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# Spatial and temporal chromatic contrast: Effects on chromatic discrimination for stimuli varying in L- and M-cone excitation

ANDREW J. ZELE, VIVIANNE C. SMITH, AND JOEL POKORNY

Department of Ophthalmology and Visual Science, The University of Chicago, Chicago, Illinois

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## Abstract

Discrimination for equiluminant chromatic stimuli that vary in L- and M-cone excitation depends on the chromaticity difference between the test field and the surrounding area. The current study investigated the effect of the proximity in space and time of a surround to the test field on chromatic contrast discrimination. The experimental paradigm isolated spatial, temporal, and spatial-and-temporal chromatic contrast effects on discrimination. Chromatic contrast discrimination thresholds were assessed by a four-alternative spatial forced-choice procedure. Stimuli were either metameric to the equal energy spectrum, or varied in L-cone activation along a line of constant S-cone activation. A model based on primate parvocellular pathway physiology described the data. Spatial and temporal contrast produced equivalent reductions in chromatic discriminability as the chromatic difference between the test and surround increased. For all test chromaticities, discrimination was best in the absence of chromatic contrast. Chromatic contrast discrimination is determined by either the spatial or temporal contrast component of the signal.

**Keywords:** Parvocellular, chromatic contrast discrimination, spatial contrast, temporal contrast

## Introduction

What are the effects of spatial and temporal chromatic contrast between an adapting surround and a test chromaticity on chromatic contrast discrimination? Psychophysical chromatic discrimination thresholds for stimuli that differ from a chromatic surround take the form of a V-shape, with progressively poorer discrimination with increasing chromatic difference (Shapiro & Zaidi, 1992; Watanabe et al., 1998). A chromatic surround serves the purpose of maintaining adaptation to its chromaticity (Brown, 1952; Pointer, 1974; Loomis & Berger, 1979) and acts to displace the detection threshold minimum toward it (Krauskopf & Gegenfurtner, 1992; Miyahara et al., 1993; Smith et al., 2000). The reduction in chromatic discrimination ability with increasing chromatic difference between the test and surround reflects the spatio-temporal properties of the stimulus (Krauskopf & Gegenfurtner, 1992; Smith et al., 2000), however the independent effects of spatial or temporal chromatic contrast have not been previously considered.

An appropriately designed spatio-temporal stimulus can be used to compare V-shape results obtained in chromatic contrast discrimination tasks with the contrast gain functions found for cells in primate parvocellular (PC) retinal ganglion and lateral

geniculate nucleus cells (Pokorny & Smith, 1997; Smith et al., 2000). Chromatic contrast discrimination data are well described by a model of cone spectral opponency that has spatial and temporal components (Smith et al., 2000). Using the model as a framework, the current experiment investigates the effect of the proximity in space and time of a surround to the test field on chromatic contrast discrimination. The test paradigms isolated the effects of spatial, temporal and spatial-and-temporal chromatic contrast. Discrimination in the absence of chromatic contrast between the test and surround was also studied. The model with shape parameters fixed from physiological data requires only scaling parameters to fit the psychophysical data.

## Materials and methods

### Observers

Two women (VCS and LK) and one man (AJZ), all with normal color vision (assessed with the Ishihara pseudo-isochromatic plates and the Neitz OT anomaloscope) served as observers. All had Farnsworth–Munsell 100-hue error scores below 40. Two of the observers were well-practiced psychophysical observers. The third, a naïve observer (LK), was allowed sufficient practice sessions to become familiar with the task requirements. The Institutional Research Board at the University of Chicago approved all experimental procedures and participants gave informed consent.

Address correspondence and reprint requests to: Joel Pokorny, Visual Science Laboratories, The University of Chicago, 940 East 57th Street, Chicago, IL 60637. E-mail: j-pokorny@uchicago.edu

### Apparatus and calibration

Stimuli were displayed on a high resolution Sony Trinitron (GDM-F520) CRT graphics monitor controlled by a 10-bit Radius video card hosted in a 3200 power Macintosh computer. The CRT monitor was run at a frame rate of 75 Hz to ensure artefacts generated by the raster scan would not be resolved by the mechanisms mediating detection (Zele & Vingrys, 2005). The calibration procedures are described in detail elsewhere (Smith et al., 2000).

### Stimuli

Smith et al. (2000) measured chromatic contrast discrimination using a  $2^\circ$  square stimulus array containing four  $1^\circ$  squares (separated by small gaps) and set within a larger uniform surround. One square was designated as the test square and its position randomly changed in each trial. The stimulus paradigm included steadily viewed pedestal and pulsed-pedestal conditions. In the current study, a  $4.0^\circ$  square pedestal stimulus appeared within an  $18.5^\circ \times 13.8^\circ$  rectangular adapting surround that was  $12 \text{ cd.m}^{-2}$  ( $\sim 115$  effective Td). Thresholds were measured for a  $1.0^\circ$  test square presented in an inner quadrant (a corner of the test square located at the center of the pedestal) or an outer quadrant (a corner and two borders of the test square abutting the surround) of the larger  $4.0^\circ$  square pedestal. Fig. 1 shows the spatial arrangement of the stimuli. In the pulsed-pedestal condition, the  $4^\circ$  square pedestal appeared only during the trial period as a pulsed-pedestal at a higher or lower chromaticity relative to the surround. The observer maintained adaptation to the uniform 115 Td surround between trials. For the steady-pedestal condition, the  $4^\circ$  pedestal was continually present as a steady pedestal within the surround during the entire protocol. Observers adapted for two-minutes to the surround before measurements began, with an additional one-minute for subsequent pedestal chromaticities. The pedestal and test stimuli were either an L-Troland increment or L-Troland decrement presented as one cycle of a 1.5 s raised cosine envelope. During a trial, the  $1^\circ$  test square randomly positioned in one quadrant of the  $4^\circ$  square changed chromaticity and the observer had to identify the quadrant and the direction of the chromaticity change. A 1.5 s inter-stimulus interval separated the stimulus presentation. A schematic representation of the temporal sequence of the steady- and pulsed-pedestal paradigms is shown in Fig. 1.

A control condition evaluated the possible effects of contrast and more peripheral field locations using chromatic backgrounds and pulses. In this case, thresholds were measured for the  $1^\circ$  test square set within the rectangular surround ( $18.5^\circ \times 13.8^\circ$ ) that varied in L Td. One corner of the test was positioned at the centre of the rectangular field. The Smith et al. (2000) paradigm was also replicated to confirm that the outer quadrant condition with different pedestal area and target placement provided comparable results.

### Specification of chromatic stimuli

The stimuli were specified in a cone chromaticity space  $(l, s, Y_J)$ , using the Smith and Pokorny (1975) transformation of the Vos–Judd observer,  $(x_J, y_J, Y_J)$ . Using the relative Troland space (Boynton & Kambe, 1980), normalization was achieved with  $\bar{l}(\lambda) + \bar{m}(\lambda) = \bar{y}_J(\lambda)$ , and the  $\bar{s}(\lambda)$  fundamental equivalent to  $\bar{z}(\lambda)$ . For an illumination metameric to an equal energy spectrum,  $S$  is set to equal  $y$ . Surround and test chromaticities were arranged on a

constant  $s$ -line in  $(l, s)$  relative cone Troland space with a relative  $s$ -Troland value of 1.0, metameric to the equal energy spectrum (EES) at an  $l$ -chromaticity of 0.665. In this system an L-cone Troland is the  $l$ -chromaticity of a given stimulus multiplied by the luminance in Trolands. There were a series of eight test and pedestal stimuli that varied in  $l$ -chromaticity at equal luminance (115 effective Td) on a line through equal energy spectrum from  $l = 0.62$  to  $l = 0.74$ . The eight  $l$ -chromaticities with their respective log L-Troland values specified in brackets are: 0.62 (1.853), 0.64 (1.867), 0.66 (1.880), 0.68 (1.893), 0.7 (1.906), 0.72 (1.918), 0.74 (1.930), and 0.76 (1.942). There were three surrounds on the  $l$ -line, a control surround set at an  $l$ -chromaticity of 0.665 (EES) and two surrounds with  $l$ -chromaticities equal to 0.62 and 0.74 on a constant  $S$ -cone line.

### Rational for the approach

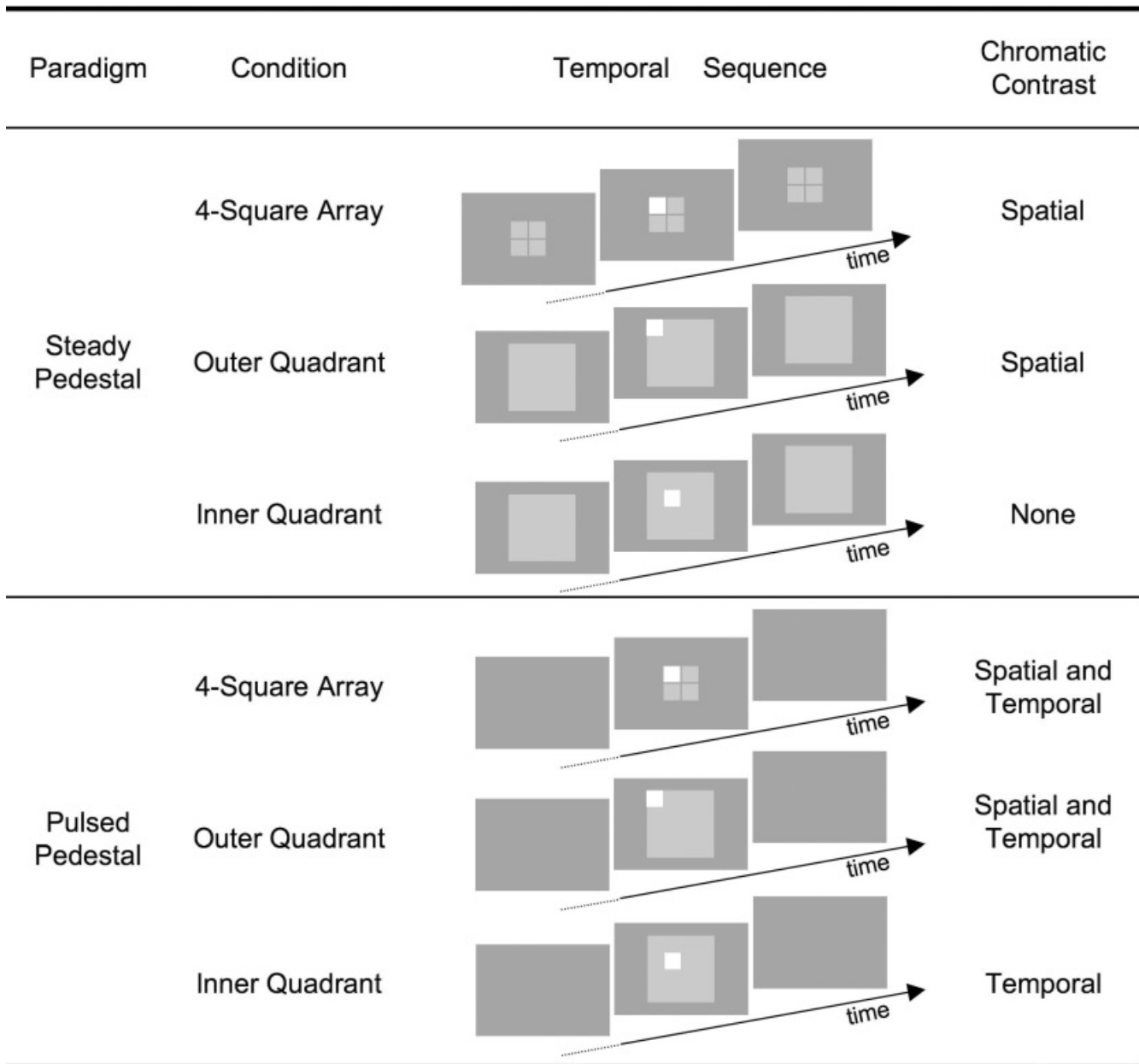
The spatial parameters of the Smith et al. (2000) paradigm were modified to describe the effects of chromatic spatial and temporal contrast on chromatic discrimination. Spatial chromatic contrast is defined as the contrast between the test and surround. The small magnitude of the temporal edge produced by the test stimulus presentation at threshold is expected to generate little or no temporal contrast. Therefore, temporal chromatic contrast is specified relative to the chromatic contrast change introduced by the pedestal over time. Fig. 1 shows the spatial arrangement of the inner and outer quadrant conditions and gives the spatial and temporal chromatic contrast in each paradigm. In the Smith et al. (2000) paradigm, the steady-pedestal condition generated spatial contrast at the test-surround border; the pulsed-pedestal introduced a spatial and temporal chromatic contrast step (Fig. 1, 4-square array). In the current paradigm, the steady-pedestal paradigm produces either spatial chromatic contrast signals for a test stimulus abutted with the border between the test and the surround (outer quadrant), or no spatial or temporal chromatic contrast when embedded within the pedestal (inner quadrant). The pulsed-pedestal paradigm produces spatial and temporal contrast (outer quadrant), but only temporal contrast for the inner quadrant condition.

### Psychophysical threshold estimation

Trials were specified according to a two-yes-one-no double random alternating staircase. One staircase measured thresholds in an increment direction and the other in a decrement direction. On each trial the test appeared in one quadrant as a small chromaticity difference from the pedestal (4-alternative spatial forced choice). For a correct response the observer was required to identify the quadrant and whether the direction of the chromatic change relative to the pedestal was an increment or decrement in L-Trolands. No feedback was given. On the first trial an easily discriminable test contrast was present, and the step size was halved until a criterion step of 0.0015 log unit was attained. Once the criterion step size was reached, staircases continued without further change in step size. Ten reversals at the criterion step size were measured for both staircases and the average of the reversals was defined as the threshold measure.

### Procedure

Observers binocularly fixated in the center of four fiduciary lines that abutted the edges of the stimulus. There was a 2 min adaptation period before the beginning of each condition. Head position



**Fig. 1.** The schematics show temporal sequence of the three conditions (4-square array, outer quadrant and inner quadrant) using the steady-pedestal and pulsed-pedestal paradigms. The chromatic contrasts generated by the paradigms are indicated. Further details are given in the text.

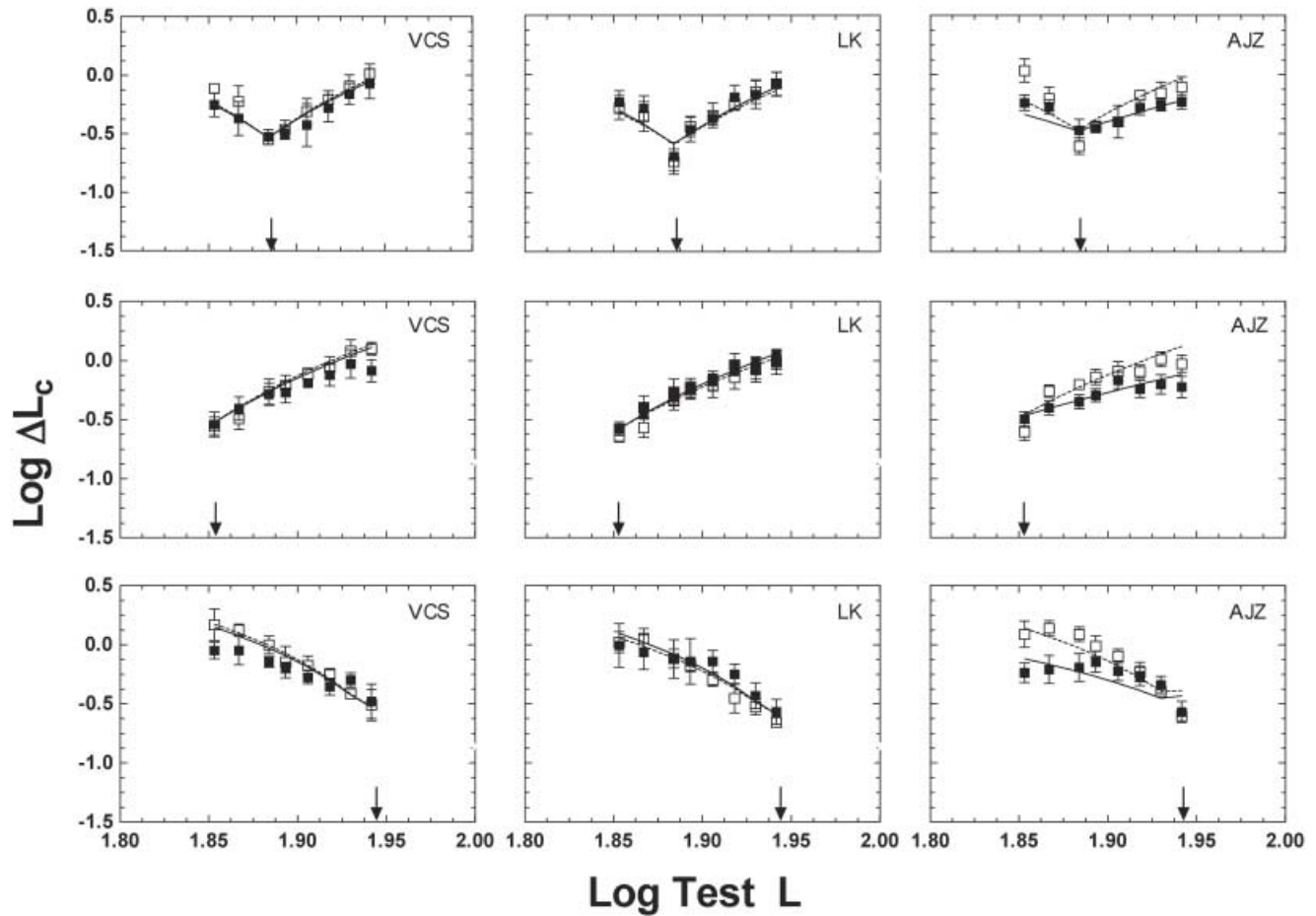
was maintained by a chin and head-rest. Observers wore their normal refractive correction (non-tinted) if required. Stimuli were presented randomly during a single 20–30 min test period with rest breaks allowed between conditions when desired. Chromatic pulsed- and steady-pedestal data were measured in separate sessions. The experimental design offers the advantage that the stimulus presentation for steady- and pulsed-pedestal paradigms is identical, differing only in pre- and post-adaptation. Each datum represents the average ( $\pm$  standard deviation) of three measurements.

**Results**

The results for the control condition (not shown) indicate that detection thresholds are always minimal for test stimuli measured

in the vicinity of the adaptation point set by the surround chromaticity. The control condition implies that there was no Weberian adaptation when detection was measured for test stimuli under adaptation to the test chromaticity (Krauskopf & Gegenfurtner, 1991). These data are consistent with the model (see Appendix), which allows only partial cone adaptation to the background and thus consistent with the conclusions of Krauskopf and Gegenfurtner (1991) that there is no evidence of Weberian adaptation of individual cones prior to the calculation of retinal opponency.

Fig. 2 shows chromatic discrimination thresholds for three observers measured in the outer quadrant of the 4° pulsed- or steady-pedestal (unfilled and filled symbols respectively). The upper panels give the data for the surround metameric to the *EES* and the middle and lower panels for biased chromatic surrounds



**Fig. 2.** Chromatic discrimination thresholds for the 1° test pulse that abutted the edge of a larger 4° pedestal (outer quadrant condition) that was steady (filled squares) or pulsed (unfilled squares). The chromaticity of the adapting background in Log L Td (indicated by an arrow) was metameric to an equal energy spectrum,  $l = 0.665$  (upper panels), or had L-cone chromaticities of  $l = 0.62$  (middle panels) and  $l = 0.74$  (lower panels) on a constant S-cone line ( $l, s$ ). The dashed and solid lines show the results from the model described in the Appendix (Eq. (6)) for the pulsed- and steady-pedestal data, respectively.

with  $l$ -chromaticities equal to 0.62 and 0.74, respectively (downward pointing arrows). For all conditions, the minimum is at the surround chromaticity and discrimination is degraded for increasing chromatic differences away from the surround. For conditions that contained either spatial contrast alone or spatial-and-temporal chromatic contrast, the contrast gain was equivalent (filled and unfilled symbols, respectively). The data are concordant with previous results for the 2° array (Smith et al., 2000). The larger pedestal area used in the present study (4° vs. 2°) did not alter discrimination for the 1° test positioned in the outer-quadrant, except for a small difference in absolute sensitivity due to more peripheral viewing. The dashed and solid lines in Fig. 2 are the fits from the model based on PC retinal ganglion cells in the Macaque retina for the pulsed- and steady-pedestal paradigms respectively. The best fitting parameters are given in Table 1.

Fig. 3 show the effects of temporal contrast or no contrast on chromatic discrimination. The inner quadrant data are presented in the same format as Fig. 2. In the presence of temporal chromatic contrast, thresholds created the standard V-shape function (pulsed-pedestal paradigm; unfilled symbols). A minimum is observed at the surround chromaticity. Discrimination functions for a steadily viewed light that contains no chromatic contrast were flatter and less dependent on test or surround chromaticity (steady-pedestal;

filled symbols). These functions indicate that there is almost complete adaptation to the test stimulus and discrimination is better at all test contrast. The dashed and solid lines represent the model

**Table 1.** Parameters for the chromatic discrimination model based on spectral-opponent cells in the Macaque retina

Condition	Observer	Variable parameters			Adjusted $r^2$	Fixed parameters	
		$K$	SAT	$p$		$k_1$	$k_2$
Outer	VCS	0.024	8.33	0.95	0.83	$l_{max}$	0.63721
	LK	0.019	9.53	1.08	0.89	$m_{max}$	0.39241
	AJZ	0.023	9.91	0.52	0.68	$k_1$	0.95
Inner	VCS	0.016	7.19	—	0.63	$k_2$	0.8
	LK	0.007	14.19	—	0.67	$k_3$	0.33
	AJZ	0.013	11.33	—	0.65	$k_4$	0.5

$l_{max}$  and  $m_{max}$  from Smith & Pokorny (1975)  
 $k_1$  from Hood & Finkelstein (1986)  
 $k_2$  from Smith et al. (1992)  
 $k_3$  and  $k_4$  from Miyahara et al. (1996)

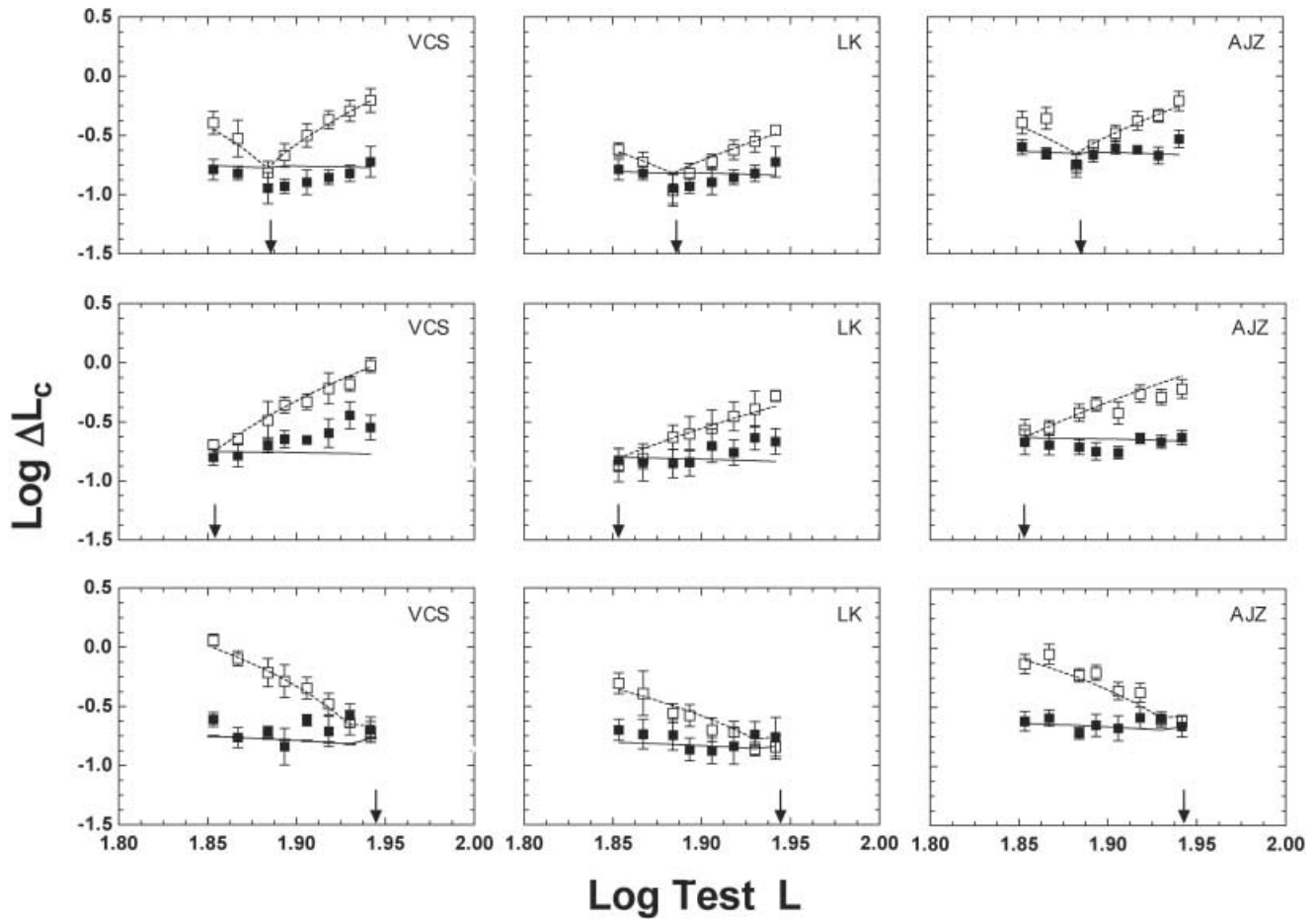


Fig. 3. Chromatic discrimination data for the inner quadrant condition. The data follow the same format as Fig. 2.

fit to the pulsed- and steady-pedestal paradigm data and best-fitting parameters are given in Table 1.

**Discussion**

The present work used a psychophysical paradigm that can be compared to the physiological properties of the primate PC-retinal ganglion and LGN cells chromatic response to consider the effect of spatial, temporal, spatial-and-temporal contrast between the surround and test field on chromatic discrimination. Spatial and temporal contrast had equivalent effects on chromatic discrimination, as did the joint presence of spatial-and-temporal chromatic contrast. Irrespective of the spatial-and-temporal properties of the stimulus, chromatic discrimination was always best at the surround chromaticity, which is consistent with previous observations (e.g., Brown, 1952; Krauskopf & Gegenfurtner, 1991; Watanabe et al., 1998; Smith et al., 2000).

Local spatial structure is important for chromatic discrimination in the presence of a steadily viewed light. Previously investigations have demonstrated that surround chromaticity (Smith et al., 2000) and structure (Boynton et al., 1977; Watanabe et al., 1998) can determine discrimination ability. This study is consistent with the Smith et al. (2000) observation that inferred PC-ganglion and LGN driven chromatic discrimination is degraded by border contrast (Fig. 3, filled symbols). Eye movements produce retinal contrast signals and prevent the fading of steadily viewed equi-

luminant chromatic images. Cells adapted to the border maintain the adaptation state and the continuous spatial chromatic contrast generated at the border (Smith et al., 2000). However, discrimination is improved at all test chromaticities in the absence of spatial and temporal chromatic contrast between the test and surround. The slight but systematic deviation from linear functions may indicate some adaptation to the temporal chromatic contrast of the 1.5 sec raised cosine test stimulus, or perhaps a minor degree of adaptation from the remote surround (Fig. 3, filled symbols).

For conditions in which the stimulus presentation contains only temporal chromatic contrast (inner quadrant pulsed-pedestal: Fig. 3, unfilled symbols), discrimination is regulated by the magnitude of the spatio-temporal chromatic contrast step relative to the surround. The position of the border is not important for temporal contrast changes. Although fewer receptive fields are located at the border of the test and surround compared to the number of receptive fields within the test area, the effect of a temporal contrast step is equivalent to that observed for spatial chromatic contrast. It can be inferred from the results that the temporal and spatial components of the Smith et al. (2000) model produce similar changes in chromatic contrast discrimination.

**Summary**

The present study used a paradigm that differentiated the effects of temporal and spatial chromatic contrast on chromatic discrimina-



tion. When the test stimulus was set entirely within a chromatic surround, chromatic discrimination for a steadily viewed light was best. Border elements adjacent to the test and surround generate continuous spatial contrast that degrades discrimination (Boynton et al., 1977; Smith et al., 2000). The temporal contrast of a chromatic light degrades chromatic discrimination irrespective of the location of the surround border to the test stimulus. Both spatial and temporal contrast produce equivalent decreases in discrimination for a fixed contrast step away from the adapting chromaticity. Consequently, chromatic contrast discrimination is determined by either the spatial or temporal contrast component of the signal.

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### Appendix

#### Model of chromatic contrast gain

The chromatic discrimination data were described using the Smith et al. (2000) model of the physiological data of spectral-opponent PC-cells in Macaque retina. The model has separate spatial and temporal components. The first stage of the temporal component of the model includes a multiplicative gain control, followed by a second-site of cone spectral opponency, which is subject to subtractive feedback, and a static non-linearity. The spatial component of the model is distinguished from the temporal component by an additional parameter that reduces the strength of the opponent signal in the presence of continuous spatial contrast. Each component will be briefly considered. A comprehensive account of the model is described by Smith et al. (2000).

The first stage of partial multiplicative gain (Swanson et al., 1987; Lee et al., 1990; Smith et al., 2001) reflects cone-specific adaptation in L- and M-cones. The opponent signal strength at the second site is controlled by partial multiplicative gain. The multiplicative gain terms  $G(L_A/l_{max})$  and  $G(M_A/m_{max})$  at the adapting chromaticity are given by an equation of the form:

$$G(L) = \frac{1}{\left(\frac{(1 + k_3 L_A)}{l_{max}}\right)^{k_4}}, \quad (1)$$

where  $L_A$  is in cone Trolands and  $k_3$ ,  $k_4$  are constants and  $l_{max}$  and  $m_{max}$  are the maximal sensitivities of the Smith and Pokorny (1975) cone fundamentals. The gain is dependent on the retinal illuminance (Purpura et al., 1990). The second stage incorporates a cone spectral-opponent site for each of the four subtypes of long- and medium wavelength sensitive PC-retinal ganglion cells, (+LWS –MWS), (+MWS –LWS), (–LWS +MWS), and (–MWS +LWS). The response of a spectral opponent cell to a chromaticity change,  $C$  from a fixed adapting chromaticity,  $A$  is:

$$R = R_{max} \left( \frac{OPP_C}{(OPP_C + SAT)} \right), \quad (2)$$

where  $OPP_C$  is a spectral opponent term and  $SAT$  is the static saturation. A static non-linearity characterizes the retinal ganglion cell response to contrast changes from their steady-state adaptation level (e.g., Shapley,

1990). It is an intrinsic non-linearity that renders the cell response asymmetric such that it acts as if it is partially rectified. For a (+LWS –MWS) cell, the spectral opponent term at the test chromaticity would be given by

$$OPP_{(+LWS, -MWS)} = \left[ \frac{L_T}{l_{\max} G(L_A/l_{\max})} - \frac{k_2 M_T}{m_{\max} G(M_A/m_{\max})} \right] \quad (3)$$

where  $L_T$  and  $M_T$  are the cone Trolands at the test chromaticity,  $L_A$  and  $M_A$  represent the cone Trolands at the adapting chromaticity. The constant  $k_2$  represents the surround strength of the spectral opponency.

Subtractive feedback follows at the site of spectral opponency (Yeh et al., 1996) and acts to cancel the net signal from the adapting chromaticity. At the adapting chromaticity, subtractive feedback is described by,

$$OPP_c = OPP_T - k_1 OPP_A, \quad (4a)$$

where the spectral opponent term is  $OPP_T$  at the test chromaticity and  $OPP_A$  at the adapting chromaticity. The parameter  $k_1$  is subtractive feedback strength, which can be as high as 90% (Hood & Finkelstein, 1986). Under conditions where continuous spatial contrast is generated at the test-surround border (outer quadrant, steady-pedestal paradigm), it is necessary to allow some reduction in the spatial contrast signal (Smith et al., 2000). The decrease in the strength of the opponent signal due to spatial chromatic contrast can be described by,

$$OPP_c = OPP_T - k_1(p OPP_A + (1 - p) OPP_T) \quad (4b)$$

where  $p$  is the proportion of the adapting chromaticity in the subtraction. A reduction in the strength of the opponent signal is not required for the inner quadrant, steady pedestal paradigm, because cells in the test area are adapted to the pedestal chromaticity and there is no edge to produce spatial chromatic contrast and drive the opponent signal.

In a single cell, three parameters, the criterion response,  $\delta$ , maximal response rate,  $R_{\max}$ , and the semi-saturation value,  $C_{sat}$ , uniquely determine contrast discrimination (Smith & Pokorny, 2003). Psychophysical thresholds however, involve higher order processes that combine inputs from arrays of retinal cells (Smith & Pokorny, 2003). To compare contrast discrimination data in humans to single cells, the shapes of the contrast discrimination functions and not the absolute levels are considered. A free vertical scaling parameter,  $K$ , incorporates  $(\delta/R_{\max})$ . The chromatic dis-

crimination threshold for an optimal spatio-temporal stimulus at the adapting chromaticity is based on the derivative of Eq. (2), such that

$$\log(\Delta L_A) = \log(K) - \log \left[ \frac{1}{(G(L)/l_{\max})} + \frac{1}{(G(M)/m_{\max})} \right] + \log \left[ \frac{(OPP_A + SAT)^2}{SAT} \right]. \quad (5)$$

In Eq. (5), the second term represents the luminance gain response, and the third term is the opponent term. The threshold test chromaticities away from the adapting chromaticity depend on the size of the contrast step,  $\Delta OPP$ , between the adapting and the new test chromaticity. Including the term  $\Delta OPP$  in Eq. (5) gives Eq. (6) such that,

$$\log(\Delta L) = \log(K) - \log \left[ \frac{1}{(G(L)/l_{\max})} + \frac{1}{(G(M)/m_{\max})} \right] + \log \left[ \frac{(\Delta OPP + OPP_A + SAT)^2}{SAT} \right]. \quad (6)$$

The response for the entire chromatic contrast range utilizes pairs of cells of opposite chromatic signatures. Equation 6 describes chromatic contrast discrimination in the presence of a spatio-temporal contrast step (e.g., pulsed-pedestal paradigm). In the presence of continuous spatial contrast generated at the test-surround border (e.g., steady-pedestal condition), Eq. (4b) replaces Eq. (4a) in Eq. (6) to allow for the decrease in the strength of the opponent signal (Smith et al., 2000).

The model was simultaneously fit to individual observer data from the steady- and pulsed-pedestal paradigms for the inner quadrant condition at each of the three surround chromaticities, by minimizing the sum-of-square differences between the 48 data points and the model with two free parameters ( $K$  and  $SAT$ ). For the outer quadrant condition, an additional parameter,  $p$ , is required to account for the presence of continuous spatial chromatic contrast in the steady-pedestal paradigm. Values for the remaining parameters were set in accord with physiological data (Lee et al., 1990, 1994; Shapley, 1990; Yeh et al., 1996). The variable and fixed physiological parameters for the model fits for each observer and condition are given in Table 1. The percent variation accounted for by the model (adjusted  $r^2$ ) for each observer is given in Table 1.