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S-cone discrimination for stimuli with spatial and temporal chromatic contrast

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Abstract

In the natural environment, color discriminations are made within a rich context of spatial and temporal variation. In classical laboratory methods for studying chromatic discrimination, there is typically a border between the test and adapting fields that introduces a spatial chromatic contrast signal. Typically, the roles of spatial and temporal contrast on chromatic discrimination are not assessed in the laboratory approach. In this study, S-cone discrimination was measured using stimulus paradigms that controlled the level of spatio-temporal S-cone contrast between the tests and adapting fields. The results indicate that S-cone discrimination of chromaticity differences between a pedestal and adapting surround is equivalent for stimuli containing spatial, temporal or spatial-and-temporal chromatic contrast between the test field and the surround. For a stimulus condition that did not contain spatial or temporal contrast, the visual system adapted to the pedestal instead of the surround. The data are interpreted in terms of a model consistent with primate koniocellular pathway physiology. The paradigms provide an approach for studying the effects of spatial and temporal contrast on discrimination in natural scenes.

Keywords: Chromatic discrimination, Cone, Chromatic contrast, Koniocellular pathway, Parvocellular pathway

Introduction

Chromatic discrimination refers to an observer's ability to detect the difference between two equiluminant lights that differ only in chromaticity. Depending on the involvement of the three cone types, chromatic discrimination can be further classified as L/M cone discrimination that is based on the relative L- and M-cone excitations at equiluminance, and S-cone discrimination that is based on only S-cone excitations (e.g., Zaidi et al., 1992; Smith et al., 2000). Interest in the detection and discrimination properties of the S-cone pathway has been long-standing. An early study by Wald (1964) suggested that the spectral sensitivity of S-cones could be measured by pulsing brief short-wavelength lights on an intense long wavelength background (Stiles, 1949, 1972, 1978). The spectral sensitivities measured in Stiles's two-color threshold studies (Stiles, 1949) revealed cone-specific adaptation mechanisms. In an elegant analysis, Pugh and Mollon (1979) showed that S-cone detection data could be explained by postulating two sites of adaptation in the S-cone pathway, first, a multiplicative gain obeying Weber's Law in the cone receptors, and second, a gain control in the opponent pathway following spectral opponency of S-cones and L- and M-cones. Zaidi et al. (1992) developed a more general S-cone model that predicts sensitivity for lights of away from the adapting light, extending the Pugh and Mollon model that accounted solely for discrimination at the adaptation point. Boynton and Kambe (1980) studied chromaticity discrimination using modern cone axes (MacLeod & Boynton, 1979) and equiluminant stimuli without a surround. Their S-cone discrimination data assumed the form of an increment threshold function (Boynton & Kambe, 1980). In the presence of a surrounding field, S-cone discrimination is best at the adaptation point (Krauskopf & Gegenfurtner, 1992; Zaidi et al., 1992; Miyahara, 1993; Shapiro et al., 2003). For most spatio-temporal stimulus configurations however, the increment threshold procedure does not isolate the spectral response of cone mechanisms.

Modern studies of anatomy and physiology have identified three major pathways, the magnocellular (MC), parvocellular (PC), and koniocellular (KC) pathways. Each pathway consists of groups of cells that feed signals forward from the photoreceptor to the lateral geniculate nucleus, and to the visual cortex (reviewed by Dacey, 1996; Lee, 1996; Kaplan, 2004). Cells in the MC pathway sum signals from L- and M-cones in centers and surrounds and have bandpass spatio-temporal characteristics with high temporal frequency sensitivity. Cells in the PC pathway difference the L- and M-cone signals to generate spectral opponency, and have a low-pass spatio-temporal characteristic to chromatic stimuli and a bandpass spatio-temporal characteristic to achromatic stimuli. Cells in the KC pathway obtain spectral opponency by differencing

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S-cones from the sum of L- and M-cones, and have a low-pass spatio-temporal characteristic to chromatic stimuli (Yeh et al., 1995). In a cone space, such as the relative cone Troland chromaticity space (Smith & Pokorny, 1996), the L/M axis and S axis reflect post-receptoral spectral processing in the PC and KC pathways. Therefore, psychophysical measurements of L/M cone discrimination and S-cone discrimination can be linked to physiology. In fact, a model based on primate ganglion cell responses has been developed and successfully describes L/M and S-cone discrimination (Smith et al., 2000; Pokorny & Smith, 2004; Zele et al., 2006).

Classical studies of chromatic discrimination typically presented a standard light of fixed chromaticity and a test light of variable chromaticity in different spatial locations, either surrounded by darkness (e.g., Boynton & Kambe, 1980), or by an illuminated surround (Miyahara et al., 1993). Krauskopf & Gegenfurtner (1992) and Zaidi et al. (1992) concurrently introduced paradigms that simultaneously pulsed standard and test fields. More recently, Smith et al. (2000) designed a paradigm that presented stimuli either in a pulsed or steady format, and found no difference in L/M discrimination between the pulsed- and steady-pedestal conditions. These studies showed that L/M and S-cone discrimination thresholds depend on the chromatic contrast between the pedestal and adapting surround, with best discrimination at the adapting chromaticity. Discrimination is characterized as a V-shape in a plot of log threshold as a function of log pedestal L- or S-Tds, indicating spectral opponency in the PC or KC pathway (for review, see Pokorny & Smith, 2004). All of these paradigms included a spatial chromatic contrast signal (border) between the test field and the adapting surround. Zele et al. (2006) investigated the effect of spatio-temporal chromatic contrast between the test field and the adapting surround on the L/M cone discrimination with different pedestal chromaticities. The study found that there was no difference in the V-shape for L/M cone discrimination for the paradigms with spatial, temporal, and spatial and temporal chromatic contrast. Under stimulus conditions that provided no chromatic contrast between the test and surround, discrimination was best with a shallower V-shape. Here we extend the work of Zele et al. (2006) to study the discrimination of stimuli varying in S-cone excitation. There is evidence that the receptive field characteristics including the size and temporal response differ in the PC and KC units (for review see Kaplan, 2004). The purpose of the research reported here is to investigate the effect of spatial and temporal chromatic contrast between the test field and adapting surround on S cone discrimination and to compare the findings to those for L/M discrimination. The paradigms provide a strategy for evaluating the functional properties of cone pathways, and may serve as a bridge to the study of the effects of spatial and temporal contrast on real-world discrimination abilities.

Materials and methods

Apparatus and calibration

The stimuli were generated using a 9500/132 Power Macintosh computer and were displayed on a well-calibrated 17″ NEC CRT color monitor controlled by a 10-bit Radius video card. The CRT display was run at a refresh rate of 75 Hz to ensure artifacts generated by the raster scan would not affect discrimination threshold (Zele & Vingrys, 2005). Calibration procedures have been described fully elsewhere (Smith et al., 2000).

Stimuli

The spatial and temporal properties of the stimuli were the same as those used to investigate the spatial and temporal contrast effect on discrimination along the L/M direction (Zele et al., 2006). A 4° square pedestal was set within an 18.5° × 13.8° rectangular surround. A 1° test square differed in S-cone excitation from the pedestal and was randomly presented in one of the four quadrants of the pedestal (see Fig. 1). The test square was presented either in an inner quadrant of the pedestal (one corner of the test square was adjacent to the pedestal center) or an outer quadrant (a corner and two edges of the test square abutted the surround). The pedestal was either pulsed simultaneously with the test square during the trial period (pulsed-pedestal condition) or presented continuously (the steady-pedestal condition). The experiment therefore controlled the spatio-temporal chromatic contrast between the test

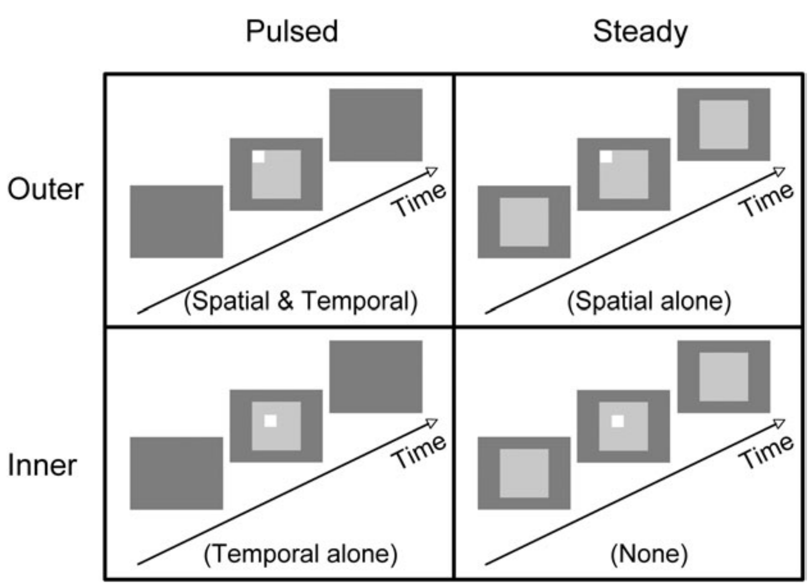

Fig. 1. (**A**) schematic representation of the stimuli used to control the spatio-temporal chromatic contrast between the test and adapting surround. Left and right columns show the temporal sequences for the pulsed- and steady-pedestal paradigms. The upper and lower rows show the spatial arrangements of the outer and inner quadrant conditions. Further details are given in the text.

field and the adapting surround using four paradigms: (1) the pulsed outer quadrant paradigm with simultaneous spatial and temporal contrast, (2) the steady outer quadrant paradigm with spatial contrast alone, (3) the pulsed inner quadrant paradigm with temporal contrast alone, and (4) the steady inner quadrant paradigm with no spatial or temporal contrast. The four conditions are shown schematically in Fig. 1. A control experiment measured S-cone discrimination with no pedestal; the test square was located at the center of the surround.

The luminance of the stimulus was $11.3\ \mathrm{cd \cdot m^{-2}}$ throughout the experiment, corresponding to 108 effective Trolands (Le Grand, 1968). The stimuli were specified in a cone chromaticity space (l, s, Y_J), using the Smith and Pokorny transformation (Smith & Pokorny, 1975) of the Vos-Judd (Vos, 1978) observer, (x_J, y_J, Y_J). Normalization was made such that the sum of L- and M-cone Trolands equal to luminance and the s value for an equal-energy-spectrum light (EES) is 1.0. This is called a relative cone Troland chromaticity space (Smith & Pokorny, 1996).

The surround and pedestal chromaticities were arranged on a constant l-line ($l = 0.667$) in the relative cone Troland chromaticity space. There were three surrounds with s chromaticities of 0.4, 0.997, and 5.0, respectively. For mnemonic purposes, the surrounds were labeled according to their approximate appearance, i.e., yellow, white, and purple, respectively. For each surround, eight pedestals varied with s-chromaticity between 0.4 and 5.0.

Procedure

Prior to each session, observers first adapted to the dark for 3 min, followed by a 1 min adaptation period to the surrounding light. Each session consisted of one surround and four pedestal s-chromaticities for one of the four paradigms. Discrimination threshold was measured using a random double four-alternative forced choice staircase procedure, with one staircase for an s-increment and the other for an s-decrement. During each trial, the pedestal was steady or pulsed, and the test square, with either higher s-chromaticity (increment) or lower s-chromaticity (decrement) than the pedestal, was randomly presented to one of the four inner or outer quadrants. Observers were instructed to located the quadrant and identify the direction of color change by pressing buttons on a gamepad sensed by the computer. The staircase procedure continued until 10 reversals occurred for each staircase. The last six reversals were averaged and counted as the threshold value for the pedestal and surround. The staircase procedure was repeated for another pedestal chromaticity. Each session lasted about 30 min. Thus two sessions were required to obtain full data for one surround chromaticity and one paradigm. Each session was repeated three times on three different days. Discrimination threshold for s-increment and s-decrement were essentially the same for each combination of the surround and pedestal, therefore the discrimination threshold for increment and decrement were averaged. The thresholds in log S Trolands were plotted as a function of the pedestal chromaticity in log S Trolands.

Observers

Two observers, DC and IS, participated in the study. Both have normal color vision (assessed by the Neitz OT anomaloscope) and hue discrimination (assessed by the Farnsworth-Munsell 100-hue test). DC, an author, was an experienced psychophysical observer. The second observer, IS was a paid undergraduate student who was naïve to the purpose and design of the experiment. All experimental procedures were approved by the Institutional Review Board at the University of Chicago.

Model

The model of S-cone pathway spectral processing is based on the spectral response of primate bistratifed ganglion cells. It provides a link between primate physiology and human psychophysical measurements by fitting S-cone discrimination data with the majority of parameter values obtained from published physiological and psychophysical results (Smith et al., 1992, 2000; Miyahara et al., 1996). The model postulates two sites of adaptation in the S-cone pathway, first a multiplicative gain in the cone receptors and second a negative feedback in the opponent pathway following spectral opponency of S cones and the sum of L and M cones (Pugh & Mollon, 1979). The cone responses to a light of a given L, M, S cone Trolands are given by

$$R_L = L/l_{\max} \tag{1}$$

$$R_M = M/m_{\max} \tag{2}$$

$$R_S = S/s_{\max} \tag{3}$$

where L, M, and S are cone Trolands, and l_{max}, m_{max}, and s_{max} are maximal sensitivities of the Smith and Pokorny (1975) cone fundamentals. The cone responses are subject to multiplicative sensitivity regulation (gain control):

$$G(L_A) = 1/(1 + k_1 L_A/l_{\max})^{k_2} \tag{4}$$

$$G(M_A) = 1/(1 + k_1 M_A/m_{\max})^{k_2} \tag{5}$$

$$G(S_A) = 1/(1 + k_1 S_A/s_{\max})^{k_2} \tag{6}$$

where L_A, M_A, and S_A are the cone Trolands at the adapting chromaticity in the surround and k_1 and k_2 are constants. The value of k_1 is about 0.33 Trolands and the value of k_2 is about 0.5 (Miyahara et al., 1993).

The spectral opponent term for the +S/−(L+M) cell is given by

$$\begin{aligned} OPP_{+S/-(L+M)} &= S_T/s_{\max} G(S_A) \\ &\quad - k_3[pL_T/l_{\max} G(L_A) + (1-p)M_T/m_{\max} G(M_A)] \end{aligned} \tag{7}$$

where L_T, M_T, and S_T are cone Trolands of the test chromaticity in the pedestal, k_3 is the surround strength of the opponent signal, and p refers to the relative weight of L cones in the MC pathway for a Vos-Judd observer and has a value of 0.6189.

The spectral opponency signals are subject to a subtractive feedback, which is determined by the strength of the opponent signal at the adapting chromaticity:

$$OPP_C = k_5 \cdot (OPP_T - k_4 OPP_A), \tag{8}$$

where OPP_C is the spectral opponent signal to a chromaticity change, C is from a fixed adapting chromaticity, A is to a test chromaticity, T. OPP_T is the spectral opponent term at the test chromaticity, OPP_A represents the spectral opponent term at adapting chromaticity, k_4 represents the subtractive feedback strength, and k_5 represents an adaptation parameter (for an achromatic adapting field, $k_5 = 1$; for a non-achromatic adapting field, $k_5 < 1$). If $C = 0$ (i.e., the test and adapting chromaticity are equal), then OPP_T is substituted by OPP_A in Eq. (8). The response of a spectral opponent cell to a chromaticity change, C is from a fixed adapting chromaticity, A is:

$$R_{OPP} = R_{\max} \cdot OPP_C/(OPP_C + SAT), \qquad (9)$$

where OPP_C is a spectral opponent term in Eq. (5), $R_{\max}$ is the maximum response, and SAT is the static saturation. Given that the criterion for discrimination δ is small relative to $R_{\max}$, the threshold of chromatic discrimination based on S-cone excitation can be deduced by the derivative of R_{OPP} in Eq. (9):

$$\log(\Delta S_c) = \log(S_{th}) - \log[G(S_A)/s_{\max}] + \log[(OPP_C + SAT)^2/SAT], \qquad (10)$$

where S_{th} represents $\delta/R_{\max}$, a vertical scaling factor. Therefore, S-cone discrimination is determined by three terms; the first related to the criterion and static saturation, the second related to gain, and the third related to opponency. Smith et al. (2000), Pokorny and Smith (2004), and Zele et al. (2006) provide further details of the modeling of chromatic discrimination thresholds for stimuli varying in either L/M-cone or S-cone excitation.

Results

Fig. 2 shows S-cone discrimination thresholds, expressed as log S Trolands as a function of pedestal log S Trolands. The top two rows show the results for the white surround, the middle two rows for the yellow surround, and the bottom two rows for the purple surround (arrows in each panel). For each surround chromaticity, the data are organized in a 2 × 2 format: the pulsed- and steady-pedestal conditions are shown in the left and right columns, and the outer- and inner-quadrant conditions in the top and bottom rows.

The data for the two observers were very similar and are both shown in the plots. For each surround chromaticity, the effect of spatial contrast (steady-pedestal outer quadrant), temporal contrast (pulsed-pedestal, inner quadrant), and spatial and-temporal contrast (pulsed-pedestal, outer quadrant) follow the same pattern. That is, with the white and yellow surrounds, the minimum discrimination threshold was at the surround chromaticity, and discrimination degraded with increasing chromatic difference from the surround. For the purple surround, the discrimination threshold was invariant with pedestal chromaticity. Finally, in the absence of spatial and temporal chromatic contrast (steady-pedestal, inner quadrant), S-cone discrimination was similar for all three surround chromaticities, and had a pattern similar to that for the control experiment (data not shown).

To fit the S-cone discrimination model to the data, the surround chromaticity was set to equal the adapting chromaticity for paradigms with spatial or temporal chromatic contrast between the test field and the adapting surround. The free parameters included k_5 (fixed at 1 for the white surround and floated for the yellow and purple surrounds), S_{th} (a common value for the white and yellow surrounds, a separate value for the purple surround), and SAT (common value for all three surrounds). In the absence of any spatial and temporal chromatic contrast (pulsed inner quadrant), the pedestal chromaticity was set to equal the adapting chromaticity. For this condition, the free parameters included S_{th} (common value for all three surrounds), and SAT (common value for all three surrounds). The remaining parameters were fixed and are listed in Table 1 with the values of the free parameters. The fits were based on the averaged data of the two observers because their data were similar. For the model fitting, data from the pulsed outer quadrant (spatial and temporal contrast), pulsed inner quadrant (temporal contrast alone), and steady outer quadrant (spatial contrast alone) paradigms were averaged for each surround. Finally, the data for the steady inner paradigm (no chromatic contrast) for all three surrounds were averaged. The values of the free parameters were searched to minimize the residual sum of square between the averaged data and the model prediction.

The model fits are shown as solid lines in Fig. 2. In general, with only seven free parameters, the model describes the data reasonably well for all the conditions (3 surrounds × 8 pedestals × 4 paradigms × 2 observers).

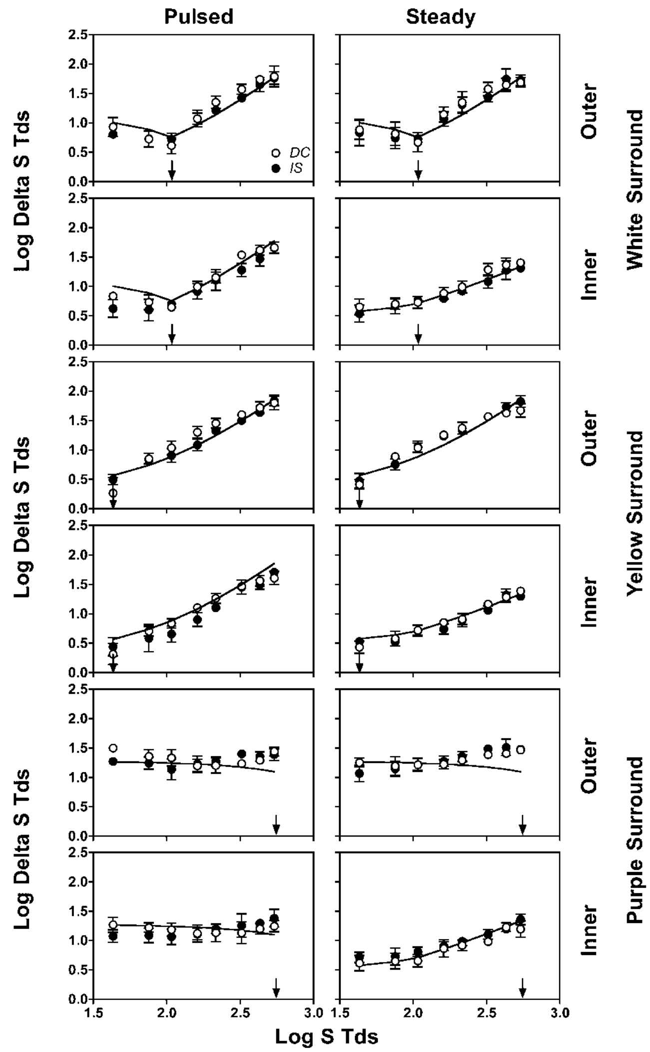

Fig. 2. S-cone discrimination thresholds for the white ($s = 0.4$), yellow ($s = 0.997$), and purple ($s = 5.0$) surrounds. For each surround, the data for the pulsed outer quadrant, steady outer quadrant, pulsed inner quadrant, and steady inner quadrant paradigms are presented in different panels. Data for observers DC (unfilled symbols) and IS (circular symbols) are plotted in each panel. The solid lines are model fits. The arrows indicate the surround chromaticity.

Table 1. *Parameters for S cone discrimination model based on the bistratifed ganglion cells in the primate retina*

Paradigm	Surround	Free Parameters S_{th}	SAT	k_5	Fixed Parameters	
Pulsed Outer	White	0.046	21.61	1	$I_{\max}$	0.63721
Steady Outer	Yellow	0.046	21.61	0.901	$m_{\max}$	0.39242
Pulsed Inner	Purple	0.080	21.61	0.1	$s_{\max}$	1.6064
					p	0.6189
Steady Inner	White	0.091	11.51	1	k_1	0.33
	Yellow	0.091	11.51	1	k_2	0.5
	Purple	0.091	11.51	1	k_3	0.6
					k_4	0.8

$I_{\max}$, $m_{\max}$, and $s_{\max}$ from Smith & Pokorny (1975)
k_1 and k_2 from Miyahara et al. (1993)
k_3 from Smith et al. (1992)
k_4 from Smith et al. (2000)

Discussion

The presence of spatial, temporal, or spatial and temporal chromatic contrast between the test field and the adapting surround had similar effects on S-cone discrimination thresholds. This parallels with the results for stimuli varying in L/M cone excitation, where spatial and temporal chromatic contrast produce equivalent changes in discrimination (Zele et al., 2006). Discrimination is degraded with increasing S-cone contrasts between the pedestal and adapting surround, with the best discrimination at the adapting surround chromaticity for white and yellow surrounds. Krauskopf and Gegenfurtner (1992), Shapiro et al. (2003), and Zaidi et al. (1992) also observed that S-cone discrimination is best at the adaptation point. For the purple surround, however, the discrimination threshold was invariant with pedestal chromaticity, most likely due to response saturation in the KC pathway to the high *s* chromaticity of the surround. S-cone discrimination functions flatten out as the *s*-chromaticity of the surround increases (Shapiro & Zaidi, 1992; Zaidi et al., 1992; Shapiro et al., 2003). Although the S-cone system shows subtractive regulation, it does not protect it from saturation (Pokorny & Smith, 2004). These results suggest it is important to have spatial or temporal proximity between the test field and the adapting surround for the visual system to use the surround information during S-cone discriminations, similar to those in L/M cone discrimination (Zele et al., 2006).

When chromatic stimuli are presented in a dark surround, L/M cone discrimination shows a V-shape with a minimum near the EES chromaticity (Le Grand, 1949; Boynton & Kambe, 1980; Yeh et al., 1993). With a 120 Trolands stimulus field in a dark surround, the function relating discrimination threshold to S-cone excitation level shows a shallower slope at low S-cone stimulation levels than at high S-cone stimulation levels (Boynton & Kambe, 1980), although some observers may show a modest amount of opponent activity (Miyahara et al., 1993). In the current study, in the absence of spatial or temporal chromatic contrast between the test and adapting surrounds, S-cone discrimination thresholds were the same for all three adapting surround and had a typical threshold versus radiance pattern. The pattern was similar to the no pedestal control experiment data with surround *s*-chromaticity variation from 0.4 to 5.0. The data suggest that for S-cone discrimination, the visual system was adapting to the pedestal chromaticity, instead of the surround. The model fits that set, the pedestal chromaticity as the adapting chromaticity could describe the data well, consistent with adaptation to the pedestal. Therefore, for steadily viewed lights, local spatial chromatic structure determines S cone discrimination. In contrast, L/M cone discrimination with the steady inner quadrant condition (no chromatic contrast) shows a flatter V-shape (Zele et al., 2006), but clearly not like a typical threshold versus radiance function. Thus there are differences in PC and KC pathway processing of spatial and temporal contrast.

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