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Spatio-Temporal Variation of Binocular Contrast Summation

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SPATIO-TEMPORAL VARIATION OF BINOCULAR CONTRAST SUMMATION

By

Amber Marie Cumings

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SPATIO-TEMPORAL VARIATION OF BINOCULAR CONTRAST SUMMATION

By

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Has been approved

2/19/2018

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Ferris State University

Doctor of Optometry Senior Paper

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SPATIO-TEMPORAL VARIATION OF BINOCULAR CONTRAST SUMMATION

ABSTRACT

Purpose: This study reports on the dependence of binocular contrast summation on the spatio-temporal properties of the stimulus in normal human visual systems. **Methods**: Monocular and binocular contrast detection thresholds were measured in 6 subjects with normal binocular function. Stimuli were Gabor (2.13 x 2.13 degrees) carrier gratings windowed with a 0.75 sigma Gaussian envelope. Contrast detection thresholds were measured for 3 spatial frequencies (0.5, 3, 9cpd) and 3 temporal frequencies (2, 8 and 16Hz) using a two-down-one-up descending staircase procedure presented with a 2 Interval Forced Choice method. Threshold was calculated as the mean of the last 6 reversals. Binocular summation ratio was calculated as the average of the monocular contrast detection threshold of each eye divided by the binocular contrast detection threshold. **Results**: Binocular summation ratios varied significantly across spatial frequency ($F(2,267) = 5.634$, $p = 0.004$), but not with temporal frequencies over the 3 octave range investigated in this study ($F(2,267) = 1.516$, $p = 0.222$). Mean binocular summation ratios ranged from 1.48 (+/-0.06, SEM) to 1.84 (+/-0.07, SEM). Neither the quadratic summation model nor the two-stage model in their current forms were capable of accounting for the spatial frequency dependent change in binocular summation. **Conclusions**: Binocular summation depends on the spatial frequency of the stimulus; being maximal for spatial frequencies about 3cpd. The quadratic summation and the two-stage models at minimum, require model parameters that should scale with the spatial frequency composition of the stimulus.

ACKNOWLEDGEMENTS

This study was supported by a Ferris Faculty Research Grant and a MFVA research grant to A Raghunandan.

TABLE OF CONTENTS

Page

CHAPTER

CHAPTER 1

INTRODUCTION

Binocular summation generally refers to enhanced detectability of targets during binocular viewing over monocular viewing. In the specific case of contrast detection, binocular contrast detection thresholds have been shown to be significantly lower than monocular detection thresholds.[1-5] This superiority declines as contrast increases above detection thresholds.[6,2] While earlier reports have attributed this superiority to probability summation,[7] specifically, if each eye is considered to be an independent detector, however, evidence for the existence of cortical neurons that are driven binocularly, have discounted this theory.[4] Furthermore, when stimulus properties favor sensory fusion, then binocular summation exceeded predictions based on probability summation,[9,10] thereby providing further evidence that the binocular summation of contrast signals must involve a combination of signals between eyes. One enduring theory proposed by Legge[1,6] asserts that the effective binocular contrast signal is equivalent to the square root of the sum of each eye's contrast signal squared. This theory is known as the quadratic summation theory and predicts a $\sqrt{2}$ improvement in binocular detection thresholds over monocular detection if each eye has equal detectability. This value is also equivalent to the simple summation theory proposed by Campbell and Green[11] in which each eye's contrast signal and the variance of independent noise from each eye sums linearly at a binocular site. More recently, Meese et al.[2] proposed an alternative model, termed the two-stage model. This model comprises an early stage of suppression where monocular contrast is controlled by the ipsilateral and contralateral contrast signals in a divisive gain pool, followed by binocular summation between the left and right eyes which is then followed by a second stage of contrast gain control. This model has fared well in accounting for sub-threshold contrast summation and supra-threshold contrast interactions (in addition to other properties of contrast interactions) between eyes of normal human visual systems.[2,13]

On a related note, it has long been known that contrast detection thresholds vary considerably with the spatio-temporal properties of a stimulus.[3,14] Similarly, cortical cells in higher primates also display spatio-temporal specificity.[15-17] However, in the case of binocular summation, psychophysical studies have suggested no systematic effect of spatial frequency on binocular summation,[11,12,1,18] specifically for stationary grating stimuli. As a side note, Pardhan[30] reported spatial frequency dependence of binocular contrast summation in older subjects (58.4 ± 7.3 years) but not within a sample of younger subjects (22.6 ± 3.8 years). Anderson and Movshon[20] also reported that the spatial frequency (1.5 to 6cpd) nor the nature of temporal modulation (4Hz sinusoidal modulation, targets flashed on and off at 1 Hz, targets with no temporal modulation) had an effect on their binocular summation results. However, contrary to these reports, Levi et al.[18] reported a significant effect of in-phase temporal contrast modulation frequency on binocular summation for normal subjects. In this study, binocular summation ratios (~2-3) peaked around 1 – 2 Hz flicker and decreased progressively reaching ratios of approximately 1 around 20-50 Hz. Similarly, Harwerth and Smith[21] also showed significant decreases in binocular contrast summation for temporal contrast modulation frequencies in excess of 20Hz. Rose[22] also reported a decrease in binocular summation ratios in 0.5 cpd and 5 cpd gratings from approximately 2.0 for temporal frequencies up to about 10Hz followed by a gradual decrease toward ratios of 1 for temporal frequencies between 20 to 30Hz. Similarly, Arditi et al.[5] (1981) reported a progressive decrease in binocular summation ratios for binocular in-phase drifting gratings as spatial frequency increased from 0.3cpd to 9 cpd, there was also an indication of an adverse effect of temporal frequencies in excess of 8 Hz.

Currently, both the quadratic summation model[1,6] and more recently the two-stage model[2] do not incorporate parameters that address the spatio-temporal effects of binocular summation, as these models have largely assumed binocular summation to be relatively independent of the spatial frequency (and temporal frequency) content of the stimuli used as base data for these models. Furthermore, these considerations are becoming increasingly important and clinically relevant as there are attempts to apply these models to abnormal binocular conditions such as strabismic amblyopia.[12]

Hence, there is a need for an investigation of the spatiotemporal properties of binocular summation, and, more specifically, to weight its relevance to the predictions of existing models of binocular summation. In this study, the authors measured contrast detection thresholds for monocular and binocular grating stimuli for 3 spatial frequencies presented with 3 temporal frequencies. We report a significant effect of spatial frequency on the binocular summation of contrast in grating stimuli. Furthermore, we also show that the quadratic summation model[1,6] and the two-stage model[2] in their current forms, are unable to account adequately for variations in binocular summation observed with spatial frequency.

CHAPTER 2

METHODS

All stimuli were generated using Matlab on a MacBook Pro and presented on a gamma corrected Dell Trinitron CRT interfaced with a DataPixx™ hardware system using Psychotoolbox.[23] This allowed 16 Bit grayscale look up table resolution.

CHAPTER 3

STIMULI

Stimuli were 2.13^0 x 2.13^0 Gabor gratings presented with one of 3 cosine carrier spatial frequency gratings (0.5, 3 and 9cpd) presented within a circular Gaussian window of sigma = 0.75 degrees. A cosine temporal envelope modulated the contrast of the carrier grating at one of 3 temporal frequencies (2, 8 and 16Hz) about a mean luminance of 3.21 cd.m^{-2} (measured through the phoropter and monitor polarizing filters). The luminance modulation of the stimulus across space and time ($L_{(x,t)}$) was determined as follows:

$$L(x,t) = cos(2 * pi * f * x) * cos(2 * pi * tf * t) \; ... \; (1)$$

f = carrier spatial frequency (cpd)

tf = carrier temporal frequency (Hz)

For monocular contrast detection tasks, the Gabor stimulus was presented in the square region visible by the tested eye, while the contralateral (non-tested) eye viewed a gray square region of the same angular size and mean luminance. These two square regions were positioned side-by-side with a lateral separation of 0.57 degrees. Crossed polarized filters were placed over the left and right square regions on the monitor and over the right and left viewing apertures of a phoropter to allow each square region to be viewed dichoptically through the phoropter. The polarizing filters on the monitor and within the phoropter viewing apertures were oriented so that the right eye viewed the left image and vice versa.

Thus, all viewing conditions were consistent with a crossed-fusion setup. The screen background was dark, and viewing distance was set at 1.19m.

For binocular contrast detection tasks, the Gabor stimulus was presented simultaneously in both square regions.

CHAPTER 4

PSYCHOPHYSICAL TECHNIQUE

A 2-down-1-up descending staircase method using a two-interval forced choice (2IFC) method was used to present the stimuli. Each subject was required to report whether the stimulus was presented in the first or second interval using a left and right mouse-click, respectively. A beep of different frequency indicated the start of each interval comprising the 2IFC sequence. Each 2IFC sequence was repeated three times for a given stimulus contrast. The stimulus duration of each temporal interval was set to 1 second, with an inter-stimulus interval set at 1 second. The peak contrast of the carrier grating was decreased by 0.2 log units following three consecutive correct responses and was increased by 0.1 log unit if there was at least one incorrect response. Auditory feedback was provided after each correct and incorrect response. The staircase was terminated after 8 reversals, and the threshold was calculated as the average of the last 6 reversals. Monocular right, monocular left and binocular conditions were randomly interleaved within a single block of trials. Separate blocks of trials were run for each spatial and temporal condition. A completed block comprised 5 repetitions for each of 9 conditions (3 spatial frequencies x 3 temporal frequencies).

CHAPTER 5

SUBJECTS

Six (6) normal sighted adult subjects participated in the study. All subjects had best corrected visual acuity of 20/20 or better in each eye, stereoacuity of 40 arc seconds or better of local stereoacuity and 250 arc seconds of global stereoacuity using the Randot Stereotest, a dissociated phoria measurement between 6 prism diopters of exophoria and 3 prism diopters of esophoria at the viewing distance of 1.19m, no clinical evidence of amblyopia, strabismus, and suppression. All subjects provided signed informed consent for voluntary participation in the study. Approval for the use of human subjects was granted by the Ferris State University IRB.

CHAPTER 6

SUBJECT SETUP

Prior to the start of the test, each subject had their dissociated horizontal and vertical phoria measured at the viewing distance (1.19m) using a method similar to the Von Graefe method.[24] The respective prism values that were determined using this technique were used by each subject to fuse the stimuli for the rest of the data collection session. Each subject viewed the stimuli through the phoropter using their best corrected distance prescription (if applicable) and the neutralizing prisms described in the preceding statement. Contact lenses or habitual distance spectacle prescription could be used behind the phoropter, if desired by the subject.

CHAPTER 7

RESULTS

Analysis of the spatio-temporal variation of contrast sensitivity:

Contrast sensitivity functions for monocular and binocular viewing conditions for the 3 temporal frequencies are shown in Figure (1 A-C). Each datum represents the mean (+/- 1SEM) averaged across 6 subjects. A two-way ANOVA (Spatial Frequency x viewing condition) showed significant main effects of spatial frequency (2Hz: $F(2,263) = 176.509$, $p < 0.001$; 8Hz: ($F(2,266) = 161.483$, $p < 0.001$; 16 Hz: $F(2,272) = 169.720$, $p < 0.001$) and viewing condition (2Hz: $F(2,263) = 48.547$, $p < 0.001$; 8Hz: $F(2,266) = 38.501$, $p < 0.001$; 16 Hz: $F(2,272) = 34.580$, $p < 0.001$) for all 3 temporal frequency conditions. Furthermore, there was a significant interaction effect between spatial frequency and viewing condition across all 3 temporal frequency conditions (2Hz: $F(4,263) = 8.345$, $p < 0.001$; 8Hz: $F(4,266) = 6.356$, $p < 0.001$; 16Hz: $F(4,272) = 5.411$, $p < 0.001$). Using the Holm-Sidak method as a Pairwise Multiple Comparison Procedure, there was no significant difference between the contrast sensitivities of right and left eyes across all spatial frequencies ($p>0.05$) and all 3 temporal frequency conditions, with an exception for the 0.5cpd condition at 16Hz which showed a slightly higher contrast sensitivity confined to the left eye ($p = 0.002$). Furthermore, while the magnitude of binocular contrast sensitivity was significantly higher than monocular contrast sensitivities, this trend was confined to the 0.5, and 3 cpd carrier spatial frequency conditions ($p < 0.01$), but not for the 9 cpd condition, regardless of the temporal frequency of the stimulus. Hence, it appears that facilitation of contrast sensitivity observed with binocular viewing did indeed depend on the carrier spatial frequency of the stimulus.

Analysis of the spatio-temporal variation of binocular summation ratios:

In an attempt to explore the above trend in greater detail, binocular summation ratios were calculated for each spatial frequency and temporal frequency condition. Binocular summation ratio was calculated as the mean of the right and left monocular thresholds divided by the binocular threshold. These results are plotted in Figure 2 which displays the mean binocular summation ratios (+/- 1 SEM) pooled across 6 subjects for each spatial frequency and temporal frequency. A Two-way ANOVA (Spatial frequency x Temporal Frequency) was conducted on the binocular summation ratios. There was a significant main effect of spatial frequency ($F(2,267) = 5.634$, $p = 0.004$), however there was no significant effect of temporal frequency ($F(2,267) = 1.516$, $p = 0.222$) nor any significant interaction effect between stimulus spatial and temporal frequency ($F(4,267) = 0.909$, $p = 0.459$). Hence, binocular summation was most evident for the lower spatial frequencies, while the highest spatial frequency employed in this study (9cpd) failed to produce significant binocular summation regardless of the temporal frequency of stimulus. Temporal frequency across the 3 octave range tested in this study, also failed to display any significant effect on binocular summation regardless of stimulus spatial frequency.

Comparison of binocular summation ratio data to the quadratic summation model:

The dashed line in Figure 2 displays the $\sqrt{2}$ rule proposed by Campbell and Green[11] and is also consistent with the prediction of the quadratic summation model in cases with equal monocular detectability. It is evident that both these predictions fail to account for the significant variation of binocular summation observed with changes in carrier spatial frequency. This data is also replotted as a binocular summation contour in Figure 3. A value of 1 on the abscissa and ordinate axes represent the monocular contrast detection threshold of the right and left eye normalized to itself, respectively. The binocular contrast threshold is also expressed as a ratio relative to its respective right and left eye contrast detection thresholds. When represented in this manner, the data can be fit by the following equation to determine the type of summation between eyes:[20]

$$\left[\frac{CL}{\mathrm{CL(thres)}}\right]^{n} + \left[\frac{CR}{\mathrm{CR(thres)}}\right]^{n} = 1 \ldots \quad (2)$$

CR = Contrast presented to right eye

CR(thres) = Contrast detection threshold of right eye

CL = Contrast presented to left eye

CL(thres) = Contrast detection threshold of left eye

n = excitatory exponent

When the exponent $n = 1$, this will be consistent with simple linear algebraic summation of the contrast signals between the two eyes. However, when $n = 2$, this is consistent with quadratic summation of contrast signals between eyes. These forms of binocular summation are indicated in the Figure 3, and labelled with its corresponding value of the exponent n adjacent each dashed line. The solid lines emanating from an abscissa and ordinate value of 1, represent complete independence between eyes, excluding probability summation. It is evident from Figure 3 that the data obtained with the 3cpd (2, 8 and 16Hz) and 0.5cpd (2, and 8Hz) data are not completely consistent with the prediction of linear summation nor quadratic summation, but rather fall between these two forms of summation. However, the 9 cpd data (2, 8 and 16Hz) and the 0.5cpd (16Hz) seem to cluster close to the quadratic summation contour (n ~ 2). This representation provides fairly convincing evidence that the value of the summation exponent (n) must scale with carrier spatial frequency to provide an adequate account for the data obtained in this study. We determined the best fit exponent (n) for the empirical data for each temporal/ spatial frequency combination pooled across 6 subjects. We used a GRG Nonlinear Solving method which solved for the value of exponent n that provided the closest solution to equation (2) using the binocular data obtained in this study as input contrast. The mean value of exponent n (+/- 1SEM) for each spatial and temporal frequency condition is represented in Table 1. It is evident that the value of n exhibits significant variation with spatial frequency and displays a tendency to be much lower for the lower spatial frequencies. A two-way ANOVA (Spatial Frequency x Temporal frequency) conducted on the values of exponent n showed a significant main effect of spatial frequency ($F(2,50) = 6.350$, $p = 0.004$), but no effect of temporal frequency ($F(2,50) = 0.886$, $p = 0.420$), and no interaction effect between temporal and spatial frequency (($F(4,50) = 0.860$, $p = 0.496$).

Comparison of binocular summation ratio data to the two-stage model:

As mentioned earlier, the two-stage model proposed by Meese et al.[2] comprises an early stage of suppression where monocular contrast is controlled by the ipsilateral and contralateral contrast signals in a divisive gain pool, followed by binocular summation between the left and right eyes followed by a second stage of contrast gain control. The interaction between each eye can be expressed mathematically by the following equation for stages 1 and 2:

$$\text{Stage 1(L)} = \frac{CL^{\text{m}}}{\text{s+CL+CR}} \ldots (3)$$

$$\text{Stage 1(R)} = \frac{CR^{\text{m}}}{\text{s+CL+CR}} \ldots (4)$$

$$\text{Stage 2} = \frac{[(\text{Stage1(L)+ Stage1(R)}]^{\text{p}}}{\text{z+[Stage1(L)+}Stage1(R)]^{q}} \ldots (5)$$

CL = Contrast presented to left eye

CR = contrast presented to right eye

m = First-stage excitatory exponent

p = second-stage excitatory exponent

q = second stage inhibitory exponent

s = stage 1 saturation constant

z = stage 2 saturation constant

In an attempt to ascertain if the two-stage model was capable of accounting for the results of the present study we conducted an analysis in which all 5 parameters were fixed according to the published values of Meese et al.[2] and a separate analysis in which only parameters m and s were varied (p, q and z were fixed). The authors deem the comparison of the current data to those of Meese et al.[2] plausible, as the psychophysical method (2IFC presented within a 2-down-1-up adaptive staircase procedure), the independent stimulus variable (contrast), and the methods of stimulus presentation (monocular and binocular) were comparable to the Meese et al.[2] study. While the methods of threshold computation and spatio-temporal manipulation of the stimulus differed from their study, and may limit comparisons of absolute thresholds, however, in this study we were concerned primarily with the relative changes in thresholds and binocular summation with spatio-temporal properties of the stimulus. Additionally, given the generic parameters comprising their model, we reasoned that application of their model to the current study remains appropriate.

With respect to the first analysis, the input binocular contrast was varied using a GRG Nonlinear Solving method so as to minimize the squared difference in responses generated at stage 2 between the monocular input contrast (average of left and right eye contrast detection thresholds) and the binocular contrast for fixed values of parameters m (1.28), s (0.985), p (7.99), q (6.59), and z (0.077). This iteration provided the predicted binocular contrast threshold for a given spatial and temporal frequency pair. With respect to the second analysis, as a first approximation we constrained the fit by varying the values of m and s whilst keeping the values of p, q and z equal to 7.99, 6.59, and 0.077, respectively.[2] In fitting the data, parameters m and s were allowed to vary freely so that the squared difference in responses at stage 2 between the empirically determined monocular (average of left and right eye contrast detection thresholds) and binocular thresholds (for each subject, and each spatial/temporal frequency condition) was minimized using a GRG Nonlinear Solving method. The starting parameter values for the iterations using the above method, was first set equal to the respective values reported by Meese et al.[2] The means

(+/- 1SEM) pooled across 6 subjects, for each parameter are tabulated in Table 2 when the input contrast for equations 3, 4 and 5 was expressed as percent contrast.

A three-way ANOVA (Spatial Frequency, Temporal Frequency, and Parameter) conducted on fitting parameters (m and s) across 6 subjects showed a significant interaction effect between spatial frequency and parameter ($F(2,90) = 3.705$, $p = 0.028$). This effect was confined to parameter "s" (Holm-Sidak method: $p < 0.05$) but not parameter "m". There was also no significant interaction effect between temporal frequency and parameter ($F(2,107) = 3.128$, $p = 0.05$) and no significant three–way interaction effect between spatial frequency, temporal frequency and parameter ($F(4,107) = 1.120$, $p = 0.352$).

The results of the fits are presented in Figure 4 (A-C) which plots the mean binocular thresholds (+/- 1 SEM) obtained in this study and the predictions of the two stage model (Solid lines = fit with parameters set equal to Meese et al.,[2] dashed lines = optimized fit by varying parameters m and s only) for each spatial frequency separated according to temporal frequency. Corresponding binocular summation ratios are plotted in Figure 4 (D-F). While the general trend of the variation in binocular summation ratio with spatial frequency is captured with the two-stage model using a fixed set of 5 parameters, however, at least to a first approximation, a cursory constrained iteration (where only parameters m and s were varied) provides fairly convincing evidence that the parameters comprising the two-stage model would need to invoke at least a spatial frequency dependent scaling factor to account adequately for the sub-threshold summation (and binocular summation ratio) trends observed in the current study (see RMS values in Table 2). More specifically, it seems that the scaling factor "s" governing the magnitude of monocular and interocular divisive gain exhibits a greater dependence on stimulus spatial frequency than the monocular excitatory exponent (m). We express caution in this inference at this point, as the model fits were constrained to allow only parameters m and s to vary freely. Furthermore, given that these fits were limited to sub-threshold summation, it remains to be seen if these spatial frequency dependent parameters will also account for supra-threshold contrast effects. On a related note, Baker, Meese and Hess,[25] used a two-stage model constrained to two free parameters (k and s) to fit to their sub-threshold summation and supra-threshold contrast masking functions in normal human observers for 0.5 cpd and 3cpd grating stimuli (parameter m was fixed at the same value (1.28) for both spatial frequencies). They obtained adequate fits to their empirical data by scaling parameter "s" with spatial frequency.

CHAPTER 8

DISCUSSION

In this study, the authors aimed to investigate the joint effects of spatial and temporal frequency effects on the magnitude of binocular summation. This study provides fairly convincing evidence that binocular summation does indeed exhibit significant variation with spatial frequency over the ~4 octave range of spatial frequencies and 3 octave range of temporal frequencies employed in this study. More specifically, while temporal frequency failed to exert significant effects on the magnitude of binocular summation, carrier spatial frequency, specifically higher than about 3cpd, produced smaller magnitudes of binocular summation. The secondary aim of this study was to explore the predictions of two dominant theories that have been proposed regarding the combination of binocular contrast signals, specifically in the case of normal human binocular systems. Once again, this study shows that the quadratic summation model,[1,6] nor the two-stage model[2] in its current form were capable of accounting for the variation of binocular summation observed with the spatio-temporal frequency variation of the carrier grating. At first glance, both models require at least a spatial frequency dependent scaling of parameters to capture the trends of the data adequately.

Notwithstanding the above, it remains unclear why binocular summation exhibits a decrease with increasing spatial frequency. A possible basis for such a trend could potentially reflect an underlying velocity limitation endemic to binocular summation processes. Given that stimulus velocity of a grating stimulus is equivalent to the grating temporal frequency divided by its spatial frequency, therefore manipulations of the spatio-temporal frequency of a grating stimulus will produce corresponding changes in the velocity of the grating stimulus. Figure 5 replots the binocular summation data presented in figure 2 with the abscissa reflecting the velocity of the grating stimulus. While in the specific case of the 0.5 cpd data, there seems to be a gradual decrease in the binocular summation ratios with increasing stimulus velocity, however, this scaling effect is not evident with the 3cpd and 9 cpd data. Most notably, there is clear departure of the 9cpd data from the trends exhibited by the 3 cpd data for comparable stimulus velocities. Hence, the data trends do not provide unequivocal support for the velocity limitation hypothesis, specifically for the stimulus velocities represented in this study. This inference is also consistent with the reports of Arditi et al.[5] in which they showed no systematic scaling of binocular summation for binocular drifting gratings presented dichoptically with different spatio-temporal frequency pairings that produced a constant stimulus velocity.

There is also converging lines of evidence supporting the existence of two distinct streams of visual processing which segregate at the level of V1 and perhaps earlier.[26] Functionally, these pathways can be segregated broadly into a visual motion analysis stream (Magnocellular pathway) and a form and color analysis pathway (Parvo cellular pathway). It is conceivable that the reduced binocular summation noted with higher spatial frequencies across temporal frequencies in this study may reflect a difference in binocular summative properties between these two putative processing streams. In support of such an inference, Rose[4] measured binocular summation ratios with counterphase modulated gratings and stationary gratings for the same spatial frequency, and reported larger magnitudes of binocular summation with temporally modulated gratings which tended toward that obtained with stationary gratings as spatial frequency increased. This result seemed to support the proposal that the form analysis pathway (Parvo cellular pathway) may be inherently less efficient at binocular summation than the motion analysis pathway (Magnocellular pathway). However, while Blake and Rush[10] did report a gradual decrease in binocular summation ratio with increasing spatial frequency at a fixed temporal frequency (3.5Hz), however, in stark contrast to Rose,[4] they reported no difference in binocular summation ratios obtained with stationary gratings, flickering gratings and counterphase modulated gratings. However, they also reported interocular temporal phase selectivity for dichoptic grating for low spatial frequencies only but not for high spatial frequencies. Based on this result, they accept the assertion of two separable mechanisms that differ in their capacity to integrate information across eyes. Medina and Mullen[27] measured binocular summation ratios for luminance and iso-luminant Red-Green Gabor gratings (1.5cpd) across 3 temporal frequencies. While both types of stimuli displayed significant binocular summation, iso-luminant gratings displayed consistently lower magnitudes of binocular summation compared to luminance-defined gratings. Thus, when taken cumulatively, there is suggestion that both form and motion analysis pathways are capable of binocular summation, but perhaps to different degrees.

However, one additional hypothesis requiring further investigation is the role of fixation eye movements. Fixation eye movements typically comprise 3 major types of eye movements, namely, microsaccades, slow drifts and high frequency tremor.[28] While there is evidence that saccades and perhaps slow drifts to a certain extent are correlated between eyes (in direction and magnitude), it appears that high frequency tremor may not be.[28]

Uncorrelated (or poorly correlated) eye movements between eyes creates time-varying horizontal and vertical fixation disparities. When applied to a viewing situation with gratings, this could translate into induced phase disparities between dichoptically viewed gratings. Thus, the higher the spatial frequency, then small fixation disparities could induce much larger effective interocular phase disparities. Furthermore, given that binocular summation does depend on interocular disparity,[29] therefore, it is conceivable, that decreasing binocular summation noted with progressive increases in spatial frequencies may reflect the effect of eye movement-induced interocular phase disparities which could affect binocular summation adversely. The authors are currently exploring this hypothesis.

In summary, the current study shows a spatial-temporal dependency of binocular summation in normal human binocular systems and suggests that the magnitude of binocular excitatory interactions involved in sub-threshold binocular contrast summation may exhibit significant variation across the spatial frequency domain. Currently, these variations are not addressed adequately by existing models proposed to account for binocular combination of sub-threshold contrast signals and, as a first approximation, require model parameters that should scale with the spatial frequency composition of the stimulus. Additionally, stimulus velocity limitations are unable to account completely for the spatio-temporal variation noted with binocular summation.

LIST OF TABLES

	0.5 cpd	3 cpd	9 cpd
2 Hz	1.42 +/- 0.13	1.22 +/- 0.13	1.79 +/- 0.18
8 Hz	1.43 +/- 0.09	1.47 +/- 0.14	2.04 +/- 0.21
16 Hz	1.59 +/- 0.16	1.32 +/- 0.15	1.59 +/- 0.25

Table 1

Parameter	2 Hz			8 Hz			16 Hz		
	0.5 cpd	3 cpd	9 cpd	0.5 cpd	3 cpd	9 cpd	0.5 cpd	3 cpd	9 cpd
m	1.11+/-0.041	1.09+/-0.037	1.14+/-0.033	1.23+/-0.032	1.18+/-0.059	1.16+/-0.047	1.24+/-0.079	1.07+/-0.038	1.09+/-0.056
s	1.04+/-0.039	1.35+/-0.248	1.00+/-0.004	0.99+/-0.011	1.065+/-0.056	0.98+/-0.006	0.99+/-0.015	1.01+/-0.019	0.99+/-0.006
RMS (%) All 5 fixed	0.2293			0.3668			1.8410		
RMS(%) m and s optimized	0.0165			0.1441			0.9894		

Table 2

LIST OF FIGURES

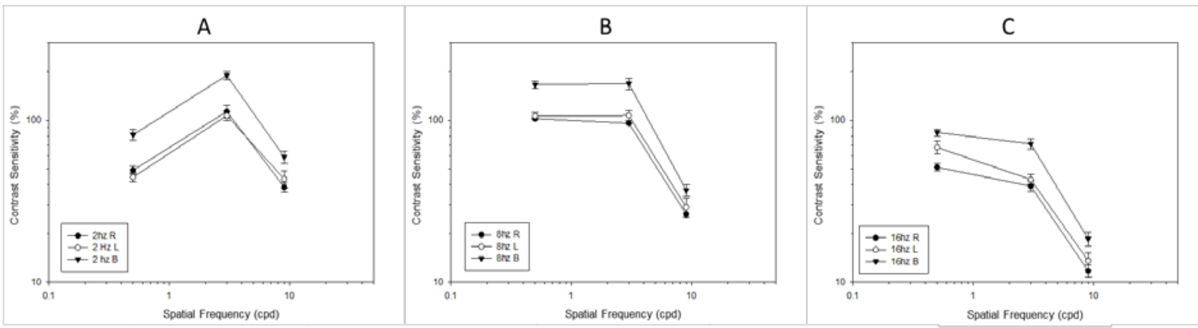

Figure 1

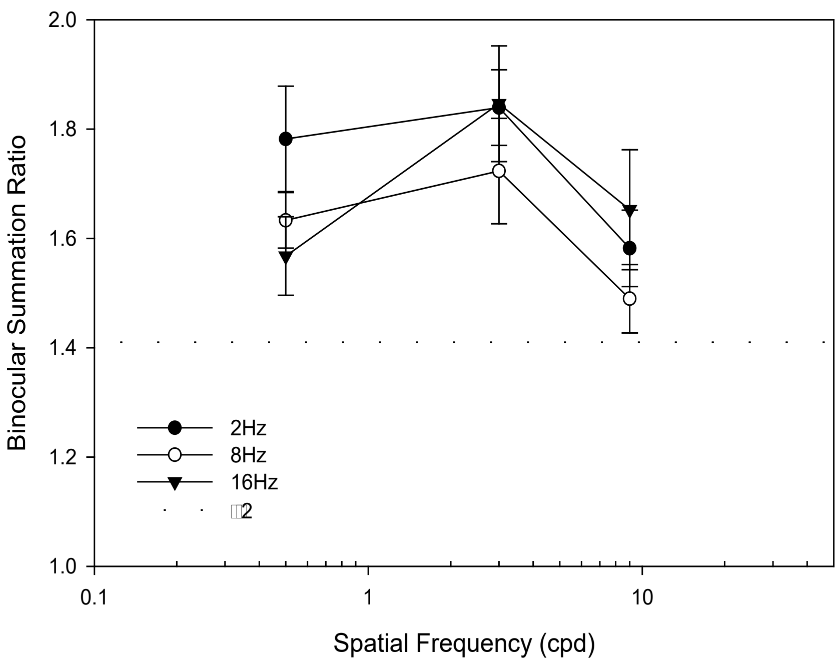

Figure 2

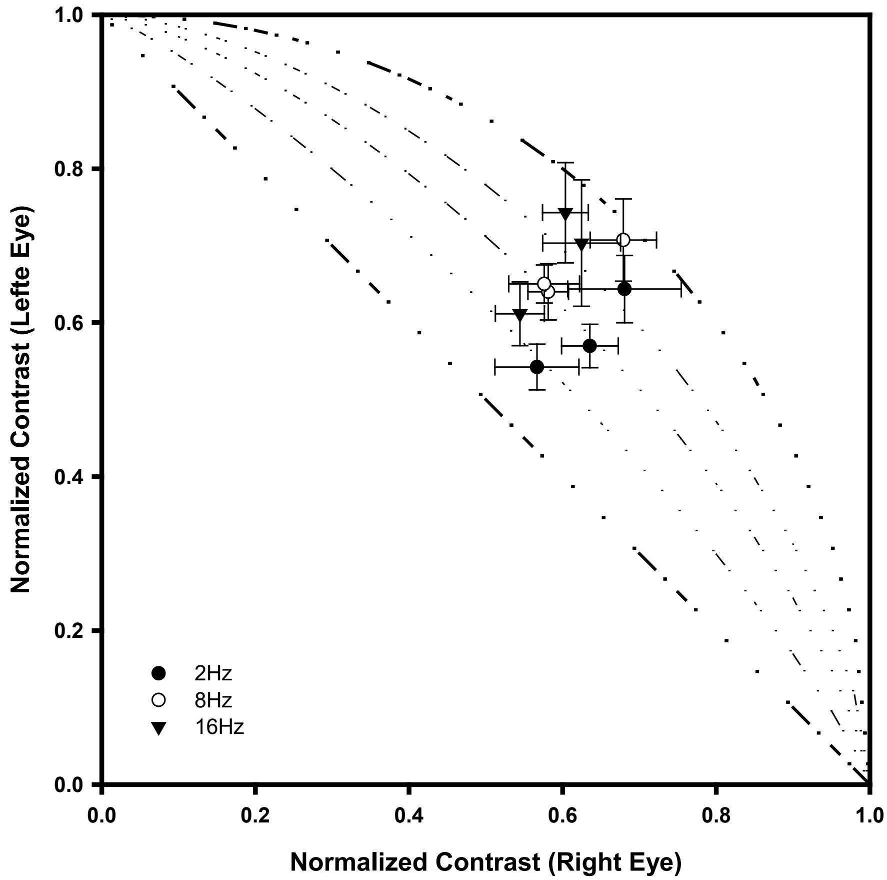
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
Normalized Contrast (Lefte Eye)
Normalized Contrast (Right Eye)
2Hz
8Hz
16Hz

Figure 3

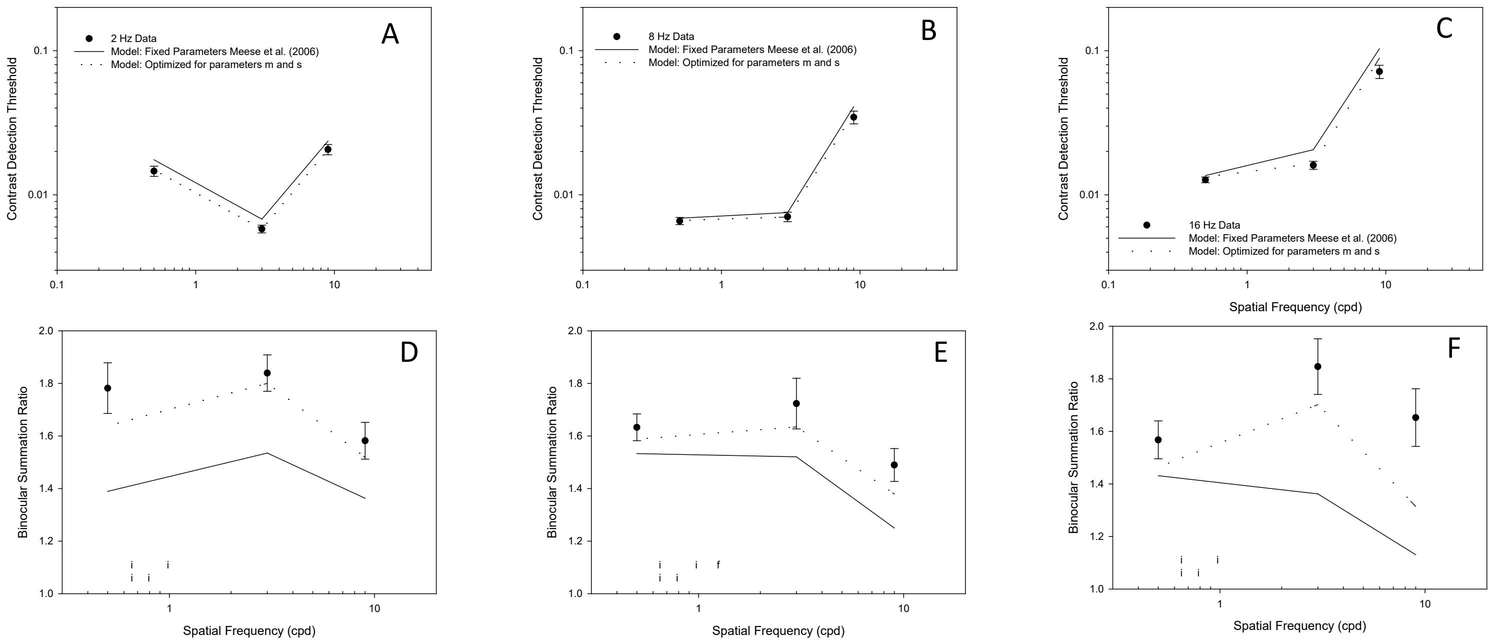

Figure 4

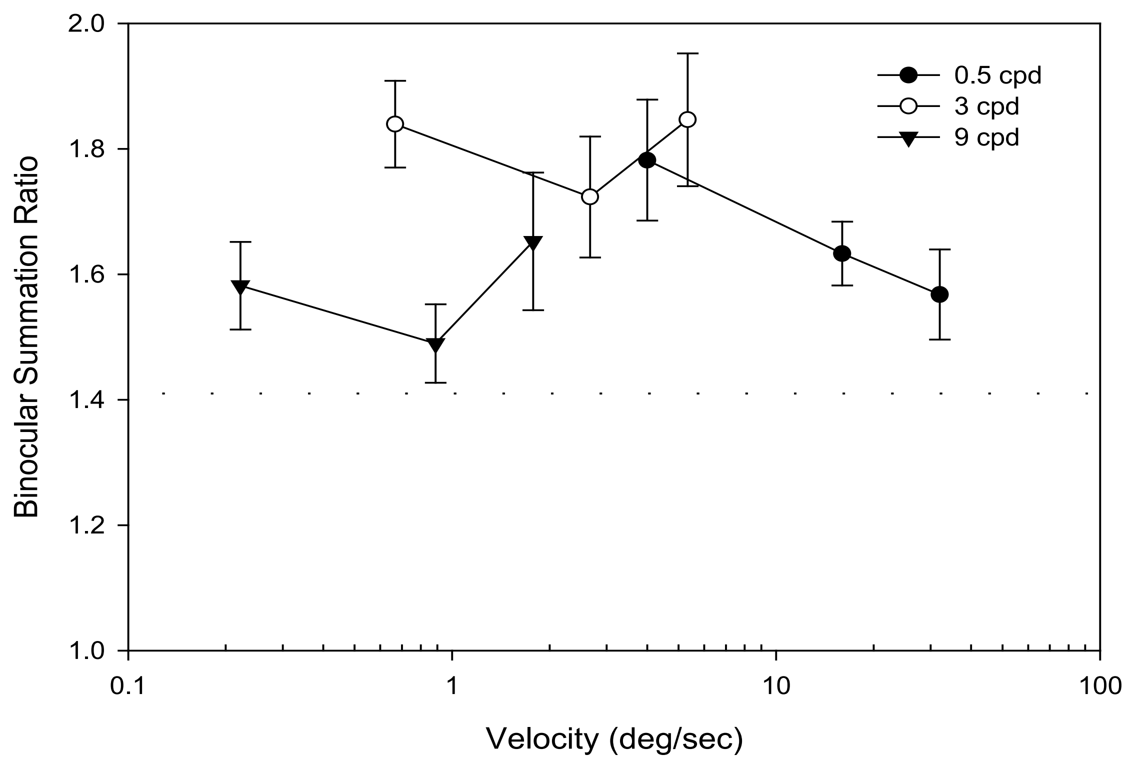

Figure 5

LEGENDS

Figure 1A,B,C: Mean (+/- 1SEM) monocular (R, L) and binocular (B) spatial contrast sensitivity functions for 2, 8 and 16Hz. Data pooled across 6 subjects.

Figure 2: Mean (+/- 1SEM) binocular summation ratios for 2, 8 and 16Hz as a function of spatial frequency. Binocular summation ratio = average of right and left monocular contrast detection threshold/ Binocular Contrast threshold. Dashed line depicts prediction of the √2 rule of binocular summation.

Figure 3: Binocular Summation Contour: Mean Binocular threshold (+/- 1SEM) expressed relative to its respective right and left eye contrast detection threshold for each spatial frequency (number adjacent to datum) and temporal frequency. The number adjacent to each dashed line represent exponent (n) values (see equation 2 in text) associated with each dashed curve. These contours can be compared to the values of exponent (n) derived from the best fits to the empirical data using equation 2.

Figure 4: Mean (+/- 1SEM) binocular contrast detection thresholds for each spatial frequency are plotted with the predicted binocular thresholds of the two-stage model when **(A-C).** Mean (+/- 1SEM) for each spatial frequency are plotted with the binocular summation ratios predicted from the binocular contrast detection threshold predictions of the two-stage model **(D-F)**. Solid lines: All 5 parameters were fixed according to Meese et al. (2006). Dashed lines: Optimized fit using the parameters reported in Table 2.

Figure 5: Mean (+/- 1SEM) binocular summation ratios plotted according to the respective velocity (degrees/sec) of the grating stimulus, separated according to the carrier spatial frequency (cpd). Dashed line depicts prediction of the √2 rule of binocular summation.

Table 1: Mean (+/-1 SEM) of exponent n derived by determining the best fit to the empirical data using equation 2 for each spatial and temporal frequency condition.

Table 2: Mean (+/-1 SEM) of parameters m and s of the two-stage model derived by determining the best fit to the empirical data using equations 3,4 and 5 for each spatial and temporal frequency condition. The last 2 rows represents the RMS values (in percent contrast) derived for the fitted data when all 5 parameters were fixed according to the values of Meese et al. (2006) and when parameters m and s were optimized in the current study.

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FERRIS STATE UNIVERSITY

Institutional Review Board for Human Subjects in Research

Office of Research & Sponsored Programs, 1010 Campus Drive, FLITE 410G · Big Rapids, MI 49307

Date: August 11, 2017

To: Dr. Avesh Raghunandan

From: Dr. Gregory Wellman, IRB Chair

Re: IRB Application #140902 *(A Study of the spatio-temporal characteristics of inter-ocular suppression and binocular summation in normal and strabismic human visual systems)*

The Ferris State University Institutional Review Board (IRB) has reviewed and approved your request for an extension to continue using human subjects in the study, *"A Study of the spatio-temporal characteristics of inter-ocular suppression and binocular summation in normal and strabismic human visual systems"* (#140902). This approval has an expiration date of one year from the date of your previous expiration. **As such, you may collect data according to the procedures outlined until September 6, 2018.**

Your project will continue to be subject to the research protocols as mandated by Title 45 Code of Federal Regulations, Part 46 (45 CFR 46) for using human subjects in research. It is your obligation to inform the IRB of any changes in your research protocol that would substantially alter the methods and procedures reviewed and approved by the IRB in your application. Thank you for your compliance with these guidelines and best wishes for a successful research endeavor. Please let us know if the IRB can be of any future assistance.

Regards,

Ferris State University Institutional Review Board
Office of Research and Sponsored Programs