University of Nevada, Reno

Minimally distinct border judgments and contrast: effects of eccentricity

A thesis submitted in partial fulfillment of the requirements for the degree of
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by

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Abstract

Precise isolation of individual chromatic mechanisms is useful for investigations of vision. One technique for isolating chromatic pathways is “silent substitution” (modulating colors along specific color directions). The minimally distinct border (MDB) technique can be further used to determine the specific color direction that isolates the S-cones (tritan axis). However, macular pigment distribution may render a foveally-measured tritan line imprecise when stimuli are large or peripheral. We had subjects make MDB judgments at five retinal eccentricities, and compared the results to a model of macular distribution. The model predicted the direction of chromatic rotation but the predicted magnitude was less than observed. We hypothesized that the neural properties that underlie MDB judgments in the fovea may not be valid for the periphery. For example a decrease in L-M sensitivity across the visual field may result in minimum border detection shifted near the L-M axis.

We investigated this issue by using a suprathreshold contrast matching task to examine the perceptual scaling of chromatic and luminance as a function of eccentricity. Subjects made contrast matches between Gabor patches across the visual field, comparing chromatic and achromatic stimuli to a foveal achromatic stimulus. Our results show a falloff in L-M and luminance sensitivity, relative to S-cone sensitivity with increasing eccentricity. Our suprathreshold results mirror those of threshold measures for chromatic pathways but not for luminance, consistent with known physiology of magno and parvo luminance pathways. Our results indicate that MDB may not be a valid peripheral indicator of the tritan axis.
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Minimally distinct border judgments and contrast: effects of eccentricity

Introduction

Humans are able to perceive color based on the activities of three types of cone photoreceptor in the retina. Each cone type is maximally sensitive to a particular range of wavelengths of light: L cones are specialized for long-wavelength light, M cones for the middle wavelengths, and S cones for the short wavelengths. The inputs to each cone type are compared to one another to produce the percept of “color” (a perceptual, rather than physical, quality). We have the impression of a unified visual experience; that is, we perceive objects or regions as being one color, rather than a mix of wavelengths of light or differential cone activations. Despite this percept, visual information is relayed to the brain and processed along multiple, parallel pathways. One aspect of this parallel processing is cone opponency. The “red-green” color opponent mechanisms difference the outputs of the L and M cones to provide red-green information; another compares the output of the S cones to the summed activity of the L and M cones to provide blue-yellow opponency, and a third sums the activity of the three cones (in particular the L and M cones) to provide luminance information. Each of these pathways is associated with a distinct physiological substrate, and each has unique spatial and temporal properties. By creating appropriate models of color vision, and stimuli that isolate individual mechanisms, we can design experiments that investigate these properties.
In cone-based color space, axes can be determined that selectively modulate different cone or cone-opponent systems. For example, in the cone-based color space described by Macleod & Boynton (1978), modulations along any horizontal axis correspond to a selective activation of the opponent pathway that differences the L and M cones while holding S-cone activation constant. Similarly, modulations in the vertical directions selectively modulate the S cones and subsequently the S-(L+M) opponent pathway while holding the L and M cone activations constant. Many studies have employed this space as well as another cone-based color space that was modified to include an orthogonal luminance dimension (Derrington, Krauskopf, & Lennie, 1984). The cardinal axes in this space correspond to physiological channels in the retina and lateral geniculate nucleus (ibid.). In cone-based color spaces such as these, dichromatic individuals (i.e. those that are missing one of the cone types) would be unable to distinguish between colors along certain lines in this space. A tritanope (somebody who has only L and M cones) would be unable to discriminate any pair of colors along S-(L+M) axes (the cardinal axis, as well as any line parallel to it) in an equiluminant plane, since modulation along these lines changes only the activity of the missing cone type. These lines are collectively called “tritan confusion lines”, while protanopic and deuteranopic confusion lines radiate diagonally outwards from the lower corners of the MacLeod Boynton space.

Applications and definitions of these cone-based color spaces vary from study to study. In the most common application the space is calculated from tabled values of corneal-based cone spectral sensitivities (so-called “fundamentals”) that represent the
average data from many individuals collected under specific experimental conditions. Since each individual’s cone spectral sensitivities are unlikely to exactly match the tabled fundamentals, individual axes can vary between individuals and within individuals when measured in different ways. Consequently, actual confusion axes may vary from person to person and from one experimental condition to another depending on the individual factors such as optic media (Ambach et al., 1994), ratios of photoreceptor types (Smith & Pokorny, 1995), genetic variation in peak cone sensitivities (Merbs & Nathans, 1992; Neitz, Neitz, & Jacobs, 1991), and stimulus parameters such as retinal location, spatial frequency, and even temporal timing.

There are several techniques for determining an individual’s tritan line, including minimally distinct border (MDB) (B. W. Tansley & Boynton, 1976), minimum sensitivity (Sankeralli & Mullen, 1996), transient tritanopia (Mollon & Polden, 1975, 1977; Smithson, Sumner, & Mollon, 2003), and adaptation (Webster & Mollon, 1994). In the MDB technique, subjects are shown a circular patch divided in half (a bipartite field), with each half of the field comprising a different chromaticity with the same luminance. Depending on the particular version of the task, subjects either adjust both chromaticities simultaneously (as in Experiment 1 of this paper), or adjust the chromaticity of one side of the field while the other is held constant. The goal of the task is to find a combination of colors for which the perceived border between the two halves of the field is minimally distinct. These two colors should form a tritan pair. The reason this works is because S cones have a sparse representation in the retina (Curcio et al., 1991) and provide minimal contribution to luminance (Eisner & MacLeod, 1980; Ripamonti, Woo, Crowther, &
S-cones are thus poor at forming perceptual borders and when isolated will produced the “minimally distinct border” effect.

The minimum sensitivity paradigm takes a similar approach: subjects adjust both chromaticities of a grating until the stimulus as a whole is minimally visible (or more formally that threshold is greatest), indicating a tritan line (Sankeralli & Mullen, 1996). This technique works on the same principles as the MDB method.

Finally, a tritan line can be found by taking advantage of the “transient tritanopia” phenomenon, wherein the extinction of adaptation to a bright yellow field (which adapts the L & M cones) paradoxically raises detection threshold for an S cone stimuli (Mollon & Polden, 1975). Colored patterns composed of tritan metamers therefore exhibit the greatest loss of sensitivity compared to patterns composed of other colors (Smithson et al., 2003).

Studies seeking to characterize the S-cone pathway often need to make a determination of the tritan line, since modulation along such a line preferentially activates the S cones. While it is often convenient to speak of the nominal tritan line for the average observer, in practice there is little reason to believe that this nominal axis will hold for any individual observer. That is, a modulation in color that would be predicted to isolate the activity of the S cones for the “standard” observer will very likely also change the activity of the L and M cones in a real observer, due to the reasons described above. Thus, when minimal intrusion from L and M cone mechanisms are desired, the tritan axis ideally is measured in each subject and for each experimental condition using one of the techniques listed above. Traditionally, these methods are used to determine the tritan axis
in the center of gaze (fovea) in the retina. However, the central ~3° of visual angle contains the greatest concentration of macular pigment (Howells, Eperjesi, & Bartlett, 2011), which has great influence on the spectral content of the light that impinges upon the photoreceptors. Consequently, changes in the density of macular pigment with retinal eccentricity will cause a concomitant change in the tritan line.

Macular pigment (MP) is a carotenoid-based prereceptoral filter found in the fovea that selectively absorbs light between ~380 and 550 µm, with a peak absorbance at ~460 µm (Sharpe, Stockman, Knau, & Jägle, 1998; D. M. Snodderly, Brown, Delori, & Auran, 1984). The function of macular pigment appears to be protection of the retina from the relatively higher energies found in the short-wavelength end of the spectrum (e.g. UV rays from the sun), as well as preventing oxidative stress to the retinal pigment epithelium (Frank, Amin, & Puklin, 1999; W. M. Snodderly, 1995). Optical density of MP varies widely between individuals, and can be measured in a variety of ways direct and indirect, including Raman detection (Bernstein, Yoshida, Katz, McClane, & Gellermann, 1998), microspectrophotometry (D. M. Snodderly et al., 1984), fundus reflectometry (Zagers & van Norren, 2004), and flicker photometry (e.g. Sharpe et al., 1998).

As noted above, macular pigment is found nearly exclusively in the fovea and diminishes rapidly beyond roughly 3° of eccentricity (although see Berendschot & van Norren, 2006). Because MP effectively acts as a filter for short-wavelength light, its presence affects the amount of light available to be absorbed by photoreceptors at the retina, thus changing their activity in the fovea versus the periphery. For experiments that
stimulate the retina outside the fovea (e.g. fields larger than about 3 degrees) and attempt to maintain S cone isolation, this is a significant consideration. These types of large-field stimuli are used to study the development (Crognale, 2002) and pathology (Crognale et al., 1993) of the S cone pathway. Visual evoked potentials (VEPs) record, at the scalp, the electrical activity generated by the brain in response to different types of stimuli (e.g. those that isolate S cones). The use of large-field stimuli can increase the amplitude of the VEP (Parry & Robson, 2012; Rabin et al., 1994), which can be desirable not only for subjects with normal color vision but those who normally show reduced responses, such as infants (Crognale, 2002). Since these types of experiments (and others, including threshold psychophysics) depend upon the isolation of the S cones, differences in macular pigment between the fovea and periphery become especially important.

In Experiment 1, we attempted to establish a method for determining the tritan axis in both the fovea and periphery using MDB judgments. Our results were mostly consistent with previous findings and the predictions of our model, but differed enough from the expected models to encourage additional experimentation. That is, the rotation of color angle on the periphery of the visual field necessary for an MDB setting was, on average, 8.07° relative to our nominal tritan line. This is more than three times greater than the 1.59 degrees of rotation predicted by our model. One possible explanation of these results is the wide variation in individual MPOD mentioned previously; however, the variance in settings between individuals was greater in the periphery than in the fovea. Since all subjects presumably had an MPOD of zero in the extrafoveal region, then that should have been the condition with the least variance.
One factor that was not taken into account in Experiment 1 is the difference in cone opponency between the center and the periphery of the visual field. The cone mosaic in the fovea is characterized by densely-packed L and M cones, with relatively few rods and S cones. In addition, the center of the receptive fields of the midget (parvocellular) cells in the fovea receive input from a single cone photoreceptor, allowing high acuity. The high ganglion cell to L and M cones ratio also allows for strong red-green opponency in the fovea; there are many spatially distinct L and M signals, providing a great deal of input to the L-M differencing pathway (Dacey, 2000). In contrast, each ganglion cell receptive field region in the periphery samples from a large population of cones, including both L and M cones. This mixed input to the L-M differencing signal essentially reduces red-green opponency (ibid.). The S cones are distributed in a nonrandom fashion that “tiles” the peripheral retina (Curcio et al., 1991). The anatomical connection between S cones and ganglion cells is distinct from that of L and M cones, and thus the S-(L+M) pathway may not suffer the same deficit in opponency that the L-M pathway does. Additionally, since the luminance (L+M) pathway simply sums its inputs, it may be minimally affected by eccentricity (Dacey, 2000; Mullen & Kingdom, 2002; Mullen et al., 2005) as well.

Modulation along any tritan line changes only the activity of the S cones, while holding the relative activities of the L and M cones constant; thus tritan lines can be considered “constant LM” or “LM-silencing” axes (Derrington et al., 1984). Note also that by definition this axis also silences the L+M (luminance) pathways. In the peripheral retina, an area with reduced opponency between the L and M cones, the axis that silences
the L-M pathway while passing through a chosen white point should be shifted relative to
the fovea due to macular absorption and its effects on the L and M cone spectral
sensitivities. While this shift has been modelled (Smith & Pokorny, 1995) and measured
(Smithson et al., 2003), it has not been established how closely the MDB technique
agrees with other methods of determining the S axis. As noted above, the perception of a
distinct border between two equiluminant colors depends upon the L-M and L+M
mechanisms (Tansley & Boynton, 1978). Perhaps, then, a reduction of L-M opponency in
the periphery might cause the border between two chromaticities to be minimally distinct
closer to the L-M axis than the S cone-isolating direction. Experiment 2 investigated this
issue.

It has been established experimentally that contrast between stimuli modulated
along different cone and cone-opponent axes can be equated perceptually, a method
known as suprathreshold contrast matching (SCM). Switkes & Crognale showed that
subjects were able to reliably make perceptual contrast matches between gratings along
the cardinal L-M, L+M, and S-(L+M) axes, as well as unipolar +L and +M directions (E.
Switkes & Crognale, 1999). This result was then built upon by demonstrating similar
results for axes intermediate to the cardinal axes (Eugene Switkes, 2008). Other studies
have used contrast matching to examine the effect of spatial frequency on perceptual
matches (e.g. Georgeson & Sullivan, 1975; Tiippana et al., 2000). Experiment 2 was
designed to expand upon this line of research. To the author’s knowledge, the question of
how (if at all) perceptual contrast matches vary with eccentricity has not been
investigated. Due to the aforementioned changes in the physiological substrates of
perception across the visual field, the SCM task may help to elucidate the role of L-M opponency in the results of Experiment 1. Specifically, do subjects require relatively more L-M contrast to make a match at greater visual eccentricities? If so, this explanation for the greater-than-expected magnitude of rotation seen in the MDB task becomes more likely.

**Experiment 1**

**Methods**

Five females aged 20 to 28 and five males aged 21 to 35 participated in the experiment. All subjects had normal color vision as assessed by the 38-plate Ishihara test, and normal or corrected-to-normal visual acuity. Subjects gave informed consent to participate and all procedures were first approved by The University of Nevada, Reno’s human subjects institutional review board and were in accord with the Declaration of Helsinki. Stimuli were presented on a 39cm x 29cm Sony Triniton Multiscan 20seII CRT monitor from a distance of 57cm, and consisted of circular bipartite patches presented at five retinal eccentricities. The patch sizes and eccentricities are listed in Table 1. These circular fields comprised two colors with chromaticities at opposite ends of a line in a scaled MacLeod-Boynton color space, with the initial chromatic direction selected randomly. The CIE coordinates of the average chromaticity were $x = 0.313$, $y = 0.313$ while luminance was held at 18 cd/m$^2$. In the first step, the colors in the bipartite field were equated flicker photometrically for each of the two nominal opponent axes and defined individual isoluminant planes. This procedure was repeated for each of five eccentricities. These isoluminant settings were then applied to the stimuli used in the next
step, a modified MDB procedure. The bipartite fields themselves were constantly rotating in orientation at a rate of approximately 180° per second to reduce Troxler fading in the periphery. Visual angles subtended by the patches across eccentricities are listed in Table 1. In this procedure, participants pressed the left or right keys on a keyboard to rotate the color axis in color space around the white point, thereby changing the colors of both halves of the bipartite field(s) simultaneously while holding the mean chromaticity and luminance constant. Subjects were instructed to adjust the color angle in increments of 1° until the border between the two chromaticities was minimally distinct. When subjects were satisfied that this criterion was fulfilled, they pressed a key to move to the next level of retinal eccentricity. For each level, previous stimuli were not shown, creating expanding annuli of bipartite fields (see Figure 1). The final eccentricity contained two layers of circles, with the second layer filling in the rectangular space left on the outside of the stimulus ring. This sequence of five minimally distinct border judgments was repeated three times per participant and the chosen angles were averaged across trials to yield a mean estimate of the tritan direction for each eccentricity.

**Model of the tritan line**

In order to have a point of comparison for our experimental results, we calculated how the tritan axis would be transformed in the absence of macular pigment (i.e. in the periphery of the visual field). To do this we modified the 2-degree quantal cone fundamentals tabled by Stockman & Sharpe (2000) by subtracting the influence of macular pigment as tabled by Stockman, Sharpe, & Fach (1999). Our model assumed a
peak macular pigment optical density of 0.5, which we considered a reasonable estimate, although the tabled optical density values of

<table>
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<th>Level</th>
<th>Centroid</th>
<th>Diameter</th>
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<td>3</td>
</tr>
<tr>
<td>2</td>
<td>2.5</td>
<td>3.4</td>
</tr>
<tr>
<td>3</td>
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<td>5</td>
</tr>
<tr>
<td>4</td>
<td>9</td>
<td>5.6</td>
</tr>
<tr>
<td>5</td>
<td>13; 17.5</td>
<td>7.2</td>
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</tbody>
</table>

**Table 1**: locations of bipartite fields. All measurements are in degrees of visual angle. The size of stimuli scale upwards with retinal eccentricity; this was to allow border judgments despite decreased visual acuity in the periphery.

**Figure 1**: An example of the minimally distinct border stimulus described in Experiment 1; the fourth eccentricity level is shown here.
Stockman, Sharpe, & Fach (ibid.) peak at 0.35. Our calculations predicted a clockwise shift of 1.59° for the S axis, relative to the nominal angle of 90°, as well as an extension of the line segment in MacLeod-Boynton space. These results are largely in agreement with a similar model plotted in cone-troland space by Smith & Pokorny (1995), who also showed that stimuli originally calculated to be on a tritan axis rotated counterclockwise without macular pigment. This counter-clockwise rotation of the stimuli in color space would predict an equal and opposite (clockwise) rotation of the peripheral (without macular) tritan axis when plotted in a color space using foveal-based fundamentals (with macular).

**Results & Discussion**

The MDB judgments made by the experimental subjects agreed in direction with the predictions of our model. The angles in cone-excitation space corresponding to the participants’ choices are shown in Figure 2. The angles chosen close to the fovea are close to the expected 90° given a nominal tritan axis, and increase in distance with increasing eccentricity. The final eccentricity gave a clockwise angle of 8.07° relative to the vertical S axis. Our participants’ mean MDB angles in the periphery are similar to those determined by Smithson et al (Smithson et al., 2003) in a non-foveal transient tritanopia experiment. It should be noted that initial MDB attempts proved difficult as reported previously due to fading. However, the introduction of slow rotation of the patches greatly reduced the fading of the peripheral stimuli and consequently the difficulty of the task. Interestingly, the magnitude of color angle change required for a
minimally distinct border was greater than the model predicted. This is possibly due to significant variation between individuals in density of macular pigment (Sharpe et al., 1998). This explanation is rendered less likely by the fact that the variance between subjects was greater for peripheral than for foveal judgments (see Figure 2). If our results are due to individual variation in MPOD, it would be expected to have its effect in the fovea where the macular pigment is present rather than the periphery where it is absent. An alternative explanation is that a paucity of red-green opponency in the periphery of the visual field is causing the border to be minimally distinct closer to the L-M axis than would be seen otherwise. Experiment 2 was designed to investigate this possibility, as well as expand upon previous research on contrast matching between chromatic- and luminance-modulated stimuli.

Figure 2: MDB settings averaged across subjects. The angles shown on the Y-axis are angles in the MacLeod Boynton space listed in the Results & Discussion section. Error bars represent standard error of the mean.
Experiment 2

Methods

Suprathreshold Contrast Matching (SCM)

Two females aged 26 and 37 and four males aged 28 to 57 (median age 29) participated in the experiment. Three subjects viewed the stimuli on the same monitor and with the same viewing conditions as in Experiment 1. For the remaining three subjects, stimuli were presented on a 39cm x 29cm Mitsubishi Diamond Pro 2070SB (see below), with viewing conditions the same as in Experiment 1. Each subject had their isoluminant plane determined flicker photometrically before completing the suprathreshold contrast matching (SCM) task. SCM was determined using the method of constant stimuli in a 2 alternative forced choice procedure. In the SCM task, subjects were sequentially shown a test and a comparison Gabor patch (sine wave gratings spatially filtered with a Gaussian function). Test patches varied along three axes: two chromatic axes, as in Experiment 1, as well as the orthogonal luminance axis. Comparison patches were a fixed-contrast (Michelson contrast = 0.09) achromatic, luminance patch presented in the fovea. The characteristics of the color space and mean chromaticity were as specified in Experiment 1. Gabors are ideal stimuli for selectively stimulating the LM and S pathways, as they contain no hard edges and thus minimize the likelihood of luminance artifacts. In a given trial, either the test or the comparison stimulus was shown on the screen in a square-wave temporal pattern, accompanied by a
tone. The stimulus remained on the screen for 1s. Then the first stimulus disappeared and the second stimulus was shown in the same manner. The same five eccentricity levels were used here as in Experiment 1, and test stimuli that appeared in the periphery were presented as annuli of identical configuration, but composed of gabor patches rather than bipartite fields (see Figure 3). Subjects maintained fixation throughout, and were instructed to judge whether the first or the second stimulus had higher contrast, indicating their judgment with a key press. On each trial, eccentricity and chromatic contrast varied pseudo-randomly for the test stimulus. The temporal order of the test vs. the comparison

**Figure 3:** An example of the suprathreshold contrast matching stimulus described in Experiment 2; the fourth eccentricity level is shown here.
stimuli varied randomly. The axis of the test grating was varied in a fixed order (LM, S, luminance, LM ...) across trials. The spatial frequency and size of the stimuli were held constant at each eccentricity; spatial frequencies were comparable to those used by Mullen & Kingdom (2002). Specific stimulus properties are listed in Tables 2 & 3.

The optimal properties of the comparison patches were determined by measuring detection thresholds for achromatic gratings using a 2 alternative forced choice task (i.e. is the grating on the right or left side of the screen?). Spatial frequency, luminance contrast, and eccentricity were varied throughout this experiment. We determined that 1 cpd gratings could be detected the most reliably, with detection approaching chance with decreasing spatial frequency. Threshold for detection was defined as the contrast level at which a grating could be detected 50% of the time. The primary reason for this measurement was to ensure that the contrast used for the comparison patch in the SCM task is at least two times threshold level. The approximate threshold (in Michelson cone contrasts) in this experiment was $L = 0.0578$, $M = 0.0578$, $S = 0.0578$, and the contrast for the comparison grating was $L = 0.578$, $M = 0.578$, $S = 0.578$, ten times threshold. Threshold detection level for achromatic stimuli did not vary appreciably across retinal eccentricities, consistent with previous findings (Mullen & Kingdom, 2002). We used these results to set the properties of the comparison patch in the SCM task. This comparison patch modulated along the luminance axis, and had a fixed cone contrast of $L = 0.578$, $M = 0.578$, $S = 0.578$ and spatial frequency of 1 cycle per degree. The
percentage of times that the test patch was chosen at each contrast level was fit to a Weibull function, with the point of subjective equality (test patch chosen 50% of trials) comprising the “contrast match” for that subject; this was equated separately for each of the three stimulus axes.

<table>
<thead>
<tr>
<th>LM Axis</th>
<th>Contrast 1</th>
<th>Contrast 2</th>
<th>Contrast 3</th>
<th>Contrast 4</th>
<th>Contrast 5</th>
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<tr>
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<td>0.354</td>
<td>0.404</td>
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**Table 2:** Michelson cone contrasts for the LM and S axes in a cone excitation space.

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<td>Cycles per Degree</td>
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<td>1</td>
<td>0.46</td>
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</table>

**Table 3:** Spatial frequencies (cycles per degree) and centroids (degrees of visual angle) for each of the five eccentricity levels. Diameters of stimuli for each eccentricity are listed in Table 1.

Subjects judged each unique combination of stimulus characteristics ten times per run. The first run was used as task training and to determine a custom contrast range for each subject. The contrast range of the initial run was determined via pilot testing to be
ostensibly reasonable for the “average” subject. After the first run, the points of subjective equality for each subject were averaged across contrasts separately for each axis. This average axis value was set as the mean in each subject’s custom range; a total of six contrast levels were determined for each axis, in three equal steps on either side of the mean. Each subject then performed two more runs using their custom contrast ranges. The PSEs for each of the second two runs were averaged together to yield a contrast matching function for each axis. For three subjects the maximum contrast of the S cone stimuli, which was limited by the gamut of the Triniton monitor, was not high enough for them to make a match to the comparison stimulus. These subjects completed their second two runs on the Diamond Pro monitor, which was able to generate higher contrasts for the S axis stimuli. For these subjects all stimuli except those of the S cone conditions were identical to those generated on the Triniton monitor. Subjects were excluded from further runs or final data analysis if functions were unable to be fit to their data (e.g. if they chose the test stimulus for one axis every time, regardless of contrast level), or if their data indicated the use of a criterion dissonant with the given instructions. Six subjects were excluded in this manner; the data presented here are those of the remaining six subjects who completed all three runs.

Results & Discussion

Points of subjective equality averaged across subjects are shown in Figure 4. In general, as stimuli moved farther into the periphery, subjects required more LM contrast to match them to the foveal comparison stimulus. This is consistent with previous findings that contrast sensitivity (at threshold) for red-green stimuli decreases with
eccentricity (Hansen et al., 2009; Mullen & Kingdom, 2002; Mullen et al., 2005). However, our data also show a similar increase in required contrast for luminance-modulated gratings across the visual field, which is at odds with previous research showing that contrast sensitivity for luminance gratings remains relatively constant as eccentricity increases (Mullen, 1991; Mullen & Kingdom, 2002). This can likely be explained (at least in part) by the fact that the stimuli used in our contrast matching task were well above threshold, while stimuli used in previous studies often were close to threshold. Of the physiological pathways from the retina through the lateral geniculate nucleus to the visual cortex, the magnocellular pathway is especially sensitive to low-contrast stimuli and would be preferentially engaged by patterns near threshold (Lee et al., 1990; Smith & Pokorny, 1997). The input to the magnocellular pathway remains fairly constant across the visual field (Baseler & Sutter, 1997; Livingstone & Hubel, 1988), and thus is consistent with a steady level of contrast sensitivity for achromatic stimuli in previous research. The parvocellular system is strongly driven by higher-contrast stimuli of the type that were displayed in Experiment 2 (Smith & Pokorny, 1997). Unlike the magnocellular system, the input to the parvocellular system decreases with eccentricity (Baseler & Sutter, 1997); it is likely that the LM and luminance stimuli used in this experiment were engaging these cells, and thus both axes required higher contrast to make a match in the periphery.

One consistent pattern of results from Experiment 2 was a decrease in the amount of contrast necessary to match the S cone stimuli to the comparison patch as the stimulus moved from the fovea to the periphery. This effect also seems to be unique to
suprathreshold S cone stimuli, as Mullen & Kingdom’s near-threshold measures of S cone sensitivity showed little change across the visual field (2002). In particular, necessary S cone contrast decreased as the stimulus moved beyond the fovea, but remained fairly constant across the rest of the visual field. This finding is consonant with the distribution of macular pigment across the retina: the fovea contains the greatest concentration of macular pigment, and thus it is there that subjects required the highest contrast for S cone stimuli. The second level of eccentricity is 2.5 degrees and thus may still be within a region of macular pigment, but the results suggest that at least for suprathreshold stimuli, the optical density is low enough at this eccentricity not to influence contrast matches compared to the far periphery.

To quantify these observations, a repeated-measures factorial ANOVA was performed using stimulus axis and eccentricity as factors. Mauchly’s test showed that the assumption of sphericity in this data set was not violated (axis: p = 0.7; eccentricity: p = 0.35); as such, no corrections to degrees of freedom were made. There were significant main effects of axis, $F(2,10) = 9.99$, $p < 0.01$, $\eta^2 = 0.67$, and eccentricity, $F(4, 20) = 4.27$, $p = 0.01$, $\eta^2 = 0.46$. A significant interaction between axis and eccentricity was also found, $F(8, 40) = 5.47$, $p < 0.001$, $\eta^2 = 0.52$. Due to the relative similarity in subjects’ matches along the L-M and luminance axes, both the main effect of axis and the interaction appear to be driven by the difference between these and the S axis, both overall and as a function of eccentricity. One possible factor in subjects’ judgments that we are unable to rule out is the effect of stimulus size. As noted above, the size and number of gratings in the periphery was larger than in the fovea; this was done in order to
increase visibility, since the measure of interest was a comparison of the relative changes between pathways. Contrast matching judgments between chromatic and achromatic stimuli rely in part on the salience of the stimulus, and in conditions of roughly equal perceptual contrast, salience might have come instead from stimulus size.

![Figure 4: Points of subjective equality as a function of stimulus eccentricity, which each data point normalized with respect to the fovea. Red line: LM stimuli. Blue line: S stimuli. Black line: luminance stimuli. Each data point is an average across subjects; error bars correspond to one standard error of the mean.](image)

It is difficult to predict exactly what the effect of stimulus size might have on the data, but overall it ought to increase the likelihood of subjects choosing more peripheral stimuli as having higher contrast. This could be expected to minimize the effect of the independent variable; that is, a smaller peripheral stimulus would require more contrast in order to be matched. In Figure 5, this would manifest as more negative slopes for the LM
and S functions. One subject was run on a control experiment wherein the comparison stimuli were single Gabor patches presented symmetrically on both sides of the visual field along the horizontal meridian. These patches occupied the same eccentricities as the corresponding patches that were embedded in annuli in the main experiment. With these stimulus conditions, the subject required more contrast to match both the LM and S stimuli, a finding consonant with the size effect proposed above and with previous studies demonstrating that the deleterious effect of eccentricity upon color vision can be ameliorated by increasing stimulus size (Abramov et al., 1991; Hansen et al., 2009; Noorlander et al., 1983). Thus, the positive slopes seen for the LM and luminance stimuli may be flatter than they would be if size was held constant.

**Conclusion**

Experiment 1 sought to investigate whether the minimally distinct border method of determining an individual’s tritan axis is viable in the periphery of the visual field. Our results show that while the direction of rotation of the tritan axis is consistent with previous results, and the predictions of a model, the magnitude of the rotation was greater than expected (8.07 degrees observed vs. 1.59 degrees predicted). Taken alone, this result is somewhat ambiguous. Previous studies have shown a consistent decrease in the strength of red-green opponency as visual eccentricity increases (Mullen, 1991; Mullen & Kingdom, 2002). It remains a possibility that this decrease, rather than an indistinct border due to an isoluminant tritan pair, drove the results of Experiment 1.

Experiment 2 was designed to investigate this possibility, as well as expand upon previous research on suprathreshold contrast matching. It has been established that
perceptual contrast matches can be made reliably between the cardinal chromatic and luminance axes (Switkes & Crognale, 1999) as well as intermediate axes (Switkes, 2008). The current study had subjects make contrast matches between suprathreshold chromatic and luminance stimuli across the visual field. Our results show that on average, more L-M contrast was required in the periphery than in the fovea to match an achromatic comparison grating, lending support to the interpretation of the data collected in Experiment 1 as being due in part to reduced L-M opponency in this area. Because the MDB technique relies on the assumption that the least distinct border will be formed by isoluminant colors comprising a tritan axis, the validity of this technique appears to be suspect when the results of Experiment 2 are taken into account.

The data collected in Experiment 2 are consistent with contrast sensitivity experiments (Mullen, 1991; Mullen & Kingdom, 2002). However, subjects in this study also required more achromatic contrast with greater eccentricity. This finding, as well as a decrease in the S cone contrast necessary to match from the fovea to the periphery, are at odds with studies using low-contrast stimuli. One interpretation of these results is that suprathreshold stimuli preferentially engage the parvocellular system, giving rise to properties discrete from those of near-threshold stimuli, which would be more likely to engage the magnocellular system.
References


