# **ORIENTATION TUNING IN HUMAN COLOR VISION:**

# IS THERE COLOR WITHOUT FORM BEYOND MONOCULAR

# **DETECTION?**

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## **Contribution of Authors**

The contribution of authors to the work presented in this thesis are as follows:

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ASC and KTM contributed to the conception of all of the experiments. MG also contributed to the conception of the first experiment, developed its model, and collected half of its data. All other data collection was done by ASC. ASC completed all analyses, created all figures, and wrote the thesis under the supervision of KTM.

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## List of Abbreviations

2AFC	Two-Alternative-Forced-Choice				
2x2FC	Two-by-Two-Forced-Choice				
c/deg	Cycles Per Degree				
CRT	Cathode Ray Tube				
deg	degree				
LSF	Low Spatial Frequency				
MSF	Medium Spatial Frequency				
PSE	Point of Subjective Equality				
RMS	Root Mean Square				
SE	Standard Error				
SEM	Standard Error of the Mean				
SF	Spatial Frequency				
SR	Summation Ratio				
ViSaGe	Visual Stimulus Generator				

#### Abstract

Orientation processing is fundamental to the encoding of form. While it was once thought that form and color were entirely segregated, there is now evidence for both orientation tuned and untuned color mechanisms. A previous psychophysical experiment found a monocular color vision mechanism, revealed at low spatial frequencies, that lacks orientation tuning and may act as a surface color or 'blob' detector. However, monocular color vision at mid spatial frequencies and achromatic vision both displayed orientation tuning, and are therefore capable of form processing. This research thesis tests the limitations and extent of the proposed untuned mechanism in color vision in three investigations of related visual behaviors with both color and achromatic stimuli at different spatial frequencies. First, we asked if binocular vision also has mechanisms that are not tuned for orientation. Using the technique of subthreshold summation, we measured binocular summation of dichoptic plaids over a range of component orientation differences. An orientation tuned model provided a good fit to all conditions with similar bandwidth estimates. Binocular summation in color vision is orientation tuned. Next, we examined the perception of high contrast stimuli to see if an untuned color mechanism influences vision above threshold. We employed a contrast matching paradigm in which high contrast orthogonal monocular plaids were perceptually matched with their component gratings. Summation was calculated as a ratio of contrast of the plaid to its perceptually matched grating. High summation could indicate an influence of untuned mechanisms. While low spatial frequency color plaids had the highest average summation of perceived contrast, it was statistically indistinguishable from achromatic stimuli. In the final experiment, we used the assumption of labelled lines to test for isotropic mechanisms in identification. We asked if identification of oriented gratings is possible at detection threshold and so concurrently measured identification and detection thresholds. While orientation discrimination was worse for low spatial frequency color stimuli, orthogonal gratings could be distinguished at threshold. Identification at threshold in monocular color vision is orientation tuned. We find no direct evidence of an untuned color mechanism beyond monocular detection. When any potentially untuned signals go through the additional processing inherent to these tasks, orientation tuning is imposed. Form and color appear intertwined beyond early vision.

#### Resume

Le traitement de l'orientation est essentiel pour l'intégration des formes. Alors qu'il a longtemps été considéré que la forme et la couleur étaient séparées, il y a désormais des preuves que des mécanismes de couleurs sélectifs et non-sélectifs à l'orientation existent. Une étude psychophysique antécédente a déterminé un mécanisme monoculaire de vision de la couleur, révélé à basse-fréquence spatiale qui ne présente pas de sélectivité à l'orientation et qui pourrait agir en tant que détecteur de surface de couleur ou de 'blob'. Cependant, la vision chromatique monoculaire à moyennes fréquences spatiales ainsi que la vision achromatique ont présenté une sélectivité à l'orientation et sont donc capables de traiter la forme. Cette thèse de recherche teste les limites et l'étendue du mécanisme non-sélectif proposé pour la vision de la couleur par trois expériences sur les comportements visuels liés entre des stimuli chromatiques et achromatiques à différentes fréquences spatiales. Premièrement, Nous nous sommes demandés si la vision binoculaire a aussi des mécanismes non-sélectifs à l'orientation. En utilisant la technique de sommation sous-liminaire, nous avons mesuré la sommation binoculaire de plaids dichoptiques pour une gamme de composantes d'orientations différentes. Un modèle sélectif à l'orientation représente correctement toutes les conditions avec la même bande-passante estimée. La sommation binoculaire en vision chromatique est sélective à l'orientation. Ensuite nous avons étudié la perception des stimuli à haut contraste afin de déterminer si un mécanisme de couleur non-sélectif influence la vision supra-liminaire. Nous avons employé un paradigme d'ajustement de contraste dans lequel des plaids orthogonaux monoculaires à hauts contrastes étaient perceptuellement ajustés avec leurs composantes réseau. La sommation a été calculée par un ratio du contraste du plaid en fonction du réseau perceptuellement ajusté. Une large sommation pourrait indiquer la présence de mécanismes non-sélectifs. Alors que les plaids de couleur basse-fréquence avaient la plus grande sommation moyenne de contraste perçu, elle n'était statistiquement pas distinguable des stimuli achromatiques. Dans la dernière expérience, nous avons utilisé l'hypothèse de détecteurs labellisés afin de tester les mécanismes isotropes d'identification. Nous nous sommes demandés si l'identification de réseau orientés était possible au seuil de détection et pour cela nous avons mesuré simultanément les seuils d'identification et de détection. Alors que la

discrimination d'orientation était pire pour les stimuli chromatiques à basse-fréquence, les réseaux orthogonaux pouvaient être distingués au seuil. L'identification au seuil en vision chromatique monoculaire est sélective à l'orientation. Nous n'avons trouvé aucune preuve directe d'un mécanisme de couleur non-sélectif au delà de la détection monoculaire. Quand un quelconque signal non-sélectif potentiel passe par le traitement additionnel inhérent à ces tâches, une sélectivité à l'orientation s'impose. La forme et la couleur apparaissent ainsi entremêlées au delà des premiers stades de la vision.

#### INTRODUCTION

Color adds a distinct richness to our visual world. In the early days of color research, Newton pictured colors exciting our nerves like notes on a musical scale, each associated with a particular tone (Newton, 1704). Indeed it can be very evocative; the most common forms of synesthesia involve attaching color to letters, numbers, time, and sound (Day, 2005). Yet, we can easily imagine a scene without color, it is felt to be a unique and separate perceptual quality. When most media was still shown in black and white, psychologists alleged that we predominantly dreamed without color (Hall, 1951). In vision research, color is often a secondary visual property, removed for ease of study. However, it is a meaningful and critical part of normal human vision. From form perception to cognition, it aids fast recognition and easier remembrance (Gegenfurtner & Rieger, 2000). Historically overlooked, we are now uncovering the complex ways color is ingrained into our basic visual abilities. We have recently begun to understand its contributions to visual tasks such as motion perception (Michna & Mullen, 2008), stereopsis (Kingdom & Simmons, 1996), shape formation (Mandelli & Kiper, 2005), and orientation discrimination (Beaudot & Mullen, 2005; Webster, De Valois, & Switkes, 1990). For this graduate research thesis, I have completed a series of experiments investigating the orientation processing abilities of color vision, an essential property of form encoding. These experiments are a continuation of the work by Gheiratmand et al. (2013; 2014) who identified a psychophysical color vision mechanism that appears to lack any orientation tuning (isotropic). As orientation tuning is necessary for shape perception, an untuned mechanism could be primarily used as a 'blob' or surface color detector. This research thesis tests the limitations and influence of the proposed untuned color vision mechanism in related visual

behaviors. To this end, I examine color vision's orientation processing properties in binocular vision, high contrast perception, and orientation identification.

#### **CHAPTER 1: BACKGROUND**

### 1.1 Psychophysics and Physiology of Color and Form

Classically, color vision was thought to be somewhat segregated from form processing as it was demonstrated to be selectively poor at tasks that require fine discrimination including motion discrimination (Ramachandran & Gregory, 1978), stereo acuity (de Weert, 1979; Lu & Fender, 1972), three dimensional shape from shading (Cavanagh & Leclerc, 1985), and other depth cues (Livingstone & Hubel, 1988). Livingstone & Hubel (1984) proposed color vision was mainly used as a surface detector and for filling in the spaces defined primarily by luminance contours, and they called color vision "form blind" (Livingstone & Hubel, 1987). However, over the last twenty five years, visual neuroscience and psychophysics have found linkages between form and color that complicate the classical segregated view.

In psychophysics, the contrast sensitivity function of color vision is spatially low-pass (Mullen, 1985), seemingly favoring segregated color vision theories. However, researchers later ifound that the broad low-pass function actually contains many narrow spatial frequency tuned functions, which may be used for form processing tasks such as edge detection and orientation discrimination (Beaudot & Mullen, 2005; Bradley, Switkes, & De Valois, 1988; Losada & Mullen, 1994). Indeed, the well-known perceptual effect of color constancy is dependent on the interaction of form and color. The spatial properties of a surface must be concurrently

processed with its spectral reflectance in order to keep its color constant despite changes in illumination (Brainard & Radonjić, 2004).

Current physiological research in color vision proposes two separate color sensitive systems based on distinct neural substrates (Friedman, Zhou, & von der Heydt, 2003; Johnson et al., 2001; Johnson, Hawken, & Shapley, 2008). These two systems partially dissociate form and color while still allowing for one to influence the other. Single cell recordings have identified two subsets of color responsive neurons in V1 (Johnson et al., 2001; Johnson, Hawken, and Shapley, 2008; Livingstone & Hubel, 1984; Thorell, De Valois, & Albrecht, 1984). Single-opponent neurons, so called for having their input built from just two opposing cone types, are maximally sensitive to a patch of color that covers their entire receptive field (De Valois, 1965). Classically, these cells were thought to be the main mediators of color vision in V1, supporting the segregated view as they lack any orientation selectivity (Livingstone & Hubel, 1984). Double opponent color-sensitive neurons were hypothesized, but they were thought to have circularly symmetric organization and lack orientation selectivity (Livingstone & Hubel, 1984). However, Thorell, De Valois, & Albrecht (1984) estimated that close to 80% of all macaque V1 neurons are color sensitive, with complex cells responding to multiple color regions. Recent recordings systematically characterized large samples of V1 neurons and found significant populations that are responsive to both color and orientation (Friedman, Zhou, & von der Heydt, 2003; Johnson et al., 2001; Johnson, Hawken, and Shapley, 2008). These newly defined double-opponent neurons have an oriented side-by-side spatial organization with each region composed of cone signals that are opposite in sign and imbalanced in magnitude. This

configuration allows double-opponent neurons to respond equally well to both achromatic and color edges. While these cells are therefore not exclusively color sensitive, they do afford color vision the orientation selectivity necessary for form processing. **Figure 1** is a reprint from Johnson, Hawken, and Shapley (2008) that illustrates this double-opponent model (**1.a**) and other receptive field models. Receptive fields like those in **1.c** and **1.b** are both color blob detectors, with **1.b** also responding to color contrast but lacking orientation selectivity, as it is circularly symmetric. Single opponent color cells with **1.c** receptive fields are like those found in V1 by De Valois (1965), while **1.b** remain hypothetical. Despite color vision's classical shapeless and segregated roots, most modern behavioral research supports a role for color that is highly linked to form processing and physiology supports *both* form processing and surface blob detectors.



**Figure 1.** Hypothetical receptive field top and side representations of double opponent and singleopponent neurons. A) Oriented double-opponent model where there is an imbalance of L and M cone inputs and an oriented side-by-side organization. This receptive field model could carry both color and brightness information and was proposed by Johnson, Hawken, & Shapley (2001) to account for orientation selective color and luminance responsive neurons. B) This hypothetical receptive field arrangement would be responsive to color contrast but is circularly symmetric and lacks orientation selectivity. C) Classical single-opponent model, i.e. color surface detectors, described by Hubel and Wiesel (1968). Republished with permission of the Journal of Neuroscience, from Johnson, Hawken, & Shapley (2008).

## 1.2 Evidence for an Isotropic Color Mechanism

In contrast to its historical import, there was until recently no known psychophysical color vision mechanism that was truly "form blind" and little behavioral evidence of the noted

V1 population of 'surface blob detector' color-only responsive single opponent neurons. However, recent research has provided evidence for an analogous isotropic behavioral mechanism in monocular color vision. Gheiratmand, Meese, and Mullen (2013) examined the orientation tuning of monocular color vision at threshold using the technique of subthreshold summation. They found that orthogonally oriented low spatial frequency (LSF) color stimuli were detected at significantly lower contrast levels when summated, indicating that they were processed by the same, potentially isotropic, mechanism. These high summation ratios were in contrast to those from orthogonal medium spatial frequency (MSF) color stimuli or achromatic stimuli at either spatial frequency. Gheiratmand and Mullen (2014) continued their investigation of the orientation tuning of visual detection mechanisms by repeating their previous technique with stimuli at multiple orientation differences. Their goal was to investigate how summation levels decreased with increasing orientation differences. With the resulting response curves, and a model that accounts for stimuli bandwidth and neural and spatial summation, they were able to estimate the orientation bandwidths of detection mechanisms for color and luminance vision at low and medium spatial frequencies. The model estimates support a monocular LSF color vision detector that is very broadly tuned or has no orientation tuning. This isotropic mechanism may be a psychophysical parallel to the nonoriented color responsive single opponent cells in V1.

## 1.3 Research Questions

An isotropic LSF color contrast detector has ecological utility as a mechanism for detecting patches of color or for filling otherwise defined shapes with their color content.

Gheiratmand et al. (2013; 2014) identified this detector under monocular threshold viewing conditions. It is possible that the mechanism is best seen in these conditions, although much of our visual behavior is conducted binocularly and in high contrast. Furthermore, identification of detected oriented stimuli is implicit in normal vision but would be impossible through an isotropic mechanism. This research thesis probes the ways that color vision may or may not use an isotropic mechanism in a greater representation of visual behavior: in binocular and suprathreshold vision, and identification. My thesis is therefore subdivided into three investigations comparing color and achromatic vision at different spatial frequencies as summarized below:

- 1. Does an isotropic detector extend to binocular color vision? There is evidence for both isotropic and orientation tuned responses in binocular color vision. We measure binocular summation as a function of the orientation difference between stimuli presented dichoptically to the two eyes. We then estimate orientation bandwidths of these binocular contrast detection mechanisms using modeling. If an isotropic detector is present in binocular color vision, then very broadly tuned or untuned model estimates will best fit binocular summation across stimuli orientation.
- 2. Does an isotropic color vision mechanism influence perception at higher contrast levels? An isotropic mechanism may also cause greater summation in high contrast color plaids. We measure subjective contrast perception of plaids and component gratings with a contrast matching paradigm. If an isotropic mechanism is used, and there is greater

summation for LSF color plaids, they will be perceived to have higher contrasts compared to component gratings.

3. Can we distinguish between orthogonally oriented color stimuli at detection threshold? According to labelled line theory (Watson & Robson, 1981), an isotropic detection mechanism is also an isotropic identification mechanism, and would then not be able to distinguish between oriented stimuli at threshold. We concurrently measure detection and identification thresholds for oriented chromatic and achromatic gratings. If the identification mechanism is also isotropic, identification thresholds will be higher than detection for LSF chromatic gratings. However, if we are able to identify oriented stimuli at threshold, then we need to question the original interpretation of an isotropic color detector and/or the accuracy of labelled line theory.

These three inquiries correspond to the three main experiments that make up the current research. By their examination I hope to investigate how, when, and if an isotropic color mechanism behaves in human vision.

#### **CHAPTER 2: MATERIALS AND METHODS**

#### 2.1 Apparatus

The stimuli were presented with a ViSaGe video-graphics card with a 14 bit contrast resolution (Cambridge Research Systems, Kent UK). A CRT computer monitor was used for display (Iiyama Vision Master Pro 513, Iiyama Corporation), its resolution was 1024 X 768 and the refresh rate was set to 120 hz. Gamma correction of the luminance display from the

monitor was calibrated with a ViSaGe program and OptiCal photometer from Cambridge Research Systems. Red, green, and blue phosphor displays were measured and calibrated using a PR-645 Spectrascan spectroradiometer (Photo Research Inc., Chatsworth, CA, USA). CIE 1931 x-y chromaticity coordinates for their outputs were red: x= 0.624, y = 0.335, green: x = 0.293, y= 0.608, and blue: x = 0.147, y = 0.073. For all experiments, the background was achromatic with a mean luminance of 43 cd/m<sup>2</sup>. All stimuli viewing was done with a mirror stereoscope, and the observer was 58 cm from the screen center. When stimuli were viewed monocularly, the other eye was observing the mean luminance background.

#### 2.2 Observers

All participants had normal or corrected-to-normal visual acuity and normal color vision, as assessed with the Farnsworth-Munsell 100 Hue test. The experiments were performed in accordance with the Declaration of Helsinki and approved by the institutional ethics committee of McGill University Health Centre. All participants agreed with and signed an informed consent form.

*Experiment 1* - For the binocular subthreshold summation experiment there were 7 participants. Two were authors (AC and MG) while the remaining five were naive (AB, IO, MS, RSE, and SK). Not all subjects completed all the conditions. In total there were 3 participants for each color and achromatic condition at the MSF, 1.5 c/deg, and 4 participants for each color and achromatic condition at the LSF, 0.375 c/deg.

*Experiment 2* - The contrast matching experiment has seven total participants. However, the experiment was first conducted with just two participants, AC (author) and AF (naive). These subjects completed the experiment at four different plaid contrasts (1x, 2x, 3x, and 5x threshold). The remaining participants (BD, CC, JT, MS, and SP, all naive) completed the experiment at just one plaid contrast level (3x threshold). There were three conditions for each test: color at 0.375c/deg, color at 1.5 c/deg and achromatic at 0.375 c/deg.

*Experiment 3* - For the identification and detection experiments there was one participant, the author (AC), who completed all three experimental versions: (a) original, (b) phase jittered, and (c) phase jittered with smaller orientation difference. One naive participant (MS) completed the (b) phase jittered and (c) phase jittered with smaller orientation difference experiments. All experiments were done with three conditions: color at 0.375c/deg, color at 1.5 c/deg and achromatic at 0.375 c/deg.

## 2.3 Stimuli

All stimuli used in each experiment were either isoluminant red-green or achromatic sine-wave gratings. Orientation of stimuli was set depending on the experiment and condition and could vary between ±0-45 deg away from vertical. The spatial frequency of the sine-wave grating was either 0.375 c/deg (LSF) or 1.5 c/deg (MSF) displayed in a 10 deg circular patch, centered to the viewing eye on the screen. Edges were contrast enveloped with a spatial raised cosine of 2.5 deg. All stimuli were static and presentation happened within a contrast modulated temporal Gaussian envelope with a sigma of 0.125 s, an overall stimulus duration of 0.5 s, and an interstimulus interval of 0.4 s. Whenever stimuli were combined, be it two components of a plaid or a superimposed mask, they were drawn on the screen independently and combined by interleaving on alternate frames through the ViSaGe. While interleaving effectively halves the contrast displayed on the screen, this presentation method was kept consistent across all experiments, including threshold detection. Therefore contrasts for single gratings are actually half reported contrast, while two combined gratings (of the same contrast) are the reported contrast.

## 2.4 Color Space

The stimulus contrast for each cone type is defined within a 3-dimensional conecontrast space (Cole, Hine, and McIlhagga, 1993). For details on the calculation of this conecontrast space, please refer to Gheiratmand and Mullen (2014). Stimulus contrast is defined as the vector length in cone contrast units (CC):

$$Cc = \sqrt{(L_c)^2 + (M_c)^2 + (S_c)^2}$$

where  $L_c$ ,  $M_c$ , and  $S_c$  represent the L, M, and S Weber cone-contrast fractions in relation to the L, M, and S cone values of the achromatic background. Each observer had their spatial frequency specific red-green isoluminance point measured using a minimum motion task (Cavanagh, Tyler, & Favreau, 1984).

#### **CHAPTER 3: EXPERIMENT 1 - BINOCULAR ORIENTATION BANDWIDTHS**

### 3.1 Introduction

Binocular processes combine the inputs of the two eyes into a coherent representation of the world. Here we ask if an isotropic color contrast detector extends to binocular vision. In this experiment, we investigate the orientation tuning of binocular sub-threshold summation for color and luminance stimuli at low and medium spatial frequencies. While it is possible that the isotropic color contrast detector is purely monocular, monocular neurons in layer 4 of V1 are thought to be mostly combined into binocular neurons in layers 2/3 (Blasdel & Fitzpatric, 1984), therefore orientation tuning, or a lack of, may be carried forward *or* it may be imposed by the integrating binocular neuron.

Color vision performs poorly in stereopsis (de Weert, 1979) and consequently has been thought to be weak or even absent in binocular mechanisms (Livingstone & Hubel, 1988). In a psychophysical exploration of binocular color vision, Simmons & Kingdom (1998) examined the binocular summation of color stimuli. They found that color stimuli are binocularly combined and that chromatic binocular summation was greater than in the luminance condition.

Additionally, recent neurophysiological research by Peirce, Solomon, Forte, & Lennie (2008) revealed a population of neurons in the early visual cortex with a binocular and huespecific response to color. While these neurons lacked spatial selectivity, responding to both uniform fields and drifting gratings, the researchers also identified a second population of binocular cells that were responsive to both color and spatial detail but were not selective for

binocular chromaticity. That is, this second group of binocular cells responded to color stimuli but preferred hues that were not necessarily matched between the eyes. The existence of binocular V1 cells that are responsive to color and also lack spatial selectivity parallels the previously and similarly described single opponent neurons (De Valois, 1965; Johnson et al., 2001; Johnson, Hawken, and Shapley, 2008; Livingstone and Hubel, 1984). With physiological evidence of isotropic color processing in binocular vision, we may also assume a corresponding isotropic behavioral mechanism, an extension of the previously identified monocular LSF isotropic channel.

Here we repeat the subthreshold summation technique used in previous studies that examined orientation tuning in monocular color vision (Gheiratmand, Meese, and Mullen, 2013; Gheiratmand and Mullen, 2014). The orientation tuning of binocular summation was first examined using the technique of subthreshold summation by Blake & Levinson (1977). They found that binocular summation in luminance vision has narrow orientation tuning at spatial frequencies of 2 and 4 c/deg. The method of subthreshold summation has specific advantages in measuring orientation tuning by using threshold contrasts. Adaptation or masking methods use suprathreshold stimuli which introduce complicating masking effects of contrast gain control. Subthreshold summation presents near threshold level oriented stimuli to each eye. The orientation tuning of the binocular mechanism reflects the binocular summation at different dichoptic orientation differences. For example, if a plaid with orthogonal component gratings and a 'plaid' with co-oriented component gratings produce relatively similar levels of binocular summation, then the corresponding binocular contrast detector may be inferred to

be very widely tuned or isotropic. However, if summation is only large at co-oriented and small orientation differences in dichoptically presented stimuli, then the binocular mechanism has narrow orientation tuning. The more intricate relationship between the orientation bandwidth of the binocular detector and binocular summation levels across orientation difference will be further detailed in our model. A modeling approach is necessary to determine orientation tuning of the underlying detectors because the stimuli themselves have different orientation bandwidths. Additionally, neural and spatial summation has to be accounted for as it significantly affects binocular contrast detection (Meese, Georgeson, & Baker, 2006).

It is prudent, when studying the detection of plaids and gratings, to note that there is some debate as to whether plaids are detected by specialist 'conjunction detectors' (Peirce, 2007) or, as we assume, by the same detectors that are used for their component gratings. Peirce proposes that first order neurons may saturate or supersaturate in response to a plaid conjunction, and then sum into a secondary detection that would be sensitive to the resulting nonlinearities, as a 'conjunction detector'. However, May and Zhaoping (2013) disagree that supersaturation of a neuron would be useful for conjunction detection. They contend that it actually reduces performance for conjunction detection in addition to being a messy coding mechanism for the visual cortex.

In this experiment, we use the same methods as in Gheiratmand and Mullen (2014), with the exception that stimuli are presented dichoptically rather than monocularly. We measure subthreshold summation across a wide range of orientation differences in both color

and luminance at the LSF and MSF. From this method we obtain a full response tuning function across orientation which we can fit with a model modified from a previous paper and the work of Meese, Georgeson, & Baker (2006). This experiment was conducted in collaboration with Mina Gheiratmand, following the methods developed in her thesis (Gheiratmand, 2014). This experiment is currently in preparation for submission (Gheiratmand, Cherniawsky, & Mullen, 2016).

## 3.2 Specific Methods

## 3.2.a Protocols

Our experimental protocol is identical to that outlined in Gheiratmand and Mullen (2014) with the modification of dichoptic instead of monocular presentation of stimuli. This experiment was done in multiple sittings and with a pseudo-randomized balanced block design. Stimuli had two chromaticity conditions (chromatic and achromatic), two spatial frequency conditions (LSF and MSF), and 8 orientations  $(0, \pm 5, \pm 8, \pm 11.25, \pm 16, \pm 22.5, \pm 30, \text{ and } \pm 45$  degrees away from vertical), (Chromaticity (2) x SF (2) x orientation (8)). An example of the LSF stimuli is illustrated in **Figure 2**. We measured detection thresholds for component stimuli, left oblique and right oblique each presented monocularly in either right eye or left eye, and combined stimuli, when both left oblique and right oblique were presented together dichoptically. Thresholds were obtained using a two-alternative-forced choice method of constant stimuli. One temporal interval had a stimulus, the other a blank, and the participant indicated which interval contained the stimulus. Feedback was provided for correct and incorrect responses. Detection thresholds, corresponding to 81.6% correct, were then

calculated from fitting a standard Weibull function to the psychometric curve (Weibull, 1951) with the psignifit toolbox in Matlab. Psychometric functions all had six or more contrast levels with 100-140 trials per contrast level. Data collection took place over multiple sessions. Detection thresholds for component gratings did not significantly vary across orientation or between eyes. Therefore, we collapsed these monocular data so that component grating thresholds were determined from all oriented gratings from both left and right eyes in one condition for each subject (300-660 trials per contrast level). For ease of comparison between conditions, stimulus contrast in this, and future experiments, is often represented in dB where a contrast of 1% is 0 db.



Figure 2. Example component color and achromatic gratings at the LSF with different orientations.

## 3.2.b Analysis

## 1-Summation Ratios:

Summation ratios (SRs) are measured using the psychophysical method of subthreshold summation (Bergen, Wilson, & Cowan, 1979; Meese & Baker, 2011). SRs are measured at each relative orientation between the two component gratings, ( $\vartheta$ ), and are a ratio of a monocular grating to its dichoptic combined presentation.

$$SR = \frac{C^*_{mon}}{C^*_{dich}}$$
(Eq 1.)

where C\* is grating contrast at detection threshold,  $C^*_{mon}$  is the detection threshold contrast for a component monocular grating, and  $C^*_{dich}$  the threshold contrast for the associated dichoptic gratings. There are typically five levels of SR that correspond with different types of binocular summation (Simmons, 2005): An SR of 1 indicates inter-ocular suppression; SR  $\approx$  1.2 correlates approximately to probability summation; SR > 1.2 would indicate some level of neural summation; and SR = 2 denotes full linear summation between the eyes. An SR < 1 would be rare at threshold contrasts and indicate high amounts of suppression between the two components.

## 2- Modeling

In Gheiratmand et al. (2016, in prep) we developed a model in order to estimate the orientation bandwidths of the underlying binocular neural detector mechanism based on an earlier monocular model (Gheiratmand & Mullen, 2014). A brief outline of the model will follow with greater detail provided in Gheiratmand, (2014, phd dissertation). The model incorporates three properties of the psychophysical response: (1) spatial summation, (2) stimulus orientation bandwidth, and (3) detector bandwidth. (1) To account for spatial summation, the model uses Minkowski summation to combine the outputs of different neural detectors. (2) Stimulus orientation bandwidth is represented in the model by two-dimensional stimuli input specific to each spatial frequency. The stimuli have a fixed size, so their orientation bandwidth differs between low and medium spatial frequencies. Therefore, the stimulus dimensions, specifically in relation to their aspect ratio, are represented in the model.

(3) The model's aim is to estimate the detector bandwidth that best fits each orientation tuning curve. Detector bandwidths are represented by a bank of orientation and spatial tuned filters.

#### 3.3 Results

## 3.3.a Orientation Tuning Curves

Figure 3 shows example psychometric functions for subject AC (author) in the LSF color condition when stimuli have an orientation difference of 90 degrees. Detection thresholds are derived from these functions to calculate summation ratios and resulting orientation tuning curves as outlined in the methods section. Figure 4 displays the average orientation tuning curves for all conditions (3 subjects for MSF, 4 subjects for LSF). As expected, binocular summation is greatest when component gratings are co-oriented. For all co-oriented gratings, binocular summation exceeds levels associated with probability summation (> 1.2), indicating some degree of neural summation and the presence of binocular neural mechanisms in both luminance and color vision (Simmons, 2005). Additionally, co-oriented chromatic stimuli binocularly summate at greater levels than achromatic stimuli, consistent with the findings of Simmons and Kingdom (1998). LSF chromatic stimuli have the highest binocular summation ratio (1.75), followed by MSF chromatic stimuli (1.56), and then LSF and MSF achromatic stimuli (1.44 for both). A linear mixed model analysis of the co-oriented SRs (0°) with two factors (2 (chromaticity) x 2 (spatial frequency)) reveals that there is a significant effect of chromaticity, F(1, 7.63) = 9.487, p = 0.016, no effect of spatial frequency, F(1, 7.63) = 2.101, p = 0.187, and no interaction, F(1, 7.63) = 2.058, p = 0.191.



**Figure 3.** Example psychometric functions from subject AC (author) in the LSF color condition where percent correct detection is plotted against contrast (in dB, where 0 dB is 1% contrast). Percent correct detection for dichoptically presented plaids with an orientation difference of 90 degrees is plotted in purple. Percent correct detection for pooled monocular gratings, from both eyes and all orientations for subject AC in the LSF color condition, is plotted in blue.



**Figure 4.** Orientation tuning curves for chromatic (red circles) and achromatic stimuli (black triangles) at the MSF, 1.5 c/deg (left) and LSF, 0.375 c/deg (right). Error bars are the standard error of the mean. Summation ratios are plotted against the relative orientation difference of the component stimuli. Data points are averages with standard errors of the mean (S.E.M.).

When looking at the complete orientation tuning curves, we used a linear mixed model with three factors (8 (orientation) x 2 (chromaticity) x 2 (spatial frequency)). There is a main effect of orientation difference, F(7, 14.636) = 27.471, p < 0.001, due to decreasing summation ratios over increasing orientation differences. There is a main effect of chromaticity, F(1,47.695) = 31.809, p < 0.001, with chromatic stimuli having higher SRs than achromatic stimuli. A main effect of spatial frequency, F(1, 47.695) = 27.445, p < 0.001, reflects larger SRs in the LSF. Furthermore, there is a significant interaction of chromaticity and spatial frequency, F(1,47.695) = 13.943, p = 0.001. This interaction underlines an interesting result, that in the LSF, color vision has larger SRs of a near uniform difference across orientations. Interactions between orientation difference and chromaticity and/or spatial frequency were all nonsignificant, p > 0.05.

#### 3.3.b Model

Details on the model are presented in Gheiratmand, (2014, phd dissertation) and will be published in Gheiratmand, Cherniawsky, and Mullen (2016, in prep). The model is modified from Gheiratmand and Mullen (2014), where it was used to find the estimated orientation bandwidths of monocular contrast detectors, to be applicable to a binocular summation stage with dichoptic presentation of stimuli, as depicted in the schematic in **Figure 5**. The model uses a bank of Cartesian-separable log gabor filters of different orientations that are spatial frequency and orientation tuned. The spatial frequency bandwidths of the filters are 2.2 and 1.6 octaves for filters tuned to 0.375 c/deg and 1.5 c/deg respectively. The output of these filters is rectified and the binocular response is found by the non-linear summation across monocular responses, using a non-linear transducer, *b. b* is a fixed parameter and is an empirically derived exponent from average or individual co-oriented binocular summation ratios (SR<sub>bin</sub>) using the following equation (Legge, 1984):

$$SR_{Bin} = 2^{1/b}$$

These outputs are then spatially summated according to Minkowski summation (m=6 provided the best fit). We find the model response for individual gratings and dichoptic stimuli, which produces estimates of SR as a function of orientation difference. We then find the model output from different orientation tuning bandwidths (from 5-62 degs in steps of 1 deg) that

best fits our data by producing the least RMS error between the model and empirical data.



Therefore, all parameters were fixed in the model except orientation tuning bandwidth.

**Figure 5.** Schematic of the binocular tuned model. This is reproduced from Gheiratmand (2014, phd dissertation) with permission. The first stage of the model is a bank of filters that are tuned to spatial frequency and orientation. These outputs are then full wave rectified and binocularly summated through nonlinear summation. The entire binocular array goes through Minkowski summation for both space and orientation. Model outputs are determined for monocular and dichoptic stimuli. Summation ratios are then calculated from their ratio.

**Figure 6** illustrates the model fits to the average data from all conditions. **Figure 7** shows the individual data and their model fits. The orientation bandwidth estimate (BW), R<sup>2</sup> goodness of fit measure, and the sum of squared errors (SSE) are included on each graph. The assumption of tuned binocular mechanisms fit the data well for all four averaged conditions, the lowest R<sup>2</sup> is 0.82 for LSF achromatic stimuli. Half-width half-height bandwidths are as follows: 23 deg for LSF color, 19 deg for MSF color, 31 deg for LSF achromatic, and 24 deg for MSF achromatic. **Figure 8** shows the individual BWs with their average for each condition. **Table 1** includes orientation bandwidths and fit parameters from the tuned model for all average and individual data. Note that there are both orientation bandwidth estimates from model fits to the averaged response data, as reported above and on separate rows in the table, and an average of orientation bandwidth estimates from model fits to individual data, which are reported in a separate column. A linear mixed model test of individual orientation BWs with two factors (2 (chromaticity) x 2 (spatial frequency)) reveals that there are no main effects of chromaticity, F(1, 8.771) = 0.279, p = 0.611, or spatial frequency, F(1, 8.771) = 2.633, p = 0.140. Likewise, there is no significant interaction of chromaticity x spatial frequency, F(1, 8.771) = 0.366, p =0.560. A model with untuned filters was also tested with two different Minkowski exponents (M) of 6 and 3 but each produced poor fits to the data (Figure 9). M = 3 was tested, as it provided the best fit to the previous monocular isotropic model (Gheiratmand & Mullen, 2014). We used the previous binocular model but replaced the orientation tuned filters with isotropic filters with no orientation and spatial frequency tuning. Therefore, all values were fixed in this model. An attempt to find the best M by including it as a free parameter resulted in poor fits ( $R^2$ < 0) even with a large range of M values.

Condition	Subject	Subject Filter SSE	SSE BMSE	R <sup>2</sup>	Ave of individual BW ±	
	Jubject		55L	JJL INVIJL	IX.	s.e.m
Col – 1.5 c/deg	MG	23	0.020	0.0532	0.90	
	SK	10	0.013	0.0428	0.91	19.7 ± 4.91
	AB	26	0.013	0.0440	0.93	
	Ave	19	0.006	0.0301	0.96	
Ach – 1.5 c/deg	AC	25	0.068	0.0988	0.70	
	10	15	0.049	0.0838	0.85	26.7 ± 7.26
	MS	40	0.025	0.0592	0.69	
	Ave	24	0.028	0.0635	0.85	
Col – 0.375 c/deg	AC	22	0.060	0.0925	0.92	33.7 ± 6.83
	SK	19	0.089	0.1125	0.57	
	MG	44	0.120	0.1308	0.71	
	RSE	50	0.040	0.0758	0.75	
	Ave	23	0.011	0.0404	0.96	
Ach – 0.375 c/deg	AC	34	0.068	0.0985	0.39	33.3 ± 2.08
	SK	42	0.040	0.0759	0.69	
	10	40	0.035	0.0710	0.72	
	MS	17	0.210	0.1730	0.55	
	Ave	31	0.025	0.0599	0.82	

**Table 1.** Estimated orientation tuning bandwidths and fit parameters from all subjects and averages for each condition. SSE is sum of squared errors, RMSE is root mean squared errors, and R<sup>2</sup> is how close the data fit to the model.


SF = 1.5 c/deg

**Figure 6.** Model fits (dashed lines) for the average orientation tuning data for color (red diamonds) and achromatic (black diamonds) at the MSF, 1.5 c/deg (top) and the LSF, 0.375 c/deg (bottom). The detector bandwidth estimates (BW) and goodness of fit measures, R<sup>2</sup> and SSE (sum of squared errors) are displayed on each graph but are also available in **Table 1** (above). Summation ratios are plotted against the relative orientation difference of the component stimuli. Data points are averages across subjects within conditions with S.E.M. error bars.



SF = 1.5 c/deg

Relative orientation (deg)



SF = 0.375 c/deg

**Figure 7.** Model fits (dashed lines) for average and individual subject orientation tuning data for color (red diamonds) and achromatic (black diamonds) at the MSF, 1.5 c/deg (a) and the LSF, 0.375 c/deg (b). The detector bandwidth estimates (BW) and goodness of fit measures, R<sup>2</sup> and SSE (sum of squared errors) are displayed on each graph and are also available in **Table 1** (above). Summation ratios are plotted against the relative orientation difference of the component stimuli. Data points for the averages include S.E.M. error bars.



**Figure 8.** Bandwidth estimates for individual data (symbols) and the average (line) for each condition. Chromatic data are displayed with red circles, and achromatic data with black triangles. LSF is on the left and MSF is on the right.

# SF = 0.375 c/deg

Average of 4 subjects



**Figure 9.** Isotropic model fits to the average colour (left) and achromatic (right) data for the LSF, 0.375 c/deg, condition. Goodness of fit measures, R<sup>2</sup> and SSE (sum of squared errors) are displayed on each graph. Model outputs with a minkowski exponent (M) of 6 are shown in red for colour and black for achromatic. Model outputs with an M of 3 are shown in blue for colour and grey for achromatic. Average summation ratios with S.E.M. are plotted against the relative orientation difference of the components.

## 3.4 Discussion

We have begun an investigation of the properties and limitations of the proposed isotropic monocular LSF chromatic contrast detector. First, we asked if this mechanism is restricted to monocular channels, or if it is present in binocular vision as well. We determined binocular summation ratios for dichoptically presented stimuli across a range of orientation differences using LSF and MSF, chromatic and achromatic stimuli. The resulting response tuning curves for all conditions were best fit by an orientation tuned model with bandwidths that are not significantly different between conditions. Our results clearly support a role for binocular color vision that is capable of oriented edge or contour detection at different spatial frequencies. Therefore, while LSF chromatic stimuli are processed through an isotropic mechanism for monocular presentation, orientation tuning is imposed for stimuli that are dichoptically combined.

There is psychophysical precedence for purely monocular LSF isotropic mechanisms. Achromatic high temporal frequency LSF stimuli are also detected through an isotropic channel (Kelly & Burbeck, 1987) and orientation tuning is similarly imposed when stimuli are dichoptically or binocularly viewed (Meese & Baker, 2011). Detection mechanisms often represent the most sensitive pathway. While isotropic channels may be the most sensitive pathway for monocular vision, binocular vision with tuned channels may afford greater sensitivity. Those isotropic monocular pathways are still present during binocular presentation, but they are not alone, and tuned channels appear to dominate binocular mechanisms.

While we did not find psychophysical evidence for the isotropic binocular color cells described by Peirce, Solomon, Forte, & Lennie (2008), it is still ecologically sound to suppose that a binocular mechanism that matches stimuli between the eyes would require orientation specificity as a determinant. While our results are agnostic to their cortical substrates, it is intriguing to note that binocular summation ratios were significantly larger for LSF chromatic vision across all orientation differences. This larger SR difference also appears to be relatively uniform across component orientation.

We could hypothesize that there is an isotropic increase of binocular sensitivity for LSF chromatic vision due to the combined response of both tuned and isotropic detectors mediated by the tuned and untuned cells identified by Peirce et al. (2008). For monocular threshold vision, we may only access the untuned color cell first described by De Valois (1965), while binocular threshold vision may recruit additional (tuned) cellular resources as it is an inherently more complex computation. However, signals could still be concurrently processed through those untuned pathways, i.e. a tuned response superimposed onto an isotropic pedestal, resulting in larger LSF color SRs. The isotropic pedestal could be monocular or binocular. Cass et al. (2010) examined orientation tuning in adaptation for monocular and dichoptic stimuli. They also found a LSF specific isotropic raising of response that didn't affect estimated orientation bandwidths. In their adaptation studies, the isotropic pedestal didn't transfer between the eyes and was purely monocular. While adaptation may engage different mechanisms than detection at threshold, SRs could still be raised by a purely monocular isotropic pedestal with superimposed binocular orientation tuning. As a possible avenue of

future research, we may be able to test this hypothesis and the influence of any monocular or binocular isotropic mechanisms on binocular visual detection by selectively masking isotropic channels and determining resulting SRs.

Another, not necessarily exclusive possibility is that increased binocular sensitivity is due to a more linear combination of signals at the binocular LSF color sensitive neuron. Longordo et al. (2013) demonstrated that binocular neurons combine monocular signals using sublinear integration when they have higher response levels, such as when they are processing preferred orientations, binocular disparities, or higher contrasts. However if the incoming signals are weaker, binocular integration is increasingly linear. Linear integration, compared to sublinear, of monocular signals was estimated to increase orientation selectivity without changing orientation tuning bandwidth in the binocular neuron. Weaker linearly combined signals raised action potential firing rates across all orientations resulting in a response curve with the same orientation tuning bandwidth, but a less distinctive preference for a particular orientation. The relevant figure from Longordo et al. (2013) has been reprinted in Figure 10. The flat raising of response for LSF chromatic binocular SRs mirrors the linear integration estimated in binocular neurons for weaker stimuli. It is plausible that LSF color stimuli are a 'weaker' input for many binocular neurons resulting in a more linear combination. Although color is useful for binocular combination, as has been demonstrated, it is still disadvantaged in stereopsis (de Weert, 1979; Kingdom & Simmons, 1996), and orientation tuned binocular color neurons prefer mid rather than low spatial frequencies (Peirce et al., 2008).



**Figure 10.** Pink curves and bars are model estimates of linear integration, while green are observed sublinear integration data. (g) Action potential rates for model predicted linear (pink) and experimentally observed sublinear (green) integration of signals from both eyes at the binocular neuron. Orientation tuning curves are also plotted for observed sublinear and predicted linear data based on spike rates with standard error of the mean. (h, i, &j) Bars represent means and circles are individual cells for (h) direction selectivity indexes, (i) orientation tuning width in half width half height, and (j) orientation selectivity index. Figure reprinted by permission from Macmillan Publishers Ltd: [Nature Neuroscience] Longordo, To, Ikeda, & Stuart, copyright 2013.

While the mechanisms underlying increased summation in binocular LSF color vision are presently unknown, we have provided clear evidence for orientation tuning. Whereas monocular LSF color contrast detection may be isotropic or very broadly tuned, acting as a blob detector and for chromatic filling in, binocular LSF color vision appears well capable of oriented tasks such as edge detection and shape processing. These results suggest that any untuned monocular signals acquire orientation tuning with further processing through binocular mechanisms. Therefore, the remaining isotropic mechanism investigations will be conducted monocularly.

#### **CHAPTER 4: EXPERIMENT 2 - SUPRATHRESHOLD CONTRAST MATCHING**

## 4.1 Introduction

Next, we continue our investigation of how a monocular isotropic mechanism may affect a greater range of visual behavior by studying our perception of high contrast stimuli. The work of Gheiratmand et al. (2013; 2014) and the previous binocular study were conducted with threshold stimuli to reduce the masking effects of contrast gain control, which obscure orientation tuned responses at higher contrasts (Meese & Holmes, 2010). Additionally, working at threshold allows researchers to identify the detecting mechanism, an elemental visual property. However, threshold vision is a very limited visual behavior, as we mostly perceive the world in higher contrasts. Accordingly, this second experiment examines the perceived contrast of gratings and plaids at suprathreshold levels. We ask whether cross-orientation summation, which elevates contrast sensitivity and is characteristic of an isotropic mechanism response, is also evident at higher suprathreshold contrasts. To investigate this question, a contrast-matching paradigm is employed where the observer judges the relative perceived contrasts of a component grating to its combined plaid. If the monocular isotropic mechanism still operates at suprathreshold levels then the two components of the plaid could be partially processed through that same mechanism. The orthogonal components of the LSF chromatic plaid might then summate within the isotropic mechanism and appear relatively higher contrast than its component grating, compared to achromatic or MSF stimuli.

However, chromatic stimuli may also be subject to contrast constancy (Georgeson & Sullivan, 1975), wherein high contrast stimuli appear relatively equal to each other with equal

physical properties, despite any differences in detection thresholds. There are several examples in the literature of contrast constancy principles operating in color vision across different stimulus attributes. Tiippana et al. (2000) performed a contrast matching task with chromatic gratings at different spatial frequencies and found that perceived contrast became independent of spatial frequency at higher contrast levels. Similarly, Liu and Wandell (2005) determined that the near-threshold effect of reduced chromatic detection sensitivity to high temporal frequency stimuli did not extend to suprathreshold discrimination thresholds and that neural measurements in V1 mirrored these results. Additionally, Switkes and Crognale (1999) had observers compare the relative contrasts of gratings that differed in both luminance and chromaticity dimensions. They found that the relative contrasts of chromatic and luminance modulated stimuli scaled proportionately with physical contrast, again consistent with contrast constancy.

Our study aims to compare chromatic component gratings to their plaid combinations. Georgeson and Shackleton (1994) also investigated the relative perceived contrasts of plaids and their component gratings with a contrast matching task but for achromatic stimuli at a wide range of orientations and spatial frequencies. They found that gratings appeared to have stronger contrasts than their plaid counterparts across all spatial frequencies (plaid contrast was calculated as the sum of the two components). This effect increases with greater component orientation differences. They introduce a model based on contrast normalization and non-linear summation to account for this effect.

Therefore, if our LSF chromatic plaids are subject to the same processes of contrast normalization as are achromatic gratings, any effect of summation within an isotropic mechanism may be negated. Additionally, the properties of an isotropic mechanism may be negligible at high contrast levels as the principle of contrast constancy takes effect.

We examined the relative perceived contrast of gratings and plaids across chromaticity and spatial frequency conditions. Initially, for two participants, we also presented standard stimuli at a range of different contrast levels, from threshold to five times that. Finding intriguing but inconsistent results across subjects, we then focused on one standard contrast level, at three times threshold, and included five more participants.

#### 4.2 Protocols

This experiment was done entirely monocularly with the right eye and took place over multiple sessions. There are three conditions: LSF chromatic, MSF chromatic, and LSF achromatic stimuli. For each condition, contrast thresholds were first determined for a plaid presentation of two component gratings with an orientation difference of 90 degrees. Thresholds were obtained using a two-alternative-forced choice (2AFC) method of constant stimuli. One interval had a stimulus, the other a blank, and the participant indicated which interval contained the stimulus. Feedback was provided for correct and incorrect responses. Detection thresholds, corresponding to 81.6% correct, were then calculated from fitting a standard Weibull function to the psychometric curve (Weibull, 1951) with psignifit toolbox in Matlab. Psychometric functions had six or more contrast levels with 60-120 trials per level.

After finding plaid threshold contrasts, participants completed a contrast-matching paradigm. A two-alternative-forced choice design was employed where one interval contained the standard plaid stimuli and the other interval contained a single test grating stimuli which varied between trials along 6 contrast levels (step size of 2.5 db). Observers were asked to determine which stimulus appeared stronger in contrast and indicate their answer with a button box. No feedback was given for this subjective task. For two participants, this experiment was repeated with four different standard plaid contrasts based on multiples of the plaid detection threshold: 1x, 2x, 3x, and 5x. The remaining five participants completed the experiment at only 3x threshold. Grating test contrast level ranges were adjusted for each block so that resulting psychometric functions included equivalent numbers of test contrasts that were perceived to be either stronger or weaker than the given standard plaid contrast. The point of subject equality (PSE) for grating test contrasts was determined for each condition. PSEs are the 50% point on the psychometric function and were based on 60-80 trials per contrast level. For one subject, AC, the 5x threshold point for chromatic stimuli at the MSF could not be determined due to limitations of the monitor in displaying high contrast chromatic stimuli. Unlike Georgeson and Shackleton (1994), plaid contrasts are presented as equal to component contrasts, not as the sum of both components. This plaid contrast calculation was chosen so as to be consistent with plaid contrasts in previous experiments. However, as previously stated, contrast is halved from frame interleaving during presentation of a single grating, therefore total plaid contrasts are in actuality the reported contrast.

## 4.3 Results

**Figure 11** shows the psychometric functions for all conditions for the first two subjects, those that completed the experiment at multiple standard plaid contrast levels. The plots show the percentage stronger contrast judgements for each observer (AC and AF) and condition (0.375 c/deg chromatic, 0.375 c/deg achromatic, and 1.5 c/deg chromatic). On each graph there are separate psychometric functions for the different standard plaid contrast levels (1x, 2x, 3x, and 5x threshold). Psychometric functions are not displayed for the five other subjects as PSE points are more meaningful for interpretation.





**Figure 11.** Psychometric functions for the contrast matching experiment for subject AC (a) and subject AF (b). The percentage of times that the test grating was judged to have a greater contrast is plotted against the test grating contrast. The different curves on each graph correspond to different standard plaid contrasts that increase with purple shade darkness from 1 times to 5 times threshold. LSF chromatic data are shown on the top graphs, LSF achromatic data are shown on the middle graphs, and MSF chromatic data are shown on the bottom graphs.

Figure 12 illustrates the PSEs for those first two participations for each condition and at all standard plaid contrast levels. There is a dashed blue line for standard plaid contrasts on the graph, where standard plaid contrast is determined as component contrast. Data points falling on or close to this line would indicate that there was little to no summation effect between plaid components. Component gratings would be perceived to be as equally high contrast as their plaid counterparts. One participant, AF, perceived MSF chromatic plaids at threshold in this manner. They also perceived LSF achromatic plaids at threshold and MSF chromatic plaids at 2x threshold to be very close to component contrast. For subject AF, there was a marked trend for all conditions where higher contrast stimuli diverged more from the dashed blue line, indicating that at higher contrasts plaid components summate more and looked relatively stronger contrast than their components. Subject AC did not show these same effects for all conditions, with just a moderate similar effect for LSF achromatic stimuli. The dashed black line represents double plaid contrast, or full summation of plaid components. At this line, one would perceive a plaid to be twice the contrast as its component. As in Georgeson & Shackleton (1994), plaids were perceived to be weaker than full summation between component gratings. However, for subject AC, LSF chromatic plaids appear to perceptually summate more, almost falling on the double contrast line for all contrast levels. Subject AF does not show this same effect, but their LSF chromatic plaid PSEs do appear much closer to this line than their MSF chromatic plaid PSEs and slightly closer than LSF achromatic plaid PSEs. They found LSF chromatic plaids to be of stronger contrast than their component gratings more so than MSF chromatic plaids and slightly more so than LSF achromatic plaids.



**Figure 12.** PSEs of the gratings are plotted against standard plaid contrasts for subjects AC (a) and AF (b). Contrasts are plotted in decibels. LSF chromatic data are shown with red circles, LSF achromatic data are shown with black squares, and MSF chromatic data are shown with pink triangles. The blue dashed line represents plaid contrast, when there is no summation between components. The black dotted line is double plaid contrast, when there is full summation between components.

After finding intriguing but somewhat inconsistent results in how the two subjects perceived plaids and gratings with increasing contrast, the experiment was continued with five more subjects at just the 3x contrast point. With this larger data set, we decided to focus on the relative perceived contrast of a plaid compared to its component gratings between color and spatial frequency conditions rather than between different contrast levels. **Figure 13** displays the PSEs for all seven subjects in each condition at 3x standard plaid threshold. However, it is still difficult to tell which conditions fall closer to either dashed line. **Figure 14** displays the difference between PSEs and their respective plaid contrasts for individual subjects and condition averages. This graphs is essentially the PSEs from **Figure 11** minus the dashed blue line in dB, however raw PSEs are *divided* by plaid contrast due to the logarithmic scale. If the data points fall closer to 0 dB on the vertical axis, this indicates that the plaid was found to be the same contrast as one of its components. A data point at 6 db would mean that the subject found the plaid to be twice the contrast of a component grating. All conditions, on average, were significantly different from both 'no summation', 0 db, and 'full summation', 6 db, *p* < 0.05. A repeated measures ANOVA between the three conditions on the calculated ratio between PSEs and their relative plaid contrasts found a significant main effect of condition, *F*(2, 12) = 5.140, *p* = 0.024. Pairwise comparisons found no significant difference between LSF chromatic stimuli and LSF achromatic stimuli, *p* > 0.05. However, MSF chromatic plaids were perceived to be significantly lower in contrast than both LSF conditions, *p* < 0.05.



**Figure 13.** PSEs of the gratings are plotted against standard plaid contrasts at 3x threshold for all subjects (n=7). Contrasts are plotted in decibels. LSF chromatic data are shown with red circles, LSF achromatic data are shown with black squares, and MSF chromatic data are shown with pink triangles. S.E. is plotted but often too small to be seen. The blue dashed line represents plaid contrast, when there is no summation between components. The black dashed line is double plaid contrast, when there is full summation between components.



**Figure 14.** Difference between PSEs and respective plaid contrasts for the mean (with S.E.M.) and all subjects plotted in dB (N=7). LSF chromatic data are shown with red circles, LSF achromatic data are shown with black squares, and MSF chromatic data are shown with pink triangles.

As a point of comparison, PSE values were estimated from Figure 2 in Georgeson & Shackleton (1994) where they compared a 1 c/deg achromatic orthogonal plaid to a component grating using the method of adjustment. With a plaid contrast of 12 db (for a single component, as we calculate plaid contrast), and a grating PSE of approximately 15.5 db, a PSE ratio, like those previously calculated, is 3.5 db. This PSE ratio is similar to our observed 1.5 c/deg chromatic PSE ratios. **Figure 15** directly compares their estimated PSE ratio (3.5 db) to our condition averages. Therefore, despite using different methodology, we find very similar MSF orthogonal plaid and grating contrast matching results to those of Georgeson & Shackleton.



**Figure 15.** Georgeson and Shackleton (1994) results estimated and compared to ours. Difference between average PSEs and respective plaid contrasts for the mean (with S.E.). The Georgeson & Shackleton stimuli (G&S, black striped bar) are achromatic orthogonal plaids and component gratings at 1 c/deg. \* indicates significant difference between MSF color (1.5 c/deg) and other conditions.

## 4.4 Discussion

The current experiment examined the relative perceived contrast of plaids compared to their component gratings. At threshold, a monocular isotropic chromatic detection mechanism best explains high levels of summation between orthogonal LSF grating components of a plaid (Gheiratmand et al., 2013; 2014). We asked if this summation effect may also be present at suprathreshold contrasts, resulting in an increased perceived contrast of LSF chromatic plaids compared to component gratings. All suprathreshold contrast plaids summated at levels that were greater than zero summation but less than linear additive contrast summation. While observers perceived LSF chromatic plaids to be a higher contrast component combination than MSF chromatic plaids, they were not significantly different from LSF *achromatic* plaids (**Fig 12**). Intriguingly MSF chromatic plaids were perceived to be significantly lower in contrast than both LSF conditions. However, there is not enough consistent data to determine the course of these effects over a range of contrasts (**Fig 10**). Our results are agnostic to any effect of an isotropic LSF chromatic mechanism at high contrast, as LSF chromatic plaids were not significantly higher in perceived contrast than the achromatic condition.

In achromatic contrast matching experiments, a normalization model (Swanson et al., 1984) is sometimes employed to explain broad spatial frequency spectrum contrast matching functions in relation to more bandpass contrast sensitivity functions. In other words, contrast constancy at higher contrasts may be due to cross inhibition pooling over from activation of mechanisms well beyond threshold levels. A monocular isotropic chromatic detection mechanism may be inhibited and/or inhibiting other channels, counteracting any potential summation benefits over oriented achromatic channels.

Nonetheless, LSF plaids were perceived to be higher contrast combinations of their components than MSF plaids. At threshold, LSF color plaids also have higher summation ratios than MSF color plaids (Gheiratmand et al., 2013; 2014). While we may not draw any direct inferences to a related isotropic detecting mechanism, this is still a qualitative consistency of summation effects from threshold to high contrast. When comparing gratings of different spatial frequencies, other researchers have found a flatter contrast matching function for high contrast color stimuli (Tiipana et al., 2000; Vimal, 2000), indicative of contrast constancy. Our results partially argue against contrast constancy in the domain of plaid component summation. Color vision has greater plaid summation for LSF over MSF stimuli independent of contrast.

This result leads to a novel and unexpected finding; MSF chromatic gratings perceptually summate less than *both* LSF chromatic and achromatic gratings. We have two speculations as to why MSF chromatic stimuli may be specifically disadvantaged in summation. First, this result may be evidence of a larger spatial frequency effect wherein MSF achromatic gratings would also summate at similarly reduced levels compared to LSF stimuli. In further testing, we will repeat the experiment with MSF achromatic stimuli to test this possibility. Georgeson & Shackleton (1994) matched a 1 c/deg plaid to a component grating, similar to a MSF achromatic condition, but their presentation was binocular rather than monocular. A resulting estimated PSE summation ratio is comparable to our 1.5 c/deg chromatic PSE ratio, and well below both LSF conditions (**Fig 15**), indicating a possible overall spatial frequency effect. However, Georgeson & Shackleton (1994) found flat contrast matching functions across spatial frequency for plaids ranging between 1 c/deg and 8 c/deg, when matched to a standard grating of 4 c/deg.

Importantly, when comparing across spatial frequency, they did not test below 1 c/deg and the spatial frequency of test and standard were often different. Georgeson & Shackleton's results could argue both for and against a spatial frequency effect in the perceived contrast of achromatic plaids. Therefore, it is difficult to predict how MSF achromatic stimuli will be perceived in our experiment.

Second, lower perceived MSF chromatic summation may be due to differing levels of cross-orientation suppression. Cross-orientation masking is significantly higher for chromatic stimuli (Medina & Mullen, 2009) and suppression is estimated to have a monocular origin (Kim, Gheiratmand, & Mullen, 2013). However, this suppression effect is spatial frequency invariant and would therefore equally affect MSF *and* LSF chromatic stimuli. Increased chromatic crossorientation suppression could be a hidden reason for the less than predicted LSF chromatic summation as well. Perhaps cross-orientation suppression is responsible for reduced summation values for both MSF and LSF chromatic stimuli, however LSF chromatic plaid summation is boosted by a then respectively counteracted isotropic mechanism. In other words, for LSF chromatic stimuli, an isotropic mechanism may be boosting summation but is hidden by and hiding greater cross-orientation suppression. However, MSF chromatic stimuli doesn't benefit from an isotropic mechanism, and therefore reveals the suppression. While this remains a fascinating possibility, results from a MSF achromatic condition are still needed to provide further clarity.

A limitation of this experiment is that contrast matching is inherently subjective and this task in particular was relatively difficult. Comparing the contrast of a plaid to a grating can be an imprecise process. Do I look at the whole stimuli? Or just the highest contrast patches? In a plaid, there are areas where components overlap, doubling the contrast, and where they don't, and are the same contrast as a single component. Depending on the criterion of the observer, and how they looked at the stimuli, there could be vastly different contrast judgments. However, our mean chromatic 1.5 c/deg PSE ratios very closely matched the estimated ratios of Georgeson & Shackleton (1994), increasing the likelihood that our achromatic data is, on average, accurate and representative.

Presently, our results are unclear as to whether there is an influence of isotropic mechanisms in high contrast monocular color vision for LSF stimuli. The isotropic detector may not be evident due to the greater cross-orientation suppression for chromatic stimuli, the imprecise and subjective nature of the task, and/or effects of contrast constancy and mechanism normalization. However, summation of LSF color plaid components is greater than for MSF color plaids, in threshold and suprathreshold vision.

#### **CHAPTER 5: EXPERIMENT 3 - IDENTIFICATION AND DETECTION**

## 5.1 Introduction

The chromatic isotropic detector appears to be limited to monocular threshold vision, as we have not found any direct evidence of its influence in binocular vision or suprathreshold perception. Therefore in our third inquiry into the orientation processing of color vision, we

examine monocular orientation identification at detection threshold. Identification is a necessary step towards further conscious form processing. Importantly, studying identification with detection allows us to examine different processes that ostensibly use the same neural input (Thomas, 1985). Here we ask if the identification of monocular LSF chromatic stimuli is possible at detection threshold.

We may suppose that detection and identification are always concurrent, as visual neural representations are presumably the same. In 1826, Müller described 'specific nerve energies' wherein our sensory nerves intrinsically carry both content and modality information. That is, upon experiencing a sensation through a specific nerve we will also know what type that sensation is. In 1981, Watson and Robson published their seminal paper on labelled detectors in vision in which they described a labelled line theory of detection. If stimuli "are detected by different sets of labelled detectors, then the identity of the set mediating detection unambiguously identifies the stimulus." In their experiment they found that pairs of gratings were reliably identified as often as they were detected if they were from different sets of spatial and temporal frequency tuned detectors.

An assumption of the labelled line theory is that the input to detection and identification decisions are the same (Thomas, 1985). However, within and beyond the retina, our visual system is organized for the efficient and economical parsing of visual information. Our spatial frequency tuned visual neurons are not necessarily linear or independent and are subject to processes of gain control and squaring (Goris, Putzeys, Wagemans, & Wichmann, 2013). Additionally, there is evidence that identification may happen at a later processing stage

than detection (Neri and Heeger, 2002). Therefore it is not axiomatic that identification is always intrinsic to detection.

If LSF chromatic monocular stimuli are detected by an isotropic mechanism, then according to labelled line theory we should not be able to discriminate between orthogonal stimuli at threshold. On the other hand, if we are able to identify the orthogonal orientations of LSF chromatic stimuli at detection threshold then we may need to question a) the presence of the isotropic mechanism in identification (and detection) and/or b) the applicability and accuracy of labelled line theory. Webster, Switkes, & de Valois (1990) and Reisbeck & Gegenfurtner (1998) found that observers could reliably distinguish between two stimuli of sufficiently different orientations for both chromatic and achromatic contrast gratings at threshold. Still, discrimination was slightly easier for achromatic gratings and required smaller orientation differences. However, these experiments were not conducted monocularly and used stimuli with relatively higher spatial frequencies than our LSF condition: 2 c/deg for Webster, Switkes, & Valois (1990) and 1c/deg for Reisbeck & Gegenfurtner (1998).

This third experiment aims to examine the coincidence of identification and detection for monocular LSF and MSF stimuli. We employ the same methodology as Watson & Robson (1981) to determine identification and detection thresholds concurrently for LSF chromatic, LSF achromatic, and MSF chromatic stimuli.

## 5.2 Protocols

For these experiments, stimuli were presented monocularly in the right eye and data was collected over multiple sessions. Detection and identification thresholds were obtained simultaneously by using a two-by-two forced-choice (2x2FC) method (Nachmias and Weber, 1975). There were two intervals, one contained the stimulus, while the other did not. The presented stimulus could be randomly one of two options, a left oblique or right oblique grating. The participant had to make two responses. First, they indicated which interval contained the stimulus and this was followed by auditory feedback. The participant then indicated which stimulus orientation they perceived, with no feedback. Detection and identification thresholds, corresponding to 81.6% correct, were calculated from fitting a standard Weibull function to the psychometric curve (Weibull, 1951) with psignifit toolbox in Matlab. Psychometric functions had six or more contrast levels with 80-100 trials each. There were three version of this experiment: (a) original, (b) phase jittered, and (c) phase jittered with smaller orientation difference. The protocol was identical for each with only changes in stimuli between versions. For the (a) original experiment, the observer was identifying between a left oblique and right oblique stimulus with orientations of  $\pm$  45 deg and a phase of 0. The (b) phase jittered stimuli also had orientations of  $\pm$  45 deg but their phase was randomly varied from 0-180 degrees between trials. For the last version (c), the two stimuli had random phases but with a smaller orientation difference of  $\pm$  16 deg. The experiments were all completed with three conditions: LSF chromatic, MSF chromatic, and LSF achromatic stimuli.

#### 5.3 Results

**Figure 16** displays thresholds with standard errors for all conditions and experimental versions. Red and black stars indicate that the standard errors do not overlap for identification and detection thresholds. Standard errors are calculated by fitting the psychometric function and performing parametric bootstrap to obtain confidence intervals. Red stars denote lower identification thresholds, while black stars are used for higher identification thresholds.



**Figure 16.** Identification, ID (solid bars), and detection, det (patterned bars), thresholds for all experimental versions and all conditions: LSF, 0.375 c/deg, achromatic (grey), LSF chromatic (red), and MSF, 1.5 c/deg, chromatic (pink). Error bars are ±1 standard error. Asterisks indicate that the standard errors do not overlap for ID and det thresholds. Red asterisks are for lower identification thresholds, while black are for higher identification thresholds. Thresholds are plotted for experiments a) with subject AC and stimuli that are orthogonal with a phase of 0 degs, b) with subjects AC and MS when stimuli are orthogonal with random phases, and c) with subjects AC and MS when stimuli were ± 16 degs with random phases.

## a) Stimuli with Orientation of ± 45 deg and Phase of 0 deg

**Figure 17** shows the percentages of correct detections and identifications of the stimuli for all three conditions for subject AC (the author). The identification and detection psychometric functions appear to mostly overlap. Identification and detection thresholds are all within each other's standard error ranges for all conditions. At threshold the observer was able to distinguish between the two orthogonal gratings.



**Figure 17.** Subject AC's psychometric functions for experiment a) where stimuli had a phase of 0 degrees and an orientation difference of ±45 degs. Percentage correct is plotted against the contrast in decibals of the stimuli. Detection (Det) data are shown with solid lines and identification (ID) data with dashed lines. LSF, 0.375 c/deg, achromatic data is shown in black, LSF chromatic in red, and MSF, 1.5 c/deg, chromatic in pink.

## b) Stimuli with Orientation of ± 45 deg and Random Phase

**Figure 18** (left) shows the percentages of correct detections and identifications of the stimuli for all three conditions and the two observers (AC and MS). Introducing a random phase to the stimuli does not produce higher identification thresholds. Participant MS had lower identification thresholds for both chromatic conditions.

## c) Stimuli with Orientation of ± 16 deg and Random Phase

**Figure 18** (right) shows the percentages of correct detections and identifications of the stimuli for all three conditions and the two observers (AC and MS). When lowering the orientation difference of the stimuli, both AC and MS have *higher* identification thresholds for LSF chromatic stimuli. At detection threshold, they were not able to reliably distinguish between a left and right oblique stimuli. AC also had lower identification thresholds for LSF achromatic stimuli.



**Figure 18.** Psychometric functions for subjects AC and MS for experiment b) (left) in which stimuli had a random phase and an orientation difference of  $\pm$ 45 degs and experiment c) (right) where stimuli had a random phase and an orientation difference of  $\pm$  16 degs. Percentage correct is plotted against the contrast in decibals of the stimuli. Detection (Det) data are shown with solid lines and identification (ID) data with dashed lines. LSF, 0.375 c/deg, achromatic data are shown in black, LSF chromatic in red, and MSF, 1.5 c/deg, chromatic in pink.

## 5.4 Discussion

This third experiment examined the coincidence of identification and detection for orthogonal gratings. While orientation discrimination is worse for monocular LSF chromatic stimuli, identification of orthogonal gratings is possible at detection threshold. If monocular LSF chromatic orthogonal stimuli are processed through the same isotropic detector, then according to labelled line theory we should not be able to distinguish between them.

Nonetheless, identification thresholds were not higher than detection thresholds for any orthogonal condition.

In an attempt to remove potential gross spatial cues to identity, we added phase randomization. Instead of making identification more difficult, there were several instances where observers had *lower* identification thresholds. Somehow, observers appear able to reliably identify a stimulus even when they had not detected it. Lower identification thresholds have been found in a wide range of detection and identification experiments (i.e. in Wandell, Sanches, & Quinn, 1982 and Allik, Dzhafarov, & Rauk, 1982). While better identification performance may be due to inhibitory interactions in detection for some studies (Thomas, 1985), signal detection theory actually predicts this initially baffling observation. As Haase, Theios, & Jenison (1999) explain, in signal detection theory yes and no responses in a detection task are represented by two separate regions with a normal distribution. These regions are separated by the observer, who uses their own criterion to define the boundary. This observerdefined boundary does not necessarily represent absolute conscious perception of the stimulus. It is possible for this boundary to be defined conservatively, favoring false negatives over false positives. Additionally, an assumption is made that the observer attempts to maximize correct hits on detection and identification independently. This strategy results in above-chance levels of identification within the 'no' region of signal detection space (See Haase, Theios, & Jenison, 1999 for a more in-depth review of this phenomenon).

Nonetheless, with or without a random phase, the data clearly show that identification of orthogonal LSF chromatic gratings is possible at detection threshold. There are two plausible explanations for this result; either the previous results of Gheiratmand et al. (2013;2014) have been misinterpreted as an isotropic pathway, or labelled line theory does not adequately describe all identification and detection behaviour. This second explanation is supported by more complex, newer models of identification and detection behaviour. Initially, the visual system was thought to be represented with independent parallel pathways (Campbell & Robson, 1968) with decision choices then resulting from max operator or Minkowski pooling. Goris, Putzeys, Wagemans, & Wichmann (2013) outline three main ways that physiology differs from a linear and independent encoding and decoding model. First, visual neurons are not independent from one another, as broad suppression and gain control mechanisms affect neurons that are maximally tuned to other spatial properties. Additionally, max operator decoding is inconsistent with the now large body of evidence that the brain represents information across large populations of neurons. Lastly, simple discrimination tasks are decided by pooling responses across many different sensory neurons, not just the most ideal neuron. The authors find that the biggest impedances to tasks such as detection and identification are "noise correlations between neurons and pooling inefficiencies". Identification and detection thresholds may therefore be a product of these factors, not just their similar neural input. Distinct choice behavior for each task could be represented by different suppression levels and the pooled responses and noise correlations of dynamic neural populations.

Additionally, identification may be done at a later information processing stage than detection, with a delay of 50-100 ms to identify detected image features (Neri & Heeger, 2002). Identification could take place when feedforward information has already reached a majority of other visual areas (Lamme & Roelfsema, 2000). Therefore, while inputs could be similar for the two decisions, identification outputs may be subject to much greater levels of hierarchical processing. A detecting population, located in V1 or even V2, may rely on non-oriented neurons, while identification could benefit from orientation tuning imposed by further processing through different cortical areas, V2 onwards. The amount of cone contrast for redgreen stimuli needed for detection in V2 is almost identical as that needed in V1 (Engel, Zhang & Wandell, 1997).

We did find higher identification thresholds for LSF chromatic stimuli with smaller orientation differences, confirming that orientation discrimination is worse for chromatic stimuli (Reisbeck & Gegenfurtner, 1998; Webster, Switkes, & Valois, 1990). Additionally, our results confer a potential spatial frequency dependency for weaker chromatic orientation identification at small orientation differences. It is plausible that an isotropic LSF color contrast detector could influence later identification processing, making it more difficult to discriminate close orientations. However, that hypothesis is beyond the scope of this experiment.

In the end, we did not find any evidence of an isotropic mechanism in LSF color orientation identification. We are able to distinguish orthogonal stimuli at detection threshold in all conditions. However, labelled line theories of vision are probably inadequate to describe

identification and detection behavior. Orientation tuning in identification does not necessarily equate to orientation tuning in detection. We may only conclude that isotropic filters do not extend to identification and seem thoroughly constrained to monocular LSF chromatic contrast detection tasks.

#### **CHAPTER 6: GENERAL DISCUSSION**

#### 6.1 Summary of Results

A monocular isotropic color mechanism has been proposed for color contrast detection as a behavioral parallel to isotropic color responsive cells in V1 (De Valois, 1965; Livingstone & Hubel, 1987; Johnson, Hawken, & Shapley, 2008). This research thesis examined related visual behaviors and an isotropic color pathway is not directly evident in binocular summation, suprathreshold contrast perception, or identification. The isotropic behavioral mechanism currently appears limited to the monocular detection tasks of Gheiratmand et al. (2013; 2014). Furthermore, while color vision was once called "form-blind" (Livingstone & Hubel, 1987), we found evidence for its orientation tuning and processing in all three of our experiments. Color vision has both orientation untuned (Gheiratmand et al., 2013; 2014) and tuned behavioral mechanisms that most likely correspond to the two populations of untuned and tuned color responsive cells in the visual cortex (Johnson, Hawken, & Shapley, 2008). It is not confined to blob and surface color detectors or edge detection and form processing, but is capable of both under different conditions. We examined the orientation tuning of color vision in binocular summation by measuring summation ratios for dichoptic plaids over a range of orientation differences. This study is the first thorough investigation of the orientation tuning of binocular summation using subthreshold summation. We found that an orientation tuned model fit binocular color and achromatic vision with orientation bandwidth estimates of 19 and 23 deg for the LSF and MSF color stimuli, and 24 and 31 deg for the LSF and MSF achromatic stimuli, respectively. With individual variability, none of these bandwidth estimates are significantly different from one another. Color vision has similar binocular orientation tuning to achromatic vision, an important result given past ideas of its poor orientation processing abilities (Livingstone & Hubel, 1987). On the contrary, as far as orientation tuning properties are concerned, binocular color vision appears equally capable of the oriented edge detection that is the basis for form processing.

Intriguingly, we also found that LSF color vision had increased binocular summation independent of the orientation difference of its summated components. This pedestal of increased sensitivity in the LSF color binocular summation mechanism could be due to a hidden isotropic pathway adding onto the tuned response. Alternatively, it may also be due to a more linear combination of signals at the binocular mechanism. For future investigation, one could potentially use high contrast masking to suppress isotropic channels and see whether binocular summation is then particularly reduced for LSF color plaids.
Next, we compared the contrast perception of monocular high contrast plaids and gratings to determine if there are relatively high summation effects for LSF chromatic stimuli beyond threshold vision, which could indicate isotropic processing. While LSF color plaids had greater summation than MSF color plaids, it was indistinguishable from LSF achromatic plaid summation. Therefore, although LSF color plaids had the highest average summation, we cannot propose that it is through the influence of color specific isotropic channels. Surprisingly, MSF color plaids had significantly lower perceived contrast summation than both LSF chromatic and achromatic conditions. This lower summation may be the result of an overall spatial frequency effect or increased cross-orientation suppression for all chromatic stimuli. These results are intriguing and warrant further study with the inclusion of a MSF achromatic condition.

Our final experiment examined the monocular identification of oriented gratings at threshold. According to labelled line theory (Watson & Robson, 1981), if a detecting mechanism is isotropic then an observer would not be able to discriminate between orthogonal stimuli at threshold. Although orientation discrimination was worse for LSF color stimuli, subjects were able to identify orthogonal gratings at threshold, consistent with previous (nonmonocular) literature (Reisbeck & Gegenfurtner, 1998; Webster, Switkes, & Valois, 1990). Therefore, either Gheiratmand et al. (2013; 2014) misinterpreted their detection task results as an isotropic pathway or labelled line theory inadequately describes identification and detection behavior. Due to current arguments against the simplicity of labelled line theory (Goris et al., 2013), we interpret our results only as orientation tuning in identification.

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## 6.2 Limitations

A limitation of this study and those of Gheiratmand et al. (2013; 2014) is the assumption of monocularity with our methodology. There is no guarantee that monocular presentation of stimuli, with mean luminance presented to the other eye, engages only monocular neural resources. It is entirely possible that binocular resources are also processing these signals, although perhaps at a disadvantage. Most monocular studies use similar methodology (i.e. in Meese & Baker, 2011), however that does not necessarily mean it is correct.

## 6.3 Isotropic Mechanisms in Early Vision

Behavioral evidence of an isotropic color mechanism has so far only been found in monocular contrast detection. Isotropic mechanisms are also used at the other end of low spatial frequency monocular vision, for high speed achromatic stimuli (Kelly & Burbeck, 1987), and orientation tuning is similarly imposed for dichoptic and binocular stimuli (Meese & Baker, 2011). As we didn't find evidence of isotropic processing in more complex visual tasks, we may suppose that it is only present at the very early stages of vision. Perhaps isotropic signals carried by early visual monocular channels only remain so when they encounter very little additional processing. Untuned signals arrive from the LGN at layer 4 in V1 where they may or may not acquire orientation tuning (Livingstone & Hubel, 1988). These signals are then passed to layers 2/3 where a majority are binocularly combined (Blasdel & Fitzpatrick, 1984). Additionally, approximately just 10% of color responsive V1 cells are estimated to be isotropic (Johnson, Hawken, & Shapley, 2008). Monocular contrast detection at threshold is thought to be carried out in the primary visual cortex, and these early untuned cortical areas may be

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sufficient. However, in all of our tasks, it is likely that additional neural resources were recruited, beyond the small population of isotropic color cells. For binocular summation, the signals would have to pass at the very least to binocular cells in layers 2/3. High contrast perception is affected by contrast gain control and a broad suppression pool from other visual neurons (Meese & Holmes, 2010), and identification may recruit further downstream visual areas (Neri & Heeger, 2002).

## 6.4 Conclusion

For color vision to act solely as a surface color or blob detector separated entirely from form, it must be behaviorally constrained to the very early stages of monocular contrast detection. While color surface detection and filling in could certainly be a distinct functional role with dedicated cellular resources, it is likely that this function seldom operates in isolation. For binocular summation, high contrast perception, and identification, passing low spatial frequency color information through additional neural processes appears to combine orientation and form. To suppose that color vision mainly operates independently of form would place undue emphasis on very specific and rare visual circumstances, monocular contrast detection at threshold. For the majority of visual perception, past early cortical stages, where information is distributed and combined across neural areas, form and color are inextricably linked.

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