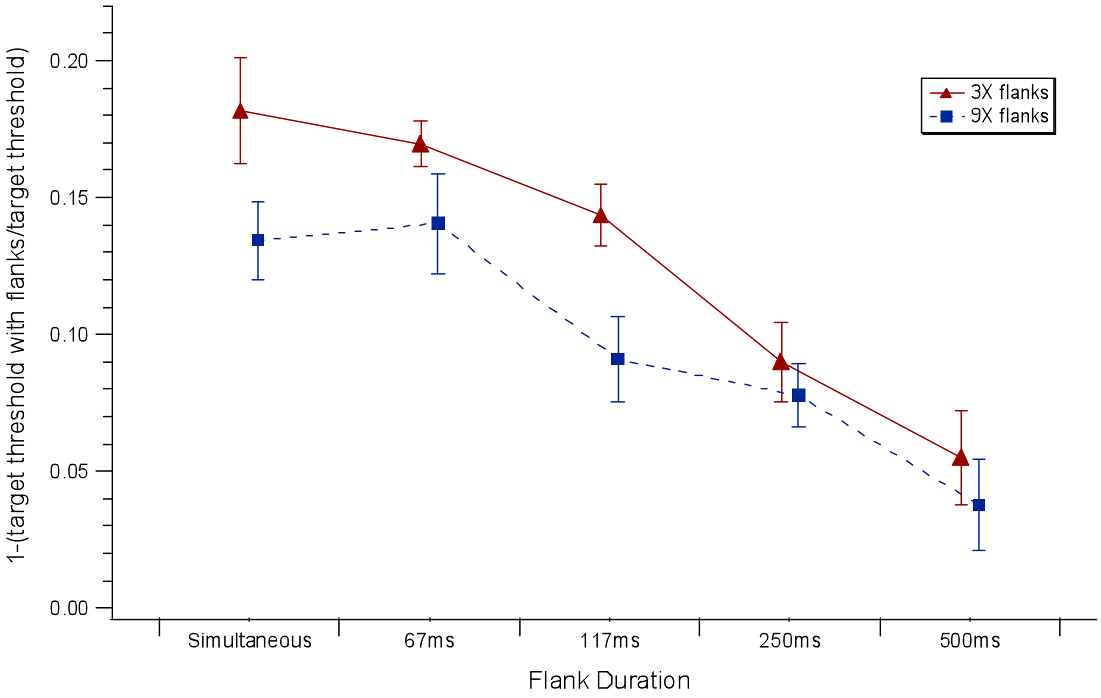


Figure 20. Monoptic 3X and 9X threshold flanks produce similar effects. Data is from a single subject (WK) and the ISI is 117ms for all data points. 3X flanks produced a slightly greater effect (CDT facilitation) than 9X flanks for simultaneous, 67ms, and 117ms flank durations. The effect of 3X and 9X flanks was very similar for 250ms and 500ms flank durations. This finding is important because it suggests that the 3X flanks used in the main experiment were consistent with the goal of obtaining facilitation in the pilot study paradigm. Error bars indicate ± one standard error.

5.6 Relative contribution of flank duration vs. interstimulus interval to the overall flank effect

The hypothesis regarding the relative contribution of flank duration vs. ISI was that the total duration from initial flank presentation to onset of the test stimulus (i.e. ISI + flank duration) is the most important contributor in determining flank effect on CDT. However, the preceding sections have only described the effect of the total duration (SOA) on CDT. These total SOA results are summarized in the followed paragraph and then a method of separating the relative contribution of flank duration vs. ISI is described.

The adjusted effect on CDT [1-(target threshold with flanks/target threshold)] was plotted against the SOA on a log scale in milliseconds. When the arithmetic means for all subjects who participated in the project were fit to an exponential function the resulting curve initially showed maximal relative facilitation at shorter SOAs. The degree of facilitation decreased as SOA increased until it approached no effect (monoptic viewing) or CDT suppression (dichoptic and half-binocular viewing) at longer SOAs and approached no effect at the longest SOAs evaluated in this study (1500-3000ms).

This finding supports the importance of SOA in determining the flank effect on CDT, but does not address the relative importance of ISI and flank durations.

To parse out the contributions of ISI versus flank duration the adjusted effect on CDT was plotted against the ratio of ISI duration to total SOA duration. This was accomplished by creating pairs of data points in which total SOA was the same, but the duration of the flanks and ISIs differed.

The first step in creating the plot was describing each flank/ISI combination as an ISI/SOA ratio. For example, the combination of a 250ms ISI and a 500ms flank presentation (750ms SOA) results in a 0.33 ISI/SOA ratio. The ISI/SOA ratios were then paired by SOA. Continuing the previous example, the 0.33 ratio would pair with the 0.67 ratio (250ms flank and 500ms ISI) to form a 750ms SOA pair. A total of 6 SOA pairs were formed (184, 317, 367, 567, 617, and 750ms).

A lower ISI/SOA ratio indicates a greater flank contribution to the total SOA and higher ISI/SOA ratios show greater ISI contributions. This plot provides a more convenient means of comparing flank/ISI duration effects. While the effect of total SOA is deemphasized, it is still visible via the Y-axis positioning of the SOA pairs. The If flank duration and ISI contribute equally to the flank's effect on CDT, a line plotted through the means at each ISI/SOA ratio (between SOA pairs) would be expected to be flat (zero slope). A positive slope would suggest that the ISI has a greater effect and a negative slope would be associated with a greater effect from flank duration.

Within each viewing condition, the mean for every ISI/SOA ratio were blocked by SOA pair creating a greater flank contribution group and a greater ISI contribution group. Table 2 displays the descriptive statistics for these groups. The groups were then evaluated for statistically significant differences using a paired two-sample t-test (SPSS version 19.0). The use of a paired t-test controlled for the effect of overall SOA and resulted in greater power than a simple t-test.

In the monoptic condition (Figure 21), a line plotted through the means at each ISI/SOA ratio has a negative slope (-0.067). A visual inspection of Figure 20 also shows that all individual ISI/SOA ratio pairings have a slightly negative slope. This suggests that the flank duration may have had greater contribution to the overall effect than ISI duration. The longer flank duration group's mean effect was 8.5% ± 2.6% (SEM) and the longer ISI duration group's mean effect was 5.0% ± 2.5%. Linear regression (Table 3) showed a highly significant correlation between the longer flank group and the longer ISI group (r^2=0.984, p<0.000, one tailed). A paired samples t-test (Table 4) gave a mean difference of 3.5% ± 0.3%. With five degrees of freedom and a t-value of 10.57, this test showed a highly significant difference (p<0.000, two-tailed) between flank longer and ISI longer

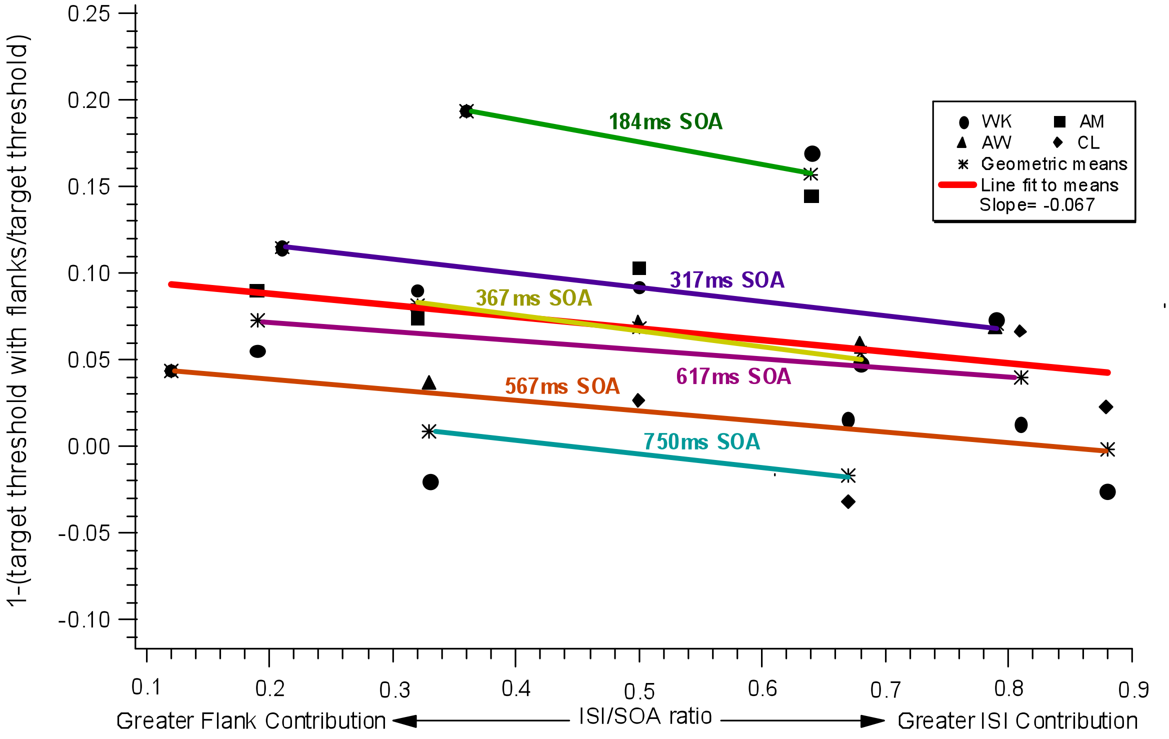


Figure 21. Monoptic flank duration and ISI component effects. Each line on the figure represents a complementary flank duration/ISI pairing that equals the same SOA. For example, the 750ms SOA pair consists of 250ms flank/500ms ISI and 500ms flank/250ms ISI points. The relative contribution of flank duration or ISI is represented on the X-axis by the ISI/SOA ratio. A lower ISI/SOA ratio indicates a greater flank contribution and a higher ISI/SOA ratio indicates a greater ISI contribution. A line fit to the means has a negative slope (-0.067) that closely resembles all of the SOA pairs and shows a greater contribution of flank duration than ISI to the overall effect.

groups. This indicates that, contrary the hypothesis, flank duration contributed more to the overall effect than ISI duration.

Analysis of the dichoptic ISI/SOA ratio plot (Figure 22) is less straightforward than analysis of the monoptic plot because at longer SOAs the flank effect changes from CDT facilitation to CDT suppression. Hence, for the 184ms, 317ms, and 367ms SOA pairs a positive slope would indicate the ISI contributed more the overall effect than flank duration. For 567ms, 617ms, and 750ms SOA pairs, a positive slope would indicate that flank duration had a greater contribution to the overall effect than ISI. However, a visual analysis of these pairs does not show any obvious trends. Since the flank effect (CDT facilitation vs. suppression) is dependent on SOA, a line was not fit to the means.

Due to the transition in dichoptic flank effect mentioned above, SOA pairs that produced CDT suppression (567ms, 617ms, and 750ms pairs) were included as absolute values in a paired t-test analysis. The longer flank group's mean effect was 4.2% ± 1.9% and the longer ISI group's mean effect was 4.5% ± 1.3%. Linear regression (Table 3) showed a non-significant correlation between the longer flank group and the longer ISI group ($r^2 = 0.236$, $p = 0.328$, one-tailed). A paired samples t-test (Table 4) gave a mean difference of -0.3% ± 1.7%. This difference was not significant ($t = -0.194$, $p = 0.854$, two-tailed) and supports the

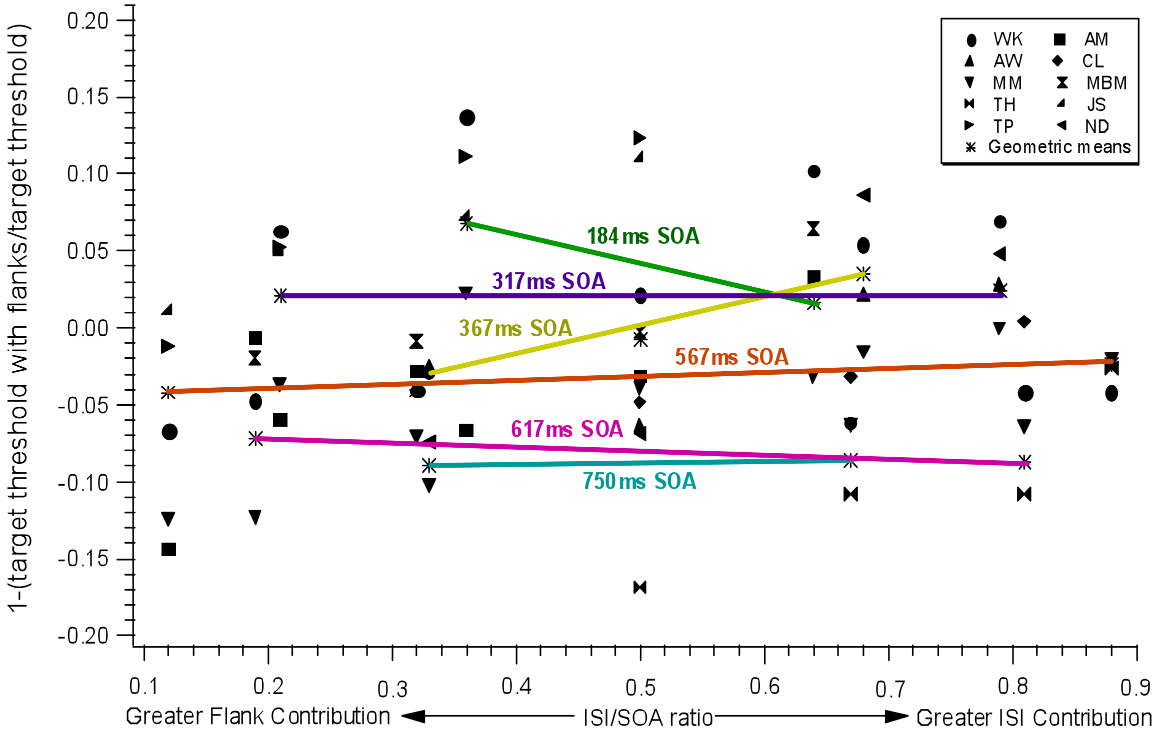


Figure 22. Dichoptic flank duration and ISI component effects. Each line on the figure represents a complementary flank duration/ISI pairing that equals the same SOA. For example, the 750ms SOA pair consists of 250ms flank/500ms ISI and 500ms flank/250ms ISI points. The relative contribution of flank duration or ISI is represented on the X-axis by the ISI/SOA ratio. A lower ISI/SOA ratio indicates a greater flank contribution and a higher ISI/SOA ratio indicates a greater ISI contribution. The 184ms and 367ms pairs show conflicting trends and the other ISI pairs do not demonstrate an overall trend.

hypothesis that overall SOA is the most important contributor to the flank effect for the dichoptic viewing.

For half-binocular viewing (Figure 23), the flank effect changed from CDT facilitation to suppression for the 750ms SOA pair. Hence, the 750ms SOA values were included as absolute values. Also, as in the dichoptic condition, since the flank effect was dependent on SOA, a line was not fit to the means. The longer flank mean effect was 9.2% ± 1.9% and the longer ISI mean effect was 5.2% ± 2.8% (Table 2).

The relationship between the longer flank group and the longer ISI group was significant (Table 3; $r^2 = 0.803$, $p = 0.016$, one-tailed). A paired samples t-test (Table 4) gave a mean difference of 4.1% ± 1.4%. The difference between the flank longer and ISI longer groups was significant with five degrees of freedom ($t = 2.886$, $p = 0.034$, two-tailed). Thus, for half-binocular viewing, flank duration contributed more to the overall effect than ISI duration. For half-binocular viewing, this result contradicts the hypothesis that overall SOA is the most important contributor to the flank effect.

To summarize, under monoptic and half-binocular viewing flank duration had a significantly greater contribution to the overall effect than ISI. This contradicted the hypothesis that flank duration and ISI contribute equally to the overall effect. Monoptic viewing produced less variability than the half-binocular or dichoptic viewing conditions that included inter-ocular flank data. The consistent, negative slopes of the SOA pairs in Figure 20 are evidence of this. Dichoptic viewing did not show a significant difference in effect contribution between flank duration and ISI. Hence, the hypothesis that total SOA has greatest effect contribution was supported for dichoptic viewing.

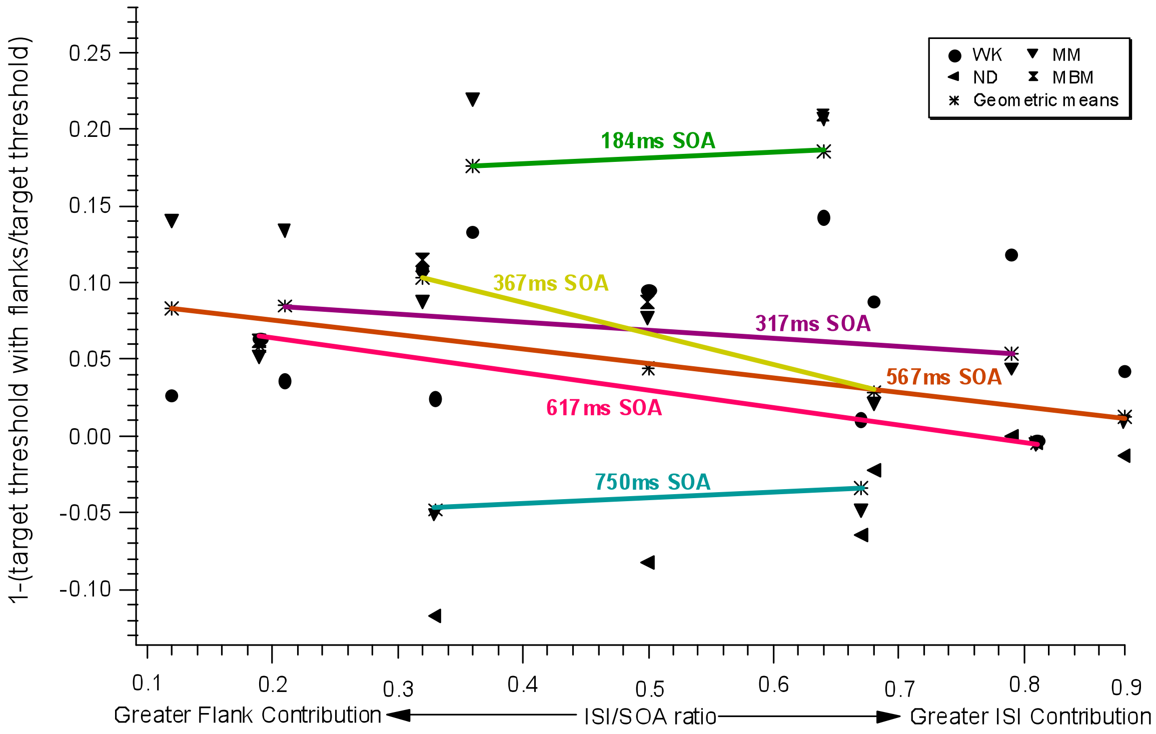


Figure 23. Half-binocular flank duration and ISI component effects. Each line on the figure represents a complementary flank duration/ISI pairing that equals the same SOA. For example, the 750ms SOA pair consists of 250ms flank/500ms ISI and 500ms flank/250ms ISI points. The relative contribution of flank duration or ISI is represented on the X-axis by the ISI/SOA ratio. A lower ISI/SOA ratio indicates a greater flank contribution and a higher ISI/SOA ratio indicates a greater ISI contribution. With the exception of the 184ms SOA pair, the SOA pairs less than 750ms show a negative slope. Since the overall effect of half-binocular flanks at SOAs less than 750ms is CDT facilitation, a negative slope for

these SOA pairs indicates that flank duration had a greater contribution than ISI to the overall effect. At the 750ms SOA, the overall effect of half-binocular flanks is CDT suppression. Hence, the positive slope exhibited by the 750ms SOA pair also indicates that flank duration had a greater contribution than ISI to the overall effect.

Table 3. Flank duration vs. ISI paired sample descriptive statistics.

		Mean	N	Std. Deviation
Monoptic	Flank longer	.085799	6	.0637786
	ISI longer	.050483	6	.0618035
Half-binocular	Flank longer	.092450	6	.0454899
	ISI longer	.051833	6	.0686469
Dichoptic	Flank longer	.042000	6	.0467974
	ISI longer	.045333	6	.0324572

Table 4. SOA paired sample correlations by viewing condition. A total of six SOA pairs were formed (184, 317, 367, 567, 617, and 750ms). Within each SOA pair, a Pearson correlation test (SPSS version 19) was used to examine the relationship between the point with a greater flank contribution and the point with a greater ISI contribution. The resulting correlation values demonstrate strong, statistically significant correlations for the monoptic and half-binocular flanks. Dichoptic flanks show a much weaker correlation that is not statistically significant.

Viewing Condition		N	Correlation (r^2)	Sig.
Pair 1	Monoptic	6	.992	.000
Pair 2	Half-binocular	6	.896	.016
Pair 3	Dichoptic	6	.486	.328

Table 5. Paired samples t-tests evaluating the relative contributions of flank duration and ISI. Within each viewing condition, the mean for every ISI/SOA ratio was blocked by SOA pair creating greater flank contribution and greater ISI contribution groups. The use of a paired t-test controlled for the effect of overall SOA and resulted in greater power than a simple t-test. The difference between greater flank contribution and greater ISI contribution groups was significant for the monoptic and half-binocular viewing conditions. However, there was not a significant difference between the greater flank and greater ISI contribution group with dichoptic viewing.

		Paired Differences					
		Mean	Std. Deviation	Std. Error of Difference Between Means	t	df	P-value (2-tailed)
Pair 1	Monoptic	.03532	.00818	.00334	10.58	5	< .001
Pair 2	Half-binocular	.04062	.03448	.01407	2.89	5	.034
Pair 3	Dichoptic	-.00333	.04202	.01716	-0.19	5	.854

5.7 Monoptic and dichoptic orthogonal flank results

In an effort to explain the unexpected suppression seen with long SOA dichoptic and half-binocular flanks, a supplemental experiment was run using orthogonal flanks under monoptic and dichoptic viewing. For efficiency, half-binocular, orthogonal flanks were not included since their inclusion was not expected to yield any information that could not be gleaned from the dichoptic data. Simultaneous presentation of monoptic, orthogonal flanks produced CDT facilitation (10.6% ± 2.3%) that generally decreased as SOA increased until it approached no effect at the 1000ms SOA (1.3% ± 0.3%). The two subjects who participated in the monoptic, orthogonal flank experiment (CP and WK) showed similar responses at all six evaluated SOAs (Figure 24).

Simultaneous presentation of dichoptic, orthogonal flanks produced CDT facilitation (12.3% ± 6%). As with monoptic presentation, the degree of facilitation decreased as SOA increased until it approached no effect at the 1000ms SOA (2.1% ± 1.8%). Three of the four subjects showed consistently small amounts of inter-subject variability (Figure 25). The fourth (MM) showed minimal inter-ocular contrast transfer, as demonstrated by low degrees of CDT facilitation. Subject MM's dichoptic, collinear flank findings (Figure 16) also show minimal effects of inter-ocular contrast transfer at shorter SOAs (where most subjects showed facilitation). However, at longer SOAs subject MM demonstrated CDT suppression at levels comparable to the group means.

Both monoptic and dichoptic orthogonal flank means were fit to the same exponential function ($Y = y_0 + A\exp[-(x-x_0)/\tau]$) as in the main experiment (Table 1). A comparison of the monoptic and dichoptic orthogonal flank functions (Figure 26) shows that the functions are very similar in shape and vertical placement on the plot. Here, the most pertinent finding to the experiment's purpose is that dichoptic, orthogonal flanks did not produce CDT suppression at any of the evaluated SOAs. This supports the hypothesis that the long SOA CDT suppression produced by inter-ocular flank contrast is due to adaptation to an illusory contour (see section 6.4 of the Discussion).

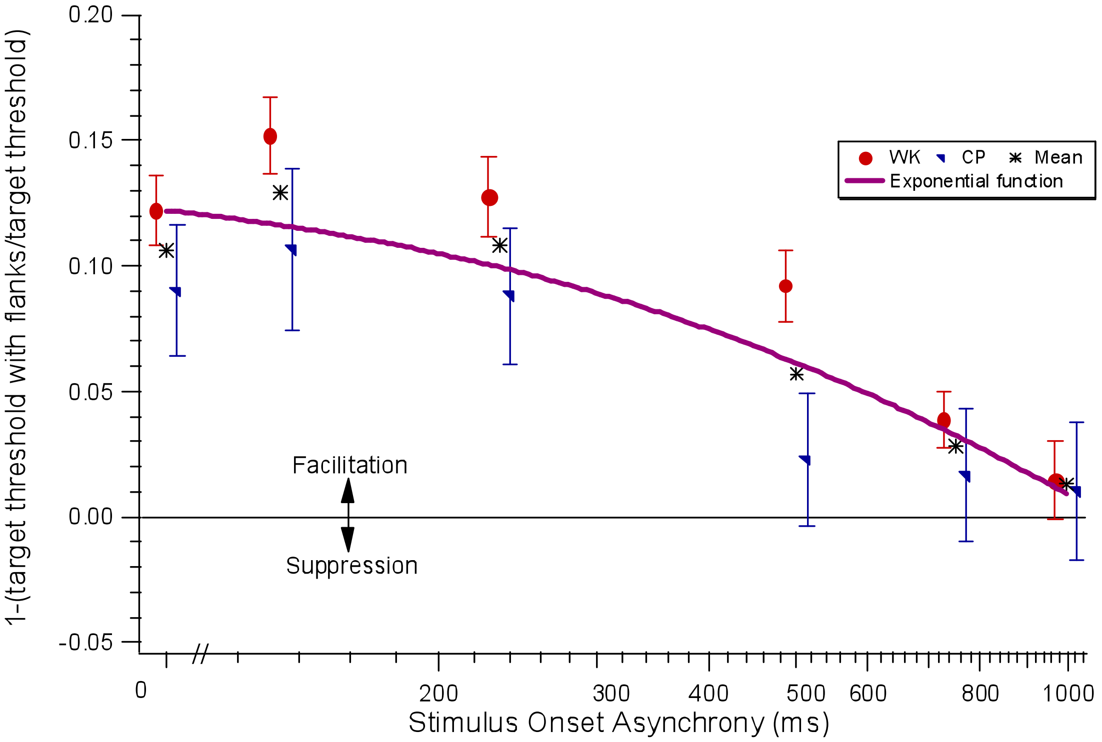


Figure 24. Monoptic, orthogonal flanks produce CDT facilitation. Error bars represent ± 1 SD. The degree of facilitation decreases as SOA increases. At the 1000ms SOA, the flank effect approaches no effect.

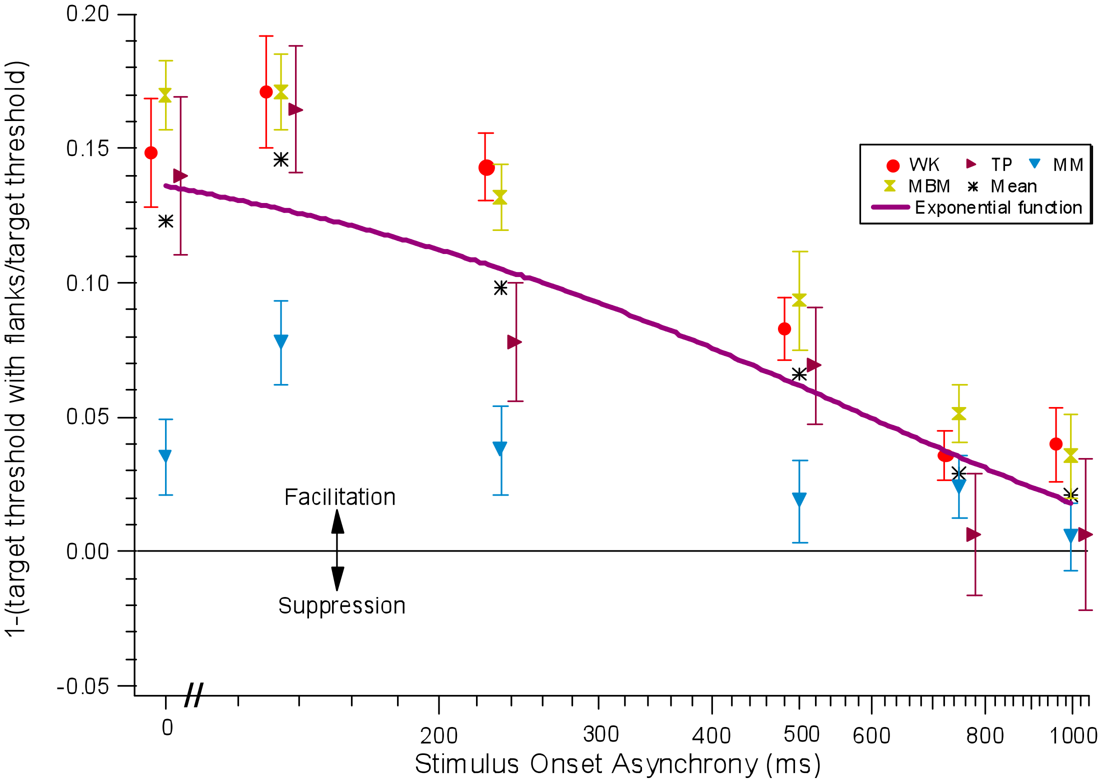


Figure 25. Dichoptic, orthogonal flanks produce CDT facilitation. Error bars represent ± 1 SD. The degree of facilitation decreases as SOA increases. At the 1000ms SOA, the flank effect approaches no effect.

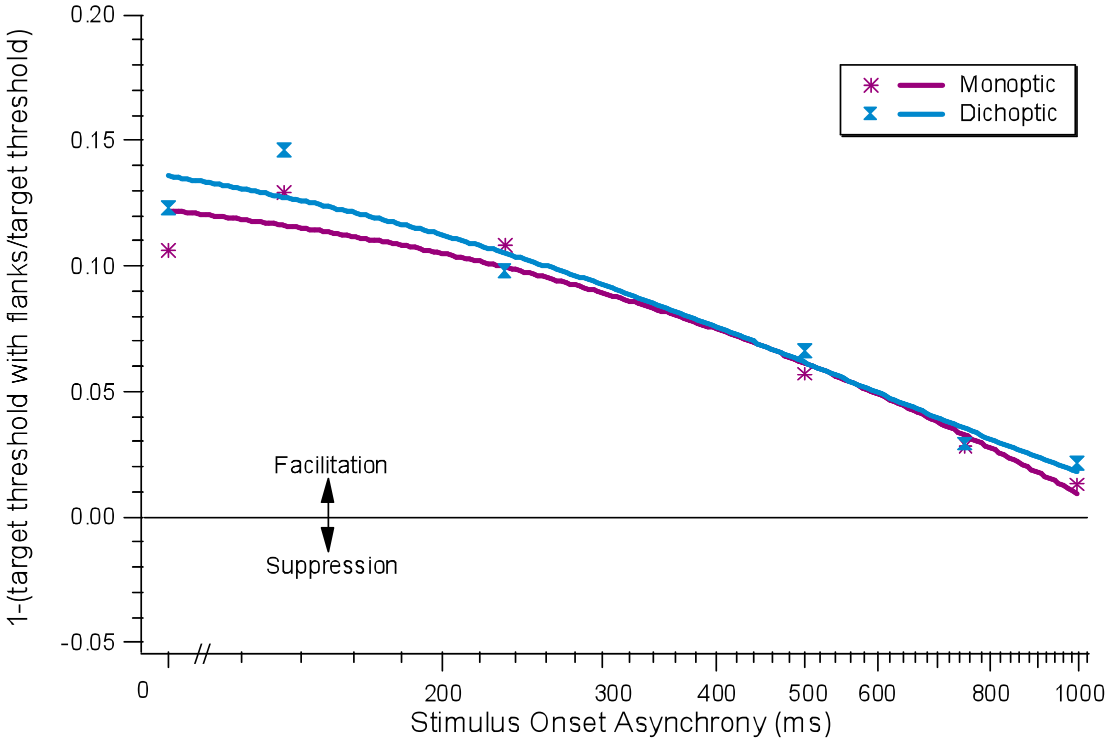


Figure 26. Orthogonal flanks under monoptic and dichoptic viewing produce very similar exponential functions. Data points represent arithmetic means of all available thresholds.

5.8 Relationship between CDT and slope of the psychometric function

To better understand the relationship between detection threshold and the slope of the Weibull psychometric function, slope was plotted against CDT for each of the main (collinear flank) experiment viewing conditions. Thus, each point on the scatter plots (Figures 27-30) represents the CDT and slope of a Weibull function and is the result of approximately 700 trials (see section 3.7 of the Methods). A regression line was then fit to the points on the scatter plot.

Analysis of 35 monoptic contrast detection thresholds (Figure 27) shows a regression line with a positive slope (0.174 ± 0.042 (SD)) indicating a positive relationship between CDT and slope (i.e. as threshold increased slope also tended to increase). The Pearson correlation between threshold and slope is 0.595 ($p < 0.001$, 1-tailed). The r^2 value is 0.354 indicating that 35.4% of the variability in slope values is directly predictable from the variability in threshold values.

Analysis of 81 dichoptic collinear flank thresholds (Figure 28) shows a positive relationship between CDT and slope (regression line slope = 0.103 ± 0.029). The Pearson correlation between slope and threshold is 0.369 ($p < 0.001$, 1-tailed) and the r^2 value is 0.136 indicating that 13.6% of the variability in slope values is directly predictable from the variability in threshold values. Fifty half-binocular collinear flank thresholds were analyzed (Figure 29) and show a positive relationship between CDT and slope (regression line slope=0.180 ± 0.023). The half-binocular viewing condition's Pearson correlation between slope and threshold is 0.746 ($p < 0.001$, 1-tailed). The corresponding r^2 value of 0.556 indicates that 55.6% of the variability in slope can be explained by the variability in CDT.

Figure 30 shows all three viewing conditions plotted on a single graph. The most apparent observation is the similarity of the monoptic and half-binocular regression lines. The slopes of the monoptic and half-binocular regression lines (0.174 ± 0.042 and 0.180 ± 0.023 respectively) are similar and the lines on the plot almost completely overlap. They also show a stronger correlation between CDT and slope ($r^2 = 0.354$ and 0.556 for monoptic and half-binocular respectively) than the dichoptic condition ($r^2 = 0.136$), which also has a flatter slope.

In summary, an analysis of the relationship between detection thresholds and slopes of the psychometric function suggests similarities between the monoptic and half-binocular viewing conditions, both of which contain intra-ocular flank contrast. This analysis also shows a trend toward differences between intra-ocular flanks contrast integration (monoptic and half-binocular viewing) and inter-ocular contrast integration (dichoptic viewing). However, due to high variability, the 95% confidence intervals overlap for all three viewing condition's regression line slopes. This high variability also precluded an analysis that included SOA.

Shallower psychometric function slopes are generally associated with threshold reductions. The positive correlation between CDT and slope for all three viewing conditions in the present study is consistent with this association. The relatively flat slope of the dichoptic regression line (compared with the monoptic and half-binocular regression line) appears to be primarily the result of greater dichoptic threshold variability at steeper slopes (Figure 30). Even at low thresholds some dichoptic slopes were relatively steep. This is consistent with dichoptic contrast integration being a fundamentally more difficult task. In total, although not statistically significant, these results agree with prior findings (see sections 5.2, 5.3, and 5.4 of the Discussion) that intra-ocular, collinear contrast integration is governed by a different neural mechanism than inter-ocular, collinear contrast integration.

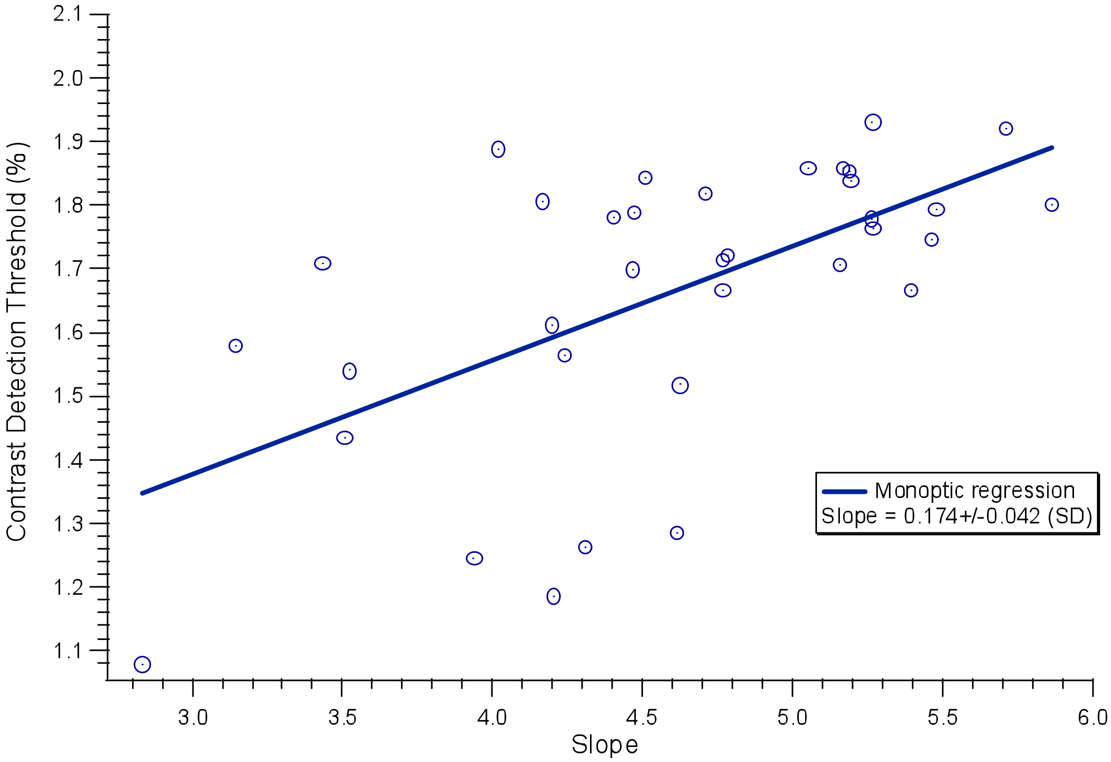


Figure 27. Slope vs. contrast detection threshold regression for monoptic viewing. The mean slope value is 4.60 ± 0.74 (SD).

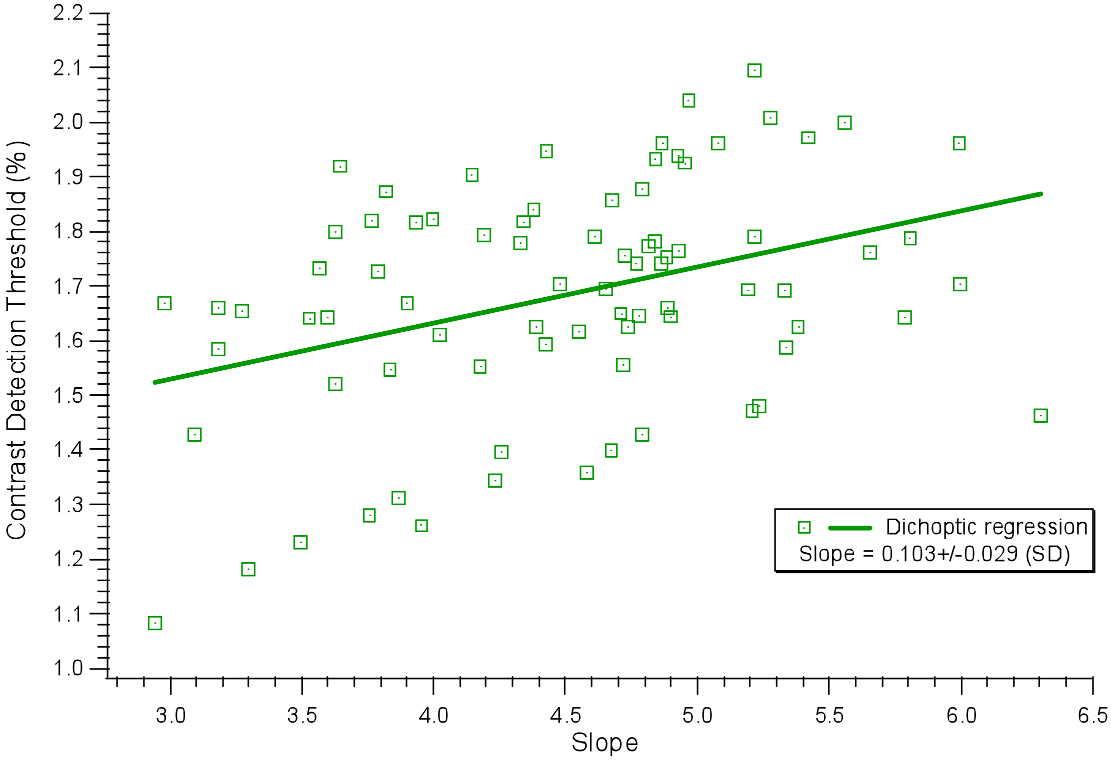


Figure 28. Slope vs. contrast detection threshold regression for dichoptic viewing. The mean slope value is 4.50 ± 0.76 (SD).

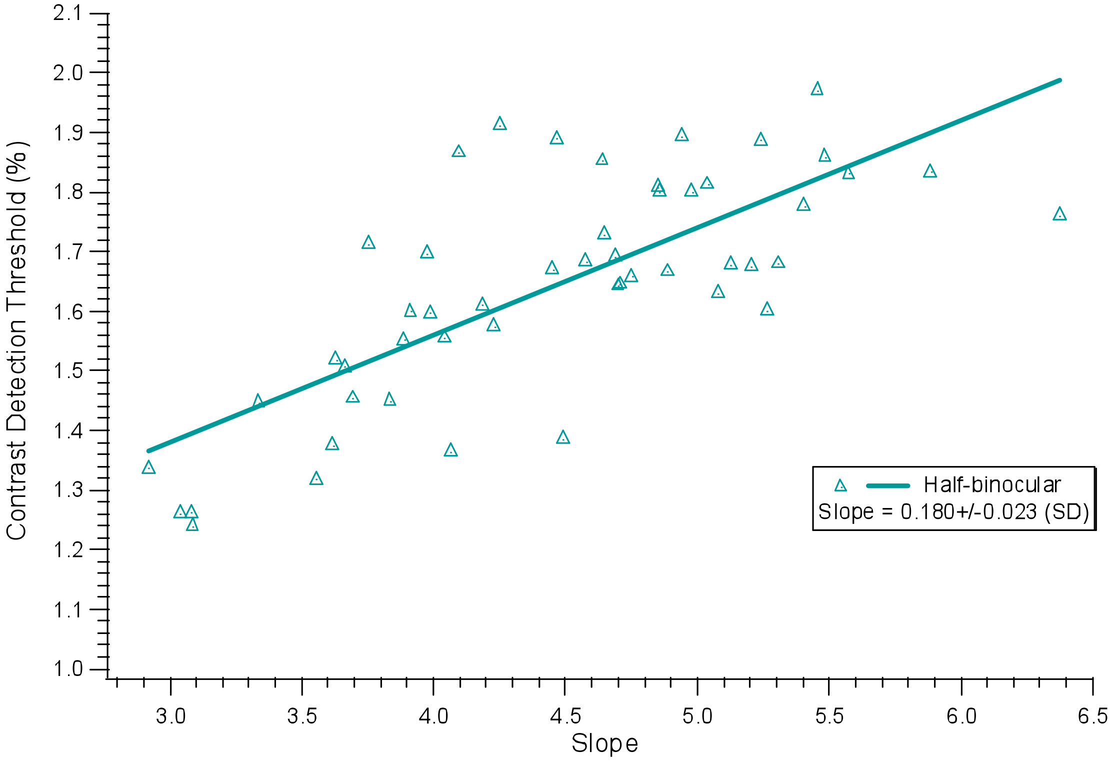


Figure 29. Slope vs. contrast detection threshold regression for half-binocular viewing. The mean slope value is 4.46 ± 0.78 (SD).

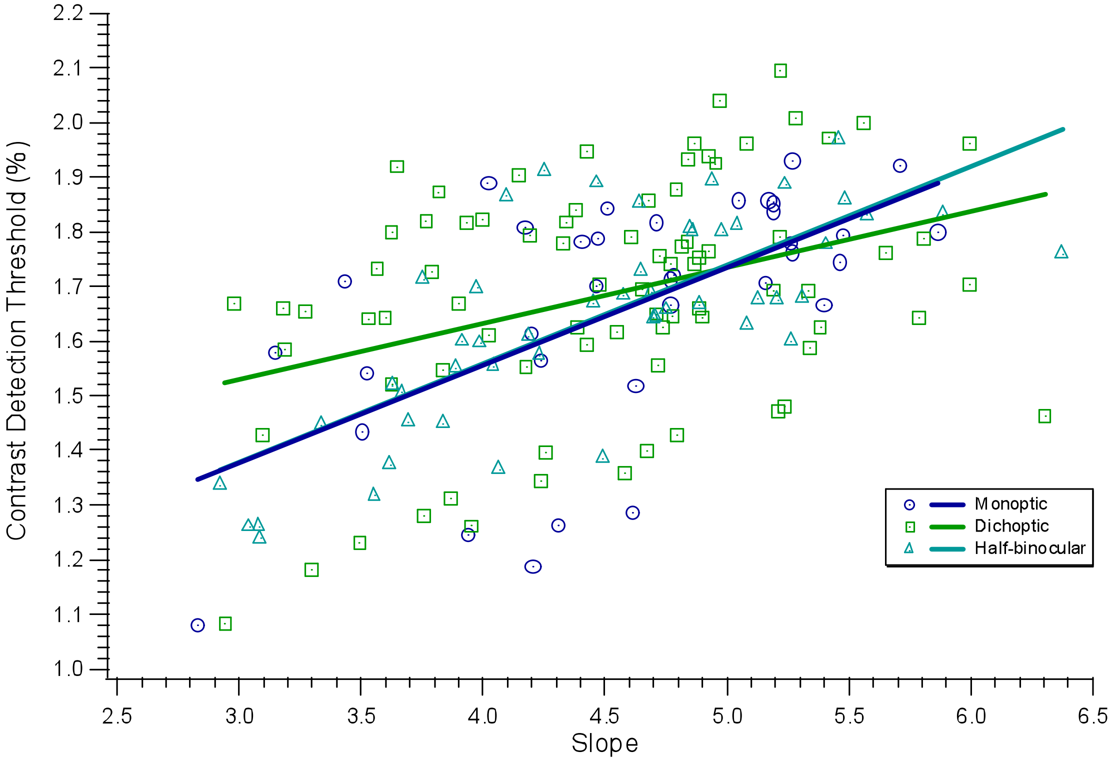


Figure 30. Weibull function slope plotted against contrast detection threshold by viewing condition.

Table 6. Relationship between CDT and slope of the psychometric function by viewing condition. Errors represent ± one standard deviation.

	Regression Slope	Pearson Correlation	r^2
Monoptic	0.174 ± 0.042	0.595 ($p < 0.001$)	0.354
Dichoptic	0.103 ± 0.029	0.369 ($p < 0.001$)	0.136
Half-binocular	0.180 ± 0.023	0.746 ($p < 0.001$)	0.556

5.9 Summary of results

Collinear flank effects on contrast detection thresholds (CDT) were measured under monoptic, dichoptic and half-binocular viewing conditions at SOAs ranging from 0ms (simultaneous presentation) to 3000ms. Monoptic flanks (Figure 12) produced CDT facilitation at shorter SOAs. Simultaneous presentation produced maximal facilitation (18.9% ± 3.86% (SE)). Monoptic flank effects approached zero at the longest SOAs evaluated, but never produced CDT suppression.

As expected, simultaneously presented collinear, dichoptic flanks (Figure 14) produced less CDT facilitation (13.9% ± 4.00%) than simultaneous monoptic flanks. This is evidence of decreased inter-ocular contrast integration. At longer SOAs (500-1000ms), dichoptic flanks produced unexpected CDT suppression (9.9% ± 5.1% at the 1000ms SOA). This suppression was statistically significant at all five longer SOAs (500ms, 567ms, 617ms, 750ms, 1000ms; $p < 0.05$).

Half-binocular flanks (Figure 18) produced CDT facilitation levels similar to monoptic viewing at shorter SOAs (18.0% ± 4.20% with simultaneous presentation). The degree of half-binocular flank facilitation decreased with increasing SOA until the effect changed to CDT suppression at the 750ms and 1000ms SOAs. However, this suppression was not statistically significant. The maximal suppression produced by half-binocular flanks was approximately one-half of the maximal suppression produced by dichoptic flanks (5.3% ± 4.7% at the 1000ms SOA), suggesting that the intra-ocular flanks mediated the effect of the inter-ocular flanks.

The individual contributions of collinear flank duration and ISI to the overall effect were also examined. In the monoptic condition, there was a trend toward flank duration having a greater contribution than ISI duration. However, this trend was not statistically significant ($p > 0.05$). In the dichoptic condition, ISI tended to have a greater contribution to the overall effect than flank duration. Again, this trend was not statistically significant ($p > 0.05$). Overall, the complete SOA (flank duration + ISI) appeared to make the greatest contribution to effect size.

To evaluate the hypothesis that the unexpected inter-ocular flank suppression at long SOAs was due to adaptation to an illusory contour, orthogonal flanks effects were measured under monoptic and dichoptic viewing. Intra-ocular (monoptic) and inter-ocular (dichoptic) flanks produced similar levels CDT facilitation with simultaneous presentation (monoptic 10.6% ± 2.3%, dichoptic 12.3% ± 6.0%). Figures 23 and 24 show individual subject and mean data for orthogonal flank monoptic and dichoptic viewing, respectively. For both orthogonal flank viewing conditions, the degree of facilitation decreased with increasing SOA until the flank effect approached zero at the 1000ms SOA.

Figure 25 demonstrates the similarity of exponential functions fit to the monoptic and dichoptic orthogonal flank means. The absence of orthogonal flank CDT suppression at longer SOAs supports the hypothesis that adaptation to an illusory contour produced the CDT suppression observed with inter-ocular, collinear flanks at longer SOAs (500-1000ms).

Chapter 6

Discussion

6.1 Comparison of intra-ocular and inter-ocular lateral contrast integration across space

Collinear flanks

As expected, flank contrast did transfer inter-ocularly to affect target detection thresholds under dichoptic and half-binocular viewing conditions. Intra-ocular flank contrast (monoptic viewing) produced CDT facilitation with simultaneous presentation. The facilitatory effect decreased as the temporal separation between initial flank presentation and target presentation (SOA) increased until it approached minimal effect at the longest SOAs. Inter-ocular flank contrast also produced CDT facilitation at simultaneous and shorter SOAs. However, at longer SOAs (500-1000ms for dichoptic viewing and 750-1000ms for half-binocular viewing) inter-ocular flank contrast produced CDT suppression that approached no effect beyond 1000ms.

Monoptic and half-binocular viewing produced similar degrees of facilitation at simultaneous and short SOAs. At the same SOAs dichoptic viewing

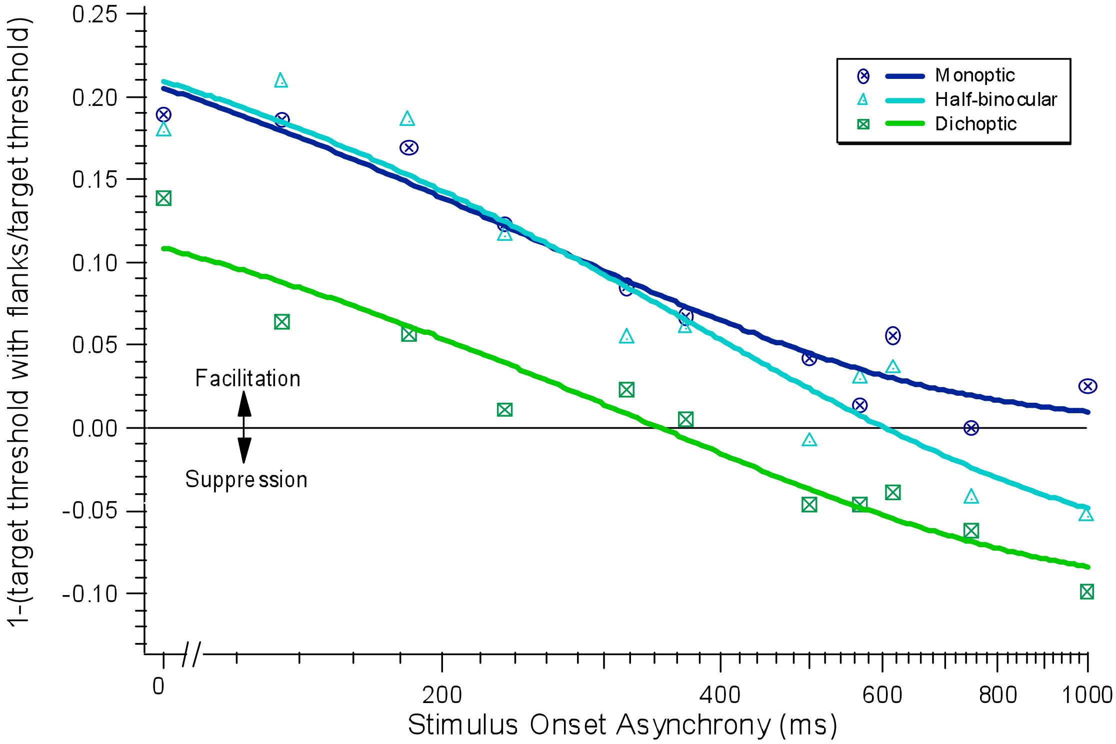


Figure 31. The mean effect of monoptic, dichoptic, and half-binocular collinear flanks on CDT up to the 1000ms SOA. Exponential functions are fit to each viewing condition. The monoptic and half-binocular functions appear very similar up to approximately 400ms SOA. Beyond 400ms, they diverge with the monoptic function asymptoting at approximately no effect and the half-binocular function transitions to CDT suppression at the longest SOAs. The dichoptic function is shaped similarly to the monoptic function, but shifted vertically such that beyond 400ms dichoptic flanks produced CDT suppression.

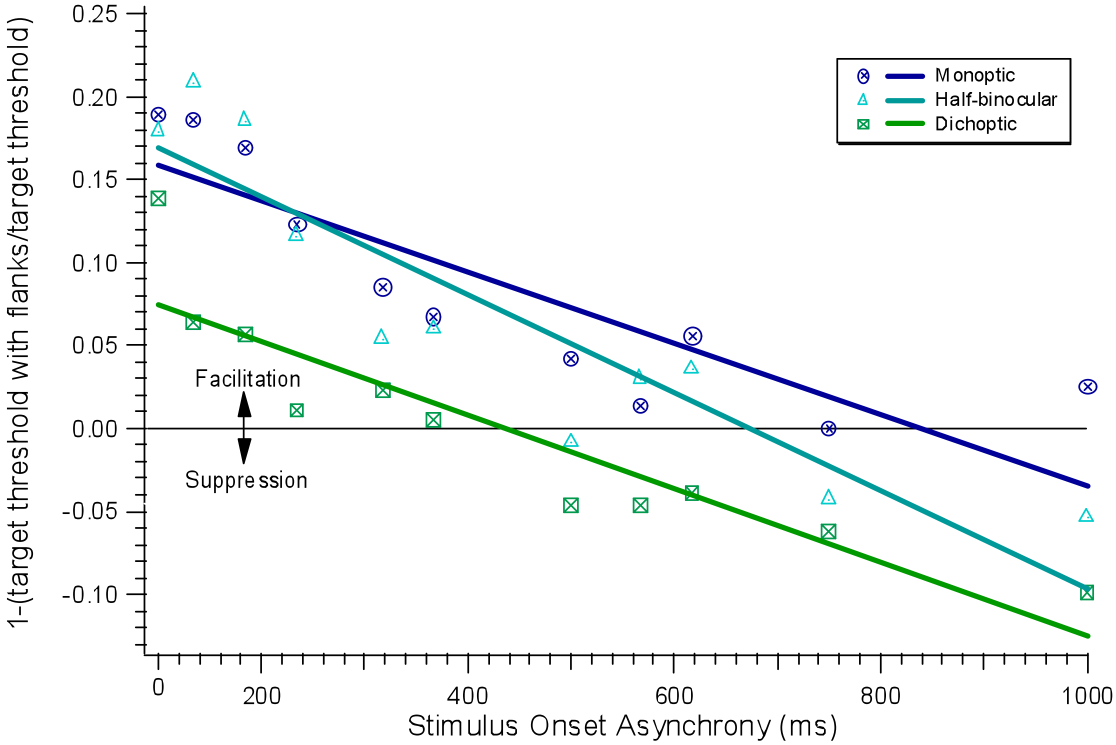


Figure 32. Line functions fit to collinear flank data up to the 1000ms SOA. Line functions provide reasonable fits to the dichoptic and half-binocular data. However, for the monoptic data, an exponential function (Figure 30) provides a better fit than a line function. This poor fit is especially noticeable at longer SOAs where the line function predicts CDT suppression that is not reflected in the data.

produced approximately one-half the degree of facilitation effect. Figure 31 shows exponential functions fit to the mean values for all subjects. These results were expected based on prior studies in our lab that demonstrated reduced inter-ocular integration of contrast across space (unpublished data). Interestingly, a visual inspection of Figure 31 shows that at SOA durations beyond 500ms the half-binocular exponential function falls approximately midway between the monoptic and dichoptic exponential functions. This matches the qualitative expectation that a viewing condition including both intra-ocular and inter-ocular flank contrast would fall between the monoptic and dichoptic flank functions.

At the longest SOAs, the collinear flank effect approached zero for both intra-ocular and inter-ocular contrast integration. In Figure 33 lines plotted through the 1500ms, 2000ms, and 3000ms SOAs for monoptic, dichoptic, and half-binocular viewing conditions converge at the 3000ms SOA. Given this convergence at a minimal level of facilitation (2.1% for monoptic, 1.4% for dichoptic, and 1.6% for half-binocular) and the relative stability of all three viewing conditions at the longest SOAs, committing subject resources beyond the 3000ms SOA seemed unnecessary.

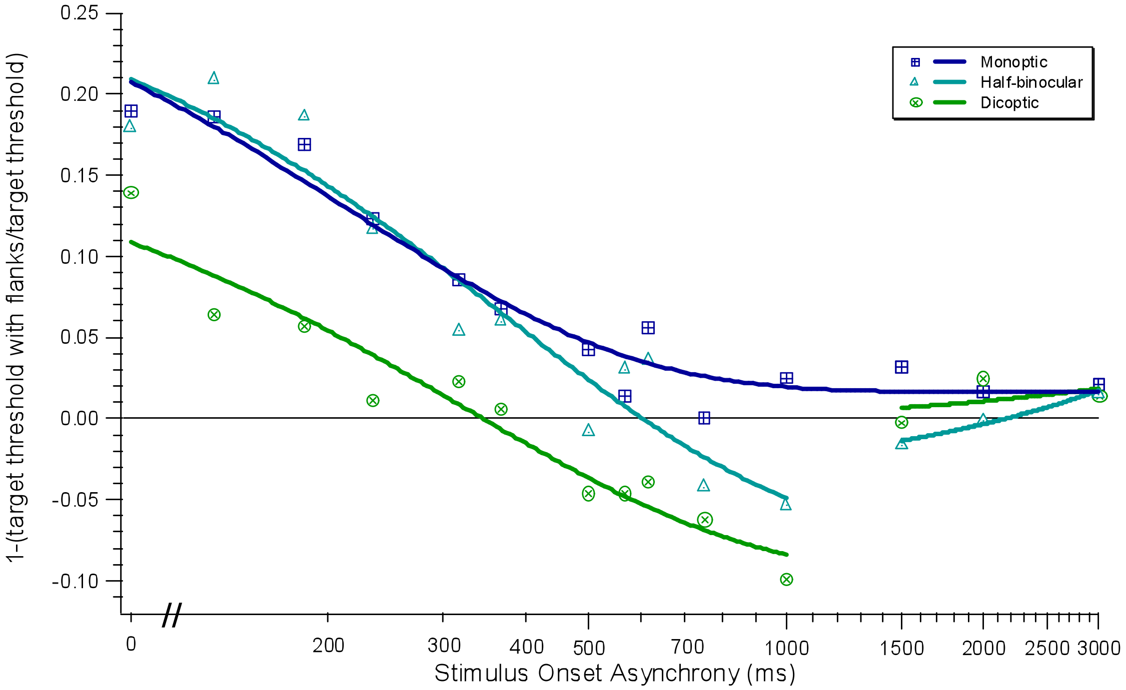


Figure 33. All three collinear flank viewing conditions approached no effect at the longest SOAs (1500-3000ms). For monoptic viewing, an exponential function is fit to the entire range of SOAs (0-3000ms) and asymptotes at minimal facilitation after approximately 750ms. Dichoptic and half-binocular viewing are fit with exponential functions for 0-1000ms SOAs. Beyond 1000ms (1500-3000ms), dichoptic and half-binocular viewing are fit with line functions and approach minimal facilitation. All three collinear viewing conditions converge at the longest SOA evaluated (3000ms).

Orthogonal flanks

Orthogonal flank contrast transferred both intra- and inter-ocularly. As shown in Figure 34, monoptic and dichoptic flank effects closely resembled one another across the entire range of evaluated SOAs (0-1000ms). This suggests that the intra- and inter-ocular mechanisms of contrast integration are similar when the target and flanks differ in orientation. With simultaneous presentation and at shorter SOAs, the effect was CDT facilitation. This effect decreased as SOA increased and approached zero at the 1000ms SOA. Of particular interest to the present study is the lack of SOA suppression under either orthogonal flanks viewing condition.

Figure 34 also allows an easy comparison of the dichoptic collinear and dichoptic orthogonal flank functions. With dichoptic, simultaneous presentation of flanks and target, the degree of facilitation is similar for both flank orientations. However, as SOA increases the vertical displacement between the dichoptic collinear and dichoptic orthogonal function increases. This suggests that the inter-ocular contrast integration mechanism is orientation channel specific.

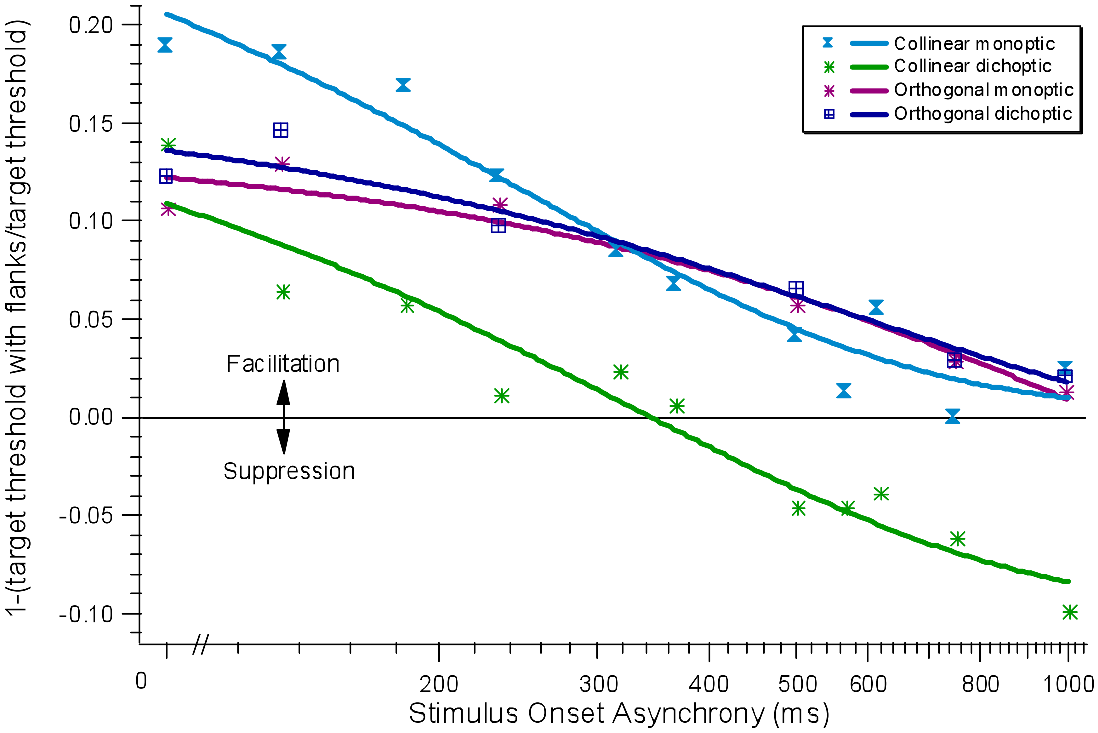


Figure 34. Comparison of collinear and orthogonal functions by viewing condition. The shape and vertical placement of orthogonal monoptic and dichoptic functions closely resemble one another, suggesting that the intra-ocular and inter-ocular mechanisms of contrast integration are similar for contrast from outside the orientation channel. The collinear monoptic and dichoptic functions resemble one another in shape, but are vertically displaced.

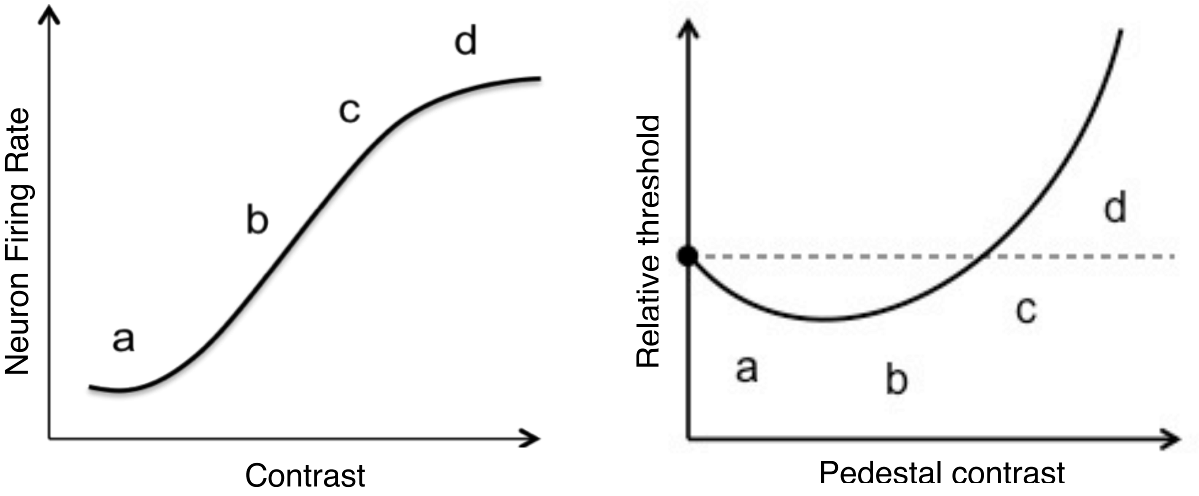
6.2 Underlying neural mechanisms

The transducer model was originally applied to same space, pedestal-type presentation of contrast, but has also been applied to spatially separated target and flank contrast (Solomon, *et al.*, 1999). In the transducer model of contrast integration, CDT facilitation is thought to be the result of interactions within a single neuron or localized group of neurons (Georgeson and Georgeson, 1987). Lower detection thresholds are caused by a criterion change in neuronal response (response threshold). At near threshold contrast levels, the neuronal response is accelerating and CDTs are lowered. At higher, suprathreshold contrast levels, the neuronal response is decelerating and CDTs are elevated. Figure 35 illustrates the contrast response function described above and explains the four stages of the function.

The non-linearity of the contrast response function described above produces a psychophysical contrast discrimination function known as the "dipper effect" (Figure 35). When a low contrast pedestal stimulus (typically from 0-1% for low spatial frequencies) is presented simultaneously with and in the same space as a target, the target just-noticable difference (jnd) contrast threshold is decreased below the target absolute detection threshold (i.e. facilitation). As the pedestal contrast increases), the target jnd then increases above the target absolute detection threshold (i.e. suppression).

Legge and Foley (1980) showed that subthreshold pedestals (the pedestal itself is not perceived) facilitate the detection of a luminance grating and suprathreshold pedestals suppress detection of a luminance grating. Based on their results, they proposed a model could account for the dipper function. The model predicts that with low contrast pedestals, target signal processing is characterized by an accelerating non-linearity that produces a reduction in target detection threshold (i.e. facilitation). Higher pedestal contrasts produce a compressive non-linearity that suppresses the target detection threshold. Again, this model refers to same space contrast integration, but has also been applied to contrast integration across space (Solomon, *et al*., 1999).

Contrast integration across space in the transducer model is expected to be rapid and have decreased effect with increasing flank separation (Huang and Hess, 2008). Neuro-physiology (Mizobe *et al*., 2001; Polat *et al*., 1998) and psychophysical (Watson *et al*., 1983) studies designed to estimate the integration time across space have suggested an upper limit of 200ms for contrast detection near threshold. This implies that, in the present study, flank contrast presented at temporal separations greater than 200ms from the target should not have an



(a) (b)

Figure 35. The contrast response function (CRF) and dipper function. (a) The CRF shows an increase in neuron response with increasing contrast and then response saturation at the highest contrast levels. Section (a) shows the response increasing in a non-linear fashion (accelerating section). In section (b) the response is increasing in a near linear manner. Section (c) shows a rapidly compressed, non-linear response (decelerating section). Finally, in section (d) the response is saturated. (b) The dipper function shows CDT facilitation at subthreshold through near threshold pedestal contrast. At suprathreshold pedestal contrast, CDT suppression is produced due to the saturating neuronal response. The horizontal dashed line represents the absolute target CDT.

effect on CDT. However, this was not observed in the present study. Temporal separations greater than 200ms (250ms and 500ms ISIs) showed flank effects that were dependant on the viewing condition. At these temporal separations, monoptic viewing tended to produce CDT facilitation (Figure 12), dichoptic viewing tended to produce CDT suppression, and half-binocular viewing produced either facilitation or suppression depending on the total SOA. These findings are not consistent with the expectations of the transducer model.

Reduction in uncertainty

A second proposed explanation for CDT facilitation in psychophysical flank studies is a reduction in uncertainty about the target location (Petrov *et al*. 2006). The uncertainty reduction explanation states that other cues could provide location information and would produce similar threshold reductions as collinear flanks. Petrov *et al*. (2006) substituted either a circle surround or a set of nonius lines for Gabor flanks as location cues. Both the circle surround and nonius line cues were very thin (1.2 arcmin width) and basically created an edge (as opposed to the sinusoid flanks used in the present experiment that had a Gaussian window applied to prevent edges). Target presentation times were also shorter than the present study (150ms and 250ms respectively). Petrov *et al*. found similar improvements in detection threshold (i.e. CDT facilitation) for all location cues. However, they did not include a flank only condition. This made comparison with their other location cues difficult (see section 2.1 of the Introduction). As a result of these issues, uncertainty reduction is not a widely accepted explanation for collinear flank facilitation.

The orthogonal flanks supplemental experiment in the present study would be expected to produce similar location cues as the collinear flanks. The monoptic orthogonal flanks did produce CDT facilitation at shorter SOAs that diminished as SOA increased, but relative to the monoptic collinear flanks they produced less facilitation (Figure 36). This suggests that, under monoptic viewing, a reduction in uncertainty is not responsible for the entire collinear flank effect.

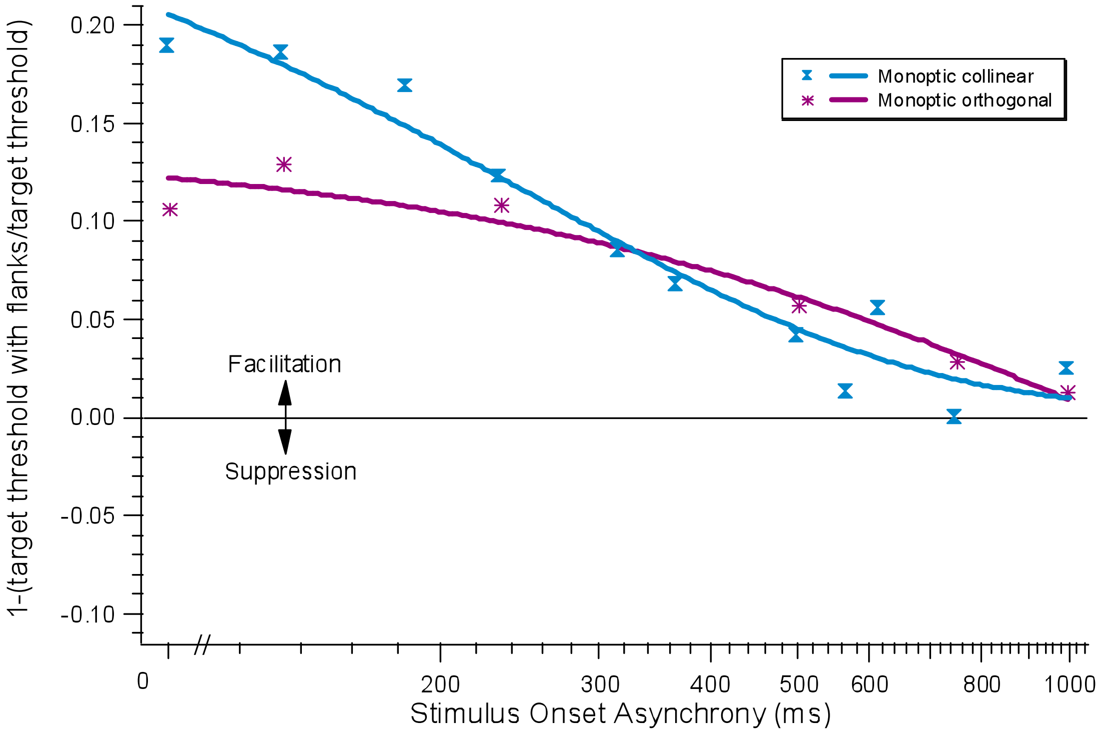


Figure 36. Comparison of monoptic, orthogonal and collinear flank effects. The curves represent exponential functions fit to means. At shorter SOAs, collinear flanks produce greater CDT facilitation than orthogonal flanks. Both decrease as SOA increases and approach no effect at the 1000ms SOA.

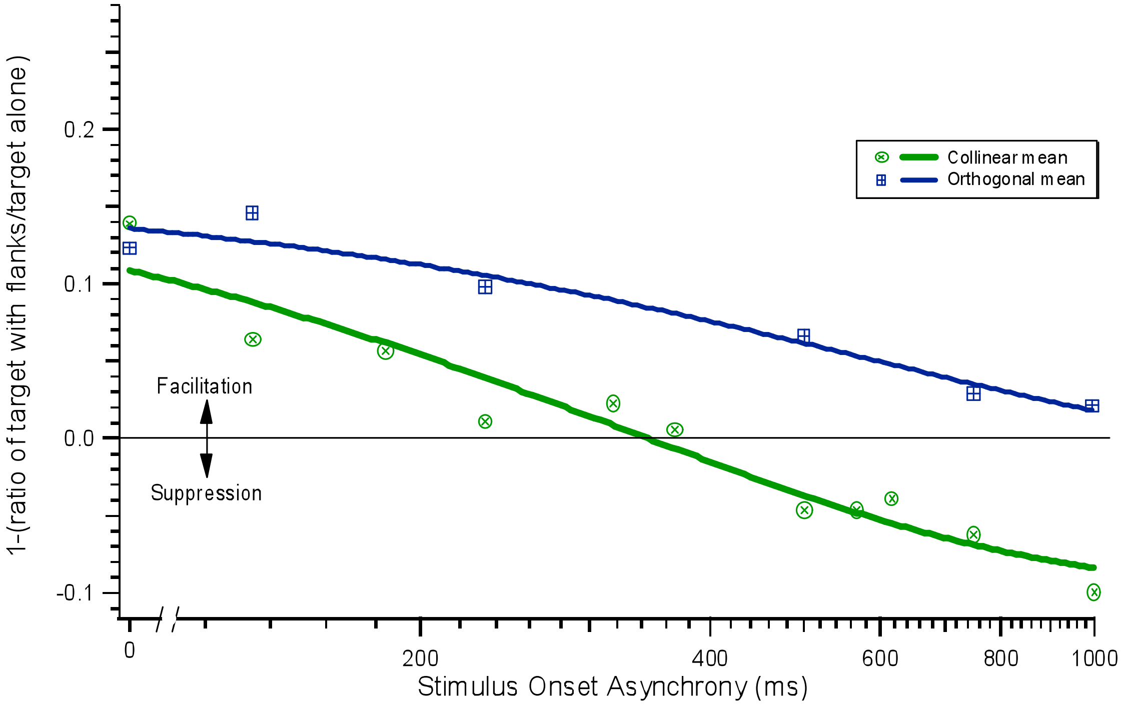


Figure 37. Comparison of dichoptic, orthogonal and collinear flank effects. Both curves represent exponential functions fit to means. Importantly, unlike the collinear flanks, orthogonal flanks did not produce CDT suppression at long SOAs. This suggests that the mechanism of contrast integration is different for orthogonal and collinear flanks.

Under dichoptic viewing, a comparison of collinear and orthogonal flank effects shows a similar effect with simultaneous presentation (Figure 37). As SOA increases the collinear flanks produce less relative facilitation than orthogonal flanks and show CDT suppression at and beyond the 500ms SOA. Here, two aspects argue against a reduction in uncertainty being the primary cause for the findings. First, the dichoptic collinear and dichoptic orthogonal functions differ markedly over time (Figure 36). Second, the CDT suppression observed at longer SOAs under dichoptic viewing is very difficult to reconcile with a reduction in uncertainty. This does not exclude a reduction in target location uncertainty as a possible effect contributor at shorter SOAs, but it seems unlikely to be the primary contributor for collinear flanks.

Lateral connections in cortex

The third neuro-physiological mechanism frequently cited as an explanation for collinear flank facilitation are long-range lateral (also referred to as horizontal) connections between two or more neuron groups in primary visual cortex (Polat and Sagi, 1993; Cass and Spehar, 2005; Polat and Sagi, 2006). This mechanism provides the most likely explanation for collinear flank CDT facilitation. One group(s) of the connected neurons is responding to flank contrast and another group is responding to the target. This mechanism is supported by physiology studies describing lateral connections parallel to the cortical surface in cat (Gilbert and Wiesel, 1979, 1983) and primate (Kapadia *et al.*, 1995 and 2000). These long-range lateral connections are un-myelinated. Consequently, they have relatively slow propagation speeds due to the slow conduction of the un-myelinated fibers. This property has been exploited to support the lateral connection mechanism by showing a positive relationship between increasing target to flank separation, and increased integration time required to reach maximal CDT facilitation (Cass and Spehar, 2005).

In the current study, the temporal properties of lateral contrast integration are consistent with what is known about the physiology of lateral connections in primary visual cortex. Intra-ocular flank effects extended to approximately 600ms SOA and inter-ocular flank effects extended up to the 1000ms SOA (Figure 30). This is in alignment with relatively slow, non-myelinated lateral connections (see section 2.6 of the Introduction).

While many neural connections exist within and between the hypercolumns of primary visual cortex, the strongest connections occur between similarly tuned neurons (Gilbert and Weisel, 1989). In primates, lateral connections between orientation-tuned hypercolumns have been shown to stretch approximately 7mm from end to end (Stettler *et al.*, 2002). Assuming an orientation column periodicity of 0.75mm, a 7mm connection would encompass about 8-10 columns (Stettler *et al.*, 2002).

Per the lateral connection model, a comparison of the current study's monoptic collinear and monoptic orthogonal flank effects (Figure 36) demonstrates the difference between orientation tuned (collinear flank) and non-orientation tuned (orthogonal flank) interactions. Here, the most pertinent finding is the relatively elevated collinear flank CDT facilitation at shorter SOAs. The collinear flank effect being greater than the orthogonal flank effect suggests that the orientation tuned cortical connections are stronger than the non-orientation tuned connections.

6.3 Application of the two-stage model of contrast integration

One recent model of contrast integration is the two-stage model proposed by Meese *et al*. (2006). This model is designed to explain the integration of contrast overlapping the same visual space, but can also be applied to the integration of contrast across space. Meese *et al.* (2006) mainly considered suppressive influences in their description of the model, but facilitative effects can be supported as well. This is demonstrated by the two-stage model's ability to support a "dipper" type function (Meese *et al*., 2006).

In the two-stage contrast gain control model (Figure 38), both intra-ocular and inter-ocular effects occur prior to binocular summation. In the present

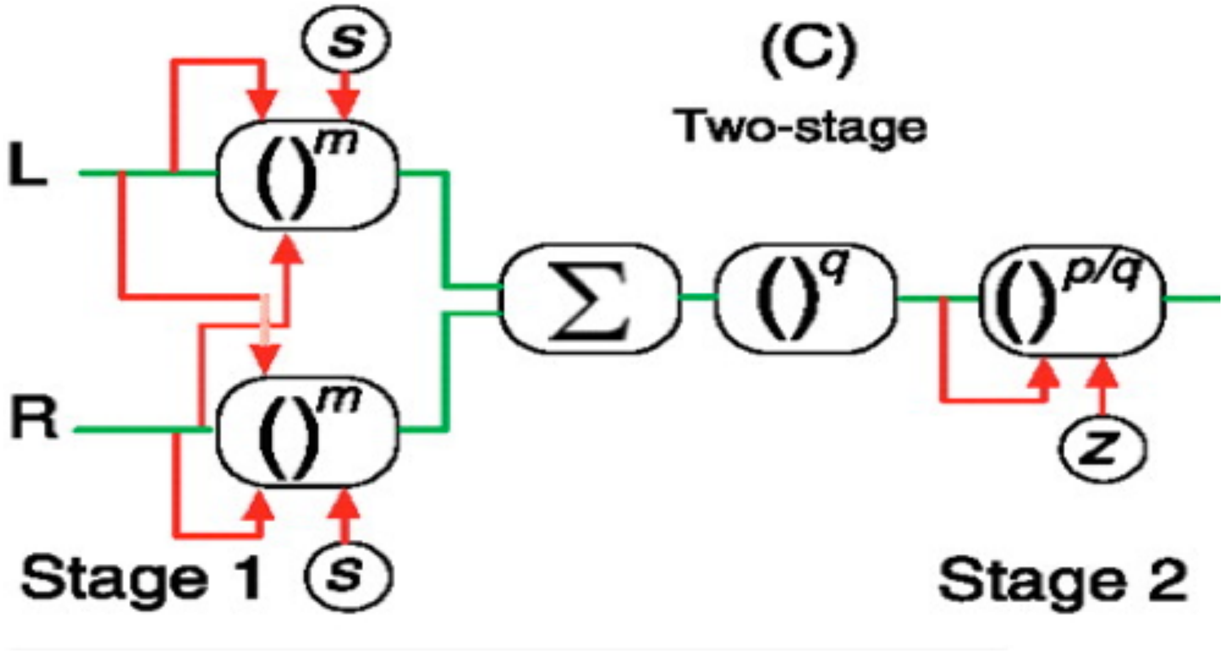


Figure 38. Model for two-stage, contrast gain control. Red arrows represent divisive suppression. R and L are right and left eye luminance contrasts, respectively. S and Z are saturation constants for the first and second stages of contrast gain control, respectively. The exponent for first stage non-linear transduction is m, and p and q are free parameters (Meese *et al.*, 2006).

Depending on the values assigned to these weights, the effect at the first monocular stage may be either suppression or facilitation of contrast detection thresholds.

study's paradigm, the intra-ocular effect is represented by the monoptic viewing condition and inter-ocular effect is represented by dichoptic viewing. The variable m is the excitatory exponent of the first monocular stage and is assumed to be the same for both eyes. The first-stage excitatory variable is represented by q. The second stage excitatory component, p, may allow deeper regions of facilitation than models with only a first stage transducer. Not shown in Figure 38 are the relative weights assigned to intra- and inter-ocular effects. These weights determine the effect (i.e. facilitation or suppression).

If we consider the possible outcomes of the half-binocular condition in terms of the two-stage model, two main alternatives emerge. The first alternative is that the additional flanks presented in the half-binocular condition enhance the effect (facilitation or suppression) due to additional inter-ocular effect. Here, under conditions that produce facilitation (e.g. shorter SOAs in the present study) additional facilitation would be expected. In the monoptic condition, collinear flank effects approached zero at the long SOAs. Following the logic of an additional inter-ocular effect, dichoptic and half-binocular flank conditions should also approach no effect at the long SOAs. However, the long SOA suppression produced by collinear, dichoptic and half-binocular flanks clearly contradicts this expectation (Figure 31).

The second alternative is that the additional set of flanks presented in the half-binocular condition activates inter-ocular suppression between the two sets of flanks. This suppression would reduce the effect of both the monoptic (same eye as target) flanks and dichoptic (fellow eye) flanks. If the original effect were CDT facilitation, then the new effect would be a reduced degree of facilitation. If, on the other hand, the original effect were CDT suppression the new effect would be a reduced degree of suppression.

At shorter SOAs, monoptic and dichoptic, collinear flanks both produced CDT facilitation (monoptic greater than dichoptic). If the flank effect is reduced by the presence of an additional set of flanks presented to the fellow eye, we would expect less CDT facilitation from both monoptic and dichoptic flanks. Depending on the relative weights assigned to intra-ocular and inter-ocular inputs, the combination of these reduced effects might result in a similar degree of facilitation as the monoptic condition. This appears to be the case when the collinear, monoptic and half-binocular conditions are compared (Figure 31). The monoptic and half-binocular exponential functions closely resemble one another at shorter SOAs. Of course, the combination of intra-ocular and inter-ocular flank effects could also result in a cumulative effect that falls somewhere between the monoptic and dichoptic conditions. Again, this would be dependant on the relative weights assigned to the inputs.

Beginning at the 750ms SOA, monoptic, collinear flanks effects approach zero. Dichoptic, collinear flanks produced CDT suppression at SOAs longer than approximately 400ms. This suppression persisted up to and including the 1000ms SOA. Reducing the effect of the monoptic flank via inter-ocular suppression would not change the overall effect significantly because the monoptic flanks already produce minimal effect at longer SOAs (Figure 12). If the dichoptic flank effect were reduced, the expected result would be decreased CDT suppression. When the minimal effect of the intra-ocular (monoptic) flanks and reduced suppressive effect of the inter-ocular (dichoptic) flanks are combined, half-binocular target CDTs would be expected to fall between the monoptic and dichoptic flank effects. Referring again to Figure 30, the results of the present study appear to support this interpretation.

To summarize, the two-stage model of contrast gain control can be applied to the integration of contrast across space. Here, the expectations of the two-stage model were applied to the results of the present study's half-binocular flank viewing condition. In the "additional inter-ocular effect" interpretation the intra- and inter-ocular flank effects are additive. This interpretation is not supported by the CDT suppression produced by collinear, dichoptic and half-binocular flanks. In an alternative interpretation, the presence of same visual space intra- and inter-ocular flank sets activates suppression between the flank sets. The effect of each flank set is subsequently reduced. Since intra-ocular (monoptic) and inter-ocular (dichoptic) flank effects are SOA dependent (Figures 12 and 13 respectively), their combined effect is also SOA dependent. This interpretation predicts that collinear, half-binocular flank effects would fall between monoptic and dichoptic effects at longer SOA. Figure 31 shows that the present study's collinear, half-binocular results support the "suppression between flank sets" interpretation.

6.4 Proposed mechanism for inter-ocular CDT suppression at longer SOAs

All 11 subjects in this study reported the perception of a filling-in effect (i.e. illusory contour) when flanks and target were presented simultaneously. For some subjects, this effect was strong enough that it was initially difficult to differentiate the appearance of the target from the fill-in effect. This observation prompted the hypothesis that the unexpected inter-ocular CDT suppression observed with collinear flanks resulted from contrast adaptation attributable to an illusory contour.

Illusory contours are known to affect perception in psychophysical studies (Tynan and Sekular, 1975; Gold *et al*., 2000; Reynolds, 1981; Ringach and Shapley, 1996; Gold and Shubel, 2006). In a neuro-imaging study, Meng *et al*. (2005) reported a strong correlation between the perception of illusory contours (termed phantoms in their study) and activity in early visual areas (V1 and V2). In addition to the suprathreshold perceptual effect of illusory contours, collinear inducing stimuli have also been correlated with subthreshold V1 activity (Kapadia *et al*., 1995; Das and Gilbert, 1999; Stettler *et al*., 2002). The area in cortex corresponding to the visual area between inducing flanks showed increases in activity even when an illusory contour was not perceived. This subthreshold (perception) correlation is important because the proposed explanation requires contrast adaptation to a subthreshold illusory contour. The sustained presence of a subthreshold, illusory contour in the same visual space and of the same orientation and spatial frequency as the target may produce contrast adaptation of cortical neurons whose receptive fields correspond to the physical target.

A walk-through of the proposed mechanism follows. First, the presentation of collinear flanks separated by a blank gap increases the firing rate of early visual cortex neurons whose receptive fields correspond to the blank gap region. This increased activity is associated with the formation of a subthreshold illusory contour. Then, the continued presence of the subthreshold contour, which may continue even after the physical inducing stimuli have been removed, produces contrast adaptation of the stimulated, binocular, cortical neurons. This adaptation desensitizes the neurons with receptive fields corresponding to the blank gap region and increases the detection threshold of a subsequently presented target stimulus.

Referring back the two-stage model of contrast gain control (Figure 38), the illusory contour formation described above would be expected to occur after binocular summation. Studies reporting the perception of illusory contours produced by dichopticly viewed flanks (upper flank shown to one eye and lower flank to the other eye) support this expectation (Tynan and Sekular, 1975; Meng *et al.*, 2007).

Does binocular rivalry contribute the threshold suppression produced by inter-ocular flanks at longer SOAs?

For several reasons it seems unlikely that binocular rivalry is the primary underlying mechanism behind the longer SOA suppressive effect produced by inter-ocular flanks. Perhaps the most apparent reason is that rivalry typically occurs when stimuli are presented in the same visual space (Alais and Blake, 2005). While the flank stimuli in the present study are basically abutting with the target, they never share the same visual space (see section 2.8 of the Introduction) and at are separated temporally at every SOA with the exception of simultaneous presentation. Stimuli also tend to produce rivalry when they have dissimilar properties, e.g. spatial frequency, color, and orientation (Alais and

Blake, 2005). All stimuli in the collinear flank experiment have identical spatial frequencies (three cpd), orientation (vertical), and are monochromatic. It seems unlikely that essentially identical stimuli would produce rivalry.

The temporal properties of binocular rivalry also seem inconsistent with the temporal properties of inter-ocular, long SOA suppression observed in the present study. Rivalry takes at least several hundred milliseconds to develop and perceptual dominance typically persists for 1-3 seconds (Brascamp *et al.*, 2005). This seems inconsistent with the time course of the present study in which inter-ocular flanks produced CDT suppression at 500-1000ms SOAs. Finally, if binocular rivalry were responsible for the longer SOA suppression produced by inter-ocular flanks, the orthogonal flank experiment would also be expected to produce CDT suppression at longer SOAs. However, this was not observed. Inter-ocular (dichoptic) flanks did not produce CDT suppression at any of the evaluated SOAs.

Why do dichoptic flanks produce long SOA suppression, but monoptic flanks do not?

A natural question is why suppression was observed under viewing conditions with inter-ocular flank contrast (dichoptic and half-binocular viewing), but not with exclusively intra-ocular flank contrast (monoptic viewing). The most apparent answer is that intra-ocular contrast and inter-ocular contrast initially integrate at different locations in the visual pathway and via different mechanisms.

The present study's analysis of the relative contributions of flank duration and ISI to the overall effect (Results section 5.6) shows that the mechanisms of intra- and inter-ocular contrast integration across space differ significantly. Viewing conditions that included intra-ocular flanks (monoptic and half-binocular) showed that flank duration had a significantly greater contribution to the overall than ISI. The inter-ocular flank viewing condition (dichoptic) did not show a significant difference between the contributions of flank duration and ISI. This suggests that the mechanism of temporal summation is different for intra- and inter-ocular contrast integration across space.

Temporal aspects of illusory contour formation

In the present study, dichoptic flanks produced CDT suppression at 500-1000ms SOAs. Half-binocular flanks produced suppression at 750-1000ms SOAs. To further examine the hypothesis that inter-ocular CDT threshold at longer SOAs results from contrast adaptation to illusory contours, it is useful to compare what is known about the temporal aspects of illusory contour formation and the temporal dynamics observed in this study. The number of prior studies examining the temporal properties of illusory contours is relatively small.

Illusory Contour Appearance

Ringach and Shapley (1996) used Kanizsa-like figures to measure binocular illusory contour formation times. For both subjects in their study, performance on a detection task asymptoted after approximately 117ms of inducing stimulus presentation time. In another, similar study Reynolds (1981) demonstrated the completion of an illusory triangle after 100ms of presentation time.

Gold and Shubel (2006) used a response classification technique to evaluate the time course to illusory contour completion. The response classification technique added luminance noise to luminance defined or illusory contours and created spatiotemporal maps by correlating subject decisions to the noise presented at each point. They concluded that the illusory contour completion process required approximately 176ms. Thus, the time required for illusory contour completion appears to be approximately 100-200ms.

Meng *et al*. (2007) used grating stimuli similar to the flanks used in this study to study the temporal dynamics of perceptual fill-in. However, unlike the flanks in this study, their stimuli were drifting and peripheral. Meng *et al*. (2007)

found that, with a two degree edge-to-edge gap between inducing elements, the mean time for an illusory contour (referred to as a visual phantom in their study) to appear ranged between 600-1300ms in four experienced subjects. In a similar experiment with 12 inexperienced subjects described in the same paper, the mean time for a phantom to appear was approximately 1075ms. Appearance time was about the same for 8% or 16% contrast inducers. Of course, these induction times include the subject's reaction time. The actual time for illusory contour completion is the observed time minus the subject's reaction time.

The inclusion of subject reaction time in the same study (Meng *et al.*, 2007) two degree gap temporal measurement makes direct comparison to this study difficult. However, they also measured illusory contour completion times for gaps up to five degrees. By subtracting the five degree and two degree gap completion times, the author's show that it took approximately 450ms to fill the additional three degrees. Assuming a linear increase in completion time with gap size, this equates to about 150ms per degree. Based on this measure (which does not include subject reaction time), it is plausible that the two degree gap in the present study would take around 300ms to be filled by an illusory contour.

Prolonged exposure to a simple pattern can alter the visibility of subsequent patterns (Blakemore and Campbell, 1969). This phenomenon is known as contrast adaptation and can occur within orientation and spatial frequency specific channels (Campbell and Sekuler, 1968; Blakemore and Campbell 1969; Blakemore and Nachmias 1971; Wilson *et al*. 1983). Adaptation desensitizes neurons responsive to contrast of that particular orientation and produces increased CDTs (suppression). Because it is orientation specific, contrast adaptation is traditionally associated with cortical neurons. However, adaptation in primates may occur as early in the visual pathway as retinal ganglion cells (Solomon *et al*., 2004). In human, psychophysical experiments contrast adaptation has been shown to occur relatively rapidly, reaching maximum desensitization to grating stimuli in less than 200ms (Foley and Boyton, 1993). For stationary, 20% contrast, two cpd mask and target gratings Foley and Boyton (1993) showed that near maximal desensitization occurred in less than 100ms.

Adding these estimates of the time required for formation of an illusory contour (300ms) and the time required for adaptation to a grating stimulus (200ms) yields a total of 500ms. This plausible approximation of the temporal properties of illusory contour formation and contrast adaptation resembles the onset time of CDT suppression observed in the present study under dichoptic viewing (500ms) and half-binocular viewing (750ms). Of course, directly comparing the temporal aspects of prior studies with the present study is complicated by the differences in stimulus type, contrast, and retinal location.

Still, what is known about the time course of illusory contour formation appears comparable to the inter-ocular CDT suppression observed in the present study.

Illusory Contour Disappearance

In the present study, the temporal limit of inter-ocular CDT suppression is shown by the SOA that produced a near zero flank effect. Under both dichoptic and half-binocular viewing, the flank effect is minimal by the 1500ms SOA and remains so up to and including the 3000ms SOA (the longest included in the experiment). Since suppression is maximal for both dichoptic and half-binocular viewing at the 1000ms, it appears that the suppressive effect expires between 1000ms and 1500ms of SOA. The next natural question is: how does the timing of suppression expiration observed in the present study compare with that in previous illusory contour studies?

In the same experiments where they examined the temporal aspects of illusory contour appearance, Meng *et al*. (2007) also investigated the timing of illusory contour disappearance. The time to disappearance for a two degree edge-to-edge gap between inducing stimuli (8% or 16% contrast) showed considerable inter-subject variability. For four experienced observers, illusory contour disappearance times ranged from approximately 600ms to 1300ms. Similarly, for 12 inexperienced subjects, the time to disappearance for the same gap size was approximately 850ms. Interestingly, the size of the gap between inducing stimuli did not seem to affect the time to disappearance.

Meng *et al*. (2007) attribute this asymmetry (illusory contour appearance being dependant on gap size while disappearance is not) to a model incorporating two sources of diffuse subthreshold input: 1) a fast component composed of feedback and feedforward connections that provide cortical input from the area corresponding to the illusory contour forming area (see section 1.1 of Chapter 1) and 2) a slow component incorporating information via unmyelinated, lateral connections (see section 1.2 of Chapter 1). In this model, only the combination of both sources of input leads to the formation of illusory contours. Input from the fast component would not be able to initiate the perception of contours by itself and would instead lead to subthreshold activity in the area of V1 corresponding to the gap region. When input from the slower, lateral connections arrives, an illusory contour is perceived. Appearance of the contour takes longer for larger gap sizes because the lateral connection input has to traverse the gap. Disappearance is not dependant on gap size because, since input from both sources is required to perceive the contour, as soon as input from the fast, feedforward/feedback source is removed the contour disappears.

To find the SOA at which it would be reasonable to expect the suppressive effects of an illusory contour to expire, the estimates of time to contour appearance and time to disappearance need to be summed. However, since for the present study's 1000-3000ms SOAs the flank (inducing stimuli) duration is 500ms and the illusory contour would not be expected to begin to process of disappearing while the inducing stimuli were still present, the flank duration (500ms) should be added to the expected time to disappearance (850ms). This summation yields a plausible estimate for illusory contour disappearance of 1350ms after initial flank presentation. This calculation falls within the observed 1000-1500ms SOA window when CDT suppression ceased and provides indirect support for the hypothesis that the inter-ocular suppression observed at long SOAs was produced by contrast adaptation to illusory contours.

Experimental support for the illusory contour hypothesis

The orthogonal flank experiment was designed to test the hypothesis that collinear flank orientation is required to produce long SOA, inter-ocular CDT suppression. Since non-collinear flanks will not produce an illusory contour, contrast adaptation will not occur, and CDT suppression would not be expected. Based on prior psychophysical studies under binocular viewing (Polat and Sagi, 1994; Polat and Sagi, 1997), CDT facilitation was expected with simultaneous, orthogonal flank presentation. These experiments have shown reduced facilitation relative to the amount produced by collinear flanks (Polat and Sagi, 1994, 1997). However, other psychophysical studies have shown CDT suppression to no effect with orthogonal flanks and in their VEP experiment Polat and Sagi (1997) showed no effect with low (8%) contrast flanks and inhibition (analogous to suppression) with 16% and 32% contrast flanks. Other neurophysiology experiments have demonstrated that orthogonal surrounds can produce a net facilitation of neuron firing rate (Jones *et al*., 2001; Sillito *et al*., 1995). As with the monoptic, collinear flanks in the main experiments, the degree of facilitation was expected to decrease as SOA increased until it approached no effect at the longest SOA (1000ms).

Both monoptic and dichoptic orthogonal flank results were consistent with the expectations described above. Exponential functions fit to the mean thresholds at each SOA show monoptic and dichoptic functions that are remarkably similar with respect to their shape and vertical placement (Figure 26). This suggests that the output of intra-ocular and inter-ocular contrast integration mechanisms is comparable for contrast from outside the orientation channel.

The finding with the most relevance to the illusory contour hypothesis is the lack of CDT suppression at longer SOAs under dichoptic viewing. This suggests that the mechanism responsible for inter-ocular suppression with collinear flanks is orientation channel specific. If CDT suppression were observed with orthogonal flanks, it would argue strongly against adaptation to an illusory contour being responsible for the dichoptic and half-binocular CDT suppression observed in the main (collinear flank) experiment. In summary, the orthogonal flank experiment findings support the hypothesis that inter-ocular, long SOA suppression resulted from contrast adaptation to an illusory contour.

6.5 Conclusion

This study investigated the temporal properties of intra- and inter-ocular lateral contrast integration in 11 adults with normal vision. The effect of collinear and orthogonal flanks on contrast detection thresholds (CDT) was measured over a wide range of flank presentations (67-500ms) and the interstimulus intervals (0-2500ms) under monoptic, dichoptic, and half-binocular viewing conditions yielding stimulus onset asynchronies (SOA) ranging from zero (simultaneous presentation) to 3000ms.

As expected, at shorter SOAs both intra- and inter-ocular collinear flanks produced CDT facilitation. Simultaneous viewing produced maximal facilitation (monoptic 18.9% ± 3.9% (SE); dichoptic 13.9% ± 4.0%; half-binocular 18.0% ± 4.2%). The facilitative effect persisted up to approximately the 600ms SOA for monoptic and half-binocular viewing, and the 400ms SOA for dichoptic viewing. The long effect duration of the collinear flanks is consistent with the temporal properties of long-range, lateral connections in primary visual cortex (Polat and Sagi, 1993; Cass and Spehar, 2005; Polat and Sagi, 2006).

Both viewing conditions that contained inter-ocular, collinear flanks (dichoptic and half-binocular) produced unexpected CDT suppression at longer SOAs. Collinear, dichoptic flanks produced statistically significant ($p < 0.05$) suppression at 500-1000ms SOAs and half-binocular flanks produced suppression at 750-1000ms SOAs. Suppression was maximal at the 1000ms SOA (dichoptic 9.9% ± 5.1%; half-binocular 5.3% ± 4.7%). This suppression was not observed with collinear, intra-ocular (monoptic) flanks and appears to be consistent with the temporal properties of illusory contour perception and contrast adaptation (see section 6.4 of the Discussion).

For collinear, intra-ocular flanks the contribution of flank duration was significantly greater than the contribution of ISI to the overall flank effect. There was not a significant difference between the contributions of inter-ocular flank duration and ISI, indicating that total SOA was the greatest effect contributor. Thus, the temporal summation of inter-ocular flank contrast across space appears to be much greater than that for intra-ocular summation. This is consistent with the longer SOA inter-ocular CDT suppression produced by collinear flanks in that both results suggest differences between the mechanisms of intra- and inter-ocular contrast integration across space.

Intra- and inter-ocular orthogonal flank viewing conditions produced CDT facilitation at shorter SOAs. Simultaneous viewing produced maximal facilitation (monoptic 10.6% ± 2.3%; dichoptic 12.3% ± 6%). For both viewing conditions, the orthogonal flank effect decreased as SOA increased until it approached zero at the 1000ms SOA. Importantly, inter-ocular (dichoptic) orthogonal flanks did not produce CDT suppression at any SOA. This suggests that the longer SOA CDT suppression produced by inter-ocular, collinear flanks is orientation channel dependent.

I propose the novel hypothesis that the CDT suppression produced by inter-ocular, collinear flanks at longer SOAs is due to a one-way, contrast adaptation from lateral propagation that produced the effect of a collinear, illusory contour. This hypothesis is supported by the dichoptic, orthogonal flank experiment that showed no CDT suppression at the same longer SOAs.

Future Directions

1. This study examined the temporal properties of contrast integration across space in adults with normal binocular vision. A natural extension of this research would be to conduct similar experiments on subjects without normal binocular vision. Ideally the non-normal subjects would have abnormal binocular vision, but normal or near normal visual acuity in each eye. This would avoid the potentially confounding influence of significant acuity differences between the eyes. Such a study would assist in the identification of visual pathway differences between normal and non-normal binocular contrast integration across space. This information could conceivably lead to clinical applications that advance the diagnosis of binocular vision deficits.

2. My hypothesis that the CDT suppression produced by inter-ocular, collinear flanks at 500-1000ms SOAs is due to a one-way, contrast adaptation from lateral propagation that produced the effect of a collinear, illusory contour was evaluated in two ways. The SOA range that produced CDT suppression was compared with a plausible range of contrast adaptation to an illusory contour based on prior studies and provided indirect support for the hypothesis. The results of the orthogonal flank study also supported the hypothesis. However, it would be preferable to directly evaluate the hypothesis without manipulating the flank

orientation and introducing the conceivably, confounding effect of the flanks and target having different orientations. It might be possible to affect illusory contour formation by introducing differences between the flanks and target that affect illusory contour formation (e.g. phase differences) without altering the orientation. Such an experiment might provide stronger support for my hypothesis.

3. One experiment that preceded this study attempted to investigate the contribution of ocular dominance to the dichoptic integration of contrast across space. That experiment was not completed due to a reallocation of human resources. However, a future attempt to correlate a measure of ocular dominance with dichoptic contrast integration strength (as measured by flank effect size) would contribute to our understanding of dichoptic contrast integration.

The presentation of targets only to the dominant eye in the present study was also a response to a finite set of resources. The dominant eye target presentation was selected due to the expectation that non-dominant eye flanks would produce a greater effect size. It would be interesting to evaluate this expectation, especially given the unexpected, longer SOA threshold suppression produced by dichoptic flanks. Would dominant eye flanks produce the same effect on detection thresholds of a non-dominant eye target? Answering this question would provide information about the role of inter-ocular inhibition in determining dichoptic flanks effects.

4. This study found that dichoptic flanks produced surprising suppression of contrast detection at longer SOAs. However, the maximum suppressive effect (approximately 10%) was relatively small. In subsequent studies larger effects sizes might be obtained by manipulating the experimental parameters. Changing from the windowed sinusoid flanks in the present study to an annulus that completely surrounds the target might encourage larger effect sizes. Altering the contrast of such an annulus might also produce larger effect sizes. Furthermore, studies that include subjects without normal binocular vision would benefit from larger effect sizes.

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