Cardinal axes are not independent in color discrimination

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We measured chromatic discrimination under conditions where the target fields could be distinguished only by the ratio of excitation of the long- (L) and middle-wavelength (M) cones. The excitation level of the short-wavelength (S) cones was varied in the experiments, although for any given measurement the S-cone excitation was common to the two target fields and could not be directly used for discrimination. Adaptation was maintained by a steady neutral background metameric to Illuminant D65. Thresholds varied substantially and systematically with the S-cone level of the target probes, but in a complex way: when the ratio of L:M cone excitation was low, an increase in S-cone excitation reduced the thresholds, but when the L:M ratio was higher, an increase in S-cone excitation raised the thresholds. To account for the pattern of results, we postulate a neural channel that draws synergistic inputs from L and S cones and an opposed input from M cones. The proposed channel has a compressive response function and is most sensitive at the point set by the steady background.

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1. INTRODUCTION

It is currently held that color information is carried at early stages of the visual system by two anatomically distinct pathways [1,2]. The small bistratified retinal ganglion cells draw excitatory input from short-wavelength (S) cones and an opposed inhibitory input from some combination of long- (L) and middle-wavelength (M) cones [3]; they project to koniocellular layers 3 and 4 of the lateral geniculate nucleus [4,5], and their signals then pass directly to layers 2 and 3 of the striate cortex [6]. The midget ganglion cells draw opposed inputs from L and M cones [2,7]; they project to the parvocellular laminae of the lateral geniculate nucleus, which in turn project to layer 4 of the striate cortex. The two morphologically distinct pathways appear to have distinct evolutionary origins [8].

The signals of the two physiological pathways correspond to the two axes of the MacLeod–Boynton diagram [9] (Fig. 1), now widely used in visual science to represent the gamut of chromaticities seen by the standard observer. The horizontal axis represents $L/(L+M)$ and the vertical axis $S/(L+M)$, where L, M, and S are the excitations of the long-, middle- and short-wavelength cones, respectively. The same two axes of color space were termed "cardinal" by Krauskopf *et al.* [10].

We ask here whether discrimination along one cardinal axis [the $L/(L+M)$ axis] is independent of the state of excitation of the other axis. The anatomical separation of the two signals, which is preserved as far as the striate cortex, hints that we might expect a large degree of physiological and psychophysical independence. The issue was directly addressed by Krauskopf and Gegenfurtner in a classic study [11]. They held constant the adaptive state of the eye and measured discrimination thresholds along one cardinal axis while varying the excitation along the second axis. The threshold at a given point on the $L/(L+M)$ axis appeared to be independent of the level of excitation of the S cones, and conversely the threshold at a given point along the vertical axis appeared to be independent of the relative excitation of the L and M cones.

The present study resembled that of Krauskopf and Gegenfurtner in that we adapted the eye to a steady background field (in our case, metameric to Illuminant D65) and probed discrimination with brief test stimuli—so that there was likely to be little adaptation during the actual test presentation. We measured thresholds in the horizontal direction in MacLeod–Boynton space. Therefore, only the ratio of L and M cone excitations would vary, and psychophysical discrimination should depend only on the pathway originating in the midget ganglion cells. We show in fact that the thresholds depend in a complex but systematic way on the excitation of the S cones.

2. METHODS

A. Apparatus and Stimuli

The same computer programs were used to make measurements in Cambridge, England, and in St. Petersburg, Russia. In both laboratories, the stimuli were presented on calibrated Mitsubishi color monitors (Diamond Pro 2070) controlled by Cambridge Research Systems graphics systems (VSG 2/3 in Cambridge, Visage in St. Petersburg). In St. Petersburg, the monitor was set to a refresh rate of 80 Hz and a resolution of 1280×980 pixels; in Cambridge, these values were 92 Hz and 1024×768 pixels. Calibration procedures and algorithms for generating colors on the CRT screen were identical in the two laboratories. The VSG system allowed a resolution of 15 bits per gun, and the Visage, 14 bits. We checked that our measured thresholds were not instrumentally limited.

Chromaticities were specified in a MacLeod–Boynton diagram (Fig. 1), which we constructed from the cone sensitivities tabulated by DeMarco *et al.* [12]. The diagram represents a plane of equal luminance for the Judd (1951) observer, where luminance is equal to the sum of the L- and M-cone signals [13]. For purposes of presentation and for consistency with our related papers, we have rescaled the vertical ordinate of the MacLeod–Boynton diagram so that a line running through 574 nm and the chromaticity of Illuminant D65 lay at −45°: under the conditions of our experiments, this "yellow–blue line" represents the set of colors that are neither reddish nor greenish (as empirically measured in our earlier studies). Since the ordinate scale of the MacLeod–Boynton diagram is arbitrary, our rescaling has no empirical effect on the measurements.

The targets were presented on a steady background metameric to Illuminant D65 [14]. The luminance of the background was set to have a value equivalent to 10 cd.m^{-2} in CIE units. The circular bipartite target field subtended 2° and was vertically divided by a thin line that had the chromaticity and luminance of the background (Fig. 1, inset). The target half-fields had a mean luminance that was 30% greater than that of the background when expressed in the (L + M) units of our space; but to ensure that the observers could not discriminate the stimuli on the basis of differences in sensation luminance, we jittered independently the (L + M) value of each target by ±5%. The duration of the target was 150 ms.

The CRT screen was viewed binocularly from a distance of 570 mm. Fixation was guided by a diamond-shaped array of small black dots surrounding the area in which the target field was presented.

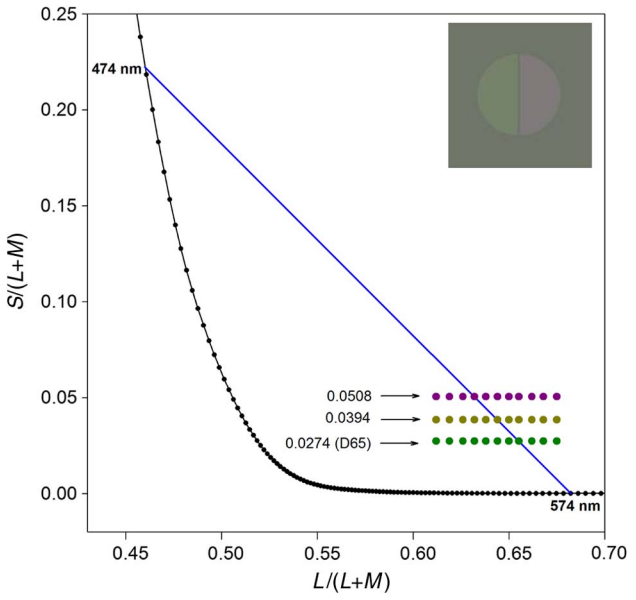

Fig. 1. (Color online) Part of the MacLeod–Boynton (1979) chromaticity diagram, showing the locations of the three sets of referent stimuli used in Experiment 1. The oblique solid line represents the set of chromaticities that appear neither reddish nor greenish under the conditions of our experiments (the "yellow–blue line") [24], and the ordinate of the diagram has been scaled so that this line lies at 45°. Each of the three sets of referents is identified by its S/(L + M) coordinate. The curved locus represents the spectrum of monochromatic lights. The inset shows the arrangement of the target field.

B. Procedures

In any given experimental session of Experiment 1, we measured discrimination thresholds along one of three horizontal lines in the MacLeod–Boynton diagram (Fig. 1). One line passes through the chromaticity coordinates of D65, the chromaticity of the steady background, and the remaining two lines have higher levels of S excitation. In the figures we refer to each line by its (rescaled) S/(L + M) coordinate. The task was a spatial forced choice. Formally the observer was asked to indicate by pushbuttons which stimulus hemifield had the lower L/(L + M) value. Informally, the target half-field could often be identified as "greener" (or "less red"), but the task was a performance one, and the observer was asked to rely on the auditory feedback that on each trial indicated the correct response. On each horizontal line there were 11 reference chromaticities. These reference chromaticities were never themselves presented, but any given pair of discriminanda lay on the same line, straddling the reference point; and their chromatic separation was increased or decreased symmetrically around the reference chromaticity according to the observer's accuracy. The staircase procedure tracked 79.4% correct [15], and it terminated after 15 reversals, the last 10 reversal points being averaged to give the threshold. The reference and test chromaticities were expressed in terms of the abscissa of the MacLeod–Boynton diagram (i.e., their L/(L + M), or l, coordinates). At any one point on the staircase, one of the discriminanda had an l coordinate l_{t1}, and the other had an l coordinate l_{t2}, where l_{t1} was equivalent to the reference coordinate l_r multiplied by a factor a and l_{t2} was equivalent to l_r divided by a, where a is always >1.0. After three correct responses, the value $(a - 1)$ was reduced by 10%, and after each incorrect response it was increased by 10%.

Within one experimental session, the 11 reference stimuli were tested in random order. The different horizontal sets were tested in random order; and six repetitions were performed for each set, the first being treated as practice and not included in the analysis (except in the case of Subject 6, who completed only five full sets of runs for two sets).

The task was not explicitly a speeded one, in that subjects could respond at their own pace. However, we routinely recorded the response time on each trial.

The stimuli and procedures were identical for Experiment 2, except that in each experimental session we tested discrimination for a set of referents that varied in S-cone excitation but had the same L/(L + M) value (Fig. 5). For each referent, discrimination was measured, as before, in the horizontal direction of the MacLeod–Boynton chromaticity space. Within one session, referents were tested in random order. There were four sets of referents, and the different sets were tested in random order. Each set was tested in six independent sessions, the first being discarded as practice.

C. Observers

All observers had normal color vision as tested by the Cambridge Color Test [16]. Observers 1 and 2 were the authors J. D. M. and M. V. D., respectively; the other observers were psychophysically practiced but were naïve as to the purpose of the experiments. Observers 2, 4, and 5 are female. All observers except observers 2 and 6 were tested in Cambridge. The experiments in both Cambridge and St. Petersburg were

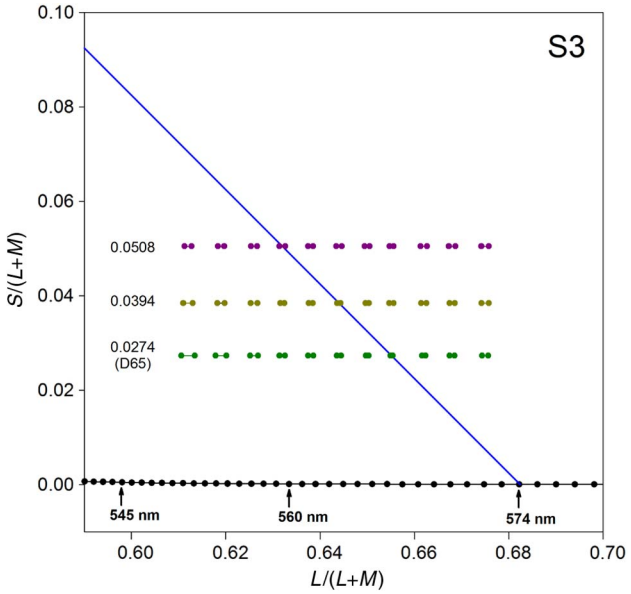

Fig. 2. (Color online) Magnified region of the MacLeod–Boynton diagram showing the results of Experiment 1 for one observer. Each yoked pair of data points shows directly how far the foveal half-fields have to differ in chromaticity if the observer is to discriminate them at the level of 79.4% correct. To the left of each of the three sets of data is shown the S/(L + M) coordinate of the targets. The line at 45° is the yellow–blue line—the set of chromaticities that look neither reddish nor greenish under our experimental conditions. Part of the spectrum locus is shown near the base of the diagram.

approved by the Psychology Research Ethics Committee of the University of Cambridge.

3. EXPERIMENT 1: RESULTS AND DISCUSSION

Figure 2 shows thresholds for one subject plotted directly in the MacLeod–Boynton diagram: each pair of yoked points shows how far the two half-fields must differ in chromaticity if the observer is to discriminate them correctly on 79.4% of trials. Two features of the results are already apparent in this direct way of plotting thresholds: discrimination is optimal at the chromaticity of the background, and it is particularly poor for the conditions where the coordinates L/(L + M) and S/(L + M) are both low (bottom left of the array).

Figure 3 shows results for all subjects. Here the threshold is plotted against the L/(L + M) coordinate of the reference stimulus. The threshold is expressed as the factor by which the two discriminanda differ—in opposite directions—from the reference stimulus. Averages are shown in the last panel.

A repeated-measures analysis of variance (ANOVA) showed highly significant main effects of both the L/(L + M) and the S/(L + M) coordinates of the referent [$F(10) = 135.03$, $p < 0.001$; $F(2) = 25.45$; $p < 0.001$]. There was also a highly significant interaction between these two factors [$F(20) = 29.16$; $p < 0.001$].

For the set of referents that pass through D65, all subjects exhibit the lowest thresholds at the chromaticity of the background. This is a classical finding, described as early as 1954 by Rautian and Solov'eva [17] and confirmed in several subsequent studies of chromatic discrimination [11,18,19]. It is analogous to the finding that differential sensitivity for luminance is optimal at the level of luminance to which the eye is currently adapted [20]. To explain such findings, in the case of both luminance and chromaticity, it is usually assumed that the response-versuss-intensity function of a visual channel will shift so that its steepest part always corresponds with the current background level [21]. Such an effect was explicitly shown for chromatically opponent neurons in the lateral geniculate nucleus (LGN) by De Valois *et al.* [22]. If discrimination in the present experiment depended only on a canonical midget ganglion cell system, drawing opposed inputs from L and M cones, the minimum threshold should always lie at L/(L + M) (the value of the D65 background), but there is some hint in the mean data that the minimum shifts to the left as the S-cone excitation increases.

However, what is particularly clear and particularly curious, for all subjects, is that for referents with low L/(L + M) coordinates (i.e., greenish colors) the threshold is reduced when S-cone excitation is increased (see Fig. 3, leftmost data points in each panel). Yet the S-cone excitation cannot directly contribute to the discrimination: it is identical on the two sides of the foveal field.

Is it possible that our observers gain sensitivity at the cost of response time; do they respond more slowly under conditions where thresholds are lowest? Although our observers were not explicitly required to react as quickly as possible, our program recorded the response time on each trial. In Fig. 4 we plot median response times for Experiment 1, averaged across subjects. To derive the medians, we included only the trials on which the thresholds are based—those encompassed by the last 10 reversals of the staircases. It is clear that observers are not trading sensitivity for speed, since the trends in the response times are in the same sense as the thresholds of Fig. 3. A repeated-measures ANOVA showed a highly significant main effect of the L/(L + M) coordinate of the referent [$F(10) = 12.6$, $p < 0.001$], no main effect of the S/(L + M) coordinate, and a highly significant interaction between these two factors [$F(20) = 3.13$, $p < 0.001$].

To explore directly the counterintuitive effect of S-cone excitation, we performed a second experiment in which the discriminations continued to be along the horizontal axis of MacLeod–Boynton space but the referent stimuli lay along vertical lines in the diagram, sampling a more detailed range of S/(L + M) values. The four sets of referents used are shown in Fig. 5, where they are identified by their L/(L + M) coordinate, which is constant for any one set. One of the four sets passes through the chromaticity of the background; the other three have lower values of L/(L + M). We extended the sets of referents to the highest values of S/(L + M) that could be achieved on our monitor while maintaining the luminance values used in Experiment 1.

4. EXPERIMENT 2: RESULTS AND DISCUSSION

Figure 6 shows data for one subject plotted directly in the MacLeod–Boynton diagram. Here the yoked data points directly show the chromaticity difference that must be obtained between the two foveal half-fields if the observer is to be correct on 79.4% of trials. Although this direct way of plotting offers only limited resolution, two interesting features can be seen: first, thresholds tend to be smallest in the vicinity of the yellow–blue line, the locus of chromaticities that look neither

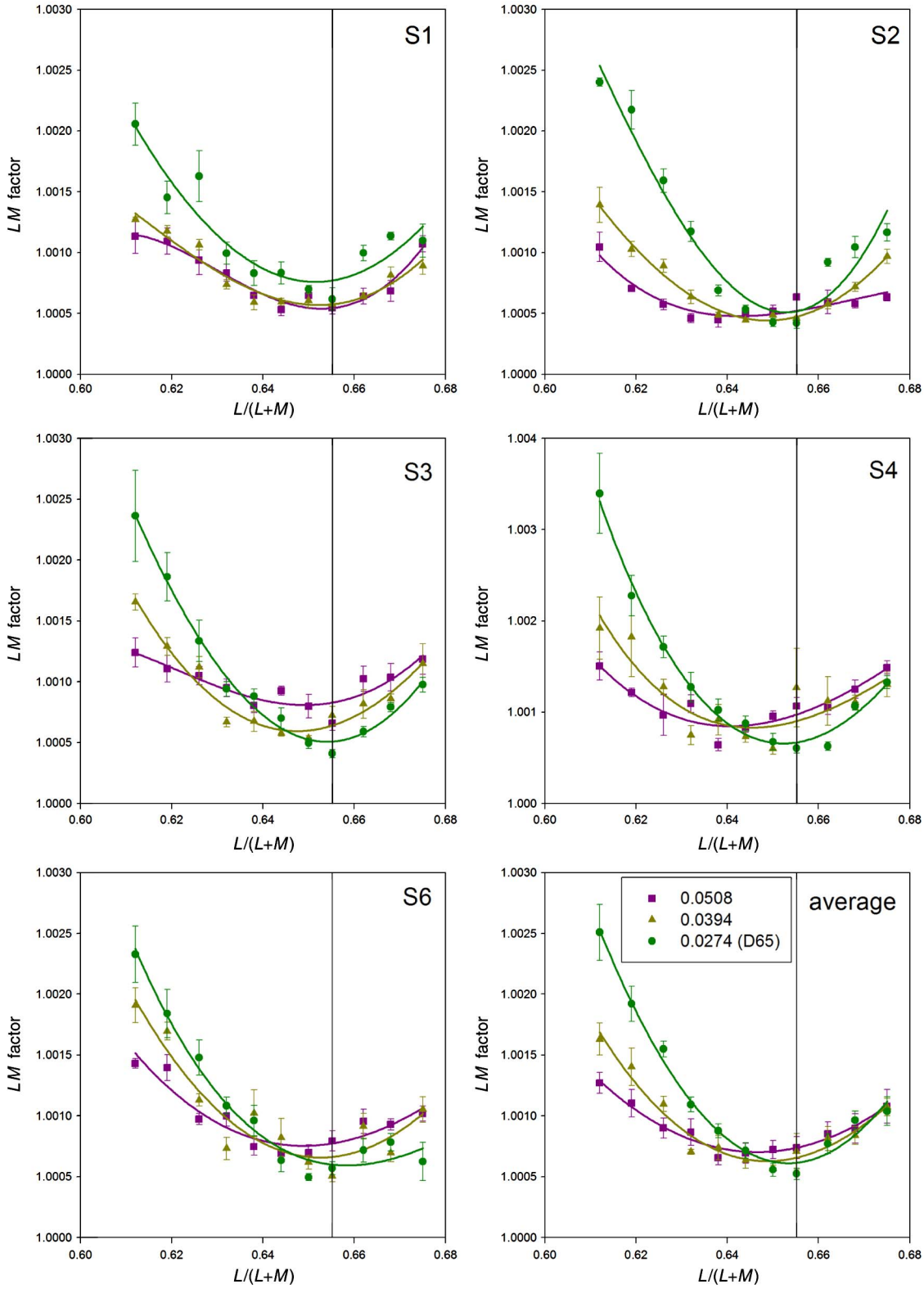

Fig. 3. (Color online) Color discrimination results for five subjects in Experiment 1; the last panel shows averages. Within each panel, each of the three sets of reference stimuli from Fig. 1 is represented by a different symbol; the inset key in last panel gives the S/(L + M) coordinate corresponding to each set. The ordinate represents the factor by which each of the discriminanda differs from the referent at threshold. These thresholds are plotted against the L/(L + M) coordinate of the referent. In each panel, a vertical line marks the L/(L + M) value of the neutral background. The functions fitted to the data sets are inverse third-order polynomials; they have no theoretical significance. Error bars for individual subjects represent ±1 SEM (standard error of the mean), based on estimates from the independent experimental sessions. Error bars for the average are based on the means for individuals.

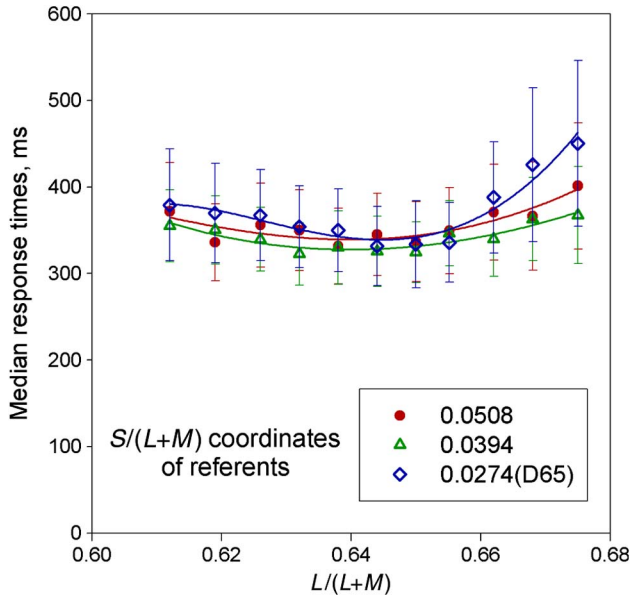

Fig. 4. (Color online) Median response times for Experiment 1, averaged across subjects. Each of the three sets of reference stimuli from Fig. 1 is represented by a different symbol; the inset key gives the S/(L + M) coordinate corresponding to each set. The curves fitted to the data are inverse third-order polynomials and have no theoretical significance. Error bars are based on between-subject variance. These results show that the observers are not gaining sensitivity at the cost of response time.

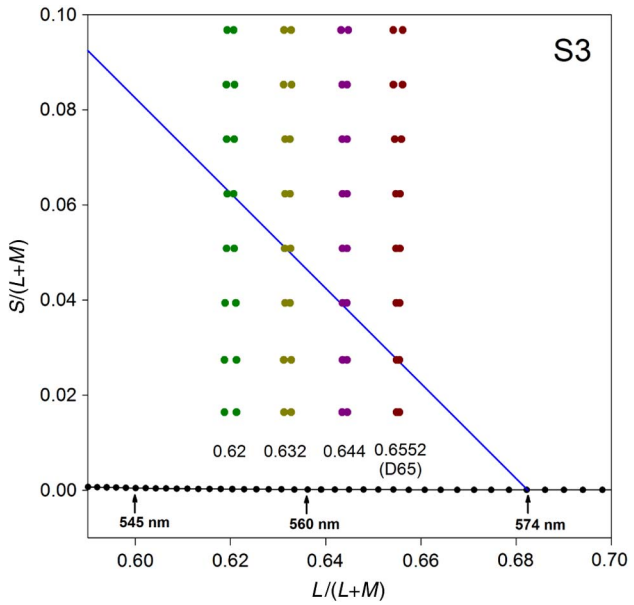

Fig. 6. (Color online) A magnified region of the MacLeod–Boynton diagram showing the results of Experiment 2 for one observer. Each yoked pair of points shows directly how the foveal half-fields have to differ in chromaticity if the observer is to discriminate them at the level of 79.4% correct. Below each of the four sets of data is shown the L/(L + M) coordinate of the targets. The line at 45° is the yellow–blue line. Part of the spectrum locus is shown near the base of the diagram.

reddish nor greenish; and second, at low values of L/(L + M) an increase of S-cone excitation improves discrimination.

In Fig. 7 thresholds for each set of referents are shown as a function of the level of S-cone excitation. The ordinates represent the factor by which the two half-fields must differ in L/(L + M) value if they are to be discriminated at the level of 79.4% correct. The final panel shows averages.

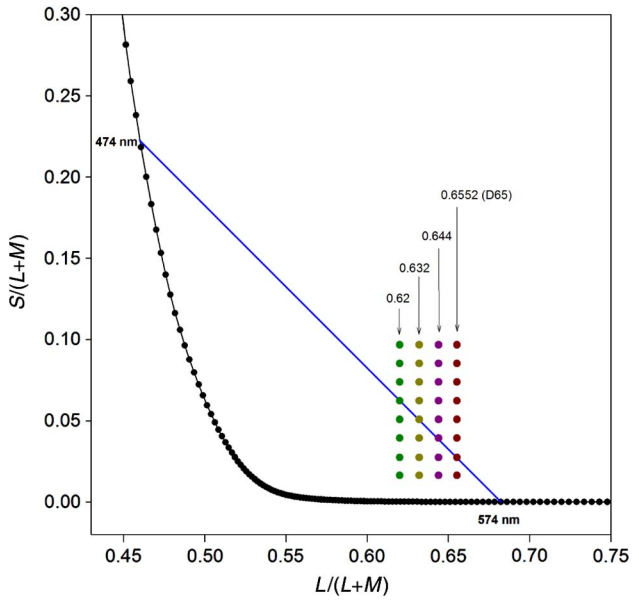

Fig. 5. (Color online) Portion of the MacLeod–Boynton chromaticity diagram showing the four sets of referent stimuli used in Experiment 2. Each set is identified by its L/(L + M) coordinate. The curved locus represents the spectrum of monochromatic lights, and the line at −45° represents the set of chromaticities that look neither reddish nor greenish under our experimental conditions.

A repeated-measures ANOVA showed highly significant main effects of both the L/(L + M) and the S/(L + M) coordinate of the referent [$F(3) = 88.95$, $p < 0.001$; $F(7) = 32.02$; $p < 0.001$]. The interaction between the two factors was again highly significant [$F(21) = 42.2$; $p < 0.001$].

The data of Fig. 7 are complex, but they are systematic and they are consistent between subjects. For the data set that passes through the chromaticity of the background (metameric to D65), the thresholds exhibit a minimum near the S/(L + M) value of the background, and indeed this threshold is lower than all others in the four data sets; for this D65 data set, thresholds then rise as S-cone excitation increases. A very different behavior is seen for the set of referents that have the lowest L/(L + M) coordinate (0.62): at low values of S-cone excitation, the average thresholds are fourfold higher than those measured near D65, but as S-cone excitation is increased, the threshold is halved. The data sets for intermediate values of L/(L + M) show behavior intermediate between the two extremes: as S-cone excitation increases, the thresholds pass through a minimum and then rise again.

5. GENERAL DISCUSSION

The present data show firmly that the two cardinal axes are not independent in color discrimination. In our measurements, the discriminanda differed only in the ratio of L:M excitation. By the standard account, discrimination should depend only on the pathway originating in the midget ganglion cells. Yet thresholds varied substantially with the level of S-cone excitation, even though the S-cone level was common to the two sides of the field.

Varying the S-cone excitation leads to a systematic but complex pattern of facilitation and impairment in discriminations

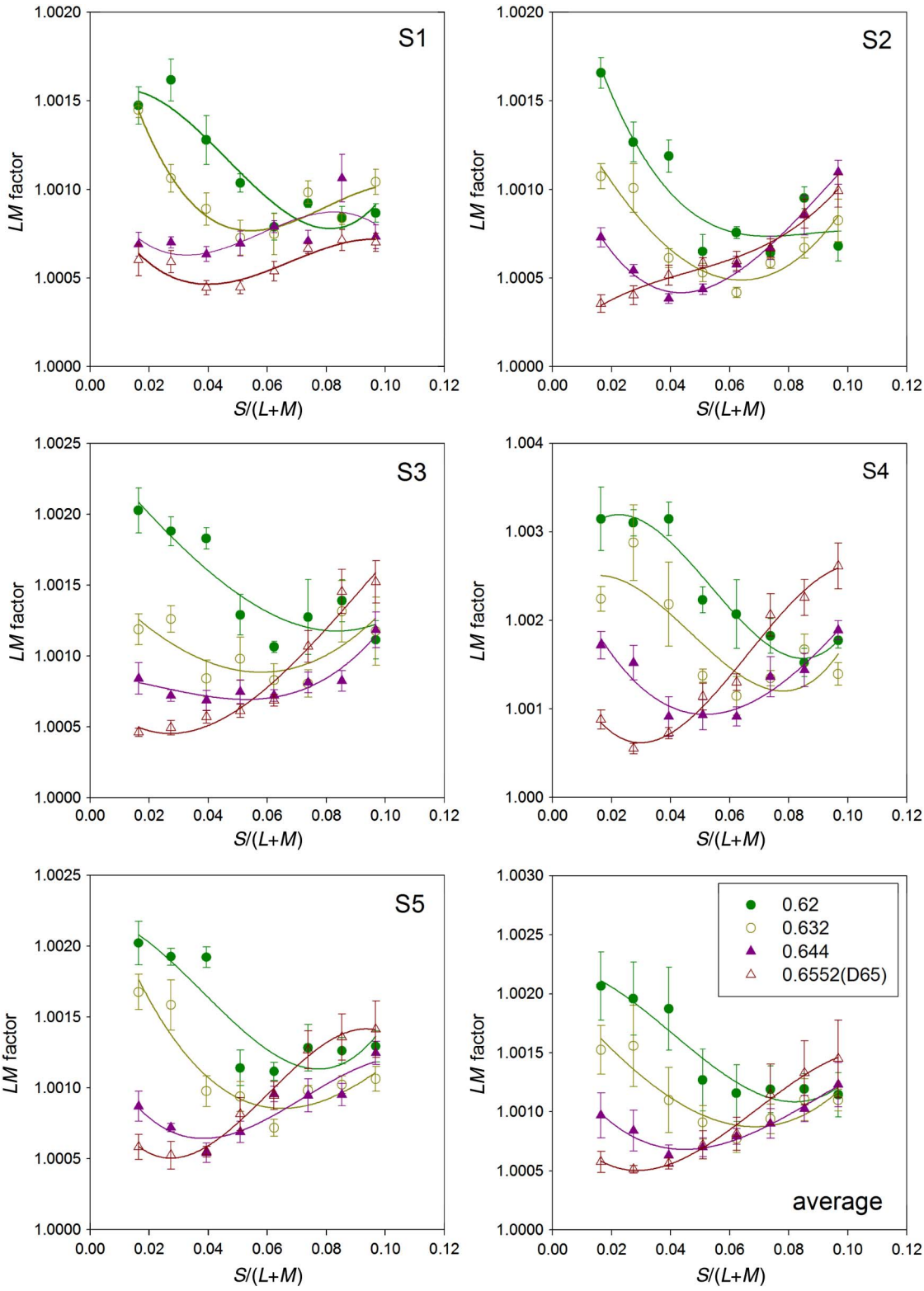

Fig. 7. (Color online) Color discrimination thresholds for five subjects in Experiment 2; the last panel shows averages. Within each panel, each of the four sets of reference stimuli from Fig. 5 is represented by a different symbol; the inset key in the last panel gives the L/(L + M) coordinate corresponding to each set. The ordinate represents the factor by which each of the discriminanda differs from the referent at threshold, and thresholds are plotted against the S/(L + M) coordinate of the referent. The functions fitted to the data sets are cubic splines; they have no theoretical significance. Error bars for individual subjects represent ±1 SEM and are based on estimates from independent experimental sessions. Error bars for the average are based on the means for individuals.

that are based on the ratio of L and M cone excitations. How can this pattern be accounted for? If the effect of S-cone excitation were always in the same direction, it would be possible to postulate, say, that the S-cone signal adds noise at a central site when it is combined with an L/M signal and that this noise varies with S-cone excitation; but in fact the *direction* of effect

of the S-cone signal varies with the value of the L:M excitation ratio.

We suggest that a possible clue lies in the fact that discrimination is optimal in the region of the yellow–blue line, i.e., near the subjective boundary between reddish and greenish colors. In previous work [23,24], we have measured chromatic discrimination along lines orthogonal to the yellow–blue line (i.e., at +45° in Fig. 1) and have found that thresholds are lowest at the transition between reddish and greenish hues, a transition that we independently measured. We were led to postulate a neural channel that was in equilibrium—and thus at the most sensitive point of its operating range—at the red–green category boundary. Such a channel would draw synergistic inputs from S and L cones and an input of opposite sign from M cones. It would thus resemble the red–green channel of classic opponent color theory [25]. The present results suggest that the putative channel may also contribute to discrimination when only L and M excitations are being reciprocally varied. The facilitatory effect of increased S-cone excitation would arise when the channel was polarized in the M direction and would act by restoring the channel to a more favorable part of its operating function. However, such a channel could not account for all the variation in our measured thresholds; the threshold is always optimal at the chromaticity of the D65 background (where all channels would be in equilibrium), and for the set of measurements for the lowest $L/(L+M)$ coordinate (Fig. 7, solid circles), the best threshold is a factor of 2 higher than that measured at D65.

A. Site of the Postulated Channel

The twofold drop in psychophysical threshold as S excitation is increased at low values of $L/(L+M)$ (solid circles in Fig. 7) does hint that our results reflect a relatively early stage of visual analysis where the representation of redness and greenness still depends on individual neurons that have a compressive response function.

The postulated red–green channel may arise cortically by recombination of the chromatic channels traditionally described in the LGN; and such a recombination has been suggested [26]. A *serial* model of this kind might account for our observation (see above) that the very lowest thresholds are recorded only at the chromaticity of the background field (D65); the explanation would be that this is the only chromaticity at which both the second-stage (L versus M) and the third-stage (red–green) mechanisms are in the middle of their operating ranges.

A more radical suggestion would be that a third chromatic channel exists in the early visual system, in *parallel* with the channels conventionally held to originate in the midget and the small bistratified ganglion cells. There have been occasional reports of retinal or LGN neurons that drew synergistic inputs from S and L cones and opposed inputs from M cones [27,28], but for at least two decades, it has been common to deny the existence of a red–green channel in the early visual system (e.g., [29]). A study of macaque LGN cells by Tailby *et al.* [30] found that cells inhibited by S cones most typically received synergistic inputs from M cones and opposed, excitatory, inputs from L cones (their Fig. 5)—although for a minority of cells the S and L signals were synergistic. One reason to reopen the issue is the demonstration that more independent channels leave the primate retina than previously suspected [31]. One candidate substrate for a red–green channel would be the large bistratified type of retinal ganglion cell, which is known to draw excitatory inputs from S cones [32]. An alternative candidate would be a subtype of midget ganglion cell that drew inputs from S cones: Field *et al.* [33], recording from peripheral retina of macaques, have reported that S-cone inputs to the center of the receptive field are frequent in the case of OFF-center midget ganglion cells and are also observed in a minority of ON-center cells.

A particularly provocative development is the description of an eleventh type of bipolar cell in Golgi-stained macaque retina [34]. These "giant" bipolars contact L or M cones, but not S cones. However, they contact only about half the cones within their dendritic field, suggesting that they are selective for either L or M cones. Such a bipolar cell would be well suited to supplying one of the inputs to a nonmidget chromatic channel that drew signals of opposite sign from L and M cones.

B. Physiological Basis for a Perceptual Category Boundary?

Our results may have implications beyond the specialized domain of color psychophysics. Hue is a paradigmatic example of a mental category: chromaticity varies continuously in a two-dimensional space, but human perception imposes discrete categories on this space. It has been a problem that no coincident neural categories have been identified—no neural signals or neural structures that map to the phenomenological categories [29,35]. The present results suggest after all that a red–green channel may still be found at a precortical or early cortical stage, a channel in which redness and greenness are represented by individual neurons with compressive response functions.

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