Chromatic parameters derived from increment spectral sensitivity functions

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We propose a mathematical model to derive the chromatic parameters from increment spectral sensitivity functions. This model was applied to determine the effective red, green, blue, and yellow mechanism contribution to the detection of the spectral stimuli of five normal trichromatic subjects. Detection thresholds were measured for a 300 ms, 1.2° circular test flash presented on a 100 cd/m^2 white background for spectral wavelengths between 410 and 660 nm. The model analysis confirmed that in the red–green wavelength area, the detection of our chosen stimuli was mediated by two distinct (L–M) antagonistic mechanisms: a red–green and a yellow, from the blue–yellow system. We inferred that the red–green mechanism receptive fields consisted of a single L- or M-cone center with a homogeneous or heterogeneous surround devoid of S-cone projections. For the receptive fields of the yellow half of the blue–yellow mechanism, we propose a similar configuration but with S-cone projections present in the surround. This proposal is not concordant with what is currently understood regarding retinal physiology. However, two L–M antagonistic mechanisms in the red–green wavelengths as proposed by our results predict what would appear as an intuitive yellow mechanism with a maximal sensitivity at the 578 nm wavelength, where the red–green mechanism sensitivity is null.

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1. INTRODUCTION

Classic theories of color vision suggest that neural signals from the three cone types are transformed at an intermediate stage into an achromatic and two chromatic signals.[1] King-Smith and Carden[2] reported that the achromatic and chromatic channels (postulated as luminance and opponent color channels) mediate the detection of test stimuli with the following properties:

(a) The detection by chromatic channels is favored for long duration and large test stimuli presented on a white background.

(b) The achromatic channel favors the detection of short and small test stimuli.

King-Smith and Carden[2] proposed that the system, which detects small targets, is the same as the one involved in flicker photometry.

With flicker photometry, it is possible to establish a good relationship between the spectral sensitivity curves and the photopigment light absorption spectrum. The fovea spectral sensitivity curves measured by flicker increment detection on a white background in a normal trichromate could be fitted by a linear combination of the cone fundamental absorption spectra.[3]

Increasing the white background luminance and the flash presentation time radically changes the shape of increment spectral sensitivity functions. The spectral sensitivity functions, measured by Sperling and Harwerth[4] in both monkeys and humans for the detection of long test flashes superimposed on the white background, present three peaks of sensitivity. While the 440 nm peak may be fitted with the spectral absorption of the S cones, the other two peaks, at about 530 and 610 nm, do not fit with the spectral absorption of the M and L cones. Sperling and Harwerth[4] suggest that there is an inhibitory mechanism related to the red–green opponent response system, originally proposed by Hering and demonstrated by Hurvich and Jameson.[1]

King-Smith and Carden[2] measured the spectral sensitivity functions for detecting and determining the color of 1°, 200 ms test flashes on a 1000 troland (td) white background. In their conclusion they suggest that, for 1°, 200 ms test flashes, superimposed on the relatively high luminance white background, the detection of spectral stimuli is mediated by the opponent color system, except for the yellow spectral region where the luminance system may be prominent. Modern studies from Kalloniatis and Harwerth[5] and Miyahara *et al.*[6] support the idea that for detection in the trough of the Sloan notch the sensitivity is more mediated by the S-cone pathway rather than the luminance pathway.

The classical model of the blue–yellow spectral opponent pathway accepted that the blue mechanism receives the signal from the S cone, in opposition to a linear sum of the L and M cones. This concept agrees with the physiological results of Wheeler and Naka,[7] where the blue color-opponent signal is performed by linear center-surround transformations in the outer plexiform layer. Modern studies[8] validate that the blue ON and yellow OFF opponent responses start from the bistratified ganglion cell where the ON bipolar cell contacts only the S cones and the OFF bipolar cell contacts L and M cones. Actual understanding regarding the yellow mechanism sensitivity is that yellow mechanism takes the signal from a linear sum of L and M cones in opposition to S-cone output. This concept was proposed to design a yellow mechanism in balanced opposition to the blue color mechanism.

Various modern studies report that it is difficult to identify the reliability between blue and yellow mechanism cone contributions by using threshold contour methods in cone-contrast space.[9] However, several studies have demonstrated that threshold contours in cone contrast space or spectral sensitivity data could be successfully fitted by a probability summation model.[3,9–11] In these studies the authors demonstrated the possibility of fitting the color sensitivity data with a probability summation vector model composed by an achromatic and two chromatic systems. However we assume that there are an unlimited number of fitting possibilities, depending on the relative cone contribution in each color system and the choice of the cone interactions in each color mechanism.

The aim of the present study was to demonstrate the possibility of deriving the chromatic mechanism parameters as a result of unique solutions of the equations with a vector color model, which can explain the increment spectral sensitivity functions.

2. METHOD

In the present study we used a vector model to fit the observed increment spectral sensitivity functions for 300 ms duration, 1.2° diameter spectral test flashes, presented on a 100 cd/m^2 white background luminance. In the above conditions, we can assume that the stimuli are detected predominantly by the opponent color systems.[2,5,6] We obtained the red–green and blue–yellow mechanism cone interaction parameters as a unique solution for the vector color model equations, which can explain the increment spectral sensitivity functions.

A. Model

The mathematical model used for calculating the increment spectral sensitivity was adopted from a vector model previously proposed by Quick.[12] The neural information from the cones is detected by an intermediate stage composed of one achromatic and two chromatic systems.

The vector model of Quick[12] can be formally expressed as

$$S(\lambda) = [S_A(\lambda)^n + S_{R-G}(\lambda)^n + S_{B+Y}(\lambda)^n]^{1/n},$$

where $S_A(\lambda)$, $S_{R-G}(\lambda)$ and $S_{B-Y}(\lambda)$ represent the spectral sensitivity of the achromatic, red–green chromatic, and blue–yellow chromatic systems, respectively.

We suggest that our chosen spectral stimuli are detected predominantly by the color opponent systems and not by the additive luminance mechanism. This proposal is also supported by the empirical data of King-Smith and Carden[2] and Kerr,[13] who demonstrated that for relatively large and long test flashes on a relatively high white background luminance, the color of the spectral stimuli could be discriminated at threshold. Other empirical data from Kalloniatis and Harwerth[5] and Miyahara *et al.*[6] support the idea that for detection in the trough of the Sloan notch the sensitivity is more mediated by the S-cone pathway rather than the luminance pathway. In this case we propose to mathematically describe our increment spectral sensitivity data by two mechanism detections: one representing a pure L- and M-cone receptive field mechanism, devoid of S-cone projections, and the second representing a mechanism field containing L-, M-, and S-cone interactions:

red – green chromatic system

$$S_{R-G}(\lambda) = a_1 * L + b_1 * M, \tag{I}$$

blue – yellow chromatic system

$$S_{B-Y}(\lambda) = a_2 * L + b_2 * M + c * S. \tag{II}$$

The values L, M, and S correspond to the Smith–Pokorny[14] cone fundamentals normalized to their peak sensitivity. Roman numerals denote equation systems.

1. Constants

The a_1 and b_1 coefficients weight respectively L- and M-cone contribution through the red–green chromatic system. The a_2, b_2, and c coefficients weight, respectively, L-, M-, and S-cone contribution from the blue–yellow chromatic system. The objective of the actual analysis was to determine the relative L- and M-cone contribution in each chromatic system. We are mainly interested in estimating the a_2/b_2 ratio parameter that characterizes the L- and M-cone interactions with the S cones. We do not make any assumption that a_1, b_1, a_2, b_2, and c parameters represent negative or positive values.

The sensitivity of the system was obtained from a probability summation, called the vector sum ($n=2$). The application of the vector sum, to describe the detection of chromatic and achromatic stimuli, has been confirmed by a large number of independent studies[1,15–19] and can be expressed as

$$S(\lambda)^2 = (S_{R-G}(\lambda)^2 + S_{B-Y}(\lambda)^2) = (a_1 * L + b_1 * M)^2 + (a_2 * L + b_2 * M + c * S)^2. \tag{III}$$

According to the present model, the overall detection $S(\lambda)$ can be expressed by the following mathematical equation:

$$S(\lambda)^2 = L^2 * m_1 + M^2 * m_2 + S^2 * m_3 + 2L * M * m_4 + 2L * S * m_5 + 2M * S * m_6, \tag{IV}$$

where [system (V)]

$$m_1 = a_1^2 + a_2^2 \quad \text{L-cone sensitivity contribution}, \tag{Va}$$

$$m_2 = b_1^2 + b_2^2 \quad \text{M-cone sensitivity contribution}, \tag{Vb}$$

$$m_3 = c^2 \quad \text{S-cone sensitivity contribution}, \tag{Vc}$$

$$m_4 = a_1 * b_1 + a_2 * b_2 \quad \text{L- and M-cone sensitivity interactions}, \tag{Vd}$$

$$m_5 = a_2 * c \quad \text{L- and S-cone sensitivity interactions}, \tag{Ve}$$

$$m_6 = b_2 * c \quad \text{M- and S-cone sensitivity interactions}. \tag{Vf}$$

To derive the m parameters, we wrote Eq. (IV) for each tested wavelength (26 wavelengths in 10 nm steps between 410 and 660 nm). We therefore obtained a system of 26 equations with 6 unknowns $(m_1, m_2, m_3, m_4, m_5, m_6)$ formulated as follows [system (VI)]:

$$\begin{bmatrix} s^2(\lambda_1) \\ s^2(\lambda_2) \\ s^2(\lambda_3) \\ \vdots \\ s^2(\lambda_n) \end{bmatrix} = \begin{bmatrix} \mathrm{L}^2_{(\lambda_1)} & \mathrm{M}^2_{(\lambda_1)} & \mathrm{S}^2_{(\lambda_1)} & 2\mathrm{L}_{(\lambda_1)} * \mathrm{M} & 2\mathrm{L}_{(\lambda_1)} * \mathrm{S}_{(\lambda_1)} & 2\mathrm{M}(\lambda_1) * \mathrm{S}_{(\lambda_1)} \\ \mathrm{L}^2_{(\lambda_2)} & \mathrm{M}^2_{(\lambda_2)} & \mathrm{S}^2_{(\lambda_2)} & 2\mathrm{L}_{(\lambda_2)} * \mathrm{M} & 2\mathrm{L}_{(\lambda_2)} * \mathrm{S}_{(\lambda_2)} & 2\mathrm{M}_{(\lambda_2)} * \mathrm{S}_{(\lambda_2)} \\ \mathrm{L}^2_{(\lambda_3)} & \mathrm{M}^2_{(\lambda_3)} & \mathrm{S}^2_{(\lambda_3)} & 2\mathrm{L}_{(\lambda_3)} * \mathrm{M} & 2\mathrm{L}_{(\lambda_3)} * \mathrm{S}_{(\lambda_3)} & 2\mathrm{M}_{(\lambda_3)} * \mathrm{S}_{(\lambda_3)} \\ \vdots & \vdots & \vdots & \vdots & \vdots \quad \vdots & \vdots \quad \vdots \\ \mathrm{L}^2_{(\lambda_n)} & \mathrm{M}^2_{(\lambda_n)} & \mathrm{S}^2_{(\lambda_n)} & 2\mathrm{L}_{(\lambda_n)} * \mathrm{M} & 2\mathrm{L}_{(\lambda_n)} * \mathrm{S}_{(\lambda_n)} & 2\mathrm{M}_{(\lambda_n)} * \mathrm{S}_{(\lambda_n)} \end{bmatrix} \times \begin{bmatrix} m_1 \\ m_2 \\ m_3 \\ m_4 \\ m_5 \\ m_6 \end{bmatrix}. \tag{VI}$$

Since equations (VI) constitute an overdetermined system, the unknown coefficients m_1, m_2, m_3, m_4, m_5, and m_6 can be computed by using the least-squares-fit method.

From equation system (V) we can see that the c parameter could be computed directly from Eq. (Vc). Furthermore, from Eqs. (Ve) and (Vf), describing the LS and MS interactions, we obtained the relative $a_2/b_2 = m_5/m_6$ describing L- and M-cone interaction from the blue–yellow system (VII):

$$m_1 = a_1^2 + a_2^2 \tag{VIIa}$$

$$m_2 = b_1^2 + b_2^2 \tag{VIIb}$$

$$m_3 = c^2 \tag{VIIc}$$

$$m_4 = a_1 * b_1 + a_2 * b_2 \tag{VIId}$$

$$m_5/m_6 = a_2/b_2 \tag{VIIf}$$

Equation system (VII) allows us to compute the a_1, a_2, b_1, b_2, and c parameters as unique solutions.

3. MONOCHROMATIC DETECTION THRESHOLDS

A. Subjects

Five normal trichromate observers with psychophysical experience, two females and three males, participated in this study. All subjects were evaluated for congenital color defects by using HRR (Hardy, Rand, Rittler) pseudoisochromatic plates and the Nagel anomaloscope.

B. Apparatus and Methods

The increment threshold sensitivity was evaluated with a standard spectral sensitivity setup (xenon arc lamp and a monochromator) mounted on an optical bench (Fig. 1). L1 and L2 correspond to lenses that focus the light at the monochromator entry slit, and D is the diffuser. The shutter, S, was placed in the light beam after the monochromator. The target stimulus was presented by opening the shutter for 300 ms. The screen, Sc, was illuminated by a standard C light source positioned to ensure 100 cd/m^2 uniform background luminance for a square area subtending 60 deg of visual angle (dva).

The 1.2 dva stimulus area was presented on the background. A rotating circular variable neutral density wedge filter in 0.05 log steps controlled the intensity of the test flash. An experimental session consisted of establishing thresholds for 26 wavelengths in 10 nm steps between 410 and 660 nm. First, the neutral density wedge was positioned so that the subject could clearly see the test flash presented for 300 ms at 2 s intervals. For each

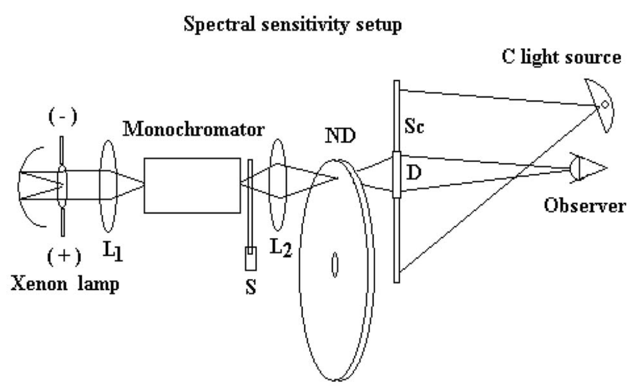

Fig. 1. Spectral sensitivity setup (xenon arc lamp and monochromator) mounted on an optical bench.

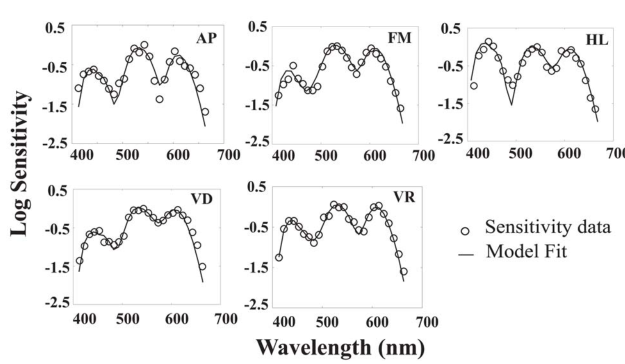

Fig. 2. Increment spectral sensitivity curve obtained from each observer, with the computed sensitivity function using the least-squares-fit method to solve equation system (VI).

Table 1. Value for m_1, m_2, m_3, m_4, m_5, and m_6 Parameters Corresponding to Each Subject[a]

m Parameters	Subject VD	FM	HL	VR	AP
m_1 (L)	4.48	4.31	4.24	5.18	3.41
m_2 (M)	6.68	6.67	6.66	8.07	6.06
m_3 (S)	0.33	0.26	1.29	0.50	0.37
m_4 (LM)	−5.17	−5.18	−5.10	−6.31	−4.45
m_5 (LS)	−3.17	3.72	−3.33	4.07	−1.74
m_6 (MS)	1.49	−2.15	0.67	−2.27	0.36
$\mathbf{m_5/m_6}$					
$\mathbf{a_2/b_2}$	**−2.12**	**−1.73**	**−4.97**	**−1.79**	**−4.83**

[a]Parameters were computed by using the least-squares-fit method to solve Equation System (VI).

Table 2. Chromatic Parameters a_1, a_2, b_1, b_2, and c Obtained as a Unique Solution of Equation System (V) Using the m Parameters Presented in Table 1

Chromatic Parameters	Subjects VD	FM	HL	VR	AP
a_1	1.82	1.85	1.94	2.09	1.79
a_2	1.09	0.94	0.68	0.89	0.42
b_1	−2.53	−2.52	−2.57	−2.79	−2.46
b_2	−0.53	−0.54	−0.14	−0.51	−0.09
c_1	0.58	0.51	1.14	0.71	0.61
$\mathbf{a_1/b_1}$	**−0.72**	**−0.73**	**−0.75**	**−0.75**	**−0.73**
$\mathbf{a_2/b_2}$	**−2.06**	**−1.75**	**−4.86**	**−1.75**	**−4.67**

step, the intensity of the flash was reduced until the subject could no longer see it: the threshold was determined as the point where the subject first reported two consecutive negative responses. The increment-threshold spectral sensitivity was computed from averaging a minimum of five descending thresholds for each wavelength.

4. RESULTS

The increment spectral sensitivity curves, obtained from each subject along with the model fits, are shown in Fig. 2. A simple inspection of the curves in Fig. 2 reveals that all the subjects demonstrate a typical normal thrichromatic increment spectral sensitivity function on a white background with three characteristic peaks for the 440, 530, and 620 nm spectral zones and two typical sensitivity dips observed for 470 and 570 nm spectral zones.

In Table 1 are shown the fitted parameters $m_1, \ldots, m_6$ for each observer. From the data presented in Table 1, we observe that there are no large individual differences concerning the m_1, m_2, and m_4 fitted parameters that describe L- and M-cone contributions and the LM-cone interactions, respectively. Significant individual differences can be noticed regarding the m_3, m_5, and m_6 parameters that describe the S-cone contribution and the SL and SM-cones interaction, respectively. Observer HL shows relatively more S-cone contribution (m_3=1.29), in contrast to other observers, who show m_3 values between 0.26 and 0.5. As shown in Figure 2, observer HL demonstrates more sensitivity for short-wavelength stimuli detection, relative to the middle and longer wavelengths.

Another noticeable difference between the subjects is represented by negative or positive values for the m_5 and m_6 parameters.

To explain this, we adopted the concept where the color-opponent signals are performed by linear center–surround transformations (proposed by Paulus and Kröger-Paulus[20]). We anticipated a middle-wavelength-sensitive mechanism with S, L, and M-cone interaction by the intrusion of S cones in the surround of the L and M cluster with variable L/M-cone inputs. There are two possible mechanisms:

(1) S−(L−M) mechanism, where the S- and M-cone signals antagonize an L-cone input and create negative SL-cone interactions.
(2) S−(M−L) mechanism, where the S- and L-cone signals antagonize an M-cone input and create negative SM-cone interactions.

In Table 2 the a_1, a_2, b_1, b_2, and c coefficients, are shown for each subject computed directly from the system of equations (VI), using the $m_1,\ldots,$ and m_6 parameters. What is interesting from the data presented in Table 2 is that all the subjects show negative values for the a_2/b_2 ratio. This result demonstrates a discriminatory S-cone interaction in relation to the L and M cones, as shown by the alternative negative and positive values obtained for the m_5 and m_6 parameters.

In Table 2 the ratios a_1/b_1 representing the relative L/M-cone contributions from the red-green system are ex-

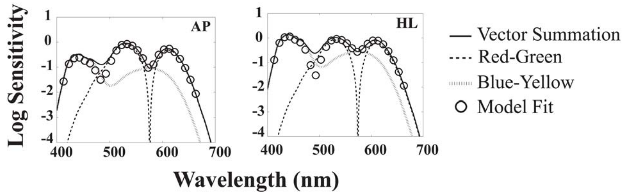

Fig. 3. Graphic representation of the two mechanisms as described by Eqs. (I) and (II) and their contributions to the overall sensitivity represented by the model fit for two representative observers.

pressed. All the subjects demonstrate negative values for the a_1/b_1 ratio in accord with an L- and M-cone red–green antagonistic mechanism. The absolute value of the a_1/b_1 ratio is similar to the $1/K_1$, where K_1 is a factor that weights the relative M- and L-cone interaction in the red–green opponent mechanism ($\mathrm{L}-K_1*\mathrm{M}$), which is consistent with other models.[11,16,21]

A graphic representation of the two mechanisms, as described by Eqs. (I) and (II) and their contributions to the overall sensitivity, is shown in Fig. 3 for two representative subjects. Figure 3 therefore suggests that our increment spectral sensitivity functions could be represented solely by two opponent color systems:

(1) A red–green system, where the L cones antagonize the M cones in a ratio that generates a null red–green sensitivity point at 578 nm. This result is in agreement with what is currently understood regarding retinal physiology.

(2) A blue–yellow system, characterized by the S-cone intrusion in a subsequent L- and M-cones opponent mechanism with maximal sensitivity for the wavelength zone, where a spectral light is perceived as yellow. We propose to call this "the yellow mechanism." This proposal is not in agreement with the actual understanding of the yellow mechanism.

5. CONCLUSIONS AND DISCUSSIONS

The major finding of our model computation predicts that two different L–M antagonistic mechanisms are required in order to explain the sensitivity in the red–green wavelength area for long test stimuli duration, presented on the relatively high background luminance. We predict a novel blue–yellow cone antagonistic system, which consists of opposing input from the L and M cones. This prediction seems not to be in agreement with earlier studies in the area of increment spectral sensitivity and also seems to be inconsistent with the majority of recent psychophysical results. At this stage, it is important to answer the following question: Are the results constrained by the spectral sensitivity model analysis [equation system (VI)]?

To answer this question, we remember that our model analysis [Eq. (IV) and equation system (VI)] has proposed to transform the increment spectral sensitivity data in a linear function with six m parameters that weight LS-, MS-, LM-cone interaction and the contribution of L^2, M^2, and S^2 cones to the overall sensitivity. This derivation is similar to the Fourier transform analysis applied to any given signal. We believe that the model analysis proposed in the present paper can be applied to any spectral sensitivity function that implies LMS-cone input. In the second step we proposed to solve the a_1, a_2, b_1, b_2, and c color mechanism parameters as a unique model solution. To confirm our model analysis, we represent the increment spectral sensitivity data and the model fit into a space with cone-contrast coordinates, such as δM/M versus δL/L, proposed by Noorlander *et al.*[17] and developed by Stromeyer and co-workers.[22,23]

Figure 4 represents the increment spectral sensitivity and the model fit data for the middle and longer wavelengths zone (490 nm to 660 nm) for each subject. The data in Figure 4 are plotted on the normalized cone contrast coordinates, where the L-cones are weighted by a factor $1/\mathrm{K}_1=0.73$, which is consistent with the average of a_1/b_1 ratio, demonstrated for the subjects in regard to the L- and M-cone interaction in the red–green opponent mechanism.

From the data represented in Fig. 4, it is noticeable that our model fits data for the sensitivity in the green (from 490 to 550 nm) and red (from 590 to 660 nm) spectral wavelength zones, which can be found on the two symmetrical lines with the positive slope. This defines the wavelength range where the sensitivity is obtained by an antagonistic L- and M-cone mechanism. For each observer representation, the 45° vector identifies the 570 nm wavelength stimulus that produces an equal stimulation of L and M cones. At this stage, our spectral sensitivity data are in agreement with earlier studies in the area of increment spectral sensitivity and with the majority of recent psychophysical results.[5,6] The disagreement between our model results and other studies is in regard to the mechanism involved in the detection of the spectral test stimulus of the 570 nm wavelength. Modern studies from Kalloniatis and Harwerth[5] and Miyahara *et al.*[6] propose an additive L+M-cone mechanism, in oposition to the S cones. Our model analysis proposes an antagonistic L–M-cones mechanism in opposition to the S-cones. Unfortunately, in a space with cone-contrast coordinate representation, it is not possible to differentiate the submechanisms inferred in our overall sensitivity data. For example, for the red–green spectral zone, our increment spectral sensitivity data can be explained by a

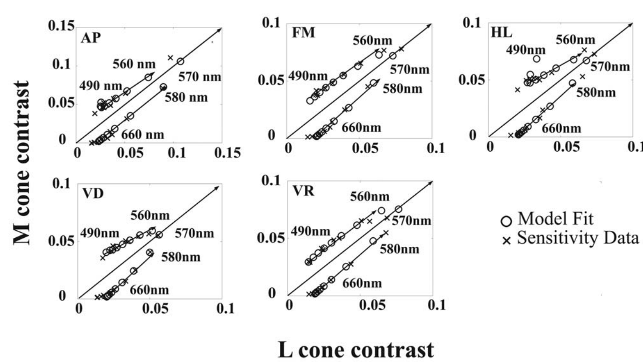

Fig. 4. Transformation of the increment spectral sensitivity and the model fit data for the middle and longer wavelength zone (490 to 660 nm) in normalized cone-contrast coordinates, where the L cones are weighted by a factor $1/K_1=0.73$, (red–green sensitivity$=0.73*\mathrm{L}-\mathrm{M}$) for each observer.

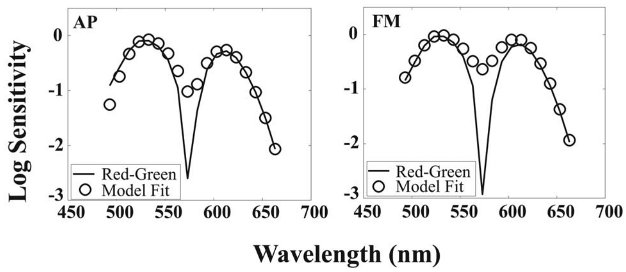

Fig. 5. Graphic representation, in the wavelength space, of the model fit sensitivity data along with the red–green mechanism sensitivity also represented in Fig. 4.

vector summation from two L–M-cone antagonistic mechanisms or by one L–M-cone antagonistic and one L +M-cone additive mechanisms. Each of these submechanisms combinations allows for generation of two identical overall sensitivity mechanisms with indistinguishable representation in cone contrast coordinates. To detect the contribution of the submechanism, it is necessary to have supplementary information concerning the zero-sensitivity setting for the red–green mechanism, or relative-mechanism cone contribution. Our prediction is very clearly marked by the negative values for the m_5/m_6 ratio relative to SL- and SM-cones interactions demonstrated by the fitting parameters (Table 1).

Another question is the following: Are the model results constrained by the actual representation that introduces SL- and SM-cone interactions? To respond, we proposed derivation with a different mechanism that ignores the S-cone connections. This new derivation also suggests a similar L- and M-cone antagonistic mechanism for explaining the sensitivity in 570 nm wavelength zone.

Figure 5 demonstrates, in the wavelength space, for two representative subjects, the model-fit sensitivity data along with the red–green mechanism sensitivity also represented in Fig. 4. From Figs. 4 and 5, it is clear that the stimuli detection in the 570 nm wavelength zone is obtained from a mechanism that is different of the red–green mechanism.

In Fig. 6 we represent the spectral sensitivity mechanism involved in the detection of the 570 nm spectral test stimulus. This mechanism sensitivity is obtained from the vector difference between the model fit sensitivity and the red–green mechanism. Figure 6 shows the data for only two representative subjects. Also, all the observers demonstrate similar mechanism detection with maximal sensitivity in wavelength zone of 570 nm. This mechanism sensitivity can be explained only from an antagonistic L- and M-cone interactions.

Another important question concerning our mechanism prediction is in regard to the model's particularity that explains the overall sensitivity from only two mechanisms expressed by equations systems (I) and (II). We proposed a new mathematical derivation by introducing a supplementary $a_0{*}\mathrm{L}+b_0{*}\mathrm{M}$ additive mechanism in a model analysis:

$$\mathrm{A}(\lambda) = a_0 * \mathrm{L} + b_0 * \mathrm{M} \qquad \text{luminance mechanism}, \qquad (\mathrm{I}_0)$$

$$\mathrm{S}_{\mathrm{R-G}}(\lambda) = a_1 * \mathrm{L} + b_1 * \mathrm{M} \qquad \text{red} - \text{green chromatic system}, \qquad (\mathrm{I}')$$

$$\mathrm{S}_{\mathrm{B-Y}}(\lambda) = a_2 * \mathrm{L} + b_2 * \mathrm{M} + c * \mathrm{S} \qquad \text{blue} - \text{yellow chromatic system}. \qquad (\mathrm{II}')$$

Equation system (V′) follows:

$$m_1 = a_1^2 + a_2^2 + a_0^2 \qquad \text{L-cone sensitivity contribution}, \qquad (\mathrm{V'a})$$

$$m_2 = b_1^2 + b_2^2 + b_0^2 \qquad \text{M-cone sensitivity contribution}, \qquad (\mathrm{V'b})$$

$$m_3 = c^2 \qquad \text{S-cone sensitivity contribution}, \qquad (\mathrm{V'c})$$

$$m_4 = a_1 * b_1 + a_2 * b_2 + a_0 * b_0 \qquad \text{L- and M-cone sensitivity interactions}, \qquad (\mathrm{V'd})$$

$$m_5 = a_2 * c \qquad \text{L- and S-cone sensitivity interactions}, \qquad (\mathrm{V'e})$$

$$m_6 = b_2 * c \qquad \text{M- and S-cone sensitivity interactions}. \qquad (\mathrm{V'f})$$

To solve equation system (V′), we found the positive values for a_0 and b_0 that reveal the real values for a_1, a_2, b_1, b_2, and c coefficients. The a_0 and b_0 values were maintained in a ratio $a_0/b_0 \sim 2$ to simulate a hypothetical luminance mechanism comparable in sensitivity with the yellow mechanism.

In Table 3 we present for each observer an example of the solution system (V′) in agreement with an additive L+M-cone sensitivity mechanism. An illustration of the mechanism's contribution to the overall sensitivity in conformity with the results presented in Table 3 is shown in Fig. 7.

From the data presented in the Table 3 and represented in Fig. 7, we understand that the a_1, b_1, and a_2, b_2 parameters that characterize the red–green system and the yellow mechanism, respectively, are not significantly affected by the luminance mechanism option in the model. This result demonstrates that our prediction concerning the second L- and M-cone antagonistic mechanism is not a consequence of the presence or the absence of the luminance mechanism contribution to the model.

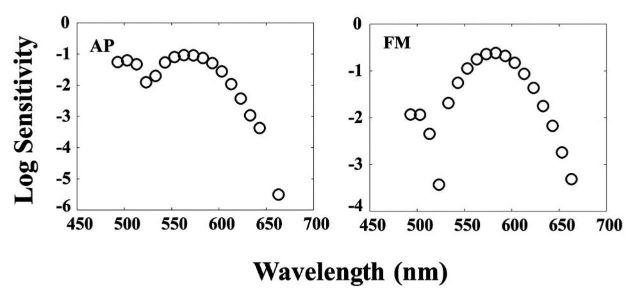

Fig. 6. Spectral sensitivity mechanism involved in the detection of the 570 nm spectral test stimulus for each observer. This mechanism sensitivity was derived as a vector difference between the model fit and the red–green mechanism represented in Fig. 5.

Table 3. Example of Results for a_1, a_2, b_1, b_2, and c Chromatic Parameters[a]

Chromatic Parameters	Subjects				
	VD	FM	HL	VR	AP
a_1	1.92	1.96	1.98	2.18	1.81
a_2	0.82	0.59	0.48	0.60	0.28
b_1	−2.55	−2.56	−2.57	−2.82	−2.46
b_2	−0.40	−0.34	−0.09	−0.34	−0.06
c	0.58	0.51	1.14	0.71	0.61
$\mathbf{a_0}$	**0.35**	**0.30**	**0.30**	**0.30**	**0.20**
$\mathbf{b_0}$	**0.15**	**0.15**	**0.15**	**0.10**	**0.10**

[a]Computed from equation system (V′) function a_0 and b_0 values. The a_0 and b_0 values were maintained in a ratio $a_0/b_0 \sim 2$ to simulate a hypothetical luminance mechanism comparable in sensitivity with the yellow mechanism.

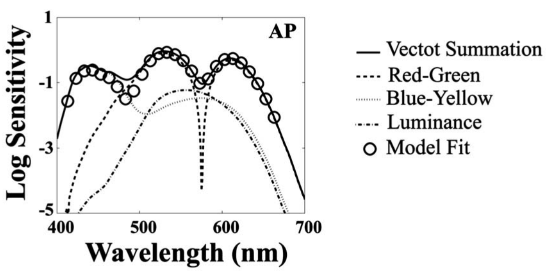

Fig. 7. Illustration for the mechanisms' contribution to the overall sensitivity in conformity with the results presented in Table 3. The sensitivity is represented by the model fit as of vector addition from a hypothetical additive (L+M) achromatic system, with the antagonistic (L−M) red–green chromatic mechanism and the blue–yellow chromatic system with S-cone interactions in a second antagonistic L- and M-cone mechanism. The mechanisms represented are obtained as a solution of the system of equations (I_0), (I) and (II) using the m parameters presented in Table 1.

Two different L-M-cones antagonistic mechanisms do not represent a consensus for understanding the actual color mechanisms. However, there is strong physiological evidence that the L cones receive inhibitory input from the M cones and excitatory input from the S cones. De Monasterio *et al.*[24] reported that even if the majority of retinal ganglions and LGN cells have been identified as having S-cone inputs opposing a summed L+M-cone signal, a small percentage (6%) of the L–M cells in the retina have an S-cone input. These cells were about equally divided between those showing an L-cone signal opposed to M+S-cones and those showing an M-cone signal opposed to L+S-cones. Furthermore Dacey and Lee[8] reported that exclusively midget ganglion cells, with S-cone input signal, convey an L–M-cone opponent signal.

There are also many psychophysical studies that are congruent with the notion that S cones can be opposed to an L–M-cone antagonistic mechanism. The present understanding concerning an antagonistic L–M-cones mechanisms is associated exclusively with the red–green mechanisms. This can be used as a possible justification to explain that the majority of recent psychophysical results associate the S-cone interaction with the red–green mechanism and not with a different L–M-cone antagonistic mechanism. Stromeyer *et al.*[25] reported that the red–green mechanism, where an L-cone signal was equally opposed to the M-cone signal, received a weak input from the short-wavelength S cones. Polden and Mollon[26] suggested two possible ways that blue sensitivity could be affected by the L–M opponent signal. The blue sensitivity cones could feed directly into the red–green pathway, or the red–green and blue–yellow opponent mechanisms may inhibit each other directly. Wisowaty[27] proposed a scheme in which all three cone types contribute to both color mechanisms. In accord with Wisowaty's proposal, the S cone contributes to an additive L+M-cone mechanism from the blue–yellow color system, but his results suggest that the S cones also contribute to the red–green color opponent mechanism. Our model computation does not exclude the possibility that there is a weak input from the S cones in red–green color mechanisms.[25] This weak input is not sufficient to explain our results concerning the m_5 and m_6 fitting parameters, which demonstrate a strong SL- and SM-cone interaction.

With respect to the S-cone pathways, McLellan[28] proposed two distinct detection mechanisms with different cone-opponent characteristics. One mechanism, representing the blue field sensitivity, was proposed as a part of S-ON pathway, receiving excitatory input from S cones and inhibitory output from L+M cones. A second mechanism explaining the long-wavelength-sensitive field "yellow" arises from L–M-cone opponent inputs as a part of S-OFF pathway. McLellan[28] concluded that the L–M-cone opponent mechanisms in connection with the S-OFF pathway could not be the same as with the L–M-red–green opponent mechanism. This conclusion is in accord with our data set results that predict two different L–M-cone antagonistic mechanisms to explain the detection in red–green wavelength zone for long test stimuli duration presented on the relatively high background luminance.

To explain how such a system is possible, we adopt the concept of retinal color coding proposed by Paulus and Kröger-Paulus.[20] The model is based on the physiological results of Wheeler and Naka,[7] where the transformation from the trichromatic into the color-opponent signals is performed by linear center-surround transformations in the outer plexiform layer. The mathematical transformation proposed by Paulus and Kröger-Paulus[20] to calculate the color-opponent signal is represented by

$$H = K * \mathrm{C}_{(\mathrm{L,M,S})} - \Sigma(F * \mathrm{C}_{(\mathrm{L,M,S})}), \qquad (1)$$

where H represents the color signal and C represents the L, M, or S cones. The receptive field center is multiplied by a factor $K=7$ to counterbalance the receptive field surround $\Sigma(F*C)$, which represents the sum of the local cone cluster assumed to be seven cones (six surrounding and one central). F represents the number of each cone type in the receptive field. For example, in the case of one central L cone and six surrounding nL and $(6-n)$ M cones (where $0 \leqslant n \leqslant 6$), Eq. (1) becomes

$$H_{(\mathrm{R-G})} = 7 * \mathrm{L} - (n+1)\mathrm{L} - (6-n) * \mathrm{M} = (6-n) * (\mathrm{L} - \mathrm{M}). \tag{2}$$

Equation (2) demonstrates that any value of n produces the same cone-opponent response shape, and the red–green color opponent response thus depends only on the L- and M-cone spectral quantum absorption.

For the blue-yellow mechanism, the model is supplemented by the intrusion of an S cone in the surround. An S-cone intrusion disturbs the opponent output described by Eq. (2):

$$\begin{aligned} H_{(\mathrm{L-M})-\mathrm{S}} &= 7 * \mathrm{L} - (n+1) * \mathrm{L} - (5-n) * \mathrm{M} - \mathrm{S} \\ &= (6-n) * \mathrm{L} - (5-n) * \mathrm{M} - \mathrm{S}, \\ & 0 \leqslant n \leqslant 4. \end{aligned} \tag{3}$$

Equation (3) represents an example of a chromatic signal from an L- and M-cone cluster with a central L cone disturbed by an S cone in the surrounding area. A point of interest from Eq. (3) is that an S cone in the surround can create a second L- and M-antagonistic mechanism $[(6-n)*\mathrm{L}-(5-n)*\mathrm{M}]$, where the M cones antagonize the L cones in a ratio of $(6-n)/(5-n)$. The n factor $(0 \leqslant n \leqslant 5)$ represents the number of L cones in a given cluster of five L and M cones and depends on the L/M-cone ratio in the retina. Paulus termed this type of mechanism a "pseudopigment cluster."

Our results point to the presence of such a yellow mechanism with variable L- or M-cone inputs and S-cone interactions. The solutions of Eq. (3) show that for an L–M–S cluster with a central L cone, the L cone is antagonized by a fraction of the M cone. This can explain our yellow mechanism results.

Concerning the S-cone pathway, our model does not exclude the possibility of explaining the sensitivity in blue wavelength area from an S-cone input and an inhibitory L+M-cone surround (Paulus and Kröger-Paulus[20] and Dacey and Lee[8]). Our data set supports a mechanism explaining the yellow wavelength sensitive field from L-cone inputs and inhibitory S+M-cone surround.[28] This scheme is congruent with the Krauskopf *et al.*[29] proposal, which suggests two different blue and yellow cardinal axes of color space. In accord with our data, one axis could be represented by the unique yellow locus or red-green equilibrium from the mechanism with an L-cone input and an S+M-cone surround. The second axis could be represented by the tritanopic line confusion from the mechanism with an S-cone input and an inhibitory L+M-cone surround.

According to the linear center–surround transformation, it is difficult to understand a field with an L+M-cone center and an inhibitory S-cone surround. It is possible that any L+M-cone center and S-cone surround predicted by the modern physiological studies represents a receptive field with L- or M-cone input centers with L-, M-, and S-cone inhibitory surrounds. This transformation represents a possible explanation of our data set results and would be in accordance with modern physiological studies. Furthermore our data are in perfect agreement with the color naming functions initially introduced by Boynton.[30] In accordance with the color-naming procedure, the normal trichromatic yellow function predicts what would appear as an intuitive yellow mechanism with a maximal sensitivity at the 570 nm wavelength, where the red–green mechanism sensitivity is null.

Therefore we argue that two different L–M-cone antagonistic mechanisms represent the best alternative for designing a color receptor system with an even color detection through all three channels (such as red, green and yellow) from two broadband spectral sensitivity receptors, such as L and M cones.

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REFERENCES

1. L. M. Hurvich and D. Jameson, "An opponent-process theory of color vision," Psychol. Rev. **64**, 384–404 (1957).
2. P. E. King-Smith and D. Carden, "Luminance and opponent-color contributions to visual detection and adaptation and to temporal and spatial integration," J. Opt. Soc. Am. **66**, 709–717 (1976).
3. J. Pokorny and V. C. Smith, "Spectral-luminosity functions, scalar linearity, and chromatic adaptation," J. Opt. Soc. Am. A **10**, 1304–1313 (1993).
4. H. G. Sperling and R. S. Harwerth, "Red–green cone interactions in the increment-threshold spectral sensitivity of primate," Science **9**, 180–184 (1971).
5. M. Kalloniatis and R. S. Harwerth, "Spectral sensitivity and adaptation characteristics of cone mechanisms under white-light adaptation," J. Opt. Soc. Am. A **7**, 1912–1928 (1990).
6. E. Miyahara, J. Pokorny, and V. C. Smith, "Increment threshold and purity discrimination spectral sensitivities of X-chromosome-linked color-defective observers," Vision Res. **36**, 1597–1613 (1996).
7. T. G. Wheeler and K. I. Naka, "The modes of chromatic interactions in the retina," Vision Res. **17**, 1015–1018 (1977).
8. D. M. Dacey and B. B. Lee, "The blue-on opponent pathway in primate retina originates from a distinct bistratified ganglion cell type," Nature **24**, 731–735 (1994).
9. K. T. Mullen and M. J. Sankeralli, "Postreceptoral chromatic detection mechanisms revealed by noise masking in three-dimensional cone contrast space," J. Opt. Soc. Am. A **14**, 2633–2646 (1997).
10. S. L. Guth and H. R. Lodge, "Heterochromatic additivity, foveal spectral sensitivity and a new color model," J. Opt. Soc. Am. **63**, 450–462 (1973).
11. S. L. Guth, R. W. Massof, and T. Benzschawel, "Vector model for normal and dichromatic color vision," J. Opt. Soc. Am. **70**, 197–212 (1980).
12. R. F. Quick, "A vector-magnitude model of contrast detection," Kybernetik **16**, 65–67 (1974).
13. L. Kerr, "Detection and identification of monochromatic stimuli under chromatic contrast," Vision Res. **14**, 1095–1105 (1974).
14. V. C. Smith and J. Pokorny, "Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm," Vision Res. **15**, 161–171 (1975).
15. D. L. MacAdam, "Color discrimination and the influence of

color contrast on acuity," Doc. Ophthalmol. **3**, 214–233 (1949).
16. K. Kranda and P. E. King-Smith, "Detection of colored stimuli by independent linear systems," Vision Res. **19**, 733–745 (1979).
17. C. Noorlander, M. J. G. Heuts, and J. J. Koenderink, "Influence of the target size on the detection threshold for luminance and chromaticity contrast," J. Opt. Soc. Am. **70**, 1116–1121 (1980).
18. V. C. Smith, R. W. Bowen, and J. Pokorny, "Threshold temporal integration of chromatic stimuli," Vision Res. **24**, 653–660 (1984).
19. D. T. Lindsey, J. Pokorny, and V. C. Smith, "Phase-dependent sensitivity to heterochromatic flicker," J. Opt. Soc. Am. A **3**, 921–927 (1986).
20. W. Paulus and A. Kröger-Paulus, "A new concept of retinal color coding," Vision Res. **23**, 529–540 (1983).
21. J. Larimer, "Opponent process additivity—I. red/green equilibria," Vision Res. **14**, 1127–1140 (1974).
22. C. F. Stromeyer, R. E. Kronauer, and G. R. Cole, "Adaptive mechanisms controlling sensitivity to red–green chromatic flashes," in *Colour Vision*, L. D. Mollon and L. T. Sharpe, eds. (Academic, 1983), pp. 313–330.
23. C. F. Stromeyer, G. R. Cole, and R. E. Kronauer, "Second-site adaptation in red–green chromatic pathway," Vision Res. **25**, 219–237 (1985).
24. F. M. De Monasterio, P. Gouras, and D. J. Tolhurst, "Trichromatic colour opponency in ganglion cells of the rhesus monkey retina," J. Physiol. (London) **251**, 197–216 (1975).
25. C. F. Stromeyer, A. Chaparro, C. Rodriguez, D. Chen, E. Hu, and R. E. Kronauer, "Short-wave cone signal in the red–green detection mechanism," Vision Res. **38**, 813–826 (1998).
26. P. G. Polden and J. D. Mollon, "Reversed effect of adapting stimuli on visual sensitivity," Proc. R. Soc. London, Ser. B **19**, 235–272 (1980).
27. J. Wisowaty, "An action spectrum for the production of transient tritanopia," Vision Res. **23**, 769–774 (1983).
28. J. S. McLellan and R. T. Eskew, Jr., "ON and OFF S-cone pathways have different long-wave cone inputs," Vision Res. **40**, 2449–2465 (2000).
29. J. Krauskopf, D. R. Williams, and D. W. Heeley, "Cardinal directions of color space," Vision Res. **22**, 1123–1131 (1982).
30. R. M. Boynton, W. Schafer, and M. E. Neun, "Hue-wavelength relation measured by color-naming method for three retinal locations," Science **146**, 666–668 (1964).