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# Discrimination of hue angle and discrimination of colorimetric purity assessed with a common metric

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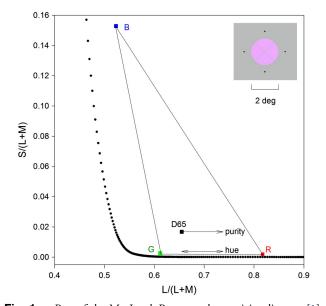
It has been suggested that thresholds for discriminating colorimetric purity are systematically higher than those for discriminating hue angle, a difference captured in Judd's phrase "the super-importance of hue." However, to compare the two types of discrimination, the measured thresholds must be expressed in the same units. An attractive test is offered by measurements along the horizontal lines in the chromaticity diagram of MacLeod and Boynton [ J. Opt. Soc. Am. 69, 1183 (1979)], i.e., a chromaticity diagram. A horizontal line that extends radially from the white point represents a variation in colorimetric purity alone (and subjectively a variation that is primarily in saturation). In contrast, a horizontal line that runs along the x axis of the diagram, close to the long-wave spectrum locus, corresponds predominantly to variation in hue angle. Yet, in both cases, only the ratio of the excitations of the longand middle-wave cones is being modulated, and so the thresholds can be expressed in a common metric. Measuring forced-choice thresholds for 180 ms foveal targets presented on a steady field metameric to Illuminant D65, we do not find general support for Judd's working rule that thresholds for purity are systematically twice those for saturation. Thresholds for colorimetric purity were only a little higher than those for hue angle, and the advantage for hue was seen in only part of the ranges that were tested. However, in the upper-left quadrant of the MacLeod-Boynton diagram, where the excitation of short-wave cones is high and where both hue angle and colorimetric purity vary along any given horizontal line, thresholds were indeed sometimes half those observed for discrimination of purity alone. © 2020 Optical Society of America

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## **1. INTRODUCTION**

There is a curious feature of color space that is seldom discussed. First, consider a horizontal line in the chromaticity diagram of MacLeod-Boynton [1], a line that passes through the white point (Fig. 1). Chromaticities along this line vary in colorimetric purity. That is to say, on one side of the white point, such lights can all be matched by mixing white light in different proportions with the same monochromatic light and, on the other, can be matched by mixing white light with the same purple light. Colorimetric purity is then defined as  $L_s/(L_s + L_w)$ , where  $L_s$ is the luminance of the monochromatic (or purple) component of a given mixture and  $L_w$  is the luminance of the white component. Saturation, the phenomenological correlate of purity [2–5], increases in each direction from the white point. As purity increases to the left of the white point in the MacLeod-Boynton diagram, stimuli become increasingly saturated teal greens; further, they become increasingly saturated cherry reds as purity increases to the right of the white point. It is true that there may be secondary shifts in subjective hue, i.e., the Abney effect [6], but the primary phenomenological variation is in saturation.

Now consider a horizontal line that lies close to the abscissa of the MacLeod–Boynton diagram. For wavelengths of  $\sim 550$  nm and above, where short-wave excitation is close to zero [7], the spectrum locus, i.e., the set of long-wave monochromatic lights, coincides with such a line. [The x axis of the MacLeod-Boynton diagram here corresponds to the diagonal of the CIE (1931) chromaticity diagram [8], i.e., the line (x + y) = 1.] Thus, for lights that fall close to the abscissa of the MacLeod-Boynton diagram, the colorimetric purity is essentially constant, at 100%, since these lights are either monochromatic or are metamers of monochromatic lights. In colorimetric terms, all that varies along the line is hue angle; indeed, subjectively such lights vary markedly in subjective hue, ranging through yellow green, yellow and orange to red. (There is also, of course, a clear variation in subjective saturation even though colorimetric purity is not varying [3,9].)



**Fig. 1.** Part of the MacLeod–Boynton chromaticity diagram [1]. The dotted line represents the spectrum locus, i.e., the chromaticities of monochromatic lights; R, G, and B mark the chromaticities of the three primaries of the monitor, delimiting the gamut of chromaticities that could be presented. D65 marks the chromaticity of the neutral illuminant to which observers were adapted in the present experiment. Along a horizontal line radial to D65, colorimetric purity is increasing. Along a parallel horizontal line, close to the spectrum locus, where the short-wave cone signal is minimal, the variation is one of hue. Note that in both cases, all that varies along the line is the value of L/(L + M), the relative excitation of the long- and middle-wave cones. Inset in the upper right of the diagram shows the arrangement of our foveal stimulus array: The observer's task is to identify which of the quadrants differs in chromaticity from the other three.

Yet, along both the lines that we have considered, all that is varying is the ratio of excitation of the long-wave (L) and middle-wave (M) cones. By definition, the x axis of the MacLeod-Boynton chromaticity diagram is computed as L/(L + M). The ordinate of the diagram represents the relative excitation of the short-wave (S) cones and is plotted as S/(L + M); thus, the excitation of the short-wave cones is constant along any horizontal line in the diagram [1,7].

These observations sit uneasily with conventional approaches to color vision. Along the long-wave spectrum locus, at low photopic levels of illumination, the normal eye is effectively tritanopic, since the S-cone excitation is close to zero. A common assumption is that the *congenital* tritanope enjoys only two residual sensations (often taken to be reddish and bluish on the basis of studies of unilateral tritanopia [10]), i.e., sensations that vary in their subjective saturation accordingly, as wavelength diverges in one direction or the other from the tritanope's neutral point near 569 nm. Yet the normal observer, under the near-tritanopic conditions of the long-wavelength spectrum locus, experiences a rich range of subjective hues. This feature of human color perception rather rarely attracts interest. We return to the issue in the General Discussion.

### A. Discrimination of Colorimetric Purity and Discrimination of Hue Angle

The feature of the MacLeod-Boynton diagram discussed above offers a fresh way to tackle a question that is currently of interest [11-13]: Is the discrimination of hue angle systematically better than the discrimination of colorimetric purity? That this was so was captured in Judd's term "the super-importance of hue differences" [14,15]: When subjective differences are estimated for surface colors along a radial line in color space-a line along which colorimetric purity varies-they are found to be smaller than those that would be expected from differences in the orthogonal direction, i.e., differences in hue angle. Judd invited his reader to consider a circle in color space centered on the white point and having a radius of *n* units of perceptual distance: The length of the circumference, a hue circle, would not be  $2\pi n$  units of perceptual distance but approximately  $4\pi n$ . There could thus be no possible Euclidean representation of color space in which chromaticities separated by equal distances were always of equal discriminability.

Judd was primarily concerned with supra-threshold color differences and with surface colors, but a general trend for forced-choice hue thresholds to be lower than purity thresholds has also been observed for self-luminous sources (see, e.g., Fig. 5 of [11]). However, any comparison of this kind requires that the two types of threshold should be expressed in a common metric. It would be intrinsically circular, for example, to express purity and hue thresholds in terms of units that have been derived by some other form of perceptual judgments, e.g., units of the Munsell system or of color spaces such CIELUV and CIELAB. Judd made a general statement about the "super-importance of hue" by estimating the total number of jnd's in a hue circle of which the radius was also expressed in jnd's. But to make a meaningful statement about thresholds locally in color space, we need some objective units in which to make the comparison. It is to emphasize the need for an independent and nonsubjective metric that we replace the term "saturation discrimination" in the present text by "discrimination of colorimetric purity."

One way to secure a common metric is to make measurements around a chromaticity that lies on a  $+45^{\circ}$  or  $-45^{\circ}$  line in MacLeod–Boynton space. In this case, the same modulation of the S-cone signal can be combined with the same modulation of the L/(L + M) signal but in different phases for saturation and for hue. Using such a procedure, we found support for the "super-importance of hue" when the observer was adapted to a neutral field and when discrimination was measured for probes of moderate levels of colorimetric purity [12]. However, neither we nor Regan and her colleagues [13] found an advantage for discrimination of hue angle when the chromaticities of the probes were close to the neutral point.

However, it is difficult to establish a common metric for points that lie on some of the most interesting radial lines in MacLeod–Boynton space, i.e., horizontal or vertical lines that align with one or other of the two cardinal axes passing through the white point. Suppose one measures discrimination for colorimetric purity at a point on a horizontal line that passes through the white point. Here, the purity threshold depends on modulation of L/(L + M), but the corresponding hue threshold (measured along an arc of a circle passing through the specified point) will depend predominantly on modulation of the S-cone signal. There is no obvious way to express the two modulations in common units. It would be dangerously circular to adopt for this particular purpose the traditional convention, e.g., [16,17] of scaling the S axis so that thresholds were equated for the two axes at the white point.

Nevertheless, an interesting test of Judd's "super-importance of hue" is offered by the feature of color perception discussed in the preceding section. If we measure thresholds along a horizontal line that passes through the white point of MacLeod-Boynton space, then we measure the discrimination of colorimetric purity alone (Fig. 1). If now we measure thresholds along a second horizontal line, corresponding to the long-wave spectrum locus, we measure discrimination of the hue angle. There is a common metric in the two cases, since the threshold measurements modulate only L/(L + M), and the excitation of the short-wave cones is held constant during any given threshold determination. Unfortunately, there is not an analogous maneuver that can be applied to the vertical axis of the MacLeod-Boynton diagram, i.e., the axis of pure S-cone modulation, for no region of the spectrum locus lies parallel to the vertical axis.

### **B.** Present Experiments

In the present study, we have made forced-choice threshold measurements along horizontal lines in the MacLeod–Boynton diagram. The observer's adaptation was held in a constant neutral state, and sensitivity was probed by brief foveal stimuli, a paradigm classically adopted by Krauskopf and Gegenfurtner [16]. In Experiment 1, we made measurement for values of L/(L + M) greater than that of Illuminant D65, the neutral chromaticity to which our observers were adapted. One of our test lines radiated from the neutral point and modulated only colorimetric purity [Fig. 2(a)]. Ideally, we would like to

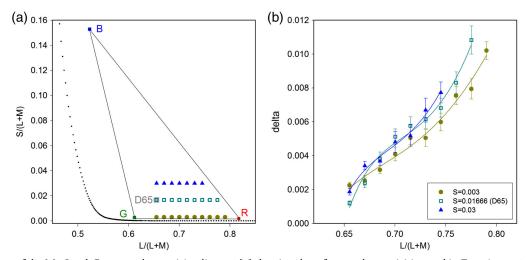
compare these thresholds with thresholds measured for lights that fall on the abscissa of the MacLeod–Boynton diagram. Using an unmodified CRT display, however, it is impossible to place a horizontal set of stimuli actually on the abscissa of the MacLeod–Boynton diagram, since the green phosphor will always give some excitation of the short-wave cones. However, our second horizontal line (set at a very low S-cone excitation value of 0.003) gave nearly constant values of colorimetric purity (see Methods). We also made measurements along a third horizontal line set at an S-cone excitation (0.03) higher than that of the neutral background [Fig. 2(a)]: Along this line, both hue angle and colorimetric purity vary.

In Experiment 2, we made measurements along the horizontal lines for values of L/(L + M) lower than that of D65, i.e., for regions on the left-hand side of MacLeod–Boynton space [Fig. 4(a)]. We have explored this region previously [18], but we now include a horizontal line critical to the present issue, one at a low level of S-cone excitation where colorimetric purity is relatively constant.

### 2. METHODS

### A. Apparatus and Stimuli

The stimuli were presented on a Mitsubishi Diamond Pro 2070 22-in CRT set at a resolution of 1024 × 768 pixels and a frame rate of 100 Hz. It was controlled by a Cambridge Research Systems (CRS; Rochester, Kent, UK) graphics board (model VSG2/5). The output of each gun of the monitor was measured with a silicon photodiode ("OptiCal"; CRS), and the spectral power distribution for each gun at maximal output was measured with a JETI spectroradiometer model Specbos 1201 (JETI Technische Instrumente GmbH, Jena, Germany). The resulting gamma functions were used to generate the required chromaticities and luminances on the screen. The VSG system allowed chromaticities to be specified with a precision of 15 bits



**Fig. 2.** (a) Part of the MacLeod–Boynton chromaticity diagram [1] showing the reference chromaticities used in Experiment 1. Discrimination thresholds were measured along a horizontal axis for chromaticities straddling each referent. The dotted line represents the spectrum locus and R, G, and B mark the chromaticities of the monitor primaries. D65 marks the chromaticity of the neutral illuminant to which observers were adapted. (b) Average thresholds obtained in Experiment 1. The ordinate represents the difference in L/(L + M) values of the tests and distractors at threshold; the abscissa represents the L/(L + M) value of the referent. The symbols correspond to those used in panel (a): the open squares correspond to purity discrimination, the circles correspond to discrimination of hue angle, and the triangles correspond to a mixed case. The error bars represent ±1SEM and are based on between-observer variance. The fitted functions are inverse third-order polynomials and have no theoretical significance.

per gun. Chromaticities were expressed in terms of the chromaticity diagram of [1] using the 2-deg cone fundamentals of DeMarco and colleagues [19]. The diagram represents a plane of equal luminance for the Judd<sub>(1951)</sub> Observer, where luminance is equal to the sum of the long- and middle-wave cone excitations. The monitor was turned on for 40 min before calibrations and before experiments to allow the outputs to reach a steady state [20].

Viewing was binocular from a distance of 570 mm and observers wore their normal corrections. Throughout the experiments, a uniform steady background field was present, with a luminance of 10 cd m<sup>-2</sup> and a spectral power distribution metameric to CIE Illuminant D65 [8]; the room was otherwise dark. The inset of Fig. 1 illustrates the arrangement of the target stimulus, which consisted of a disk subtending 2 deg of visual angle and divided into four quadrants. The oblique dividing lines were 2 pixels (approximately 4.44 arcmin) wide and had the chromaticity and luminance of the background. Their function was to enhance discrimination, since a small gap or luminance edge between stimulus fields is known to enhance chromatic discrimination [21–25]. For the same reason, a small luminance pedestal was introduced to the target quadrants: Their average luminance was set to be 10% above the background (i.e., 11 cd m<sup>-2</sup>), but the luminance of each quadrant was jittered independently and randomly in the range  $\pm 1\%$  to prevent discrimination on the basis of small luminance differences. Fixation was guided by a diamond-shaped array of black dots, which was always present. The target was centered within the fixation array and had a duration of 180 ms. The latter value represents a compromise: Longer durations favor chromatic discrimination [26-28] but potentially increase the extent of chromatic adaptation that occurs during a block of trials for probe stimuli of high purity.

### **B.** Procedures

Discrimination thresholds were measured at a number of referent chromaticities that lay along horizontal lines in the MacLeod–Boynton chromaticity diagram, i.e., along the lines on which the excitation of the short-wave cones is held constant, and only the ratio of long- and middle-wave cone excitation is varied. In Experiment 1, we used referents that had L/(L + M) coordinates higher than that of Illuminant D65; in Experiment 2, the referents had lower values than that of D65. The referents used in the two experiments are plotted in Figs. 2(a) and 4(a). These conditions were chosen on the basis of pilot experiments. The total number of referents on each line was constrained by the gamut of the display, but with this restriction the same L/(L + M) values were used for all the horizontal lines tested within a given experiment.

In both experiments, one horizontal line passed through D65, giving a range of colorimetric purity of 0% to 39.5% in each case. We chose a second line in each case to have an S-cone excitation of 0.003 (in the units of the classical MacLeod–Boynton diagram), the closest that our conventional CRT monitor would allow us to approach to the abscissa of the diagram. In both experiments, purity was almost constant along this line, ranging from 82.12% to 82.22% in Experiment 1 and from 82.22% to 82.74% in Experiment 2.

In Experiment 1, we added a third line [see Fig. 2(a)] at an S-cone excitation of 0.03, which modulated both hue angle and colorimetric purity (the latter in the range 1.58% to 31.22%); in Experiment 2, we introduced three such additional lines, at S-cone excitations of 0.03, 0.05, and 0.075 (with purities 1.58%–29.78%, 3.96%–25.34%, and 6.92%–23.66%, respectively).

Observers adapted to the neutral background for 1 min at the beginning of each experimental run. Their task was a four-alternative spatial forced choice: On each trial, three of the quadrants of the target array had the same chromaticity, while one, chosen at random, had a different chromaticity. The observers were asked to press the corresponding button in a diamond-shaped array of four buttons. Auditory feedback was given on each trial. In both experiments, the positive quadrant always had a higher L/(L + M) value than the three distractors; in all conditions, however, the instructions to the observers were expressed in terms of "odd-one-out" rather than in terms of phenomenological qualities. The referent chromaticity was never itself presented: The chromaticities of the target and the distractors "straddled" that of the referent [11]. The target chromaticity (expressed as the MacLeod-Boynton l coordinate) was obtained by multiplying the referent chromaticity by a factor and the distractor chromaticity by dividing by the same factor, and it was the factor that was adjusted in successive trials according to an adaptive staircase procedure and depending on the observer's accuracy [11]. The step size of the staircase was 10% of the fractional part of the factor. The staircase tracked 79.4% correct [29]. The staircase terminated after 15 reversals, and the threshold was estimated from the last 10 reversals, being expressed as the average difference in chromaticity between target and distractors.

In any one experimental run (taking  $\sim 30$  min), the referents lay along a single horizontal line in the MacLeod–Boynton diagram (i.e., S-cone excitation was constant). In some runs, this line passed through the chromaticity of Illuminant D65, meaning that discrimination of colorimetric purity was measured. In other cases, it ran close to the long-wave spectrum locus, meaning that predominantly hue discrimination was measured. In further cases, the S-coordinate of the line was higher than that of D65, and the stimuli were modulated in both purity and hue. Within a given run, different referent chromaticities were tested in different blocks of trials in random order. All conditions were tested six times, in independent runs, usually on different experimental days. The first run for each condition was treated as practice and not used in the analysis. Thus, any given threshold is based on five independent estimates for each observer.

### C. Observers

In Experiment 1, there were six observers (four female); in Experiment 2, there were also six observers (five female). All observers had normal color vision. The experiments were approved by the Psychology Research Ethics Committee of Cambridge University (PRE.2018.078). Participants also gave informed consent.

### 3. EXPERIMENT 1: RESULTS AND DISCUSSION

In Experiment 1, we examined three horizontal lines in the MacLeod–Boynton diagram and measured thresholds at referents that represented L-cone pedestals relative to the *l* coordinate of Illuminant D65 [see Fig. 2(a)]. One line corresponded to purity discrimination and one to discrimination of hue angle; along the third, both hue angle and colorimetric purity varied. In Fig. 2(b), we plot the resulting average thresholds obtained against the L/(L + M) value of the referent, i.e., against the *l* coordinate of the MacLeod–Boynton diagram. Several features of the results are apparent on first inspection:

- (i) The three functions are rather similar. At higher values of L/(L + M), the thresholds for discrimination of hue angle (circles) do lie below those for purity discrimination (open squares), but the differences are not large. Certainly, the functions do not differ by a factor of 2.
- (ii) In the case of purity discrimination, thresholds are lowest at the chromaticity of the neutral adapting field.
- (iii) Thresholds rise a bit more steeply for purity discrimination than for discrimination of hue angle; thus, while thresholds are lowest for purity at the referent with the lowest L/(L + M) coordinate, at higher levels the thresholds for purity (open squares) lie slightly but systematically above those for S/(L + M) = 0.003 (circles).
- (iv) At intermediate values of L/(L + M), an inflexion is apparent in the function for purity discrimination.

A repeated-measures two-way ANOVA was performed with factors LM-LEVEL and S-CONE LEVEL. Since the ranges of referents used were constrained by the monitor gamut [see Fig. 2(a)], the analysis was restricted to (L/(L + M)) values common to the three data sets. After the Greenhouse–Geisser correction, the factor LM-LEVEL was highly significant (F[1.80] = 96.77, p < 0.001), while the factor S-CONE LEVEL was only marginally significant (F[1.88] = 6.02, p = 0.022). There was also a significant interaction between the two factors, a result that reflects the increased steepness of the function for purity discrimination: (F[2.97] = 6.15, p = 0.006).

We performed a similar analysis comparing only the data for the line passing through D65 and the line close to the abscissa. This allowed us to include a larger range of L/(L + M) values where thresholds were available for both these lines (see Fig. 2). After the Greenhouse–Geisser correction, the factor LM-LEVEL was highly significant (F[2.093] = 104.05, p < 0.001), and the factor S-CONE LEVEL was marginally significant (F[1] = 9.66, p = 0.027). The interaction was highly significant: (F[3.34] = 9.027, p = 0.001). The comparison of these two lines is central to the present paper. We return to these results in the General Discussion.

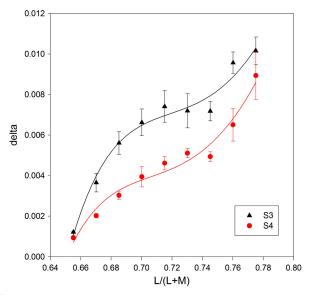
# A. Optimal Discrimination at the Adapting Chromaticity

The finding that thresholds are lowest at the chromaticity of the background [finding (ii) above] is probably the most fundamental and robust characteristic of chromatic discrimination, e.g., [30–34]. To explain a result of this kind, in the case of both luminance and chromaticity, it is usually assumed that the response-versus-intensity curve of a sensory channel will shift so that its steepest part corresponds to the current level of the background [35,36], and such a shift was shown explicitly for chromatic channels by De Valois and colleagues [37]. Such effects are perhaps seen most clearly under conditions such as the present ones, where the target is brief; thus, there is minimal perturbation of the current state of adaptation, which is in contrast to classical studies of purity and hue discrimination, such as those of Jones and Lowry [2], Martin [3,38], Wright [39], and MacAdam [40]. In the latter investigations, the observer was able to inspect the discriminanda for an extended period, and the adaptive state was therefore likely to have been different when thresholds were measured at different loci in the chromaticity diagram.

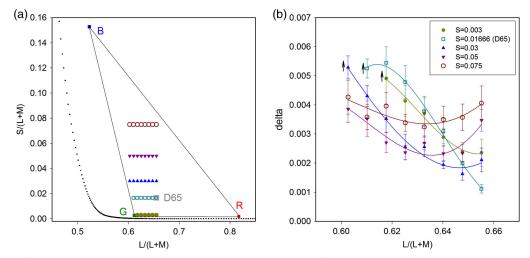
Interestingly, for the other two horizontal lines in Experiment 1, the thresholds we measured were also lowest when the target had an L/(L + M) value identical to that of D65, although the absolute values of these thresholds are higher than the equivalent threshold for the line that modulated only colorimetric purity.

#### **B.** Inflexion in the Function for Purity Discrimination

The inflexion seen in the average results for purity discrimination is particularly visible in the data for some individual observers. We show examples in Fig. 3 for two observers who differ in their absolute sensitivities to purity differences. We have regularly seen such an inflexion in pilot studies. It is unexpected, in that a single positively accelerated function might be predicted if an underlying neural channel is driven farther from its equilibrium point into a saturating region of its response function ("saturation" is used here in its neurophysiological sense.) The inflexion recalls the double branches that, classically in visual science, have suggested a transition between detection "mechanisms" or neural channels [41,42]. In the suspicion that the underlying channels might have different time or space constants, we have spent time examining whether one curve



**Fig. 3.** Results from Experiment 1 for two individual observers who show a marked inflexion in their discrimination function for purity discrimination. Error bars represent  $\pm 1$  SEM and are based on within-observer variability. Other details as for Fig. 2(b).



**Fig. 4.** (a) Part of the MacLeod–Boynton chromaticity diagram [1] showing the reference chromaticities used in Experiment 2. Discrimination thresholds were measured along a horizontal axis for chromaticities straddling each referent. The dotted line represents the spectrum locus and R, G, and B mark the chromaticities of the monitor primaries. "D65" marks the chromaticity of the neutral illuminant to which observers were adapted. (b) Average thresholds obtained in Experiment 2. The ordinate represents the difference in L/(L + M) values of the tests and distractors at threshold; the abscissa represents the L/(L + M) value of the referent. The symbols correspond to those used in panel (a): the open squares correspond to purity discrimination and the solid circles to discrimination of hue angle. Note that purity discrimination gives the steepest function, with the lowest thresholds close to D65 and very high thresholds at high purities. An upwards-pointing arrow adjacent to some data points indicates that some observers were unable to set a threshold within the monitor gamut; thus, the true average threshold lies above this point. The fitted functions are inverse third-order polynomials and have no theoretical significance.

could be displaced relative to the other by varying the duration or the size of the targets but have not so far found shifts of this kind.

One clue to the source of the inflexion might be seen in the phenomenological reports of observers: In the higher range of referents, all the target arrays appear of similar, and high, phenomenological saturation, but the discrepant quadrant in any given array is still detectable. This might suggest either (i) there is a concurrent laterally acting process, whereby the four quadrants act to set the gain control on a given trial, or (ii) over the course of a block of trials at the same purity level, there is local adaptation that cumulates in time across trials, despite the brevity of the targets and the presence of the neutral background between presentations. Both hypotheses are unconvincing, since we have seen such inflexions for purity discrimination in our separate work on comparison at a distance, where the targets are well separated in space and where they fall at different parafoveal locations on successive trials: For some observers in those experiments (see [43], especially Fig. 3(a) and the discussion at end of Section 4), the purity thresholds were almost constant for referents with L/(L + M) values in the range 0.69 to 0.73, i.e., the region in which the function is almost flat for Observer S3 in the present study (Fig. 3).

### 4. EXPERIMENT 2: RESULTS AND DISCUSSION

In a second experiment, we measured discrimination along horizontal lines at values of L/(L + M) lower than that of D65, i.e., on the left-hand side of the MacLeod–Boynton diagram. In an earlier study of this region (Expt 1 of [18]), we made measurements only for S-cone levels higher than or equal to that of Illuminant D65. Here, we introduce a horizontal line more relevant to the present issue, the line for an S-cone excitation of only 0.003 [Fig. 4(a), solid circles], which lies close to the spectrum locus and is relatively constant in colorimetric purity. We also measured thresholds along a line passing through D65, where colorimetric purity ranged from 0% to 39.5% and hue angle was constant and along three lines with higher values of S-cone excitation (S = 0.03, 0.05, 0.075). The gamut of the CRT constrains the range of L/(L + M) values to be smaller than that tested in Experiment 1 but allows a greater range of levels of S-cone excitation [see Fig. 4(a)].

The average thresholds for six observers are shown in Fig. 4(b), plotted against the L/(L + M) value of the referent. The function representing purity discrimination (open squares) is the steepest: As expected, the lowest threshold falls at the chromaticity of Illuminant D65; equally, however, the *highest* threshold obtained in this experiment is found on the same purity line at the lowermost values of L/(L + M). The set of referents with the lowest S-cone value (S = 0.003), where colorimetric purity discrimination, except that the threshold is higher at the L/(L + M) value of Illuminant D65; at low values of L/(L + M), the thresholds are lower than for purity discrimination, i.e., the overall function is less steep. This result recalls the similar finding in Experiment 1.

The functions for higher levels of S-cone excitation are flatter. At L/(L + M) values close to those of Illuminant D65, thresholds are elevated relative to the horizontal line that passes through D65. At low values of L/(L + M), however, the best discrimination is found for a level of S-cone excitation (0.05) that is approximately three times higher than the value at D65; at this level, the thresholds are half those for purity discrimination. Although the functions of Fig. 4(b) are at first sight complex, it is clear that there is a large range of chromaticity space where an increase in S-cone excitation improves discrimination, even though the discriminanda differ only in the ratio of excitation of long- and middle-wave cones.

A repeated-measures two-way ANOVA with factors LM-LEVEL and S-CONE LEVEL was performed for the range of L/(L + M) values, where thresholds could be measured for all observers. After Greenhouse–Geisser corrections, both factors were highly significant: Factor LM-LEVEL (5 levels) F[1.702] = 19.70, p = 0.001 and factor S-CONE LEVEL F[2.046], p = 0.001. There was also a significant interaction between the two factors: F[2.021] = 21.31, p < 0.001, a result reflecting the change in slope of the functions as the S-cone excitation was varied.

We performed a similar analysis comparing only the data for the line passing through D65 and the line close to the abscissa. After Greenhouse–Geisser correction, the factor LM-LEVEL was highly significant (F[1.436] = 49.926, p < 0.001), but the factor S-CONE LEVEL was not significant (F[1] = 4.186, p = 0.096). The interaction was significant: (F[1.76] = 11.087, p = 0.005).

### 5. GENERAL DISCUSSION

### A. Super-Importance of Hue?

Is it a general law that purity discrimination is always poorer than hue discrimination? Is it quantitatively the case that they differ by a factor of 2, as Judd suggests? We can firmly give a negative answer to both questions.

Perhaps there does exist an intermediate level of purity at which the circumference of the hue circle has a length of  $4\pi n$  just noticeable differences, where *n* is the length in jnd's of the radius of the hue circle. But this cannot concurrently be the case at very high purities (i.e., for monochromatic lights), since the classical results of Tyndall [44] and Haase [45] show that there is little change in hue thresholds as purity is increased from 0.6 to 1.0; indeed, in the region of 460 nm, the arc of the hue circle exhibits *fewer* jnd's at high purities than it does at very low purities [46].

Furthermore, in an earlier study ([12], Fig. 6), when measurements were made at points on  $\pm 45^{\circ}$  lines in the MacLeod–Boynton diagram and when all that varied was the phase relationship of S and L/(L + M) modulations, we found conditions where purity discrimination was better than hue discrimination. This was the case when the reference chromaticity was close to the neutral point and lay in either the upper-right or lower-left quadrant of the MacLeod–Boynton diagram. Similar results have been reported by Regan and colleagues [13]. See also Figs. 2(b) and 4(b) in the present study.

The present experiments compared purity discrimination along a horizontal line in the MacLeod–Boynton diagram with discrimination near the dichromatic region of the spectrum locus, where only hue angle is substantially changing. For increments in L/(L + M) relative to D65 (Experiment 1), there is a small advantage for hue discrimination, but the difference is not large and is restricted to high values of L/(L + M). Results are similar in the case of reference chromaticities at L/(L + M)values below that of D65 (Experiment 2): Again, close to the chromaticity of D65, thresholds are lower for purity discrimination than for hue angle, but they rise more steeply as purity increases.

We conclude that thresholds are often lower for discriminating hue angle than for discriminating colorimetric purity, but the rule is not a general one and certainly the quantitative relationship of the two thresholds varies widely.

### B. Surface Colors versus Self-Luminous Colors: Mongean Noise

Judd's concept of the "super-importance of hue" was largely based on judgments of surface colors under conditions where the presentation time was much longer, viewing was binocular, and the head was not fixed, i.e., conditions of interest to those concerned with practical tolerances in industry and commerce.

In the real world, the light reaching the eye from even a matte surface is a mixture of two components: Light that has been spectrally shaped by selective absorption by the pigments of the object and light that (in the case of most nonmetallic materials) represents the unmodified illuminant [47]. The ratio of the two components varies with angle of viewing, even when no explicit highlights are present. Thus, any surface offers a distribution of chromaticities to the eye (and often a different distribution to each eye); further, these distributions are necessarily extended along a line of purity. The existence of these distributions was first made explicit by Gaspard Monge [48,49] (see [50]). Monge himself realized that they could be used to recover the chromaticity of the illuminant and so could support color constancy. If more than one object is present in a scene, the chromaticity of the illuminant can be recovered, in modern terms, by triangulation within chromaticity space. Several modern accounts of color constancy have developed a hypothesis of this kind, e.g., [50-54]. For our present purpose, however, the interest lies in the noise that the distributions of chromaticity introduce into discriminations of surface colors. This Mongean noise is physical and will normally be greater for purity than for hue. It is an interesting question and one deserving to be explored, i.e., whether this type of physical noise is a significant factor in discriminations of surface colors. It is absent, of course, for colors presented on a display, and this is a possible explanation for why the difference between purity discrimination and hue discrimination is less marked in the case of self-luminous stimuli.

Equally, however, in so far as purity discrimination *is* the poorer of the two, even in the case of self-luminous colors, the presence of Mongean noise in natural scenes may offer an ecological explanation of why our visual system exhibits this property: It may be the hue of particular objects that we use to identify them in our world rather than their exact saturation, since the latter varies as chromaticity varies along a line joining the illuminant color to the object color. So saturation is a less reliable identifier [11].

### C. Are There Different Mechanisms for the Discrimination of Colorimetric Purity and of Hue Angle?

On the basis of Judd's "super-importance of hue," Kuehni [55,56] suggested, however, that "different mechanisms are

responsible for hue and chroma perception." He writes, "In practical terms, there appear to be two independent systems: one that assesses changes in the ratio of two opponent color signals (assuming a two-process hue detection system) and the other changes in the size of the vector sum of the opponent system (indicative of contrast) ... The two seemingly operate independently of each other and are not connected in a Euclidean sense." Regan and colleagues [13] empirically tackled the issue by asking whether the two putative mechanisms can be independently adapted. The authors measured thresholds for detecting stimuli that either were modulated in purity (stimuli corresponding to excursions on radial lines from the white point) or were predominantly modulated in hue (stimuli that described a diamond-shaped trajectory, centered on the white point). Observers were then adapted to one or the other type of modulation presented at a supra-threshold level. Detection of a given type of modulation was not selectively impaired by an adapting modulation of the same type. Regan and colleagues conclude that they "did not find psychophysical evidence for a neural channel that extracts hue thresholds more effectively than the neural channel or channels that determine saturation thresholds."

In exactly what sense might saturation and hue be represented by different channels? At what level in the visual system would such parallel channels arise? In one twentieth-century theoretical tradition, subjective saturation is derived only centrally, by taking the ratio of signals in chromatic channels to the total activity in "luminance" and chromatic channels [9,57,58]. Thus, for example, Mahon and Vingrys write: "... saturation processing requires the recombination of information from multiple channels..." [59]. In an important sense, however, the neural response to purity could be seen as more basic than that to hue. It is conventionally thought that chromatic analysis at early stages of the visual system begins with dichromatic channels that draw signals of opposite sign (excitatory or inhibitory) from different classes of cone. Such channels are in an equilibrium state in the presence of a steady adapting field, and their response to a new stimulus is greater the greater the change in the ratio of cone inputs, e.g., [37]. If the adapting field is neutral, then the channel in itself essentially signals purity [60]. In standard accounts, the axes of the MacLeod-Boynton diagram correspond to two dichromatic channels of this kind, e.g., [61-63]. A signal corresponding to the  $\gamma$  axis is thought to be carried by the small bistratified type of retinal ganglion cells [64], which project to the koniocellular laminae of the lateral geniculate nucleus [65,66], and a signal representing the ratio of long- and middle-wave cone excitation, corresponding to the x axis of the diagram, is carried by midget ganglion cells, which project to the parvocellular laminae of the LGN, e.g., [63,67].

To achieve the full range of hue discrimination, secondary stages of analysis must require the comparison of the signals in the early, dichromatic channels. Thus, it then seems odd that purity discrimination along noncardinal radial lines in the MacLeod–Boynton diagram should be poorer than discrimination in directions orthogonal to the hue circle. In our earlier paper [12], we offered an explanation that does not require wholly independent channels for saturation and hue. We drew upon the evidence that retinal and cortical neurons exhibit correlated variations in excitability, the correlation being stronger the greater the proximity of the paired cells. In particular, correlations have been found in the primate retina between the responses of small bistratified ganglion cells and those of nearby ON midget cells [68]. In the case of purity discrimination, the signals in the two channels increase or decrease together; thus, it is difficult therefore to discriminate signals from variations due to noise. In hue discrimination, however, it is the ratio of the two signals that matters, and this is relatively independent of correlated variations in the two channels.

In the present experiments, however, when discrimination along the spectrum locus is compared with the equivalent purity discrimination, thresholds do not differ to the extent that they do when discrimination is measured along 45° lines. This finding makes sense, in so far as correlated noise in the two early channels is not relevant here. In this case, the purity thresholds and the hue thresholds depend essentially on the same L/M signal.

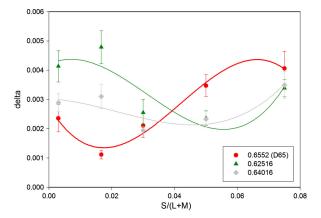
### **D.** Interactions between Cardinal Channels

Our measurements, particularly on the left-hand side of the MacLeod–Boynton diagram (Experiment 2; Fig. 4), reveal a strong interdependence of the two "cardinal" axes, an interaction we have observed previously [18]. Our discriminanda differed only in the ratio of L and M excitation; in this region, however, the measured thresholds depended critically upon the S-cone pedestal that was present. The present results only add to already extensive psychophysical evidence that S-cone signals interact with L and M signals at detection threshold ([16] Fig. 14, [69–71]).

Moreover, the effect of the S-cone excitation depends on the L/(L + M) value of the reference chromaticity. Thus, it would not be plausible simply to suppose that any change in the S/(L + M) signal adds noise at a central site when it is combined with an L/M signal. It is true that, close to the L/(L + M) value of the adapting field, both an increment and a decrement in S/(L + M) elevate threshold relative to the case (at the chromaticity of D65) where S/(L + M) is held constant when the pedestal is presented. Yet the opposite is the case at lower values of L/(L + M). In this case, both positive and negative changes in S/(L + M) are associated with lower thresholds [Experiment 2, Fig. 4(b)]. Although the data of Experiment 1 are more limited, a similar interaction is seen for decrements in S/(L + M).

The interaction discussed in the preceding paragraph is particularly clear in Fig. 5, where we re-plot data from Fig. 4(b), now showing thresholds against the S/(L + M) value of the referent chromaticity at which they were measured. Data are shown for three vertical cuts through the MacLeod–Boynton diagram. The thresholds along a vertical line at the L/(L + M)value of D65 (circles) are almost a mirror image of those along a vertical line at L/(L + M) = 0.625 (triangles). At an intermediate L/(L + M) value (0.64) the function is intermediate in form and is more nearly flat; perhaps, near this value of L/(L + M), some total signal is near-constant, or two opposed influences on the threshold remain in nearly the same ratio.

Are interactions between cardinal axes to be explained by noncardinal channels that combine S-cone signals synergistically with M- or L-cone input? Such channels have often been



**Fig. 5.** Thresholds from Experiment 2 plotted against the S/(L + M) value of the referent chromaticity. Data are shown for three vertical cuts through the MacLeod–Boynton diagram. The effects of increasing S-cone excitation along a vertical line through D65 (circles) are almost a mirror image of those for a vertical line at L/(L + M) = 0.625 (triangles). At an intermediate value of L/(L + M), the function is intermediate in form and more nearly flat (diamonds).

postulated at a central stage. There have been, however, occasional but recurrent reports of cells in the primate retina and LGN that draw synergistic inputs from L cones and S cones or from M cones and S cones, e.g., [72–74]. Some of the psychophysical variations in threshold that we observe [see e.g., Fig. 4(b)] are so large that it is plausible that they arise at any early stage in the system. It now does seem established that a subset of OFF- (but not ON-) midget ganglion cells draw input from S-cones via an S-cone OFF bipolar [75,76]. Recent work from Dacey's laboratory shows that, physiologically, such cells combine inputs along noncardinal axes [77].

### E. Colors Seen under Tritanopic Conditions

In the Introduction, we remarked on a noteworthy feature of human color perception: that, under nominally tritanopic conditions, on the long-wave spectrum locus, we see a rich range of hues, i.e., greens, citrons, yellows, oranges, and reds. Should we suppose that a congenital tritanope experiences a similar range of hues? Results from two cases of acquired unilateral tritanopia [10,78] do not give entirely clear results, as discussed by Broackes [79] in his general review of the hue sensations experienced by dichromats. Asymmetric matches, between good and tritan eyes, suggested that both cases, in tritanopic viewing, experienced blue as the dominant sensation at wavelengths shorter than their neutral point. At longer wavelengths, Graham's case called 617 nm "pink" or "golden pink" and 640 nm "reddish." The case examined by Alpern and colleagues saw long wavelengths as predominantly reddish, but, when allowed to adjust the wavelength and purity of lights in the normal eye, he made matches to desaturated yellow-greens, yellows, oranges, and reds. These long-wave matches lay on a curve in the CIE (1931) chromaticity diagram. It is not necessarily safe to extrapolate from unilateral to congenital cases ([80]; [81], pp. 631-632); however, there are certainly no grounds to rule out the possibility that a congenital tritanope experiences more than one hue at wavelengths longer than his or her neutral point.

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### REFERENCES

- D. I. A. MacLeod and R. M. Boynton, "Chromaticity diagram showing cone excitation by stimuli of equal luminance," J. Opt. Soc. Am. 69, 1183–1186 (1979).
- L. A. Jones and E. M. Lowry, "Retinal sensibility to saturation differences," J. Opt. Soc. Am. 13, 25–34 (1926).
- L. C. Martin, F. L. Warburton, and W. J. Morgan, "Determination of the sensitiveness of the eye to differences in the saturation of colours," Reports of the Committee upon the Physiology of Vision XIII (Medical Research Council, 1933).
- J. W. Onley, C. L. Klingberg, M. J. Dainoff, and G. B. Rollman, "Quantitative estimates of saturation," J. Opt. Soc. Am. 53, 487–493 (1963).
- F. Schiller, M. Valsecchi, and K. R. Gegenfurtner, "An evaluation of different measures of color saturation," Vision Res. **151**, 117–134 (2018).
- W. Kurtenbach, C. E. Sternheim, and L. Spillmann, "Change in hue of spectral colors by dilution with white light (Abney effect)," J. Opt. Soc. Am. 1A, 365–372 (1984).
- V. C. Smith and J. Pokorny, "The design and use of a cone chromaticity space: a tutorial," Color Res. Appl. 21, 375–382 (1996).
- 8. G. Wyszecki and W. S. Stiles, Color Science (Wiley, 1982).
- K. Fuld, "The contribution of chromatic and achromatic valence to spectral saturation," Vision Res. 31, 237–246 (1991).
- M. Alpern, K. Kitahara, and D. H. Krantz, "Perception of color in unilateral tritanopia," J. Physiol. 335, 683–697 (1983).
- M. V. Danilova and J. D. Mollon, "Symmetries and asymmetries in chromatic discrimination," J. Opt. Soc. Am. A 31, A247–A253 (2014).
- M. V. Danilova and J. D. Mollon, "Superior discrimination for hue than for saturation and an explanation in terms of correlated neural noise," P. R. Soc. B 283, 20160164 (2016).
- S. E. Regan, R. J. Lee, D. I. A. MacLeod, and H. E. Smithson, "Are hue and saturation carried in different neural channels?" J. Opt. Soc. Am. A 35, B299–B308 (2018).
- D. B. Judd, "Ideal color space. II the super-importance of hue differences and its bearing on the geometry of color space," Palette 30, 21–28 (1969).
- 15. D. B. Judd, "Ideal color space," Color Eng. 8, 37-52 (1970).
- J. Krauskopf and K. Gegenfurtner, "Color discrimination and adaptation," Vision Res. 32, 2165–2175 (1992).
- M. J. Sankeralli and K. T. Mullen, "Ratio model for suprathreshold hue-increment detection," J. Opt. Soc. Am. A 16, 2625–2637 (1999).
- M. V. Danilova and J. D. Mollon, "Cardinal axes are not independent in color discrimination," J. Opt. Soc. Am. A 29, A157–A164 (2012).
- P. DeMarco, J. Pokorny, and V. C. Smith, "Full-spectrum cone sensitivity functions for X-chromosome-linked anomalous trichromats," J. Opt. Soc. Am. A 9, 1465–1476 (1992).
- J. D. Mollon and M. R. Baker, "The use of CRT displays in research on colour vision," in *Colour Vision Deficiencies XII*, B. Drum, ed. (Kluwer Academic, 1995), pp. 423–444.
- R. Hilz and C. R. Cavonius, "Wavelength discrimination measured with square-wave gratings," J. Opt. Soc. Am. A 60, 273–277 (1970).
- F. Malkin and A. Dinsdale, "Colour discrimination studies in ceramic wall-tiles," in *Color Metrics*, J. J. Vos, L. F. C. Friele, and P. L. Walraven, eds. (Institute for Perception TNO, 1972), pp. 238–253.

- R. M. Boynton, M. M. Hayhoe, and D. I. A. MacLeod, "The gap effect: chromatic and achromatic visual discrimination as affected by field separation," Opt. Acta 24, 159–177 (1977).
- R. T. Eskew, "The gap effect revisited: slow changes in chromatic sensitivity as affected by luminance and chromatic borders," Vision Res. 29, 717–729 (1989).
- M. V. Danilova and J. D. Mollon, "The gap effect is exaggerated in the parafovea," Vis. Neurosci. 23, 509–517 (2006).
- 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).
- J. E. Thornton and E. N. Pugh, Jr., "Red/green color opponency at detection threshold," Science 219, 191–193 (1983).
- B. B. Lee, "Sensitivity to chromatic and luminance contrast and its neuronal substrates," Curr. Opin. Behav. Sci. 30, 156–162 (2019).
- G. B. Wetherill and H. Levitt, "Sequential estimation of points on a psychometric function," British J. Math. Statist. Psych. 18, 1–10 (1965).
- G. N. Rautian and V. P. Solov'eva, "Vlijanie svetlogo okrugenija na ostrotu cvetorazlochenija," Dokl. Akad. Nauk SSSR 95, 513–515 (1954).
- J. M. Loomis and T. Berger, "Effects of chromatic adaptation on color discrimination and color appearance," Vision Res. 19, 891–901 (1979).
- J. Krauskopf and K. Gegenfurtner, "Colour discrimination under constant adaptation," Perception 17, 352 (1988).
- E. Miyahara, V. C. Smith, and J. Pokorny, "How surrounds affect chromaticity discrimination," J. Opt. Soc. Am. A 10, 545–553 (1993).
- V. C. Smith and J. Pokorny, "Color matching and color discrimination," in *The Science of Color*, S. K. Shevell, ed. (Elsevier, 2003), pp. 103–148.
- K. J. W. Craik, "The effect of adaptation on differential brightness discrimination," J. Physiol. 92, 406–421 (1938).
- A. L. Byzov and L. P. Kusnezova, "On the mechanisms of visual adaptation," Vision Res. 11, 51–63 (1971).
- R. L. De Valois, I. Abramov, and W. R. Mead, "Single cell analysis of wavelength discrimination at the lateral geniculate nucleus in the macaque," J. Neurophysiol. **30**, 415–433 (1967).
- L. C. Martin, F. L. Warburton, and W. J. Morgan, "Some recent experiments on the sensitiveness of the eye to differences in the saturation of colours," in *Discussion on Vision* (Physical and Optical Societies, 1932), pp. 92–100.
- W. D. Wright, "The sensitivity of the eye to small colour differences," Proc. Phys. Soc. 53, 93–112 (1941).
- D. L. MacAdam, "Visual sensitivities to color differences in daylight," J. Opt. Soc. Am. 32, 247–281 (1942).
- W. S. Stiles, "The directional sensitivity of the retina and the spectral sensitivities of the rods and cones," Proc. R. Soc. B 127, 64–105 (1939).
- W. S. Stiles, "Color vision: the approach through increment threshold sensitivity," Proc. Natl. Acad. Sci. USA 45, 100–114 (1959).
- M. V. Danilova and J. D. Mollon, "Cerebral iconics: how are visual stimuli represented centrally in the human brain?" J. Opt. Technol. 85, 515–520 (2018).
- 44. E. P. T. Tyndall, "Chromaticity sensibility to wave-length difference as a function of purity," J. Opt. Soc. Am. 23, 15–24 (1933).
- G. Hasse, "Bestimmung der Farbtonempfindlichkeit des menslichen Auges bei verschiedenen Helligkeiten und Sättigungen. Bau eines empfindlichen Farbpyrometers," Ann. Phys. 412, 75–105 (1934).
- J. D. Mollon and O. Estévez, "Tyndall's paradox of hue discrimination," J. Opt. Soc. Am. 5A, 151–159 (1988).
- S. A. Shafer, "Using color to separate reflection components," Color Res. Appl. 10, 210–218 (1985).
- G. Monge, "Mémoire sur quelques phénomènes de la vision," Ann. Chim. 3, 131–147 (1789).
- G. Monge, Géométrie Descriptive; Suivie d'une Théorie des Ombres et de la Perspective, extraite des papiers de l'auteur (Bachelier, 1838).
- 50. J. D. Mollon, "Monge," Vis. Neurosci. 23, 297-309 (2006).
- H.-C. Lee, "Method for computing the scene-illuminant chromaticity from specular highlights," J. Opt. Soc. Am. A 3, 1694–1699 (1986).

- M. D'Zmura and P. Lennie, "Mechanisms of color constancy," J. Opt. Soc. Am. A 3, 1662–1671 (1986).
- A. C. Hurlbert, "Computational models of colour constancy," in Perceptual Constancy: Why Things Look as They Do, V. Walsh and J. Kulikowski, eds. (CUP, 1998).
- R. J. Lee and H. E. Smithson, "Low levels of specularity support operational color constancy, particularly when surface and illumination geometry can be inferred," J. Opt. Soc. Am. A 33, A306–A318 (2016).
- 55. R. G. Kuehni, Color Space and Its Divisions (Wiley, 2003).
- R. G. Kuehni, Color: An Introduction to Practice and Principles (Wiley, 2005).
- L. M. Hurvich and D. Jameson, "An opponent-process theory of color vision," Psychol. Rev. 64, 384–404 (1957).
- 58. L. M. Hurvich, Color Vision (Sinauer, 1981).
- L. E. Mahon and A. J. Vingrys, "Normal saturation processing provides a model for understanding the effects of disease on color perception," Vision Res. 36, 2995–3002 (1996).
- R. L. DeValois and R. T. Marrocco, "Single cell analysis of saturation discrimination in the macaque," Vision Res. 13, 701–711 (1973).
- A. M. Derrington, J. Krauskopf, and P. Lennie, "Chromatic mechanisms in lateral geniculate nucleus of macaque," J. Physiol. 357, 241–265 (1984).
- J. D. Mollon, "Cherries among the leaves: The evolutionary origins of color vision," in *Color Perception: Philosophical, Psychological, Artistic and Computational Perspectives*, S. Davis, ed. (2000), pp. 10–30.
- B. B. Lee, P. R. Martin, and U. Grunert, "Retinal connectivity and primate vision," Prog. Retin. Eye Res. 29, 622–639 (2010).
- D. M. Dacey and B. B. Lee, "The 'blue-on' opponent pathway in primate retina originates from a distinct bistratified ganglion cell type," Nature 367, 731–735 (1994).
- S. H. C. Hendry and R. C. Reid, "The koniocellular pathway in primate vision," Annu. Rev. Neurosci. 23, 127–153 (2000).
- P. R. Martin, A. J. R. White, A. K. Goodchild, H. D. Wilder, and A. E. Sefton, "Evidence that blue-on cells are part of the third geniculocortical pathway in primates," Eur. J. Neurosci. 9, 1536–1541 (1997).
- P. Gouras, "Identification of cone mechanisms in monkey ganglion cells," J. Physiol. 199, 533–547 (1968).
- M. Greschner, J. Shlens, C. Bakolitsa, G. D. Field, J. L. Gauthier, L. H. Jepson, A. Sher, A. M. Litke, and E. J. Chichilnisky, "Correlated firing among major ganglion cell types in primate retina," J. Physiol. 589, 75–86 (2011).
- A. L. Nagy, R. T. Eskew, Jr., and R. M. Boynton, "Analysis of colormatching ellipses in a cone-excitation space," J. Opt. Soc. Am. A 4, 756–768 (1987).
- 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).
- M. V. Danilova and J. D. Mollon, "Foveal color perception: minimal thresholds at a boundary between perceptual categories," Vision Res. 62, 162–172 (2012).
- F. M. de Monasterio, P. Gouras, and D. J. Tolhurst, "Trichromatic colour opponency in ganglion cells of the rhesus monkey retina," J. Physiol. 251, 197–216 (1975).
- A. Valberg, B. B. Lee, and D. A. Tigwell, "Neurones with strong inhibitory S-cone inputs in the macaque lateral geniculate nucleus," Vision Res. 26, 1061–1064 (1986).
- C. Tailby, S. G. Solomon, and P. Lennie, "Functional asymmetries in visual pathways carrying S-cone signals in macaque," J. Neurosci. 28, 4078–4087 (2008).
- K. Klug, S. Herr, I. T. Ngo, and S. Schein, "Macaque retina contains an S-cone OFF midget pathway," J. Neurosci. 23, 9881–9887 (2003).
- G. D. Field, J. L. Gauthier, A. Sher, M. Greschner, T. A. Machado, L. H. Jepson, J. Shlens, D. E. Gunning, K. Mathieson, W. Dabrowski, L. Paninski, A. M. Litke, and E. J. Chichilnisky, "Functional connectivity in the retina at the resolution of photoreceptors," Nature 467, 673–677 (2010).
- L. E. Wool, O. S. Packer, Q. Zaidi, and D. M. Dacey, "Connectomic identification and three-dimensional color tuning of S-OFF midget ganglion cells in the primate retina," J. Neurosci. **39**, 7893–7909 (2019).

- C. H. Graham, Y. Hsia, and F. F. Stephan, "Visual discriminations of a subject with acquired unilateral tritanopia," Vision Res. 7, 469–479 (1967).
- J. Broackes, "Unilateral colour vision defects and the dimensions of dichromat experience," Ophthal. Physiol. Opt. 30, 672–684 (2010).
- J. D. Mollon, "A taxonomy of tritanopias," in *Colour Vision Deficiencies VI*, G. Verriest, ed. (Dr. W. Junk, 1982), pp. 87–101.
- W. S. Stiles, ed., *Visual Problems of Colour*, National Physical Laboratory, Symposium No. 8 (Her Majesty's Stationery Office, 1959).