



Effects of eccentricity on color contrast

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Using near-threshold stimuli, human color sensitivity has been shown to decrease across the visual field, likely due in part to physiological differences between the fovea and periphery. It remains unclear to what extent this holds true for suprathreshold stimuli. The current study used suprathreshold contrast matching to examine how perceived contrast varies with eccentricity along the cardinal axes in a cone-opponent space. Our data show that, despite increasing stimulus size in the periphery, the LM axis stimuli were still perceived as reduced in contrast, whereas the S axis perceived contrast was observed to increase with eccentricity. © 2018 Optical Society of America

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1. INTRODUCTION

Humans perceive color based on the activities of three types of cone photoreceptors, each maximally sensitive to a particular range of wavelengths of light. Signals from the cones are compared to one another by “second stage” mechanisms in the retina and lateral geniculate nucleus. It is largely held that one mechanism differences the outputs of the L and M cones (L–M) to provide red–green information; another compares the output of the S cones to the summed activity of the L and M cones [$S - (L + M)$] 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 [$L + M(+S)$] [1]. It is worth noting that the terms “red–green” and “blue–yellow” as used here do not correspond to the perceptual color-opponent processes. Specifying the spatiochromatic properties of visual stimuli using a cone-opponent color space allows for the preferential modulation of individual mechanisms. Each mechanism is preferentially activated by stimuli in one of the cardinal directions of the space. These directions will hereafter be referred to as LM, S, and LUM axes. Modulations along intermediate directions will change the activity of multiple mechanisms, including those tuned to these directions [1,2].

Previous studies have shown that stimuli that vary along cone-opponent axes can be matched to one another according to perceptual salience. Switkes and Crognale [3] had subjects perform suprathreshold contrast matches along the cardinal LM, S, and LUM axes, as well as two intermediate axes that selectively change the activity of the L and M cones, respectively. They showed that these matches could be made with low within-subjects variability, and that pairwise matches showed the properties of linearity and transitivity, which allows

for a straightforward relationship between the physical and perceptual contrast of a stimulus. A later study [4] used suprathreshold contrast matching to equate salience along multiple intermediate axes, including those that include mixtures of color and luminance. It was found that matches between intermediate axes also showed transitivity, and that the ratios of contrasts between the cardinal axes were similar to those of Switkes and Crognale [3]. More recently, this technique has been used to evaluate contrast summation in plaid patterns [5] and to investigate the effects of overlaid chromatic and luminance patterns on perceived contrast [6]. Importantly, although suprathreshold matches closely predicted thresholds, the converse was not always true, since any errors in threshold values are multiplied when extrapolated to suprathreshold levels. Consequently, experiments that utilize suprathreshold stimuli would be more accurately equated across color dimensions if suprathreshold matching was used rather than the threshold equation.

In the present study, we expand upon this body of research by investigating contrast matching as a function of retinal eccentricity. There are a number of physiological differences between foveal and extrafoveal regions of the eye that may be expected to affect contrast perception. Macular pigment is found nearly exclusively in the fovea and diminishes rapidly beyond roughly 3° of eccentricity (although see [7]). This carotenoid pigment selectively absorbs short wavelength light, and thus changes the spectral distribution impinging upon the central versus the peripheral retina [8]. Ganglion cell input from cones varies with eccentricity as well. In the fovea, mid-ganglion cells' receptive field centers receive inputs from single L or M cones via a single mid-ganglion bipolar cell [9]. This arrangement is believed to provide high acuity and red–green opponency [10].

Extrafoveally, midget ganglion cells have larger dendritic trees and the receptive field centers receive inputs from large groups of both L and M cones [9]. The arrangement of cone inputs to peripheral midget ganglion cells suggests a wiring scheme that is at least somewhat random [11–13]. Even so, any bias in the ratios of L to M cones in the centers and surrounds of receptive fields would be expected to give rise to residual red–green opponency in the visual periphery [14], though the degree of opponency should decrease with increased eccentricity.

Many studies have investigated chromatic and achromatic sensitivity as a function of eccentricity. A common finding is a significant decrease in chromatic sensitivity outside the fovea, with the LM mechanism showing the sharpest decline (e.g., [12,14,15]). This deficit can be ameliorated at least somewhat by increasing the size or contrast of the peripheral stimuli [16,17]. Since these were threshold measurements, stimuli were near the limit of human perception. If one believes that fixed multiples of threshold are an appropriate metric to equate suprathreshold contrast, then a decrease in contrast sensitivity should scale directly as a decrease in perceived suprathreshold contrast.

Existing data suggest that the visual system behaves differently with threshold and suprathreshold stimuli. For instance, increasing the size of an achromatic grating lowers the threshold for detecting that grating [18–20], while stimulus size has little effect on suprathreshold discrimination [21] or matching [22], a phenomenon that has been attributed to a contrast gain control mechanism. Nor does changing the spatial frequency of a stimulus alter its perceived contrast, despite a decrease in sensitivity to that frequency [23]. Furthermore, perceptual matches between suprathreshold stimuli can show a different pattern than near-threshold measurements [3,24,25], at least at low eccentricities.

The axes of cone-opponent spaces are often scaled as multiples of thresholds such that one unit of change along a given axis is presumed to be perceptually equivalent to one unit of change along each other axis, with this step size based on threshold sensitivity [26,27]. If threshold measurements were the same as suprathreshold perceptions, then previous studies using such stimuli (e.g., [3]) should find a 1:1 ratio between the contrasts of matched stimuli, which is not always the case. In particular, extrapolation of suprathreshold data down to thresholds show reasonable agreement, while extrapolating from threshold data to higher contrasts often fails due to magnification of any error in the threshold measurements.

Thus, while threshold sensitivity in the visual periphery has been well studied, suprathreshold contrast perception may show a dissimilar pattern due to the action of contrast gain control mechanisms. The present study was conducted to quantify the dependence of the suprathreshold contrast equation on retinal eccentricity. We were particularly interested in how these dependencies may differ between the different visual pathways.

2. METHODS

A. Subjects

Six females aged 21–38 (median age 26.5) and six males aged 29–58 (median age 34) 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 accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

B. Apparatus

Stimuli were presented on CRT monitors: either a 39 cm × 29 cm Sony Trinitron Multiscan 20seII, a 39 cm × 29 cm Mitsubishi Diamond Pro 2070SB, or a 39 cm × 29 cm NEC MultiSync E1100 (see Section 2.D). Stimulus colors on all monitors were specified with linearized lookup tables and calibrated using a PR-655 SpectraScan spectroradiometer (Photo Research). Stimuli were presented using the Psychophysics Toolbox Version 3 [28] for MATLAB (MathWorks).

C. Stimuli

Stimuli were composed of circular, vertically oriented Gabor patches defined by modulations in a cone-opponent space whose axes were scaled by psychophysical thresholds [27]. Gabors comprised colors with chromaticities falling along a line in this space. Low-frequency Gabors are preferred stimuli for selectively stimulating the LM and S pathways, as they lack high spatial frequencies and thus minimize the likelihood of luminance artifacts from chromatic aberration. The end points on this line had equal chromatic contrast from the mean chromaticity, and stimuli were presented on a neutral gray background corresponding to the mean chromaticity (Illuminant C) and luminance (18 cd/m²). Stimuli were displayed at five different retinal eccentricities. In the fovea, single Gabor patches were used; outside the fovea, multiple patches equidistant from the center of the monitor were arranged in a ring, forming annuli of Gabor patches (see Fig. 1). Annular Gabor stimuli were chosen because they allow isolation of

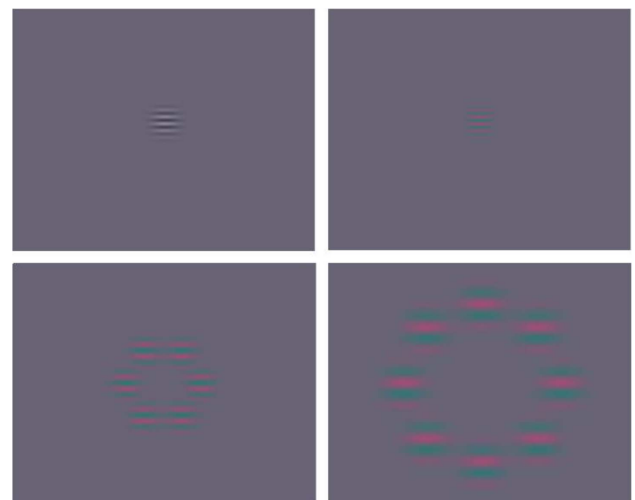


Fig. 1. Images of Gabor (foveal) and Gabor annulus (peripheral) stimuli. The stimulus in the top left panel is modulated in luminance; those in the remaining panels are modulated along the LM axis. Only eccentricities of 0, 2.5, and 5.5 deg are shown due to size restrictions. Stimulus size and contrast have been exaggerated to increase visibility.

discrete regions of the visual field while maintaining relative spatial symmetry and a minimum of sharp boundaries.

With increasing eccentricity, the size of the Gabors was increased, and the spatial frequency of the LM and S (but not LUM) Gabors decreased. This was done to compensate for decreased contrast sensitivity in the visual periphery [14], as the measure of interest is suprathreshold matching. The annular nature of the stimuli in the periphery also necessitated greater numbers of Gabors in more peripheral conditions—as annulus diameter increases, so too does the number of elements needed for consistent spacing. One desirable aspect of this arrangement is the maintenance of the spatial discretion of each annulus (i.e., further increasing Gabor size to hold their number constant across the visual field would cause annuli of greater eccentricities to “intrude upon” the domain of those of lesser eccentricities). A single subject was run in a pilot experiment wherein detection thresholds for LUM stimuli at each of the five eccentricities were measured. For this subject, achromatic contrast sensitivity did not vary appreciably across the visual field, and thus the spatial frequency of LUM Gabors was held constant across eccentricities, unlike the LM and S Gabors. The properties of the comparison patch (2 cpd, Michelson cone contrast = 0.09) were also determined by this pilot experiment, which was only used to set the stimulus parameters for the main experiment. Spatial frequency across eccentricities is the only stimulus property that varied between the three conditions. Stimulus properties at each eccentricity are listed in Table 1. Note that diameter is defined by the area subtended by ± 1 standard deviation of the Gaussian envelope of the Gabor. Each subject had their isoluminant plane determined by flicker photometry at each eccentricity [29].

D. Procedure: Main Experiment

Contrast matches were determined using the method of constant stimuli in a two-alternative forced-choice procedure. In this task, subjects were sequentially shown a test and a comparison stimulus. The test stimulus was either a patch at the fovea or an annulus at greater eccentricities. Test stimuli varied along the cardinal LM, S, and LUM axes, and were presented at six different contrast levels. Comparison patches were achromatic Gabors presented foveally and fixed in contrast (see Section 2.C).

Subjects were instructed to maintain central fixation at all times with the aid of a small black cross (0.3 deg width) present in the center of the screen throughout the experiment. 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 1 s.

Table 1. Stimulus Properties

Eccentricity (deg)	Diameter (deg)	Spatial Frequency (Cycles Per Degree)	Number of Cycles	Number of Gabors
0	3.5	2	7	1
2.5	3.8	1.1	4.2	6
5.5	4.7	0.56	2.6	8
9	5.4	0.4	2.2	12
13	5.4	0.23	1.2	32

Then the first stimulus disappeared and the second stimulus was immediately shown in the same manner. Subjects maintained central 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 versus the comparison stimuli varied randomly. The axis of the test grating changed in a fixed order (LM, S, LUM, LM...) across trials. Subjects judged each unique combination of stimulus characteristics (three axes X five eccentricities X six contrast levels) 10 times per run.

The first run was used as task training and to determine a custom contrast range for each subject. The contrast range for this run was determined via pilot testing to be ostensibly reasonable for the “average” subject. After the first run, the points of subjective equality (PSEs) for that run were calculated for each axis. This axis value was set as the mean in each subject’s custom contrast 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 subject’s settings for each of the last two runs were averaged together to yield a subject’s final contrast matching dataset. The percentage of times that the test patch was chosen at each contrast level was fit to a Weibull function (with the average of the second two runs, each psychometric function included 20 judgments at each of six contrast levels), with the PSE defined as the contrast at which the test patch was chosen 50% of the time. The PSE was calculated separately for each axis at each eccentricity, and represents the contrast match point for that combination of conditions.

Five subjects were run on the MultiSync monitor, and three were run on the Trinitron monitor. For the remaining four subjects the maximum contrast of the S axis stimuli, which was limited by the gamut of these monitors, 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 (see Section 2.B), which was able to generate higher contrasts for the S axis stimuli. Stimulus chromaticities from the calibrated monitors were identical across all monitors. Six subjects were excluded from further runs and data analysis because psychometric functions could not be well fit to their data (e.g., if they chose the comparison stimulus for one axis every time, regardless of contrast level). The data presented here are those of the remaining 12 subjects who completed all three runs.

3. RESULTS: MAIN EXPERIMENT

For statistical analysis and graphing purposes, contrast match points are represented in terms of cone contrast, calculated as

$$\left[\left(\frac{\Delta L}{L} \right)^2 + \left(\frac{\Delta M}{M} \right)^2 + \left(\frac{\Delta S}{S} \right)^2 \right]^{\frac{1}{2}}, \quad (1)$$

where L, M, and S represent the excitation of each of the three cone types to the stimulus. Points of subjective equality as a function of eccentricity, averaged across subjects and expressed in cone contrast, are shown in Fig. 2. The main finding was that the dependence of contrast perception on eccentricity

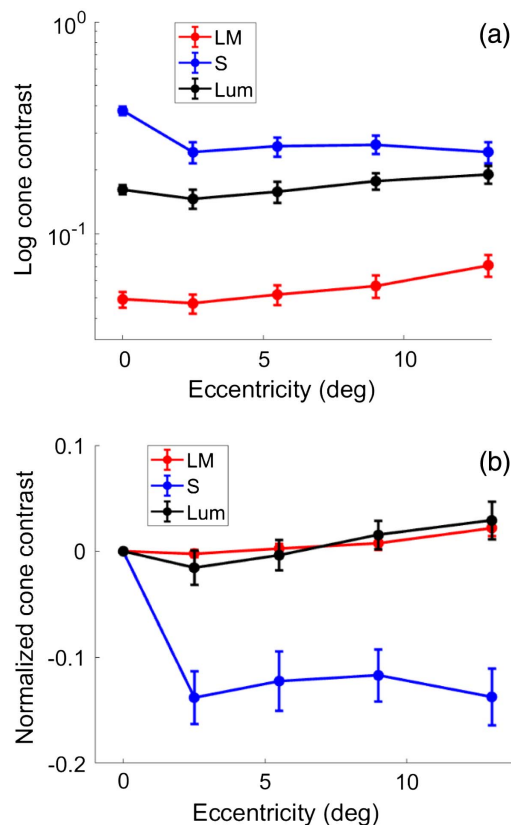


Fig. 2. Results of Experiment 1, wherein subjects matched the contrast of Gabor stimuli along cardinal cone-opponent directions at five different eccentricities. (a) Contrast matching points of subjective equality as a function of eccentricity, and expressed in cone contrast. Each data point is the average of 12 subjects. (b) The same data as (a), but normalized to the fovea to highlight the effect of eccentricity. Error bars represent ± 1 standard error of the mean across subjects.

was different between LM and S pathways; LM contrast perception decreased from the fovea with increasing eccentricity despite increasing stimulus size, while S axis contrast perception showed a minimum at the fovea and little change between 2.5 and 13 deg eccentricity. Because the size, but not spatial frequency, of the LUM stimuli varied across the visual field, they are not directly comparable to the chromatic axes. As such, data from the LUM axis are not included in the final statistical analyses; they are nonetheless shown in Fig. 2, and their significance is discussed in Section 6.

Data were analyzed using a repeated-measures ANOVA with within-subject factors of eccentricity (five levels) and axis (LM, S). Mauchly's test determined that the assumption of sphericity was violated for our data, $\chi^2(9) = 22.16$, $p < 0.01$, and thus degrees of freedom were adjusted using the Greenhouse–Geisser correction. There was a main effect of eccentricity, $F(1.99, 21.93) = 12.33$, $p < 0.001$, $\eta^2 = 0.53$; a main effect of axis, $F(1, 11) = 139.28$, $p < 0.001$, $\eta^2 = 0.93$; and a significant interaction between eccentricity and axis, $F(2.24, 24.60) = 22.58$, $p < 0.001$, $\eta^2 = 0.67$. Since absolute differences between the axes are not of direct interest here, we do not report post-hoc pairwise comparisons between them.

To investigate the interaction between eccentricity and axis, paired-sample Student's *t*-tests were run. In order to limit the number of comparisons, the foveal PSE was compared to the PSE of the furthest (fifth) eccentricity for each axis, and significance was evaluated at a Bonferroni-corrected α level of 0.025. A significant difference was found between the fovea and periphery along the LM axis, $t(11) = -2.90$, $p = 0.01$, $d = -0.98$, as well as the S axis, $t(11) = 5.16$, $p < 0.001$, $d = 1.67$.

4. PROCEDURE: CONTROL EXPERIMENT

The stimuli used in the current study had a mean luminance level of 18 cd/m², which is not sufficiently bright to ensure rod saturation. Research suggests that rod activity can influence color perception (e.g., [30,31]), which may confound our results, particularly for S stimuli. To investigate this, we calculated the amount of rod contrast evoked by both LM and S stimuli. The stimulus with the highest LM contrast produced a rod contrast of 0.11, and the stimulus with the highest S contrast produced a rod contrast of 0.13. The magnitude of these rod contrasts is unlikely to strongly influence color perception [32]. However, to be certain, three subjects were run in a rod bleach control experiment.

The bleaching procedure, outlined below, roughly doubles the time required to run each subject; the method of constant stimuli used in the main experiment was already rather lengthy, so in the interest of time an adaptive staircase procedure was adopted. This staircase procedure gives similar results to the method of constant stimuli, but regardless, the measure of interest was the comparison between the subjects' contrast matches with and without a rod bleach.

The stimulus properties and task were identical to those of the main experiment, but contrast was varied on a trial-to-trial basis depending on the subject's responses. Each condition was tested using two randomly interleaved staircases that adjusted contrast based on a two-down, one-up rule. The experiment continued until 10 reversals had occurred in every staircase. The last eight reversals within each staircase were then averaged together to yield one contrast match per staircase, and the contrast matches for each pair of staircases were averaged together to yield one contrast match per condition.

Two females (aged 23 and 24) and one male (aged 30) were run in this control experiment, with all judgments made monocularly (using the dominant eye and with the non-dominant eye covered). Each subject first completed the task normally, and then completed it again using a rod bleach procedure.

A. Rod Bleach

At the beginning of each run, a conventional Maxwellian-view optical system with a broadband light source was used to adapt the central 33.4° of each subject's visual field. Using Westheimer's method, we calculated that this light provides a retinal illuminance of approximately 3.5 million trolands [33]. The retina was exposed to this light for 15 s, which should have resulted in greater than 99% of photopigment being bleached [34]. After the light was extinguished each subject waited 4 min to allow the cones to recover (the recovery period), and then performed the contrast matching task for

5 min (the task period). At the end of the task period, the bleach \Rightarrow recovery \Rightarrow task cycle was repeated. This pattern continued until the experiment was complete.

5. RESULTS: CONTROL EXPERIMENT

The results of this control experiment are shown in Fig. 3. The basic results are unchanged after the bleach. For the LM axis, contrast perception decreases with increasing eccentricity even with partially compensating by scaling stimulus size in the periphery. The S axis results reveal lower contrast perception in the fovea with relatively little change from near to moderate eccentricities, consistent with macular distribution. If rods had a systematic effect in our main experiment, we could expect that removing their influence with a bleach would reduce, or otherwise change, contrast perception in the periphery relative to the fovea (since rod concentrations are lowest in the fovea) with a greater effect on the S axis. This effect is not observed in our control data.

6. DISCUSSION

On average, the amount of contrast required to match the achromatic foveal comparison stimulus increased as a function of eccentricity along the LM axis and decreased along the S axis. A decrease in perceived contrast along the LM axis in the periphery (which should manifest as a higher contrast required to make a match) is consistent with previous research. A series of studies measured cone contrast sensitivity at several eccentricities using either vertical [14] or radial [15] sine wave grating patterns at near-threshold contrast levels. Both studies found a sharp decrease in red–green (analogous to our LM axis) contrast sensitivity with eccentricity; blue–yellow and achromatic sensitivity decreased more gradually. Hansen *et al.* [12] measured detection thresholds at various eccentricities using uniform patches modulated along chromatic axes similar to those in the current study. They observed a similar pattern of cone contrast sensitivity loss across the visual field, albeit to a generally lesser degree than Mullen and Kingdom [14] or Mullen *et al.* [15]. However, the current study shows an increase in perceived contrast along the S axis in the periphery relative to the fovea. Given the similarities between the findings of the current study and those of the abovementioned groups along the LM axis,

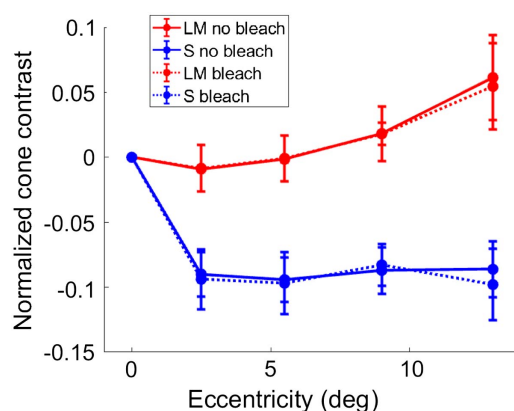


Fig. 3. Points of subjective equality, measured with and without a rod bleach and averaged across three subjects. Error bars represent ± 1 standard error of the mean across subjects.

this might be expected to have manifested as an increase in S axis sensitivity with eccentricity. In general this was not found in the studies cited above, although only Mullen and Kingdom [14] tested contrast sensitivity in the fovea.

There are a number of important differences between the stimuli used in these studies compared to the current one. Previous studies used threshold-level chromatic stimuli, while the contrasts used in the current experiment are many times greater than threshold. This allows for the action of contrast gain control mechanisms, which may act differently upon threshold versus suprathreshold stimuli. It has been shown that suprathreshold contrast matches predict thresholds well but due to error extrapolation chromatic detection thresholds are poor predictors of suprathreshold contrast matches [3,24,25]. The scaling of both size and spatial frequency across the visual field, as well as the use of Gabor annuli, are different from the studies cited above; thus, low-level stimulus attributes may play a role in the studies' respective findings. Aside from basic stimulus features, a critical difference between the current study and those discussed above is the nature of the task. Rather than detecting gratings, subjects here were contrast matching, which is a judgment of relative contrast salience. While sensitivity among the various mechanisms doubtless plays a role in salience perception, the judgment likely uses a more complex and nuanced set of criteria than a simple detection task.

When the S axis stimuli were presented beyond the fovea, there was a decrease in the amount of contrast needed to match the comparison patch. This effect also may be attributable to either the suprathreshold nature of the stimulus as a result of contrast gain mechanisms or the more complex nature of the task, as near-threshold measures of S axis sensitivity show a decrease across the visual field. Another possibility is that the choice of scaling of the size of the stimulus with eccentricity more than compensated for losses in sensitivity with eccentricity. What is important here is that independent of this choice of scaling there were clear differences in the dependence of suprathreshold contrast perception on eccentricity between the LM and S mechanisms.

In the current study, suprathreshold perceived contrast for the S mechanism increased as the stimulus moved beyond the fovea, but remained fairly constant across the rest of the visual field. Insofar as suprathreshold contrast matching relies on retinal physiology, this finding is consistent 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 was 2.5 deg and should have been within a region of reduced macular pigment. The results suggest that at least for suprathreshold stimuli, the macular density is low enough at this eccentricity not to influence contrast matches compared to the far periphery. Thus, these findings can be explained by relatively low-level physiology. Furthermore this suggests that for suprathreshold contrast matching the visual system does not compensate for macular distribution, an unexpected finding given prior evidence for adaptation to macular pigment in color vision (e.g., [35]).

As mentioned above, one possible factor in subjects' judgments that we are unable to rule out is the effect of stimulus

size. 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 been determined in part by stimulus size. It may be that increasing the size of a peripheral stimulus increases the likelihood of subjects choosing that stimulus as having higher contrast than a foveal one. Thus, if this experiment was repeated under identical conditions, but without scaling the size of the peripheral stimulus, the slopes of the LM and S functions shown in Fig. 2 might be more positive than in our results. That is, both mechanisms may show greater decreases in suprathreshold contrast perception with increasing eccentricity. Unfortunately some size scaling was necessary, as without it the monitor could not produce enough contrast for subjects to reliably choose a peripheral chromatic stimulus (assuming a reasonably suprathreshold foveal comparison stimulus).

Vakrou *et al.* [36], investigating the effect of stimulus size on sensitivity in the visual periphery, found that the LM and S directions have different scaling factors. These factors are fairly consistent with past findings on peripheral sensitivity, with LM stimuli requiring a greater size increase than S stimuli to reach a criterion threshold. Rather than choosing stimulus parameters that maximize the sensitivity of each of the chromatic mechanisms independently, in the current study size was increased and spatial frequency was decreased equally for both types of chromatic stimuli across the visual field. This was done because the measure of interest is a comparison of suprathreshold perception between mechanisms; indeed, with the right choice of stimulus parameters the contrast matching functions along the two chromatic axes could theoretically be made to be measurably identical to one another.

Both size and spatial frequency varied across the visual field for the chromatic stimuli, while the LUM stimuli only varied in size, with a constant spatial frequency. This precludes a direct comparison between the axes, but does present an estimate of the isolated effect of size scaling. For a 2 cpd grating, contrast sensitivity decreases by approximately a factor of 10 between the fovea and 14° eccentricity [37], close to the 13° of our most peripheral stimuli. If increasing the stimulus size alone completely compensated for this 10-fold loss of sensitivity, then the LUM PSEs shown in Fig. 2 would remain unchanged across eccentricities. The degree to which the PSEs increase (indicating a higher contrast required to match to the fovea) represents the degree to which increasing stimulus size fails to fully offset the loss of sensitivity in the periphery. The fact that PSEs for the LM axis still increase with eccentricity indicates that the peripheral loss of sensitivity remains, even after increasing stimulus size and decreasing spatial frequency.

A direct comparison of our results with those of Switkes and Crognale [3] and Switkes [4] at a single eccentricity is difficult, due to differences in the visual angle subtended by stimuli. Both of the previous studies used gratings presented bilaterally and offset 6.5° from the center of the screen, with gratings subtending 10°. This spans roughly the length of the center

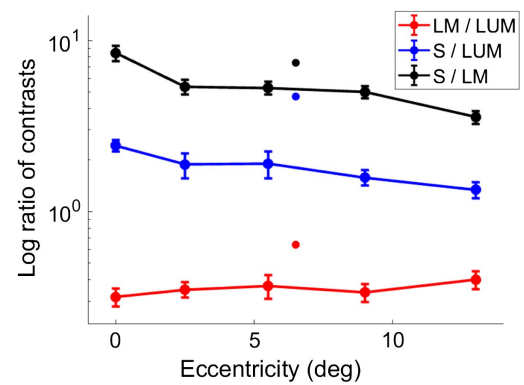


Fig. 4. Log ratios of contrast match points, expressed in units of cone contrast. The single points at 6.5 deg are the corresponding ratios of Switkes and Crognale [3]. Error bars represent ± 1 standard error of the mean across subjects.

three levels of eccentricity in the current study. Additionally, we used a standard foveal luminance grating as the comparison stimulus, rather than matching the axes directly to one another. However, insofar as a comparison is appropriate, it can be noted that all three studies showed that in terms of cone contrast subjects judged LM stimuli as more salient than both S and LUM stimuli (a lower cone contrast here indicates higher salience), and LUM stimuli as more salient than S stimuli. Figure 4 shows the ratios of cone contrasts between the axes tested in the present study. Also plotted in this figure are the approximate ratios from Switkes and Crognale [3].

The chromatic stimuli used in the current study were made isoluminant for each participant at each eccentricity, minimizing luminance artifacts from macular pigment and other retinal inhomogeneities. However, the location of the S (LM-axis silencing) axis can also vary from the fovea to the periphery as a rotation within the isoluminant plane. Consequently, it is likely that although preferentially activated, the S-(L+M) mechanism was not completely isolated at all eccentricities and may have included some small contribution from the L-M mechanism. Luminance artifacts and contrast reduction from chromatic aberration [38] are less probable due to the use of low spatial frequency Gabor patches. The specific effect that intrusion of the LM and LUM mechanisms would have on contrast matches along the S axis is difficult to predict. One might expect that adding LM contrast (for instance) would cause S matches to more closely resemble LM matches. This supposition is not supported by our results, as more LM contrast was required to match in the periphery, whereas S matches showed the opposite pattern. A more complex interaction between isoluminant mechanisms, or between color and luminance contrast, is possible; measuring detection thresholds of sinusoidal patterns on pedestals, Chen *et al.* [39] showed that interactions between cardinal axes can be either facilitative or inhibitory. Their data show that the pattern of these interactions varies between individuals and depends strongly on the contrast of both the stimulus and the pedestal, as well as which cardinal axis is given which role. This precludes a straightforward evaluation of the likelihood of LM or LUM intrusion to our S stimuli. However, while different subjects

matched the reference stimulus to different absolute levels of S contrast, the observed effect of eccentricity upon S axis contrast matches was fairly consistent across subjects (see Figs. 2 and 3). This fact alone makes these complex interactions between mechanisms less likely.

It is conceivable that the short inter-stimulus interval could have resulted in afterimages influencing the appearance of the second stimulus. This is of minimal concern for several reasons. First, the only situation in which both stimuli occupied the same retinal position was in the foveal test condition (as the reference was always in the fovea). Also, since the order of the test and fixed reference stimuli was randomized, systematic shifts due to afterimages should have been minimized. In any case, of greatest interest here is how the contrast matching functions along each of the cardinal axes change relative to each other across the visual field, not the absolute match points.

While subjects were instructed to keep their eyes fixed on a small cross in the center of the monitor, eye tracking was not used to confirm that they did so. The interpretation of the data presented here assumes a realistically maximal amount of fixation. The opposite scenario, a realistically minimal amount of fixation, has subjects moving their center of gaze to some part of the Gabor annulus at every eccentricity. In this scenario, if subjects used the foveal part of the annulus to make the contrast match, the functions should be flat across the visual field, as stimulus size and spatial frequency have been shown to have little effect on contrast perception [23]. This is not evident in our data.

This study has shown that suprathreshold contrast matches change as a function of eccentricity, and that these changes affect the chromatic pathways differently. Our results are consistent with the findings of previous studies investigating contrast sensitivity, namely a relative loss of perceived LM contrast with eccentricity. A novel result is a decrease in the amount of S cone contrast required for a match beyond the fovea, suggesting a lack of compensation for the lower density of macular pigment in the periphery by the visual system. Consequently, parallels between suprathreshold perceived contrast and threshold contrast sensitivity are likely limited by differences in contrast gain mechanisms and task complexity.

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