Chromatic contrast sensitivity: the role of absolute threshold and gain constant in differences between the fovea and the periphery

Pauline M. Pearson
Retina Foundation of the Southwest, 9900 N. Central Expressway, # 400, Dallas, Texas 75231

William H. Swanson
Retina Foundation of the Southwest, 9900 N. Central Expressway, # 400, Dallas, Texas 75231, and University of Texas Southwestern Medical Center, Dallas, Texas 75235

Received April 20, 1999; revised manuscript received October 1, 1999; accepted October 25, 1999

A model of foveal achromatic and chromatic sensitivity (Vision Res. 36, 1597 (1996)) was extended to the peripheral visual field. Threshold-versus-illuminance functions were analyzed to determine effects of eccentricity on absolute thresholds and gain constants of chromatic and luminance mechanisms. The resulting peripheral model successfully predicted peripheral contrast sensitivity as a function of wavelength, for both white and 500-nm backgrounds. We conclude that the short-wavelength-sensitive cone opponent mechanism may mediate thresholds in Sloan's notch in the normal periphery and that interpretation of reduced chromatic sensitivity in the periphery requires an explicit model of how eccentricity affects both the gain constant and the absolute threshold. © 2000 Optical Society of America [S0740-3232(00)01102-9]


1. INTRODUCTION
Understanding of foveal color vision mechanisms and the effects of disease states on these mechanisms has been enhanced by the development of a model that has provided a framework to relate data from a wide variety of clinical tests to basic studies of chromatic discrimination ability in the normal population.1–6 Although most clinical ophthalmological tests are administered foveally, peripheral assessment of chromatic sensitivity through chromatic perimetry is increasingly being used for detecting and following progression of visual diseases.7–12 However, very little is understood about the sensitivity of the mechanisms that underlie performance of chromatic perimetry. We have extended a foveal color vision model1–6 to the peripheral visual field to provide a method for integrating and comparing information gathered with a variety of peripheral chromatic tests, as well as to increase our understanding of eccentricity effects on peripheral chromatic mechanisms.

Three photopic mechanisms have been shown to be sufficient to describe foveal chromatic increment thresholds,13–22 a luminance mechanism, a red–green opponent mechanism, and a short-wavelength-sensitive (SWS) cone opponent mechanism. Over a range of retinal illuminances, contrast sensitivity for each of the mechanisms can be fully characterized with only two parameters for each mechanism: the absolute threshold and the gain constant.1,5 Two absolute thresholds of a mechanism is the increment threshold in the absence of any adaptation responses. The gain constant of a mechanism characterizes the adaptation response and is the inverse of the adapting illuminance at which threshold is twice absolute threshold. Since chromatic perimetry measures increment thresholds at a large number of visual field locations, evaluation of the absolute thresholds and gain constants of the photopic mechanisms in the peripheral visual field should increase our understanding of the mechanisms subserving chromatic perimetry. Therefore the first experiment extended the model to the periphery and evaluated the gain constants and absolute thresholds of the photopic mechanisms through an empirical evaluation of threshold-versus-illuminance (TVI) functions for chromatic increment thresholds in the fovea and at one location in the periphery. The second experiment used the absolute thresholds and gain constants derived in the first experiment to predict chromatic contrast sensitivity. This procedure provided a further test of the model and described how the responses of the mechanisms are combined to determine chromatic contrast sensitivity across the visible spectrum.

2. DETERMINATION OF ABSOLUTE THRESHOLD AND GAIN (EXPERIMENT 1)
Contrast sensitivity for both achromatic and chromatic lights of a fixed size declines as a function of eccentricity,23–26 and this decline in contrast sensitivity may be counteracted by scaling the size of the stimuli to ensure that the integration area is constant across the visual field.25,27–30 However, even when change in integration area with eccentricity is controlled for, contrast sensitivity for red–green chromatic modulation decreases more rapidly than contrast sensitivity for luminance modulation.24,31–34 This decrease in red–green sensitiv-
ity with eccentricity has been modeled as a decrease in opponency with eccentricity,\textsuperscript{23,32,35} with the implicit assumption that the decrease in sensitivity is a consequence of a reduction in the absolute threshold of the red–green mechanism in the absence of a change in gain constant.\textsuperscript{36} However, these studies evaluated relative sensitivity at a single retinal illuminance. Since contrast sensitivity of a mechanism is the ratio of the gain constant and the absolute threshold, it is uncertain whether the decline as a function of eccentricity is a consequence of an increase in the absolute threshold of the mechanism, a change in the gain constant of the mechanism, or some combination of both of these parameters. To examine the relative roles of these parameters in the decline in chromatic sensitivity in the peripheral visual field, we used an extension of the model presented by Miyahara\textsuperscript{1} to measure and fit foveal and peripheral increment thresholds for red, blue and white stimuli. To maximize the range of retinal illuminances over which the sensitivity of the chromatic mechanisms could be measured, a white pedestal and slow temporal modulation were used to decrease the sensitivity to luminance.\textsuperscript{21,33,37,38}

A. Methods

1. Participants
Two experienced psychophysical observers participated in this experiment. Both observers had 20/20 Snellen acuity with their usual correction, normal visual fields (Humphrey 30-2), and normal color vision (Ishihara Plates SPP, D-15, Desat D-15). Observers were dilated (1\% Mydriacyl) and dark adapted before testing.

2. Apparatus
All stimuli were presented by means of the three-channel direct-view optical system depicted in Fig. 1. The light source was a 450 W Xenon arc lamp (Osram) driven by a regulated power supply (Spectral Energy). The first channel provided the light for the white background. The second channel provided light for the white pedestal. The third channel provided light for the increment, modulated in intensity by a mirror galvanometer with 300-Hz resolution.\textsuperscript{1} The second and third channels were combined in an integrating sphere. With use of a beam splitter, light from the exit port of the integrating sphere formed a 3.1° circle centered on the 30°-square background (see Fig. 2). A head and chin rest was used to maintain a constant viewing distance and head position.

The apparatus was controlled by a Macintosh II computer equipped with two 6-channel 12-bit digital-to-analog boards (National Instruments NB-AO-6) wired to provide 24-bit resolution and a timing board (National Instruments NB-DMA-9-G) with 10-\textmu s resolution, which together controlled the mirror galvanometer.\textsuperscript{5} In addition, a three-port digital input-output board (National Instruments NB-DIO-24) received input from the response box used to initiate and respond to trials and controlled the position of the filter wheels containing calibrated neutral density filters and spectral filters. With use of calibrated neutral density filters, the combined illuminance of the background and the pedestal was varied from \(-1\) to 3 log tdrolands (td). At all adapting illuminances, the illumina-

Fig. 1. Schematic of the three-channel direct-view optical system used to present the stimuli. L's indicate collimating and de-collimating lenses, and M's indicate masks.

Fig. 2. Schematic representing the spatial configuration of the stimuli. The test, A, and the pedestal, B, were spatially contiguous 3.1° circular stimuli; the background, C, was 30° square. Both the pedestal and the background were white lights; the test stimulus was white, blue, or red.

The illuminance of the pedestal was 0.5 log unit higher than the background. With a pupil diameter of 8 mm, the maximum illuminance of the test increment was 4 log td. The illuminance of the test increment could be attenuated over a 7-log-unit range by using a combination of a mirror galvanometer (linear over 3 log units) and calibrated neutral density filters (4 log units in steps of 1 log unit). The color of the test increment was manipulated with broad-
band filters (Andover, 60-nm bandwidth at half-height). The increment was a Gaussian pulse with a 100-ms time constant in which 67% of the energy is contained within the central 200 ms.

3. Procedure
In separate blocks of trials, detection thresholds were measured for white, blue, and red increments on white adapting fields ranging from -1 to 3 log td (combined illuminance of the pedestal and background) in 0.5-log-unit steps. Thresholds were measured in the fovea and at 12° eccentricity in the superior temporal field. Each threshold was determined with a single staircase. The white background and the pedestal were present throughout each block of trials, and on each trial the increment was superimposed on the pedestal in one of two intervals. The luminance of the increment was varied in steps of 0.3 to 0.075 log unit with a two-down one-up rule for a total of ten reversals. Thresholds were estimated with a maximum-likelihood technique. Results are reported in illuminance units, where \( \Delta I \) is the illuminance of the increment and \( I \) is the illuminance of the pedestal and background.

4. Calibrations
The outputs of the integrating sphere and the background were measured by a photometer with a photometric head (United Detector Technology, Model 211) accurate within 5% for all visible wavelengths. The retinal illuminances of the lights were calculated on the basis of pupil and luminance measurements with the method of LeGrand. Spectroradiometric calibrations (Photo-Research, Model PR-704) yielded a color temperature of 4853 K for the white stimulus and CIE (1931) chromaticities of each of the cone types: The equivalent wavelengths for the white, blue, and red increments on white background.

Table 1. Equivalent Wavelengths for the White, Blue, Red, and Yellow Broadband Stimuli for Three Cone Types

<table>
<thead>
<tr>
<th>Color</th>
<th>Equivalent Wavelengths (nm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fovea</td>
</tr>
<tr>
<td></td>
<td>SWS</td>
</tr>
<tr>
<td>White</td>
<td>500</td>
</tr>
<tr>
<td>Red</td>
<td>554</td>
</tr>
<tr>
<td>Blue</td>
<td>472</td>
</tr>
<tr>
<td>Yellow</td>
<td>546</td>
</tr>
</tbody>
</table>

5. Data Analysis: Model
We used a previously published model of foveal achromatic and chromatic mechanisms, implementations of which have been previously used to analyze spectral increment thresholds, clinical pigment tests, and chromatic discrimination on white and chromatic adapting fields. In this model, threshold is predicted based on combinations of relative cone excitations calculated from the Smith-Pokorny cone fundamentals and the Judd luminous efficiency function. Relative cone excitations \( L, M, \) and \( S \) for each of the cone types (long-, middle-, and short-wavelength-sensitive, respectively) were calculated as follows:

\[
L = \frac{l(\lambda)}{l_{\text{max}}(\lambda)}, \quad M = \frac{m(\lambda)}{m_{\text{max}}(\lambda)}, \quad S = \frac{s(\lambda)}{s_{\text{max}}(\lambda)},
\]

where \( \lambda \) is the equivalent wavelength for the cone fundamental, \( l, m, \) and \( s \) are the Smith-Pokorny cone fundamentals, \( l_{\text{max}}, m_{\text{max}}, \) and \( s_{\text{max}} \) are the maxima of the cone fundamentals (0.53721, 0.39246, and 0.01608, respectively), and \( V(\lambda) \) is the luminous efficiency function. To extend this model to the periphery, we calculated peripheral cone excitation levels by removing the effects of macular pigment.

The white, red, and blue increment thresholds were each assumed to represent the response of a single mechanism. That is, the white increments, the red increments, and the blue increments were assumed to be mediated by the luminance \( (L) \), red-green opponent \( (M) \), and SWS cone opponent \( (S) \) mechanisms, respectively. The model was implemented in the IGOR (Wavemetrics, version 3.13) programming environment. Threshold versus retinal illumination data for each stimulus chromaticity were fitted by allowing only two parameters to vary, the absolute threshold \( T \) and the gain constant \( G \).

6. \( L+M \) Luminance Mechanism
Following Miyahara and co-workers, the luminance mechanism, \( L+M \), linearly sums the long-wavelength-sensitive (LWS) and medium-wavelength-sensitive (MWS) cone excitation levels with a single gain constant applied independently to each cone type. That is, the only difference between the LWS and the MWS cones is considered to be their spectral sensitivity, allowing them to adapt independently without a proliferation of free parameters. A number of previous studies have shown that a single gain constant implemented in this way can account for a wide range of chromatic data. On the basis of the spectral distribution of the white light, the \( L+M \) mechanism was assumed to mediate the thresholds for luminance increments. By fitting the increment thresholds \( (\Delta I) \) obtained with the white increment with the following equation, we estimated the absolute threshold \( (T_a) \) and gain constant \( (G_a) \) of the \( L+M \) mechanism:

\[
\log \Delta I = \log T_a - \log \left[ \frac{1}{1 + G_a L \Delta I} \right] + (1 - p) \log \left[ \frac{1}{1 + G_a M \Delta I} \right],
\]
where \( p \) is the proportion of LWS cones in the L + M pathway for Judd observer (0.6189), \( L_T \) and \( M_T \) are the relative LWS and MWS cone excitation levels \( 44 \) for the test increment, \( L_A \) and \( M_A \) are the relative LWS and MWS cone excitation levels \( 44 \) for the adapting field, and \( I \) is the retinal illuminance of the adapting background in photopic trolands. When the data are fitted in this way, the absolute threshold \( (T_A) \) and gain constant \( (G_A) \) of the luminance mechanism are fully determined by the cone excitation levels of the stimulus and the adapting field.

7. \([L-M]\) Red–Green Opponent Mechanism
Following Miyahara et al. \( 1,46 \) the red–green mechanism, \([L-M]\), subtracts the MWS from the LWS cone excitations with a single gain constant independent of \( G_A \) in Eq. (1). Since this mechanism is assumed to mediate red–green discriminations \( 1,15,20,37 \) the absolute threshold \( (T_R) \) and the gain constant \( (G_R) \) of the \([L-M]\) mechanism were estimated by fitting the red increment thresholds \( (\Delta I) \) with the following equation:

\[
\log \Delta I = \log T_R - \log \left( \frac{1}{1 + G_R L_A} \right) - M_T \\
\times \left( \frac{1}{1 + G_R M_A} \right),
\]

where \( L_T \) and \( M_T \) are the relative LWS and MWS cone excitation levels \( 44 \) for the red test increment, \( L_A \) and \( M_A \) are the relative LWS and MWS cone excitation levels \( 44 \) for the adapting field, and \( I \) is the retinal illuminance of the adapting background in photopic trolands. The absolute value results in equal weighting of the \( L-M \) and \( M-L \) responses and reduces the number of free parameters in the model. \( 14,17,20 \)

8. \([S-(L+M)]\) SWS Cone Opponent Mechanism
The second chromatic opponent mechanism subtracts the sum of the LWS and MWS cone excitations from the excitation of the SWS cones. Following Miyahara et al. \( 1 \) the gain constant of the \([S-(L+M)]\) opponent system is determined by the illuminance of the adapting field when a broad spectrum adapting field is used. Since this mechanism is assumed to mediate blue increments, \( 1,15,20,37 \) the absolute threshold \( (T_S) \) and the gain constant \( (G_S) \) of the \([S-(L+M)]\) mechanism were estimated by fitting the blue increment thresholds \( (\Delta I) \) with the following equation:

\[
\log \Delta I = \log T_S - \log \left( \frac{Z(\lambda_T)}{V(\lambda)} - 1 \right) - \log \left( \frac{1}{1 + G_S} \right),
\]

where \( \lambda_T \) is the SWS cone equivalent wavelength of the test (i.e., 472 nm), \( Z(\lambda_T) \) is the Judd revised color matching \( Z \) function, \( 45 \) \( V(\lambda) \) is the luminous efficiency function, \( 43 \) and \( I \) is the retinal illuminance of the adapting background in photopic trolands.

B. Results
Each panel in Fig. 3 compares the thresholds and fits obtained for one of the increments (white, blue, or red) at 12° and foveally. Thresholds for white, blue, and red stimuli were all gathered at retinal illuminances down to \( -1 \) log td. Red and blue thresholds tended to show two distinct limbs, especially in the periphery. At higher illuminances red and blue thresholds were well below white threshold and decreased linearly with retinal illuminance. Below \( 1.5 \) log td, threshold became independent of retinal illuminance and then began to decrease again following the white TVI data. This is clear evidence of the mediation of red and blue thresholds by two mechanisms with different gain constants. We interpret the higher-illuminance limbs as being mediated by chromatic mechanisms, and the lower-illuminance limbs as being mediated by the luminance mechanism. This interpretation is directly tested in experiment 2, which examines the spectral tuning of the mechanisms that mediate detection at high illuminances. Fits were made only to data on the higher-illuminance limbs, which are shown in Fig. 3. Parameters for the fits shown are given in Table 2.

For all increments the thresholds obtained at 12° eccentricity are higher than those obtained foveally at all retinal illuminances tested. For the chromatic thresholds, the difference between the fovea and the periphery appears to decrease as the illuminance of the adapting field increases. To confirm that the illuminance at which thresholds start to increase linearly (i.e., 1/gain constant) is greater at 12° than at the fovea, we compared fits to the peripheral data obtained with the gain constant constrained to be equal to that in the fovea with the fit obtained when the gain was permitted to vary. For both of the chromatic mechanisms and both subjects, the chi square for the fit to the peripheral thresholds increased at least fourfold when the gain constants were fixed to those values obtained in the fovea. In contrast, for the white thresholds, fixing the gain constant to the value obtained in the fovea did not significantly degrade the fit obtained for the peripheral data, and hence the gain constant for the peripheral luminance mechanism was fixed to the value obtained for the fovea.

Comparison of the foveal chromatic and achromatic thresholds reveals that the retinal illuminance at which thresholds increase linearly is lower for the white increments than for the red or blue increments. The difference between the retinal illuminances at which thresholds begin to increase linearly for the chromatic and achromatic increments is greater in the periphery than in the fovea.

G. Discussion
By extending the model to include peripheral sensitivity, we evaluated the role that the two parameters, absolute threshold and gain constant, play in determining the change in luminance and chromatic contrast sensitivity with eccentricity. Both the gain constant and the absolute threshold clearly play a role in the effects of eccentricity on contrast sensitivity. The gain constant was found to vary across mechanisms and for visual field location. The change in the gain constants of the chromatic mechanisms with eccentricity means that the absolute thresholds of the chromatic mechanisms cannot be approximated from measurements obtained in the Weber region. That is, estimates of the difference between the absolute thresholds of the foveal and peripheral chro-
matic mechanisms based on contrast sensitivity measurements obtained in the Weber region will underestimate the difference between the absolute thresholds of the mechanisms since there is also an increase in the chromatic gain constants in the periphery.

Our foveal data are similar to the results obtained by Miyahara et al. and extend a number of findings to the peripheral visual field. In both the fovea and the periphery, the chromatic absolute thresholds obtained from the fit of the model were similar to or higher than the achromatic absolute thresholds. Thus at low retinal illuminances it is unclear whether a chromatic or a luminance mechanism mediates detection of chromatic increments (i.e., there is no isolation of chromatic mechanism). Similar to the findings of Miyahara et al., foveal chromatic thresholds are lower than achromatic thresholds at retinal illuminances greater than 0 log td. This finding is consistent with studies that have reported that in the fovea the isolation of the chromatic mechanisms from the luminance mechanism declines as retinal illuminance decreases. In the periphery, chromatic thresholds are lower than achromatic thresholds at retinal illuminances greater than 0.5 log td. Thus the retinal illuminance necessary for isolation of chromatic mechanisms is higher in the periphery than at the fovea, and the loss of isolation of the chromatic mechanisms reported in the fovea will occur more rapidly as retinal illuminance declines in the periphery. The loss of isolation of the chromatic mechanisms in the periphery at retinal illuminances high enough for isolation of chromatic mechanisms in the fovea may explain why some previous studies have failed to maintain isolation of chromatic mechanisms in some peripheral locations. A number of previous studies have suggested that in the fovea the isolation of the chromatic mechanisms from the luminance mechanism is a consequence of differences in the absolute thresholds of the mechanisms rather than differences in the gain constants of the mechanisms. Our data confirm this finding in the fovea and extend the finding to the periphery.

A wide range of clinical studies have drawn attention to the finding that chromatic testing may reveal larger losses in increment sensitivity than standard achromatic testing. However, a number of studies have cautioned that apparent increases in the sensitivity of a test

---

**Table 2. Parameters of the Model Obtained by Fitting the Thresholds Shown in Fig. 3**

<table>
<thead>
<tr>
<th>Observer</th>
<th>Log $T_a$</th>
<th>Log $T_R$</th>
<th>Log $T_S$</th>
<th>$G_a$</th>
<th>$G_R$</th>
<th>$G_S$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fovea</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PP</td>
<td>-2.07</td>
<td>-2.09</td>
<td>-1.98</td>
<td>2.84</td>
<td>0.29</td>
<td>0.08</td>
</tr>
<tr>
<td>WS</td>
<td>-2.16</td>
<td>-1.86</td>
<td>-1.94</td>
<td>1.74</td>
<td>0.09</td>
<td>0.06</td>
</tr>
<tr>
<td>12° Eccentricity</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PP</td>
<td>-1.69</td>
<td>-0.76</td>
<td>-1.07</td>
<td>2.84</td>
<td>0.05</td>
<td>0.04</td>
</tr>
<tr>
<td>WS</td>
<td>-1.35</td>
<td>-0.72</td>
<td>-1.14</td>
<td>1.74</td>
<td>0.05</td>
<td>0.03</td>
</tr>
</tbody>
</table>
to disease may be a consequence of prereceptoral differences between the populations rather than disease-related decreases in visual function if the retinal illuminance is not high enough that the threshold is a constant fraction of the adapting field (i.e., if thresholds are not Weberian). In the model presented above, the gain constant is inversely related to the retinal illuminance at which the Weberian behavior emerges. Our results, therefore, are consistent with foveal studies that have shown that a retinal illuminance that is in the Weber region for the luminance mechanism may not be in the Weber region for the chromatic mechanisms; furthermore, we extend this result to the peripheral visual field, where the difference between the luminance and the chromatic mechanisms appears to increase. Therefore, to minimize the possibility that prereceptoral factors are responsible for differences between populations, a higher retinal illuminance is necessary in the periphery than in the fovea. Interpretation of the model or site of the decrease in sensitivity requires information about the absolute sensitivity and gain constants of the mechanisms involved. Since our data indicate that the gain constants of the chromatic mechanisms change from fovea to periphery, it is possible that decreases in chromatic sensitivity measured at a fixed retinal illuminance could be misattributed to changes in the absolute threshold of the mechanism. Our finding of differences in the gain constants of the foveal and peripheral chromatic mechanisms means that caution should be used in interpreting chromatic contrast sensitivity losses that are greater in the periphery than in the fovea.

Consistent with the finding that peripheral chromatic sensitivity declines more than peripheral achromatic sensitivity, absolute thresholds of both of the chromatic mechanisms increase more from the fovea to the periphery than does the absolute threshold for the luminance mechanism. Although a large increase in the chromatic absolute thresholds is apparent from Table 2, in Fig. 3 it appears that the thresholds for blue increase by only a small amount. This apparent discrepancy between the increment thresholds for blue and the absolute thresholds for the SWS cone opponent mechanism is a consequence of the absence of macular pigment in the periphery. The thresholds in Fig. 3 are in photopic trolands, which do not take into account the increase in the cone quantal catch for the test increment in the periphery as a consequence of the absence of macular pigment, whereas the absolute thresholds in Table 2 represent cone excitation and include the increased quantal catch of short-wavelength light that is due to the lack of macular pigment. Since macular pigment has greater absorption for short wavelengths than for middle and long wavelengths, only the SWS cone opponent mechanism shows a large difference in eccentricity effects for photometric and cone excitation units. Therefore, although the photometric thresholds for the blue stimuli and the achromatic stimuli decline by similar amounts with eccentricity, the cone-excitation-based absolute thresholds decline more for the SWS cone opponent mechanism than for the luminance mechanism.

The changes in the absolute thresholds and gain constants can be used to assess hypotheses about the underlying changes responsible for the decline in contrast sensitivity with eccentricity. For example, Greenstein and Hood have shown that a change in absolute threshold with a commensurate change in gain constant is consistent with a change in the mechanism before the gain process (e.g., receptor numerosity or quantal catch), whereas a change in absolute threshold in the absence of a change in gain constant is consistent with some postgain (i.e., postreceptoral) process. Consistent with a receptor change with eccentricity, both the absolute thresholds and the gain constant of the red–green and the SWS cone opponent processes vary with eccentricity. However, the change in absolute threshold is greater than the change in gain, indicating a role for postreceptoral changes in the decrease in chromatic sensitivity with eccentricity.

The increase in the absolute thresholds and gain constant of the blue and red–green mechanisms may be partially a consequence of changes in cone numerosity. To account for the approximate change of 1 log unit in absolute thresholds, the number of cones would have to change by 1 to 4 log units, dependent upon the model of summation used. This is not consistent with the data on SWS cone numerosity across the visual field. If the decline in the red–green absolute thresholds is a consequence of the decline in cone numerosity, then it would be expected that the absolute threshold of the red–green mechanism should decline by an amount similar to that for the luminance mechanism, since both thresholds are mediated largely by the LWS cones. In addition, it would be expected that a change in cone numerosity would cause a similar change in the absolute threshold and the gain constant. Therefore some of the decline would be expected to yield an increase in the absolute threshold of the mechanisms modeled in this experiment. We wished to examine the roles of absolute threshold and gain constants in the decline in sensitivity that cannot be accounted for by the increase in integration area with eccentricity, and hence the size of the stimulus was selected to be larger than the expected integration area for each of the mechanisms. On the basis of the receptive field sizes of the ganglion cells that contribute to the responses of the mechanisms and psychophysical measurements of spatial summation, it would be expected that the SWS cone opponent pathway would be most susceptible to changes in absolute threshold as a consequence of stimuli smaller than the integration area. Our data did not reveal changes in absolute thresholds for the SWS cone opponent mechanism that were greater than those for the red–green mechanism. Therefore we concluded that the increase in the absolute threshold of the chromatic mechanisms could not be parsimoniously explained by the
increase in integration area with eccentricity. As suggested by previous studies,\textsuperscript{23,32,35} a change in the opponency or the segregation of cone inputs may account for the portion of the decline in red–green sensitivity that cannot be accounted for by cone numerosity. It seems unlikely, however, that any change in receptive field structure can account for the increase in absolute threshold with eccentricity for the SWS cone opponent mechanism given the segregation of inputs to the small bistratified ganglion cells.\textsuperscript{59,60}

3. PREDICTING THE RELATIVE SENSITIVITY OF THE MECHANISMS (EXPERIMENT 2)

In the first experiment it was assumed, on the basis of the spectral distributions of the lights, that the response to each of the increments was mediated almost exclusively by a single mechanism. If the test increments in experiment 1 indeed isolated the response of the red–green, SWS cone opponent and luminance mechanisms as assumed, then the vector sum of the responses of the three mechanisms should predict the spectral sensitivity function.\textsuperscript{1,2,5,61,62} Therefore in experiment 2 we measured, then the vector sum of the responses of the three mechanisms obtained in experiment 1.

Calculating the vector sums of the mechanisms also allows us to compare the relative roles of the three mechanisms in the determination of threshold as a function of wavelength. Spectral sensitivity declines rapidly near 580 nm when measured on an equal-energy white adapting background. This decline in sensitivity, which is sometimes referred to as Sloan’s notch,\textsuperscript{63} is often considered to represent the neutral point for the red–green mechanism.\textsuperscript{20,62} A number of studies have shown that the depth of Sloan’s notch decreases in peripheral locations,\textsuperscript{23,35,47,56} indicating that the relative sensitivity of the photopic mechanisms varies in the periphery. The larger decline in the sensitivity with eccentricity for the red–green mechanism relative to the luminance mechanism is consistent with the suggestion that the depth of Sloan’s notch is a measure of the differential sensitivity of the red–green and luminance mechanisms.\textsuperscript{15–17,21,23,35,37}

However, Miyahara and co-workers\textsuperscript{1,46} reported that for increment thresholds for slow increments presented on a large pedestal, thresholds in Sloan’s notch were mediated by the (L + M)–S limb of the SWS cone opponent mechanism in observers with red–green sensitivity losses due to anomalous trichromacy. In our first experiment red–green sensitivity was reduced in the periphery of normal observers, so it is possible that the SWS cone opponent mechanism may mediate thresholds within Sloan’s notch in the normal periphery. The following experiment investigates whether the reduction in the depth of Sloan’s notch in the periphery is due to the decline in contrast sensitivity of the red–green mechanism relative to that of the luminance mechanism or to the decline in contrast sensitivity of the red–green mechanism relative to that of the SWS cone opponent mechanism. To determine which mechanism mediated detection of thresholds within Sloan’s notch, spectral sensitivity was measured on a broad spectrum pedestal and on a chromatic pedestal and compared with the predicted sensitivity of the chromatic and luminance mechanisms.

A. Methods

The participants, apparatus, and procedure were identical to those described for experiment 1 with the following exceptions. To minimize the free parameters, the previous model of the SWS cone opponent mechanism included a single absolute threshold and a gain constant based on the illuminance of the background. With the previous model it is not possible to distinguish the responses of the luminance and the SWS cone opponent mechanisms since they yield similar estimates for wavelengths above 500 nm. In this experiment, a more precise estimate of the gain constant and absolute threshold of both the SWS cone and the LWS and MWS responses of the SWS cone opponent mechanism was necessary to permit the (L + M)–S response to be discriminated from that of the (L + M) luminance mechanism. To discriminate the responses of these mechanisms required separate estimates of the absolute threshold and gain constant of the SWS and (L + M) portion of the SWS cone opponent mechanism. Therefore, combining the implementation presented by Yeh et al.\textsuperscript{3,5} with that presented by Miyahara et al.,\textsuperscript{1} we modeled the SWS cone opponent mechanism as the difference between SWS cone excitation and an (L + M) response, and the gain constant and absolute threshold for the SWS cone response and the (L + M) response were allowed to vary. Thus Eq. (3) becomes

\[
\log \Delta S = \log T_S - \log S_T \left( \frac{1}{1 + G_S S_A} \right) - \frac{1}{\Delta I_{LM}} \tag{4}
\]

where \( T_S \) is the absolute threshold, \( G_S \) is the gain constant of the \([S - (L + M)]\) mechanism, \( S_T \) and \( S_A \) are the relative SWS cone excitation levels\textsuperscript{44} for the test increment and the adapting fields (see Table 1), respectively, and \( \Delta I_{LM} \) refers to Eq. (1) above. When Eq. (1) was substituted into Eq. (4), the values for \( G_a \) and \( T_a \) were allowed to vary rather than being fixed to those values obtained from the fit of the luminance mechanism to the white increments.

To estimate the four free parameters in Eq. (4) required the measurement of peripheral increment thresholds for a wavelength greater than 500 nm that can be assumed to be mediated by the SWS cone opponent mechanism. Selecting a wavelength near Sloan’s notch, the neutral point of the red–green mechanism when a white background is used, makes certain the isolation of the SWS cone opponent mechanism from the red–green mechanism. To determine the parameters necessary to fit the (L + M)–S arm of the SWS cone opponent mechanism that is dominated by the response of the LWS and MWS cones at medium-to-high wavelengths, increment thresholds for a yellow (60-nm bandwidth at half-height; CIE x = 0.4124, y = 0.5803; see Table 1 for equivalent wavelengths) increment were measured on white backgrounds varying in retinal illuminance from –1 to 3 log td. Only peripheral thresholds (at the same location, 12° eccentric) were obtained. The absolute threshold (\( T_S \)) and the gain constant (\( G_S \)) of the SWS response and the absolute
threshold \((T_a)\) and the gain constant \((G_a)\) of the \((L+M)\) response were fitted by the following iterative process:

The blue thresholds were fitted by varying \(G_S\) and \(T_S\) while the \(\Delta l_{LM}\) parameters were held constant; then the yellow data were fitted by varying the \(G_a\) and \(T_a\) while the \(S\)-cone parameters were held constant; iteration was continued until no further changes were obtained for any parameters.

The use of a chromatic adapting field has been shown to shift the location of Sloan's notch to the dominant wavelength of the adapting field.\textsuperscript{14,17,64,65} To extend the model to include the influence of the chromaticity of the adapting field on the sensitivity of the chromatic mechanisms, an additional parameter \((\text{opp})\) from previous foveal implementations of the model\textsuperscript{3,5,6} was incorporated into the equation for the \(|L-M|\) opponent system:

\[
\log \Delta l = \log \Delta l_R + \text{opp},
\]

where

\[
\text{opp} = \log \left[ 1 + L_{\text{opp}} |A - W| 3.008 \left( \frac{1}{1 + G_R L_{\text{W}}} \right) \right] \quad (6)
\]

where \(\log \Delta l_R\) refers to Eq. (2) from experiment 1, \(L_{\text{opp}}\) is a new free parameter that varies the contrast sensitivity of the mechanism when the pedestal is chromatic, \(I\) represents LWS cone transduction of the adapting field \((A)\) and the white pedestal \((W)\), and \(L_{\text{W}}\) is the relative LWS cone excitation level\textsuperscript{44} for the LWS equivalent wavelength of the adapting field. Thus the new parameter, \(\text{opp}\), is 0 when the pedestal is white and affects contrast sensitivity only when the chromaticity of the adapting field is varied.

Chromatic contrast sensitivity for ten monochromatic lights (10-nm bandwidth) was measured on a white adapting field and on a 500-nm adapting field. To determine the height of the function that describes the sensitivity of the achromatic mechanism, we also measured achromatic contrast sensitivity for both the white and the 500-nm adapting fields. The combined illuminance of the background and pedestal was fixed at 150 cd/m\(^2\) for all measurements obtained on the white pedestal and at 50 cd/m\(^2\) for all measurements obtained on the 500-nm pedestal. Since the results of the previous experiment indicated that these luminances would yield contrast sensitivities in the Weber region for both observers and for all mechanisms at pupil sizes down to 1 mm, contrast sensitivity measurements were obtained with natural pupils.

To predict the chromatic contrast sensitivity data, the values of each of the parameters of the model were fixed to those values obtained from fitting the TVI functions. The combined response of the mechanisms was calculated as the vector sum (exponent of 4.0) of the three mechanisms.\textsuperscript{12,5,14,61,62}

**B. Results**

Figure 4 shows the thresholds obtained for the yellow and blue increments in the periphery. The functions represent the fit of Eq. (4) to the thresholds obtained for the blue and yellow increments. The absolute thresholds and gain constants obtained from fitting the blue and the yellow thresholds with Eq. (4) are shown in Table 3. From the figure, it can be seen clearly that although the height of the blue and yellow functions differ, the retinal illumination, in photopic trolands, at which the threshold begins to increase linearly is similar.

Chromatic contrast sensitivity on the white pedestal is shown for both observers in Fig. 5. The curves on the graph represent predictions of the contrast sensitivity of the mechanisms with use of the parameters obtained by fitting the TVI functions; that is, predictions were entirely constrained by the absolute threshold and gain constant of each of the mechanisms as determined from the TVI functions. The sensitivity of the \(|L-M|\) mechanism shows a decline in sensitivity near 570 nm for both observers. A decline in the sensitivity of the \(|S-(L+M)|\) mechanism occurs near 500 nm. Sensitivity of the \((L+M)\) mechanism was lower than sensitivity for all of the chromatic stimuli and was the same as sensitivity for the achromatic increment. The vector sum of the responses of the three mechanisms is shown by the thick gray curves and provides a good characterization of the spectral sensitivity function.

Figure 6 illustrates the data obtained on the 500-nm adapting field. The functions represent the model's predicted sensitivity of the \(|S-(L+M)|\), \(|L-M|\), and \((L+M)\) mechanisms for each of the observers. The shape of the functions for each of the three mechanisms was determined on the basis of the absolute thresholds and gain constant of the mechanisms determined from the TVI...
functions. Only the height of the function for the \(|L - M|\) mechanism was permitted to vary by an amount described by \(L_{\text{opp}}\), which was similar for the two observers (PP, 0.12; WS, 0.07). The notch in the \(|L - M|\) mechanism’s sensitivity shifted from near 570 nm to the equivalent wavelength of the adapting field (500 nm) and now coincides with the notch in the \(|S - (L + M)|\) mechanism’s sensitivity. The vector sum of the responses of the three mechanisms, represented by the thick gray curves, provides a good characterization of the spectral sensitivity for both observers with a 500-nm background.

Table 3. Parameters of the Model Obtained by Fitting with Eq. (4) the Blue and Yellow Increment Thresholds Shown in Fig. 4

<table>
<thead>
<tr>
<th>Observer</th>
<th>(\log T_a)</th>
<th>(\log T_S)</th>
<th>(G_S)</th>
<th>(G_G)</th>
</tr>
</thead>
<tbody>
<tr>
<td>PP</td>
<td>−0.42</td>
<td>−0.02</td>
<td>0.06</td>
<td>0.02</td>
</tr>
<tr>
<td>WS</td>
<td>−0.45</td>
<td>−0.09</td>
<td>0.09</td>
<td>0.02</td>
</tr>
</tbody>
</table>

C. Discussion

The model was adapted to allow us to determine the absolute threshold and gain constant of the \((L + M)\) arm of the SWS cone opponent mechanism rather than fixing the gain constant and absolute threshold for the \((L + M)\) arm equal to that of the SWS arm as was done in previous implementations of the model. The retinal illuminance at which the blue and the yellow increment thresholds begin to increase linearly with retinal illuminance is similar for the blue and the yellow increments and is at least 1 log unit higher than for the white increments. This establishes that neither the blue nor the yellow increments are detected by the same mechanism that detects achromatic increments and is consistent with reports of similar gain (in photopic trolands) for the \(S - (L + M)\) and \((L + M) - S\) limbs of the S-cone mechanism when a broad-spectrum adapting field is used. The parameters derived from fitting the white, blue, and yellow TVI data predict successfully that contrast sensitivity in the Weber region is lower for the achromatic increments than for middle-wavelength increments (Fig. 5).

It was necessary to obtain separate estimates of the gain constant and the absolute threshold of the \(S - (L + M)\)
and \((L+M)-S\) responses of the SWS cone opponent mechanism in order to discriminate the \((L+M)-S\) response from the \((L+M)\) response of the luminance mechanism at medium-to-high wavelengths. Above 500 nm the contribution of the SWS cones to the \((L+M)-S\) limb is negligible, and therefore only the height of the \((L+M)-S\) function allows it to be discriminated from the luminance \((L+M)\) mechanism. That is, above 500 nm the shape and slope of the function describing the responses of the \((L+M)-S\) arm of the SWS cone opponent mechanism is identical to that of the luminance mechanism regardless of the representation used (i.e., cone contrast space, chromaticity coordinates, or cone excitation) since both are exclusively determined by an additive combination of LWS and MWS responses of the same sign.

The vector sum of sensitivities of the luminance and chromatic mechanisms provides a good characterization of peripheral spectral increment thresholds on a white background. The predicted sensitivity of the SWS cone opponent and luminance mechanisms is consistent with the mediation of thresholds in Sloan’s notch by the \((L+M)-S\) arm of the SWS cone opponent mechanism rather than by the luminance mechanism. This confirms and extends to the normal periphery the foveal findings of Miyahara et al.\(^\text{1}\) who reported that sensitivity in Sloan’s notch can be mediated by the SWS cone opponent mechanism when a slow increment on a large pedestal is used.

To test the model further, we measured spectral sensitivity on a 500-nm adapting field, which is expected\(^\text{14,17,64}\) to shift the neutral point of the \((L-M)\) mechanism to coincide with the neutral point of the SWS cone opponent mechanism. To demonstrate this point more clearly, in Fig. 7 we show the predicted contrast sensitivity of the three mechanisms in cone contrast space.\(^{33,64,65}\) In this space the 500-nm background rotates the function describing the sensitivity of the \([S-(L+M)]\) mechanism so that the \((L+M)\) and \([S-(L+M)]\) mechanisms are more easily distinguished. The vector sums are represented by the thick gray curves. On the white background, the vector sum demonstrates that spectral sensitivity is mediated by the red–green and SWS cone opponent mechanism. In contrast, the spectral sensitivity predictions for the 500-nm background demonstrate that the SWS cone opponent mechanism mediates the majority of thresholds but the luminance mechanism mediates those in the notch of both the SWS cone opponent mechanism and the red–green mechanism.

Many studies have reported that thresholds in Sloan’s notch are mediated by a mechanism that is dependent upon the additive combination of the responses of the LWS and MWS cones.\(^{17,20,35,62}\) Our results in the periphery are consistent with the suggestion that an additive combination of the responses of the LWS and MWS cones mediates detection of chromatic increments within Sloan’s notch. The question addressed here was which mechanism, the \((L+M)-S\) arm of the SWS cone opponent mechanism or the luminance mechanism, mediates thresholds under our testing conditions. Our results indicate that thresholds in Sloan’s notch can be mediated by the \((L+M)-S\) arm of the SWS cone opponent mechanism in the normal periphery. The paradigm used in our investigation attempted to maximize the isolation of the red–green mechanism from the luminance mechanism by using a broad spectrum pedestal that decreases the sensitivity of the luminance mechanism.\(^{21,33,37,38,64,67}\) Thus, for other paradigms and stimulus configurations, responses within Sloan’s notch may be mediated by the luminance mechanism. However, our results suggest that future studies need to consider the possibility that the SWS cone opponent mechanism may mediate thresholds within Sloan’s notch and hence that a direct measurement of the sensitivity of the luminance mechanism is necessary to conclude which of the mechanisms mediates thresholds within Sloan’s notch.

4. CONCLUSIONS

The thresholds measured as a function of adapting illumination show that the peripheral sensitivity of both of the chromatic mechanisms declines more with eccentricity than does the sensitivity of the luminance mechanism. The model used here, which combines a number of earlier implementations of a foveal model\(^\text{1-6}\) and extends the model to the normal periphery, successfully predicts peripheral chromatic contrast sensitivity on white and chromatic adapting fields. Both the gain constant and the absolute threshold were shown to contribute to the decline in sensitivity with eccentricity, suggesting that both receptoral and postreceptoral mechanisms must play a role and that explicit models of adaptation should be incorporated into models of the decline in sensitivity with eccentricity. For large, slow increments presented on a spatially contiguous pedestal, peripheral thresholds in Sloan’s notch appear to be mediated by the \((L+M)-S\) limb of the SWS cone opponent mechanism rather than by the luminance mechanism.

ACKNOWLEDGMENT

This research was supported by National Eye Institute grant EY07716 to W. Swanson.
REFERENCES