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The Legacy of Perley G. Nutting Jr.: The Past and the Present of Chromatic Discrimination

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Keywords

color discrimination, wavelength discrimination, increment thresholds, chromatic adaptation, uniform color space, difference signal, double-opponent neurons, number of discernable colors

Abstract

Studies of chromatic discrimination have historically varied in their experimental procedures and in the units in which thresholds are expressed, but by 1950, it was clear that thresholds depend both on differences in the ratios of cone excitations and on the properties of post-receptoral channels. Discrimination was found to be optimal at the chromaticity to which the observer was currently adapted. Consequently, the most famous dataset in this field, MacAdam's discrimination ellipses, cannot validly be used to construct a uniform color diagram or to estimate the number of discernible colors: MacAdam's single observer, Perley Nutting, would have been in different states of adaptation when matching different colors. Furthermore, a sensation of difference is not the same as a difference of sensations: Some color discriminations may depend on channels that extract differences between adjacent regions, and different pairs of chromaticities could then give rise to the same sensation of difference.

1. INTRODUCTION

How acutely can we tell two colors apart? In the long history of visual science, this question has been tackled in three distinct literatures, which differ in their experimental procedures, in the apparatus used, and in the units in which the precision of discrimination is expressed. Sometimes these literatures have interacted, but often they have meandered independently. Although our review is necessarily selective, we draw on three domains, as described in the following sections.

1.1. Wavelength Discrimination

The classical measurements by Arthur König and his colleagues (Brodhun 1892, König & Dieterici 1884) (**Figure 1a**) already identified the main features of the curve that describes the just noticeable difference of wavelength in different parts of the spectrum. Two regions of optimal discrimination are typically found: one in the yellow region, near 580 nm, and the other in the blue-green region, near 490 nm. There is a pessimum in the green region near 540 nm, and discrimination also deteriorates at the two ends of the spectrum (Wright 1946, chapter 14). An admirable feature of the work by König and his collaborators is the use of a performance measure, the method of average error: The observer was required to make 50 matches to a given wavelength, and the dependent measure was the average error of these matches.

1.2. Discrimination of Nonspectral Colors and the Quest for a Uniform Color Space

The second half of the nineteenth century also saw attempts to measure discrimination in the interior of color space. A study of some charm and interest is one by Edward Nichols (1885), a pioneer of experimental physics in the United States and founder of *Physical Review*. For his experiments on color discrimination, he carefully created dry mixtures of white powder (magnesium carbonate) and small quantities of a colored pigment (such as ultramarine, red lead, chromate of lead, or chromic acid). In the case of each of the colored pigments, mixtures with different degrees of dilution were put into small vials. The four sets of vials were intermingled randomly, and the observer was asked to sort them by hue and by degree of saturation. Nichols reported astonishingly low thresholds: For 54 observers, on average only 25 parts of red lead needed to be mixed with 100,000,000 parts of white in order to affect the tint of the compound. When such a mixture was examined microscopically, it was seen to contain occasional, glistening, colored crystals of ~ 10 microns in diameter that were “mingled with the magnesium carbonate without imparting *any trace* of their own color to the latter” (Nichols 1885, p. 41). Nichols reported striking sex differences: For red lead, the threshold quantity was well over three times smaller for men than for women, whereas for ultramarine, there was an advantage for women.

By 1942, standard color-matching functions had been established, and the CIE chromaticity diagram had been constructed. Thresholds in the interior of color space could now be expressed in units of chromaticity and could be readily compared across laboratories. David MacAdam, working at the Eastman Kodak Company in Rochester, USA, set himself the task of measuring chromatic discrimination around 25 points in the diagram. Like König, he used the method of average error, and nearly 25,000 matches were made by his heroic observer, Mr. Perley G. Nutting Jr. (son of the first president of the Optical Society of America). MacAdam’s colorimeter was set up so that the stimuli remained at the same luminance (48 cd/m^2) while the observer adjusted chromaticity along a line passing through a given reference point in the CIE diagram (MacAdam 1942). The matching field, vertically divided, subtended a visual angle of 2° and was surrounded by a dimmer (24 cd/m^2) neutral field subtending 42° . MacAdam fit ellipses to the thresholds around each chromaticity tested, the thresholds being expressed as standard deviations of the matches (**Figure 1b**).

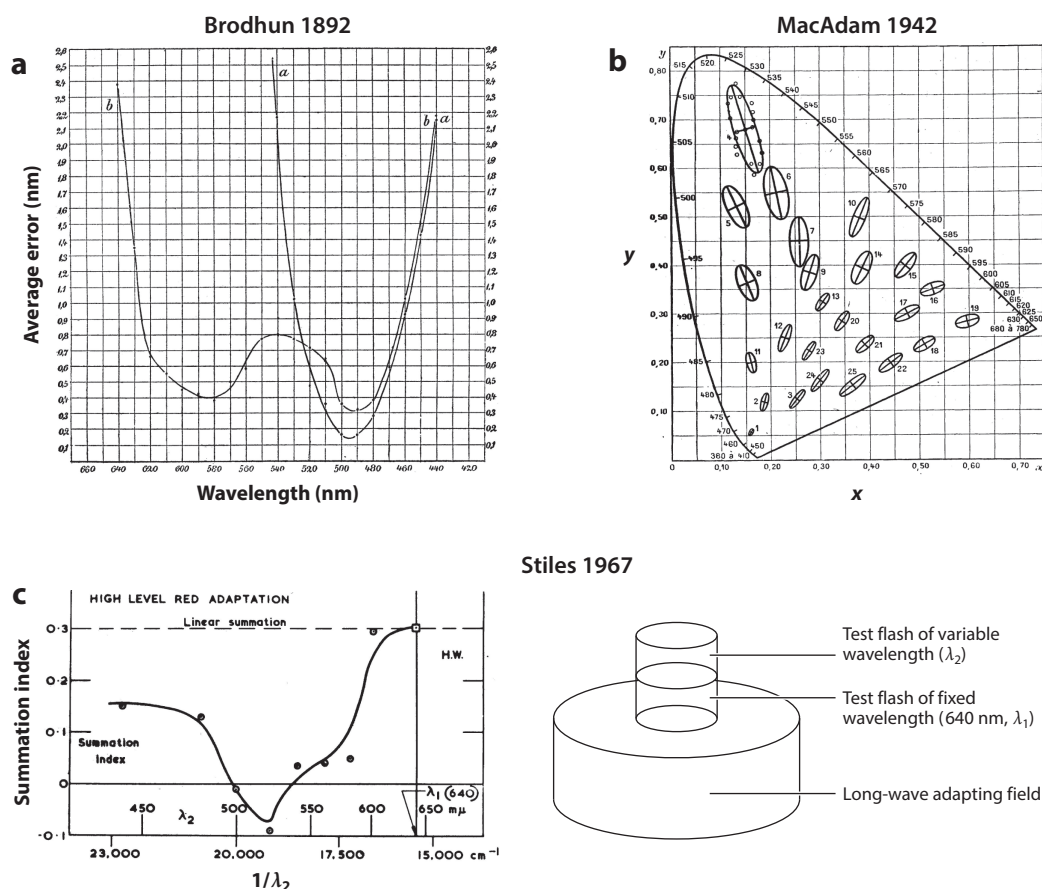


Figure 1

Three traditions in the study of chromatic discrimination. (a) Wavelength discrimination. Note that the wavelength scale is reversed relative to modern convention. The y-axis represents the average error of 50 matches. The *b* curve is for a normal trichromat (Arthur König), and the *a* curve is for a deuteranope (Eugen Brodhun). Panel adapted from Brodhun (1892). (b) The MacAdam ellipses in the CIE 1931 chromaticity diagram, as plotted by Le Grand. Each ellipse has been magnified by a factor of 10. The data represent the mean errors of 50 matches made in different directions through each of 25 reference points in the chromaticity diagram. Panel adapted with permission from Le Grand (1949); copyright 1949 IOP Publishing, all rights reserved. (c) Increment threshold measurements from Stiles (1967), with the stimulus conditions shown to the right. A red test flash of fixed wavelength (λ_1) is presented on a bright red field and is combined with a second congruent flash of variable wavelength (λ_2). The x-axis shows the wavelength (and wavenumber) of λ_2 , and the y-axis (i.e., summation index) is a measure of the degree to which the two increments add. At long wavelengths, linear summation occurs, but when λ_2 falls in the green region, the flashes appear to cancel each other's effects, and the summation index is well below even that expected for probability summation. Left side of panel adapted with permission from Stiles (1967); copyright 1967 Colour Group of Great Britain.

It was clear to MacAdam that no linear transformation of the CIE 1931 chromaticity diagram would yield a uniform color space, a diagram in which equal distances would represent equally noticeable color differences, and in which the discrimination ellipses would all become circles of equal diameter (MacAdam 1981, chapter 8). Nevertheless, Mr. Nutting's matches were to be the basis for two linear transformations that are certainly closer to a uniform color space than is the CIE 1931 diagram (the CIE 1960 u,v and 1976 u',v' diagrams). Nutting's matches have guided a host of nonlinear transformations in the quest for a truly uniform color space or an accurate

color-difference equation, practical instruments that are needed to specify tolerances in the paint, textile, paper, and many other industries (see, e.g., Brainard 2003, Candry et al. 2022, Judd & Wyszecki 1963, Kuehni 2003).

1.3. Measurements of Two-Color Increment Thresholds

In the middle of the last century, extensive measurements by W.S. Stiles, at the National Physical Laboratory in Britain, determined thresholds for detecting brief (200 ms), monochromatic increments presented on monochromatic fields (Stiles 1939, 1959). It perhaps is not widely known today that the threshold for an increment of any wavelength, presented on a background of any wavelength and of any intensity, can be estimated from three tables in chapter 7 of Wyszecki & Stiles's (1982) *Color Science*. In Stiles's working model, increments in his "two-color experiments" were detected by one or more independent, univariant neural channels ("π mechanisms"), which were explicitly not chromatically opponent. Toward the end of his experimental career, however, Stiles himself identified conditions where increment thresholds were convincingly determined by "color-differencing mechanisms": If, for example, a red (640 nm; λ_1) increment was presented on a high-intensity red field and if a superposed green increment (λ_2) was concurrently presented, then the observer's threshold for the combination was higher than would be expected if detection were mediated either by an additive mechanism or by probability summation of the responses of two independent channels (Stiles 1967; see **Figure 1c**). Such a result could be explained by supposing that the red flash on its own was detected by a chromatically opponent channel and that the added green flash drove the channel in the opposite sense. Interestingly, during the 1960s, Stiles was more ready to recognize the need for color-differencing channels than were some of his trichromatist admirers. By 1967, he knew that certain experimental conditions favored discrimination of increments by chromatically opponent channels: a large test flash, a test flash of long duration, and an adapting field of high intensity (Ikeda 1963, Stiles 1967). Soon added to this list were test flashes of short wavelength (Pugh & Mollon 1979), test flashes of low spatial frequency or with blurred edges (King-Smith & Carden 1976, Sternheim et al. 1978, Thornton & Pugh 1983), an adaptation field spatially congruent with the test field (Snelgar et al. 1987), and, to minimize the polarization of chromatic channels, a neutral adapting field (King-Smith 1975, Mullen & Kulikowski 1990).

2. PHYSIOLOGICAL MODELS OF COLOR DISCRIMINATION, 1890–2000

2.1. Line-Element Accounts

Von Helmholtz (1896, p. 463), in his celebrated line element, hoped to express the perceptual distance (ds) between two colors in terms of the changes in the signals of each of the three fundamental receptors of the retina, so that

$$ds^2 = \frac{dR^2}{(R+a)^2} + \frac{dG^2}{(G+b)^2} + \frac{dB^2}{(B+c)^2},$$

where R , G , and B are the excitations of long-, middle-, and short-wave fundamentals, respectively, and a , b , and c are constants that represent the self-light of each class of receptors. (Today we might identify the self-light with spontaneous decompositions of opsin molecules.) The signals of the three fundamental receptors are independent and represent orthogonal vectors in a 3D space. Stiles (1946), drawing on his own increment-threshold measurements (see Section 1.3), adopted different Weber fractions for the three fundamentals: He estimated values of 0.78%, 1%, and 4.46% for long-, middle-, and short-wave cones, respectively. The high value for the short-wave cones almost certainly reflects their long-suspected sparsity in the retina (Curcio et al. 1991,

Mollon & Bowmaker 1992, Roorda & Williams 1999). However, even with this refinement, it was clear that MacAdam's ellipses could not be predicted from a model in which the three fundamentals act independently. A recommended account of line-element models is that by Stiles (1972).

2.2. The Two-Subsystems Framework

A critical insight came from Le Grand (1949), who reanalyzed the MacAdam ellipses and suggested that different principles governed discriminations that depended on the short-wave (S) cones and those that depended on the relative excitations of the long-wave (L) and middle-wave (M) cones. [For an English translation of this brilliant paper, along with a valuable commentary, see Boynton & Knoblauch (1994).]

Expressing MacAdam's ellipses in terms of estimated cone sensitivities, Le Grand realized that the long axes of the ellipses were largely aligned with tritan lines in the chromaticity diagram, that is, lines along which only the S-cone excitation is varying and along which chromaticities would be confused by tritanopes (dichromatic observers who lack those cones). Le Grand supposed that the S-cones act as an independent channel and that their differential threshold depends on the level of excitation of those cones at the point in the CIE chromaticity diagram at which thresholds are being measured. However, it did not seem to be the absolute level of the S-cone excitation that set the threshold. Rather, it was the S signal divided by the current luminance level. So, expressed in modern terms, the threshold varies with the level of $S/(L + M)$, which corresponds to B_0/Y in Le Grand's terminology (left side of **Figure 2**).

In contrast, the long-wave and middle-wave cones do not act independently in Le Grand's model. Rather, the differential threshold depends on their relative excitation. Discrimination is optimal when their signals are similar (right side of **Figure 2**).

Initially unaware of Le Grand's paper, Robert Boynton developed similar analyses in the second half of the twentieth century. His method of measuring differential thresholds was very different from that of MacAdam: One half of a 2° field was fixed at the test chromaticity, and the other changed very slowly until the observer was able to report the direction of change. The surround was dark. This method led to much higher thresholds, but observers were able to maintain a stable criterion and gave a low number of false positives. At a number of positions in the CIE chromaticity diagram, discrimination was measured along the two critical directions identified by Le Grand, one that varied along a tritan line, that is, a direction where only the excitation of S-cones was changing while the ratio of L- and M-cone excitations was constant, and a second that varied the ratio of L- and M-cone excitations while holding constant the S-cone excitation. The reference luminance was held constant at 120 Td. As Le Grand's analysis had suggested, discrimination along tritan lines was independent of the L/M ratio and depended on only the S-cone excitation level of the reference stimulus. Discrimination in the L/M direction was optimal at an intermediate value of L/M , but increases in the fixed level of S-cone excitation did increase thresholds for L/M discriminations (Boynton & Kambe 1980).

The color space implicit in Le Grand's analysis was to be embodied in the chromaticity diagram of MacLeod & Boynton (1979), which has come to be widely used in visual science (see **Figure 3**). It is explicitly not a uniform color diagram, but it is more directly related to human physiology than is the CIE 1931 diagram. The ordinates of the diagram are expressed in terms of the cone excitations, L, M, S : The y -axis corresponds to $S/(L + M)$ and the x -axis to $L/(L + M)$. Importantly, these axes do not align with the yellow-blue and red-green axes of phenomenological experience.

The MacLeod–Boynton diagram represents a plane of equal luminance, since luminance is believed to depend only on the signals of long-wave and middle-wave cones (the M-cone signal is scaled to reflect the fact that L-cones make the greater contribution to luminance). For the fundamentals—the cone sensitivities—MacLeod and Boynton adopted those estimated by

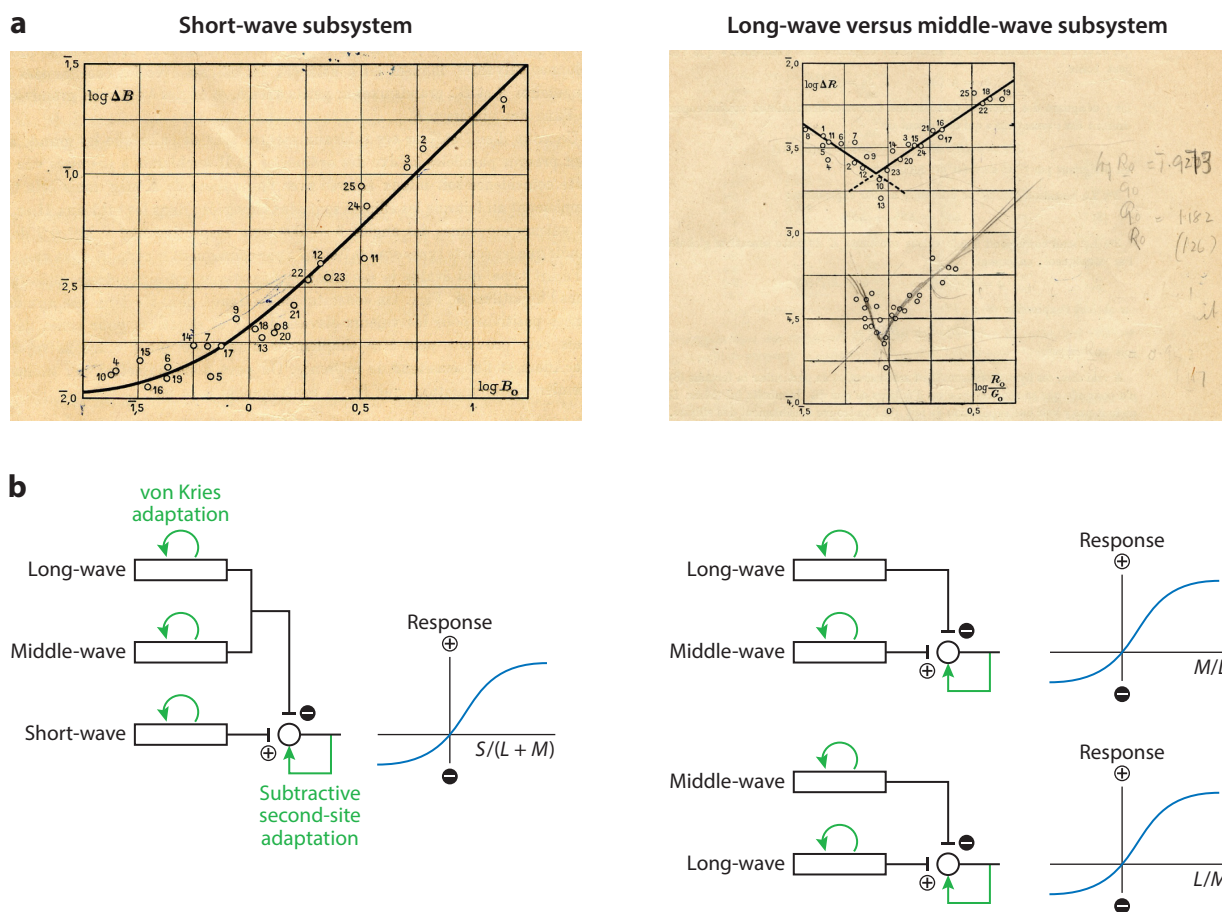


Figure 2

(a) Le Grand's analysis of the MacAdam ellipses in terms of two neural subsystems. The images are from Stiles's own offprint of Le Grand's paper, and the annotations are by Stiles. The left plot shows, for the 25 ellipses, the calculated change at threshold in the short-wave cone signal as a function of the log of the reference level of that signal. The right plot shows the calculated change at threshold in the long-wave cone signal as a function of the log L/M value of the referent. Le Grand modeled the expected values for two different estimates of the cone fundamentals (those constructed on the Fick and the König principles). Stiles has penciled a function through the König estimates. Panel adapted with permission from Le Grand (1949); copyright 1949 IOP Publishing, all rights reserved. (b) The late twentieth-century model of the two subsystems derived from Le Grand's proposal. (Left) The short-wave subsystem draws opposed inputs from S-cones and from L- and M-cones. Adaptation occurs at the receptor level ("von Kries" adaptation) and at the chromatically opponent stage (subtractive "second-site" adaptation). The hypothetical output function exhibits a compressive nonlinearity. (Right) The L/M subsystem: There are neural channels of the ON-center type either excited by M-cones and inhibited by L-cones or excited by L-cones and inhibited by M-cones. Not shown are the two corresponding types of OFF-center midjet cells. Abbreviations: L, long-wave; M, middle-wave; S, short-wave.

Smith & Pokorný (1975), which have the color-matching properties of the CIE 1931 Observer, as modified by Judd, but generic forms of the diagram can be formed for any set of fundamentals.

Essentially the same ordinates as those of the MacLeod–Boynton diagram were called "cardinal" by Krauskopf et al. (1982). They found that that adaptation to modulation along each of these two axes left the discrimination thresholds along the other almost unchanged, whereas adaptation to intermediate directions produced a much less selective loss of color discrimination (**Figure 4**).

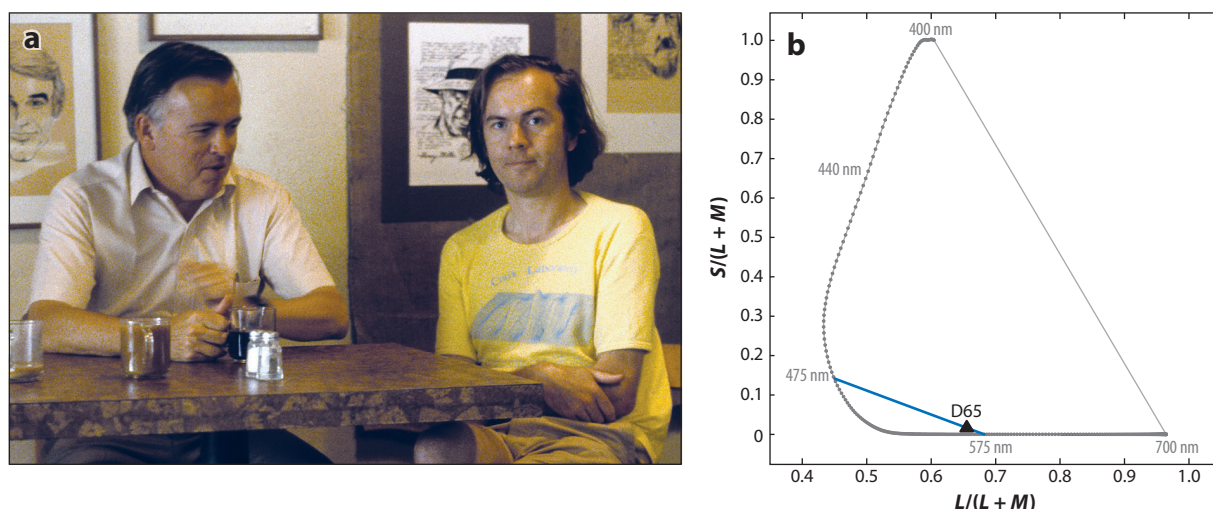


Figure 3

(a) Robert Boynton (*left*) and Donald MacLeod (*right*). The photograph was taken by J.D. Mollon in a coffee shop at the University of California San Diego, circa 1979. Donald MacLeod is wearing a Craik Laboratory T-shirt that represents a short-wave gabor stimulus on a bright yellow field, conditions under which detection is by chromatic channels. (b) The MacLeod–Boynton chromaticity diagram. The diagram represents an equiluminant plane bounded by the spectrum locus and (to the right) by the line of purples, mixtures of red and violet light. The axes correspond to the two neural subsystems identified in **Figure 2**. D65 indicates the position in the diagram of Illuminant D65, equivalent to daylight of correlated color temperature 6,504 K. The oblique blue line represents the yellow–blue line, the set of colors that appear neither reddish nor greenish. Note that it differs from a tritan line: Such lines are vertical in this diagram. Panel adapted from Danilova & Mollon (2012c).

The two channels identified psychophysically were soon taken to correspond to two neural channels found in the primate retina and lateral geniculate nucleus (LGN) (Derrington et al. 1984). These two channels appeared to have evolved at different stages and to have remained relatively independent, one overlaid on the other (Mollon & Jordan 1988, Mollon et al. 1990). The phylogenetically ancient signal was taken to be carried in the primate retina by the small bistratified ganglion cells, which were excited by S-cones and received an opposed input from some combination of L- and M-cones (Calkins et al. 1998, Dacey & Lee 1994). These small bistratified ganglion cells project to the koniocellular laminae of the LGN (Martin et al. 1997) and thence directly to layers 2 and 3 of the primary visual cortex. The phylogenetically recent signal, in contrast, was taken to be carried in the retina by the midjet ganglion cells, which were thought to draw opponent inputs from L- and M-cones (Lee 1997). The projection of the midjet ganglion cells is to the parvocellular laminae of the LGN and thence to cortical layer 4C β . The anatomical separation of the two chromatic signals reflected the psychophysical independence seen in the discrimination experiments (Krauskopf et al. 1982).

This, then, was the attractively straightforward account of color vision and of color discrimination that was dominant in the final years of the last century (Krauskopf 2001). Its structure is sketched in **Figure 2b**.

2.3. The Role of the Two Subsystems in Wavelength Discrimination

Provided that care is taken to prevent the observer from using luminance cues (see below), the discrimination of wavelength (**Figure 1a**) must ultimately be limited by the absorption curves of the three cone photopigments and, more specifically, by the local rate of change with

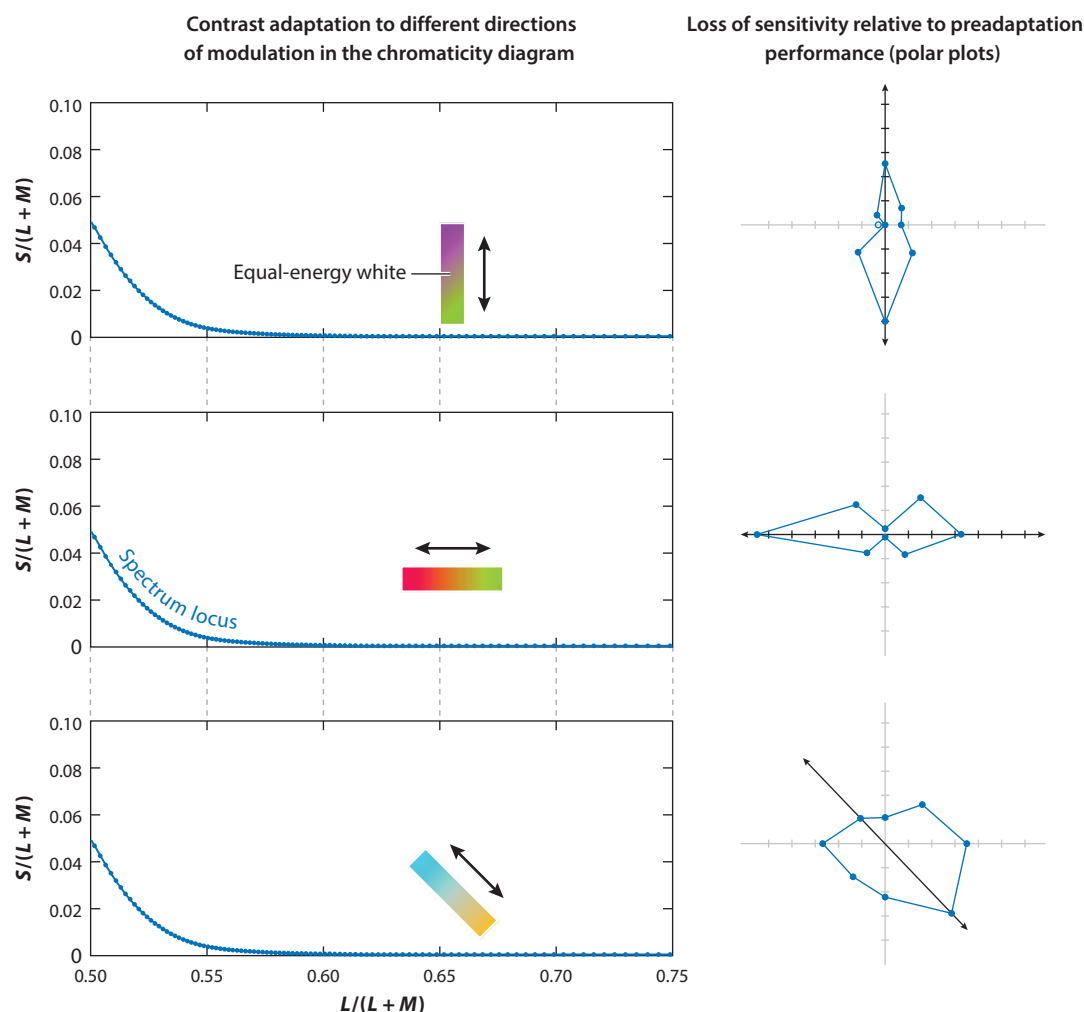


Figure 4

Cardinal directions of color space. (*Left*) A small region of the MacLeod–Boynton chromaticity diagram (**Figure 3b**). The panel illustrates (strictly schematically) the adapting stimuli used in the classic experiment on color discrimination by Krauskopf et al. (1982). The adapting field is modulated in chromaticity over time, but its time-averaged chromaticity is always equivalent to that of equal-energy white. (*Right*) Polar plots showing the loss of chromatic discrimination in different directions as a result of the adaptation on the left: Two cardinal directions produce a highly selective loss of sensitivity, suggesting that a single chromatic channel has been isolated in each case, but modulation along an oblique line (e.g., from yellow to blue) produces a more generalized loss of sensitivity. Right side of figure adapted with permission from Krauskopf et al. (1982); copyright 1982 Elsevier.

wavelength of the ratios of the cone excitations (L , M , S). Owing to the insensitivity of S-cones to long wavelengths, the ratios S/L and S/M [or $S/(M + L)$] are unlikely to be available to support discrimination at wavelengths above, say, 540 nm. However, the ratio M/L varies (and could potentially support discrimination) throughout the visible spectrum, except at long wavelengths, where it is almost constant, and at wavelengths in the vicinity of 460 nm, where M/L passes through a shallow maximum (see Mollon et al. 1990).

During the second half of the twentieth century, in parallel with the developments discussed in the previous section, the concept of two independent subsystems was applied to wavelength

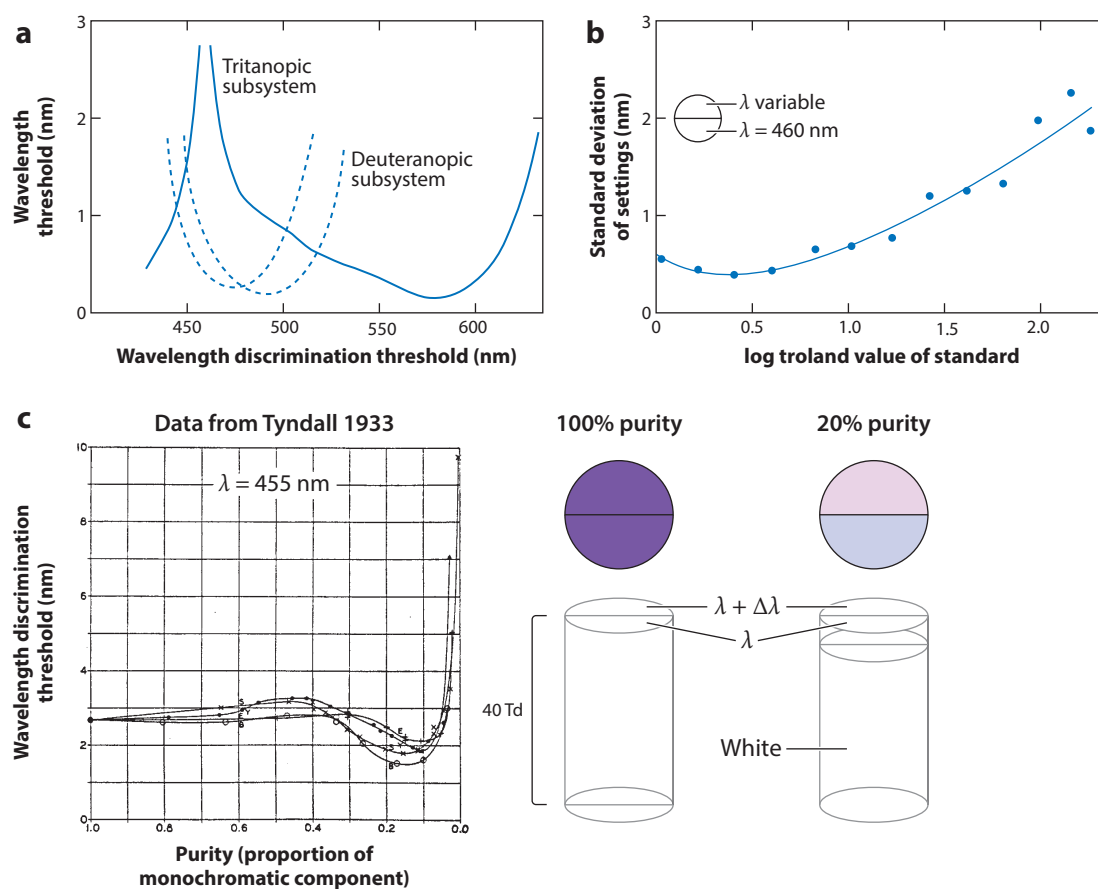


Figure 5

(a) The hypothetical role of the two chromatic subsystems in wavelength discrimination. The “tritanopic” subsystem, which relies on the ratio M/L , could potentially be used throughout the spectrum, except near 460 nm, where M/L goes through a shallow maximum. The “deutanopic” subsystem, which relies on the ratio $S/(L + M)$, is responsible for good discrimination in the short-wave region, but the region of optimal sensitivity shifts leftward as intensity or duration is reduced. (b) The König–Dieterici anomaly. The y-axis shows the standard deviation of matches to a 460-nm standard. Discrimination is optimal at a low intensity and deteriorates as the troland value increases. Panel adapted from Mollon & Estévez (1988); copyright 1988 Optical Society of America. (c) Tyndall’s paradox. The stimulus conditions are shown to the right: Varying proportions of the monochromatic half-fields are replaced by white light common to both fields. The plot to the left shows that the wavelength threshold at 455 nm changes little as purity is reduced from 100% to 30%, and, remarkably, between 20% and 15%, discrimination is much better than at 100% purity. The different curves are for white components of different color temperatures. Left side of panel adapted with permission from Tyndall (1933); copyright 1933 Optical Society of America.

discrimination. Walraven prettily characterized the normal observer as a “double dichromat,” who combined a “tritanopic” subsystem differencing L and M signals and a “deutanopic” system, which compared the S-cone signal with a combined L + M signal (Bouman & Walraven 1972, Walraven 1966). These deutanopic and tritanopic subsystems (**Figure 5a**) would correspond, respectively, to the phylogenetically ancient and modern neural subsystems discussed above.

Walraven supposed that his tritanopic subsystem was responsible for the fine discrimination observed in the 570–590 nm region (**Figure 1a**). A healthy observer is well able to discriminate the two sodium lines at 589.0 and 589.6 nm (the D1 and D2 lines of Fraunhofer), provided the retinal

illumination is of the order of 100 Td (Le Grand 1948, p. 280; Rayleigh 1910). It is remarkable that we achieve this resolution of a few angstroms by comparing the outputs of two filters (the L- and M-cones) that each have a bandwidth of more than 100 nm at half height. Near 460 nm, in contrast, not only does M/L change slowly, but any channel that extracts that ratio will be maximally polarized (i.e., driven to one extreme of its response range).

Walraven suggested that his deuteranopic subsystem was responsible for the good discrimination seen in wavelength discrimination at 490 nm or below. Strong evidence comes from the disproportionate impairment of discrimination in this region when targets are very small and especially when they are centrally fixated (McCree 1960, Willmer & Wright 1945). Under these conditions, owing to the sparsity of short-wave cones, as well as their complete absence from the very center of the foveola (Curcio et al. 1991), chromatic signals that depend on S-cones must be weak. An especially high threshold is seen near 460 nm, where the signal M/L is also not available (see the preceding paragraph).

2.4. The König–Dieterici Anomaly, the Anomalous Effect of Stimulus Duration, and Tyndall's Paradox

However, the rates of change with wavelength of the ratios of cone excitations cannot be the whole story.

In the wavelength discrimination curves of König & Dieterici (1884), a curious feature is seen near 450 nm: Discrimination improves when the light level is reduced. This König–Dieterici anomaly was confirmed by Mollon & Estévez (1988), who measured wavelength discrimination thresholds at 460 nm for lights in the range of 1 to 100 Td (**Figure 5b**). Like König and his collaborators, Mollon and Estévez used the method of average error, but with one improvement: Between settings, the computer offset not only wavelength but also intensity, and the observer used a joystick to reestablish the match in both hue and luminance. This procedure circumvents a problem that faces any study of wavelength discrimination: In spectral regions where luminance changes rapidly, the observer may base his or her settings on luminance cues. The König–Dieterici anomaly can also be seen in the data reported by McCree (1960) for retinal illuminances in the range of 0.85 to 150 Td and field sizes between 25 and 75 arcmin.

A second, and surely related, anomaly observed near 460 nm is that wavelength discrimination can be improved by shortening stimulus duration (Mollon et al. 1992), a manipulation that usually impairs chromatic discriminations (Brückner & Kirsch 1912, Scase & Foster 1988). Using a two-alternative temporal forced choice to avoid the possibility of the observer's criterion changing as duration was changed, Mollon and colleagues found that what mattered below 100 ms was the total energy in the flash; that is, a certain product of stimulus duration and intensity produced the optimal discrimination at 460 nm.

In the same spectral region, at 455 nm, a third strange phenomenon was reported by Tyndall (1933), who was working at the Bureau of Standards in Washington. Tyndall used a horizontally divided, circular field subtending 2° with a retinal illuminance of 40 Td (**Figure 5c**). The upper half-field was adjustable in wavelength, the lower was fixed at 455 nm, and thresholds were measured by a method of adjustment. Maintaining the total field at 40 Td, Tyndall reduced the monochromatic component and replaced it with white light that was common to the upper and lower halves. In other words, he reduced the colorimetric purity of his test and comparison stimuli. There was nothing in the white component that distinguished the two half-fields. Yet, astonishingly, when purity was only 15%, wavelength thresholds were substantially reduced. Using their version of the method of average error (see this section, above), Mollon & Estévez (1988) confirmed Tyndall's result. Although performance measurements are always to be preferred in studies

of discrimination, here is a rare case where it may be worth quoting phenomenological observations. Mollon & Estévez (1988, p. 152) write: “At 100% purity, the [targets] are a glaring blue and vary little in appearance as the wavelength is changed. At 20% they are of delicate pastel shades, and the variable half-field changes quickly from reddish to greenish as the joystick is moved in the direction of longer wavelengths.”

Is Tyndall’s paradox just a result of reducing the intensity of the monochromatic component (making the phenomenon equivalent to the König–Dieterici anomaly)? To test this possibility, Mollon and Estévez measured wavelength discrimination at 460 nm and added increasing amounts of a desaturating 560-nm field to the two test half-fields, which were fixed in luminance at 40 Td. Although the yellow-green, 560-nm, desaturating field would affect the quantum catch of the short-wave cones only negligibly, its addition improved discrimination.

The König–Dieterici anomaly, the duration anomaly, and Tyndall’s paradox show convincingly that wavelength discrimination at short wavelengths must depend on more than simply the rates of change with wavelength of the ratios of the cone excitations, S , M , and L . **Figure 5a** offers a late twentieth-century account in terms of two underlying and independent subsystems. Here are the essential assumptions:

1. Between, say, 450 and 500 nm, the ratio M/L extracted by the phylogenetically younger subsystem—Walraven’s tritanopic system—changes less rapidly than it does in the yellow spectral region, and it passes through an extreme value near 460 nm. Under normal circumstances, it is not used for discrimination in this spectral region.
2. Instead, wavelength discrimination depends on the phylogenetically older subsystem—Walraven’s deuteranopic system—which extracts the signal $S/(L + M)$.
3. Since the wavelength of peak sensitivity ($\lambda_{\max}$) of the short-wave cones is so distant from those of the L- and M-cones, the ratio $S/(L + M)$ exhibits a large change across the short-wavelength region of the spectrum.
4. The very high values of the ratio $S/(L + M)$ produced by short-wavelength monochromatic lights are almost never generated by natural objects, and the phylogenetically older channel is not designed to discriminate them. The channel has a compressive response function (Polden & Mollon 1980), and a bright, continuously exposed, monochromatic light in the region of 450–460 nm places the channel in a saturated part of its operating range (see **Figure 2b**).
5. Reducing the absolute intensity of the stimulus, shortening its duration, or adding a desaturant brings the channel back into a more optimal part of its operating range and changes the spectral position of optimal discrimination (**Figure 5a**).

3. CHROMATIC ADAPTATION AND THE DISCRIMINATION OF COLORS

In a classic experiment, Kenneth Craik (1938) showed that discrimination of luminance modulation is finest close to the stimulus level that the eye has been adapted to, but thresholds rise rapidly when the intensity of the test stimuli differs from that of the adapting level. Loomis & Berger (1979), explicitly citing Craik, described a corresponding effect for chromaticity when the adapting field was varied along a red-green axis, running from 633 to 502 nm. Similar results had been found in several early studies (Brown 1952, Rautian & Solov’eva 1954, Schönfelder 1933), and a physiological analogue can be seen in a classic study of wavelength discrimination by single units in the LGN of the macaque (De Valois et al. 1967). Today, one of the firmest findings in the field of color vision is that discrimination is optimal for chromaticities close to the adapting chromaticity (see, e.g., Danilova & Mollon 2014b, Hansen et al. 2008, Hong et al. 2025, Krauskopf &

Gegenfurtner 1992, Miyahara et al. 1993, Smith & Pokorny 2003, Smith et al. 2000, Thornton & Pugh 1983). Some part of the adaptation may be at the receptor level (von Kries adaptation; **Figure 2b**), but much of the adjustment has been thought to be the result of a subtractive signal at a second, chromatically opponent site (e.g., Pugh & Mollon 1979, Smith et al. 2000).

One study suggesting that chromatic adapting fields have much of their effect at a post-receptor level is that by Mollon & Cavonius (1987). Wavelength discrimination in the yellow region of the spectrum was measured by a forced-choice method after adaptation to monochromatic fields. The foveal, 2°, bipartite test stimuli had a retinal illuminance of 1,000 Td. The monochromatic adapting fields, on the other hand, were of only 10 Td illuminance, yet they had strong effects on wavelength discrimination in the yellow region. The weak adapting fields might be judged to have only a small effect on the cones, whereas, in principle, a ratio-extracting second stage should be as polarized by a 10-Td field as it would be by a brighter one. Yellow adapting fields of a wavelength similar to that of the test stimulus had the least effect on discrimination. Interestingly, a blue, 458-nm, adapting field doubled the measured thresholds and was more effective than green fields, whereas a violet adapting field of 405 nm, which appeared richly reddish, was no more effective than a yellow field. In terms of the two-channels account of the previous section, these are the expected results if the yellow test fields are discriminated by a strictly tritan channel that extracts the ratio M/L , since 458-nm light maximally polarizes such a channel, whereas 405 nm is close to a tritan neutral point and should have an effect similar to that of yellow light. The results are thoroughly incompatible, however, with a Hering account in which detection is by a “red-green” channel that is left in equilibrium by both yellow and blue adapting fields.

3.1. Implications for Uniform Color Diagrams and for the Number of Discriminable Colors

If discrimination is optimal at the chromaticity to which the eye is currently adapted, then there are strong implications for the derivation of uniform color spaces. If such a space is derived from, say, the discrimination ellipses of MacAdam, then it does not represent the instantaneous color vision of an observer in a neutral state of adaptation. Although MacAdam’s stimulus was surrounded by a dimmer white field, Mr. Nutting was not given systematic instructions to regularly look at the surround. As he made repeated settings of the variable field, he would have been partly or fully adapted to the particular chromaticity being tested in any one set of measurements. There would be a strictly local expansion of the representation of chromaticities close to the reference chromaticity, but Nutting would not enjoy concurrently such delicate discrimination elsewhere in the diagram. For an early discussion of this problem, see Judd & Wyszecki (1963, pp. 286–87).

The extent to which the observer is adapted to the chromaticity region being tested will depend on the stimulus size. Brown (1952) used the method of average error and matching fields subtending either 12° or 2°. The matched colors were white, red, green, and blue; the surrounding field could be white, black, red, green, or blue. As would be expected, discrimination was better in all cases for the larger fields. Significantly, however, it was only in the case of the smaller stimuli that a surrounding field of a different color had a detrimental effect on discrimination. In these cases, the best discrimination was obtained with either a surround of the same color as the test stimulus or a dark surround. It is plausible to assume that the 12° field allowed the observer to become fully adapted to the test chromaticity, whereas in the case of the 2° field, the observer was likely to be adapted partly to the test and partly to the surround. The problem is even more obvious in the measurements of MacAdam (1959), who measured discrimination for either a 4.4° field or two fields each subtending 3 arcmin and 6 arcmin apart. In both cases, the surround was neutral. In the case of very small fields, eye movements would ensure that there was rather little adaptation to the test stimuli themselves, and the observer’s state of adaptation would be largely set by the neutral

surround, whereas in the case of the 4.4° field, the observer would be predominantly adapted to the discriminanda.

In sum, neither linear nor nonlinear transformations of MacAdam's ellipses for 2° matches can yield a space that represents an observer's global and instantaneous sensitivity to color differences. Of course, a paint manufacturer may well want to know what tolerance to allow when a customer is adapted to a particular region of color space, and as a mnemonic record of what that tolerance may be, uniform color spaces have a valid role. But one would be mistaken to reify the space as if it corresponds to the internal representation of colors by a standard observer at a given time. It would be inappropriate, for example, to use MacAdam's ellipses, or spaces derived from them, to estimate the total number of distinct colors that can be experienced by a normal trichromat.

3.2. Sensations of Difference and Differences of Sensation

A distinct but closely related point is that a sensation of difference is not the same as a difference of sensations (Le Grand 1970). Many of the several neural channels within the early visual system appear to be designed to detect contrasts in space or time, and it may be a difference signal (or perhaps a ratio signal) that is carried forward for decision. For example, when an observer equates in luminance the two halves of a traditional photometric field, he or she minimizes the visible edge between the two half-fields, and in making this setting, the observer probably depends on a contrast signal ultimately deriving from retinal ganglion cells that draw inputs of opposite sign from photoreceptors in the center and the surround of their receptive field.

If there are conditions under which juxtaposed chromatic fields are distinguished by an analogous spatial differencing signal, then it would be invalid to use threshold data obtained under these conditions to estimate the discriminability of isolated, spatially separated colors or to estimate the number of distinct color sensations. Yet, chromaticity discrimination has a low-pass spatial contrast-sensitivity function, which does not resemble the band-pass contrast-sensitivity function found for luminance discrimination (Cavonius & Estévez 1975, Hilz & Cavonius 1970, van der Horst et al. 1967). The implication is that color is judged from signals arising in the body of a colored area and not from the transition at an edge (Gowdy et al. 1999). Conversely, however, several phenomena (such as the chromatic Chevreul illusion) do suggest a spatially differencing mechanism for color (Johnson & Mullen 2026, Shapley et al. 2019). Double-opponent cortical cells have been suggested as the physiological substrate for this type of edge detection, that is, cells that have different chromatic preferences in the center and the surround of their receptive field (Johnson et al. 2008). We suspect that in the outer reaches of the chromaticity diagram, where colorimetric purity is high, it may be the outputs of double-opponent cells that offer the lowest thresholds to an observer who is asked to discriminate the two halves of a bipartite field. When, however, the discriminanda are separated in space, the edge signals from double-opponent cells will not be available. So, an empirical prediction is that thresholds will rise with increasing spatial separation of the discriminanda, as happens for luminance and for direction of motion (Takahashi et al. 2020).

It might be asked why thresholds would ever be determined by spatially differencing, double-opponent cells when such cells are usually thought to be restricted to the cortex and might be assumed to be constructed from the outputs of single-opponent cells earlier in the visual system. Why would the threshold not always be set by single-opponent cells? An explanation could be the presence of correlated noise in single-opponent cells with adjacent receptive fields. By extracting the ratio of the signals of the single-opponent cells, double-opponent cells could recognize a difference even though there were time-varying (but correlated) fluctuations in the input signals. In a different context, a proposal of this kind was made by Regan & Beverley (1985, p. 153) for the case

of orientation discrimination: “Opponent processing has the feature that noise in the first-stage outputs. . . can be partially or even completely suppressed by the opponent elements.”

If, indeed, discrimination thresholds do sometimes depend on sensation of difference, then those thresholds cannot be taken to tell us about difference of sensation when isolated colors are considered.

4. PROBING THE DIFFERENTIAL SENSITIVITY OF THE EYE WHEN ADAPTATION IS HELD CONSTANT

A paper of great clarity and considerable significance was that by Krauskopf & Gegenfurtner (1992). They probed discrimination performance with a forced-choice task in which four stimulus patches, equiluminant with the background, were briefly presented, and the observer’s task was to identify the patch that differed from the other three. They worked with a chromaticity diagram similar to that of MacLeod and Boynton.

In one series of experiments, they adapted their observer to one of several points in the chromaticity diagram and measured thresholds for excursions from that point. In this case, thresholds along the $L/(L + M)$ axis were constant for different adaptation points, suggesting that the set point of the detecting channel had fully shifted to each fresh adapting chromaticity. Thresholds along the $S/(L + M)$ axis increased with the degree to which the background excited the short-wave cones.

In a second series of experiments, Krauskopf and Gegenfurtner held constant the observer’s adaptation while probing discrimination both around the adaptation point and around points (let us call them “referents”) elsewhere in the chromaticity diagram (**Figure 6a**). In this case, along both the $L/(L + M)$ and the $S/(L + M)$ axes, thresholds were minimal around the adaptation point but rose as the referent chromaticity became more distant from the adaptation point. Very similar, V-shaped, functions were found by Miyahara et al. (1993) when the observer was adapted to a white field. Such results confirm that chromaticity discrimination has the characteristic that Craik (1938) classically observed for luminance discrimination.

Krauskopf and Gegenfurtner’s two types of experiment firmly separate the two conditions that are probably confounded in MacAdam’s measurements: the case where the observer is fully adapted to the chromaticity at which discrimination is measured and the case where the observer’s adaptation is held constant while discrimination is tested elsewhere in the chromaticity diagram. Within the equiluminant plane displayed on their monitor, Krauskopf and Gegenfurtner suggest that a white-adapted observer could distinguish only ~448 colors.

Under neutral adaptation, at the neutral point itself and in the upper right and lower left quadrants of the chromaticity diagram, Krauskopf and Gegenfurtner find that the thresholds fall either on a circle or on an ellipse that is oriented either vertically or horizontally (**Figure 6a**). These are the results expected if there are only two channels (essentially those identified by Le Grand) and if they act independently. Consider the case where the two putative channels are equally sensitive (in terms of the arbitrary scaling of the diagram): The thresholds, then, may plot on a circle. If one mechanism is more sensitive than the other (or if the scaling of the ordinate is changed), then the circle can become an ellipse with its long axis vertical or horizontal, but an oblique ellipse should be impossible. Yet, in the upper left and lower right quadrants of **Figure 6a**, there are clearly oblique ellipses oriented toward the adapting point.

5. CHALLENGES TO THE DEFAULT MODEL OF TWO INDEPENDENT CARDINAL SUBSYSTEMS

Those oblique ellipses in two quadrants of the Krauskopf–Gegenfurtner results were an early indication that all was not well with the default model of two independent chromatic channels, a

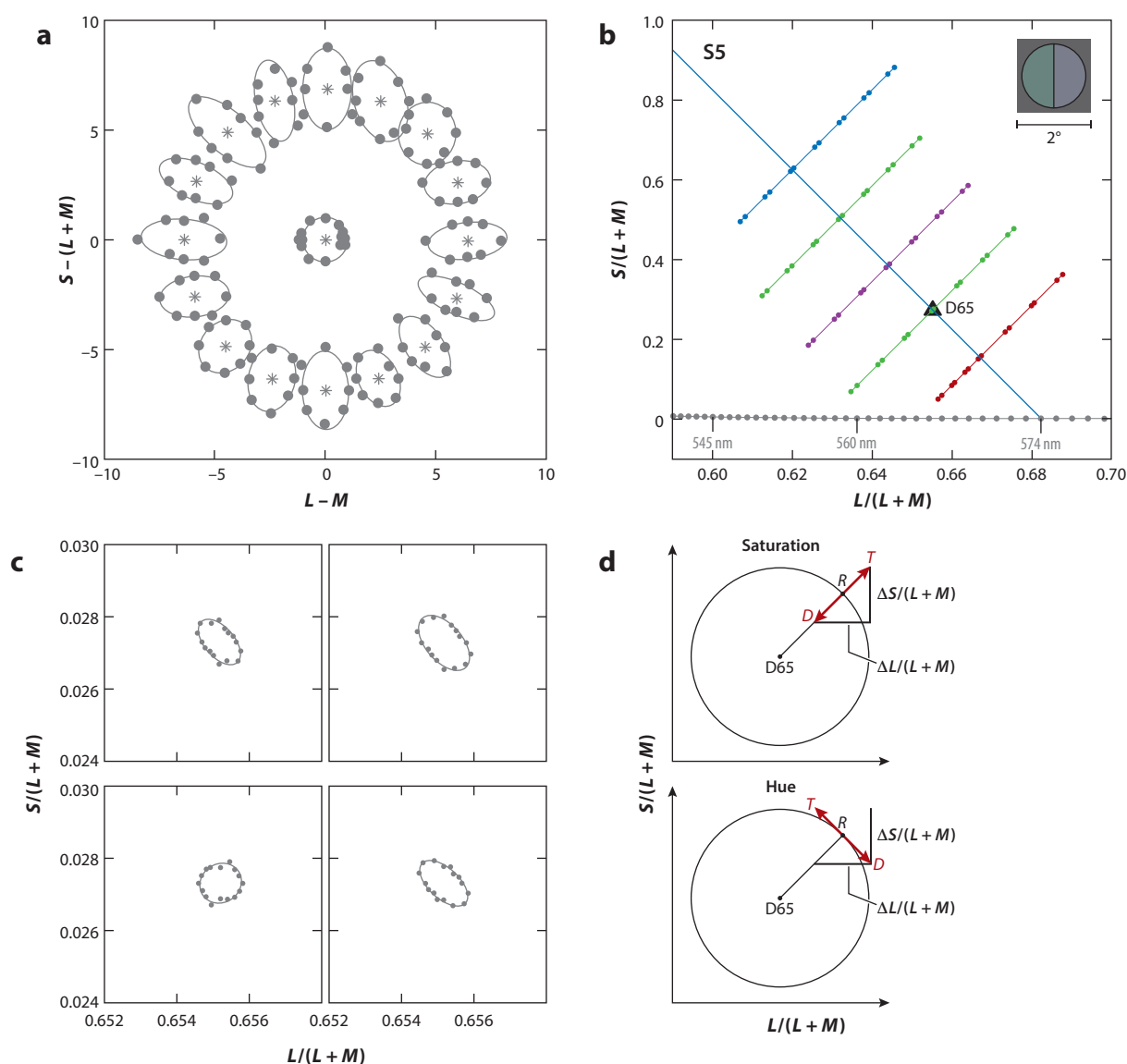


Figure 6

(a) Discrimination ellipses at different points in color space while the observer is constantly adapted to equal-energy white. Note the obliquity of the ellipses in the upper left and lower right quadrants. The chromaticity diagram used is similar to that of MacLeod and Boynton (Figure 3). Panel adapted with permission from Krauskopf & Gegenfurtner (1992) (CC BY-NC-ND 4.0). (b) Thresholds measured along lines orthogonal to the category boundary between reddish and greenish colors. The MacLeod-Boynton diagram has been scaled so that the yellow-blue line lies at -45° . The inset shows the arrangement of stimuli. The paired data points directly show how far two chromaticities must differ in order to support discrimination at a level of 79% correct. The minimal thresholds coincide with the category boundary. Panel adapted from Danilova & Mollon (2012c). (c) The central ellipse. Shown are individual examples of the discrimination ellipse around the neutral point, plotted in the MacLeod-Boynton diagram. Data from Danilova & Mollon (2025). (d) Hue versus saturation. At a given point on a radial line from the white point, saturation and hue changes require the same $S/(L + M)$ and $L/(L + M)$ signals to be combined in different phases. T and D indicate the coordinates of the target and distractors, respectively, and R indicates the reference chromaticity around which the measurements are being made. Panel adapted from Danilova & Mollon (2016).

model widely held at the opening of this century (e.g., Dacey & Lee 1999, Mollon 2000). Another counter-indication was a reanalysis of the classic adaptational results of Krauskopf et al. (1982) (Section 2.2; **Figure 4**), a reanalysis that showed residual selectivity after adaptation to intermediate directions (Krauskopf et al. 1986), although Krauskopf himself attributed this residual selectivity to adaptation of higher-order mechanisms, central to the cardinal channels (Krauskopf 1999).

5.1. Direct Tests of the Independence Hypothesis

Stromeyer et al. (1998) used a two-alternative temporal forced-choice method to measure thresholds for detecting L/M flicker. Conditions were chosen to favor detection by a chromatic channel: A bright white adapting field was present, the modulation frequency was low, and the flicker envelope was ramped on and off. If a liminal (71% detection) S-cone modulation was present in both intervals of one trial and if the observer was asked to identify the interval in which L/M modulation was present, then thresholds were lower if the S+ signal was in phase with the L+ signal. Stromeyer and colleagues concluded that L- and S-cones were acting synergistically.

Danilova & Mollon (2012a), using foveal test fields of 150 ms, measured thresholds for $L/(L + M)$ discrimination while the observer was adapted to a neutral field metameric to northern daylight. The primary question was whether the thresholds for $L/(L + M)$ varied with the level of excitation of the short-wave cones. The S-cone excitation was common to the two sides of the bipartite test field and so could not be used for discrimination. Thresholds varied substantially according to S-cone excitation level, in a complex but systematic way: When the ratio of L- to M-cone excitation was low, an increase in S-cone excitation reduced thresholds, but when the ratio of L- to M-cone excitation was high, an increase in S-cone excitation elevated thresholds. Provocatively, thresholds were minimal close to the category boundary between reddish and greenish hues, and the significance of category boundaries we must now briefly discuss.

5.2. Category Boundaries Are Not Aligned with the Cardinal Subsystems but May Be Associated with Enhanced Discrimination

Although chromaticity varies continuously across a 2D space represented by the ratios of cone excitations, human perception imposes discrete categories. Under conditions of daylight adaptation, a line that runs from unique yellow (near 575 nm) via white to unique blue (near 475 nm) divides the chromaticity diagram into two large categories: reddish and greenish colors (**Figure 3b**). This yellow-blue line explicitly does not map onto one of the two axes of the MacLeod–Boynton diagram and thus does not correspond to one of the cardinal subsystems. Nevertheless, if the ordinate [$S/(L + M)$ axis] of the MacLeod–Boynton diagram is scaled so that the yellow-blue line has a slope of -45° and if thresholds are measured along lines orthogonal to the yellow-blue line, then minimal thresholds are found to lie close to the phenomenological category boundary, independently measured under the same stimulus conditions (Danilova & Mollon 2010, 2012c) (see **Figure 6b**). This is true in both the fovea and the parafovea, and if the adapting chromaticity is changed, then the category boundary and the locus of optimal discrimination shift concomitantly (Danilova & Mollon 2012b).

In the larger field of perceptual science, it has very often been asked whether category boundaries are regions of enhanced discrimination. In the classic case of speech perception, optimal discrimination was observed at the category boundaries between consonants, for example, between the voiced stops *b*, *d*, and *g*, or between the voiced and unvoiced stops *d* and *t* (Liberman et al. 1957, 1961). In the case of color perception, it has been asked whether linguistic boundaries that are present in some languages but not in others lead to measurable differences in color

discriminations by speakers of those languages. The two Russian words for blue, *goluboy* and *sinij*, have offered a test case (e.g., Martinovic et al. 2020, Sinkeviciute et al. 2024, Winawer et al. 2007).

Here, we would make only three brief remarks on the significance of category boundaries for color discrimination. First, if the phenomenological change at a category boundary is more rapid, that does not explain any enhanced discrimination found in performance measurements: Rather, it is the explicandum. Second, thought needs to be given to the metric in which discrimination is expressed: It is inappropriate to use a space such as CIELUV or the Munsell system, since these already incorporate approximations to equal discriminability. (Equally, however, wavelength, although a physical variable, may be less appropriate than cone excitation ratios, since the broadband absorption curves of the cones interpose an arbitrary filter before sensory processing begins.) Third, enhanced perception at a category boundary is not a general rule even within the humble domain of the MacLeod–Boynton diagram: We measured thresholds along lines orthogonal to the locus of unique green (a phenomenological boundary between yellowish and bluish hues) and found no enhancement of discrimination at the category boundary (Danilova & Mollon 2014a). Instead, the minimal thresholds occurred at chromaticities with the same $L/(L + M)$ coordinate as the adapting field. Although differences in metrics and in experimental conditions mean that comparisons should be made with caution, the absence of enhanced discrimination near unique green is compatible with results from other studies (Bachy et al. 2012, Witzel & Gegenfurtner 2013).

5.3. The Orientation of the Central Ellipse

Color discrimination at the white point is of special interest. For this condition, Krauskopf & Gegenfurtner (1992) were able to fit their data with a circle (e.g., **Figure 6a**). Cole et al. (1993), measuring thresholds for Gaussian-blurred flashes embedded in a bright white field, similarly obtained ellipses that suggested independence of the cardinal mechanisms. Other studies, however, have reported that the central ellipse, measured in various ways, has a negative tilt and is, approximately, aligned with the phenomenological boundary between reddish and greenish colors (Bosten et al. 2015, Boynton et al. 1983, Danilova & Mollon 2025, Hong et al. 2025, Pearce et al. 2014, Regan & Mollon 1995, Sankeralli & Mullen 1999, Skelton et al. 2023). An ellipse whose orientation is not aligned with the vertical or horizontal axes is incompatible with an account in terms of two independent cardinal subsystems (see Section 4). But why was a tilted ellipse not observed by Krauskopf and Gegenfurtner for their single, well-practiced observer? One possible answer lies in individual differences: In a group of 10 observers, Danilova & Mollon (2025) found individuals whose data were compatible with two cardinal channels, but others had ellipses with the characteristic negative tilt, and none had an ellipse with a positive tilt (**Figure 6c**). However, Hedjar et al. (2025b), using equiluminant stimuli (as did Krauskopf and Gegenfurtner), found untilted central ellipses for all five observers. The critical difference may lie in stimulus conditions, for example, in whether the test patch is presented on a luminance pedestal (K. Gegenfurtner, personal communication) or whether it is a hue or a saturation difference that is measured.

5.4. Hue Versus Saturation

Elsewhere in the chromaticity diagram, lines radiating from the white point correspond to variation in colorimetric purity (the physical correlate of saturation), whereas an arc orthogonal to a point on one of these lines corresponds to variation in hue angle. As a general principle, the discrimination of colorimetric purity is poorer than the discrimination of hue. In the outer regions of color space, under a neutral state of adaptation, the long axes of discrimination ellipses are oriented, roughly, along lines of colorimetric purity (Danilova & Mollon 2025, Hong et al.

2025). This difference between thresholds for hue and for colorimetric purity is, *prima facie*, incompatible with two independent cardinal mechanisms. Consider a point on a radial line at 45° in MacLeod–Boynton space. If we vary either hue or purity, all that differs is the phase at which the signals of the cardinal channels are combined: Along the radial line, the signals $S/(L + M)$ and $L/(L + M)$ vary in phase, whereas along an orthogonal line, they vary out of phase (**Figure 6d**). Yet, thresholds are generally higher for colorimetric purity than for hue.

The difference in thresholds for hue and for colorimetric purity is unquestionably more marked in the upper left and lower right quadrants of the MacLeod–Boynton diagram (Danilova & Mollon 2016; Hansen et al. 2008; Hedjar et al. 2025a,b; Krauskopf & Gegenfurtner 1992). In these quadrants, the orientation of the ellipses echoes the orientation often seen for the central ellipse. Near the adapting point, however, there is little difference between thresholds for purity and hue (Danilova & Mollon 2016, Regan et al. 2018).

The asymmetry of discrimination for hue and colorimetric purity calls to mind a phenomenon much discussed in the mid-twentieth century by those concerned with practical tolerances for surface colors, a phenomenon that Judd (1969, 1970) called the “super-importance of hue differences.” If a circle is constructed in color space, centered on the white point and having a radius of n units of perceptual distance, then the circumference—a hue circle—does not have $2\pi n$ units of perceptual distance but has more like $4\pi n$ units. There could not be, Judd concluded, a Euclidean representation of color space in which equal discriminability was represented by equal distance. The classical evidence for the super-importance of hue came from judgments of Munsell papers and other surface materials (Nickerson 1936), and here there is the possibility that physical, “Mongean” noise contributes to higher thresholds for colorimetric purity (Danilova & Mollon 2016), for almost any real-world surface is represented not by a point in chromaticity space but rather by a distribution of chromaticities that extend from the body color toward the chromaticity of the illuminant (Hansen et al. 2008; Hedjar et al. 2025a; Lee 1986; Mollon 2006; Monge 1789, 1838). However, since an analogue of the super-importance of hue is found with modern self-luminous displays, it appears, at least in part, to be a genuinely visual phenomenon.

From the difference in the discriminability of purity and hue, some have argued that different neural mechanisms underlie the extraction of the two attributes (Kuehni 2003, 2005). An explicit test of this possibility was carried out by Regan et al. (2018), who found no selective effect on the two types of thresholds when they preadapted with stimuli designed to exercise either a channel extracting purity or a channel extracting hue. One way to explain the super-importance of hue within the framework of cardinal channels is in terms of noise in the two channels (Danilova & Mollon 2016): In the case of colorimetric purity, when measurements are made in oblique directions in the MacLeod–Boynton diagram, the $S/(L + M)$ and $L/(L + M)$ signals covary, and correlated noise in the two channels (Greschner et al. 2011) may make it difficult to distinguish signals from variation that is due to noise. In hue discrimination, however, what matters is the ratio of the signals in the two channels, and this will be relatively independent of correlated variation in the channels (compare to Section 3.2). But how does the independent channels model handle the limiting cases where colorimetric purity is measured along one of the cardinal axes? In these cases, at increasing distances from the white point, there will be increasing polarization of the single channel that is responding to the colorimetric purity (**Figure 2b**), whereas the orthogonal channel, responding to hue, will remain near its set point.

There is one additional complexity that we should draw attention to. A discrimination ellipse measured in the upper left quadrant of the MacLeod–Boynton diagram is certainly not aligned with one of the cardinal axes, nor is it aligned exactly with a line of colorimetric purity passing through the neutral point. Rather, it is rotated systematically toward the tritan axis (Danilova & Mollon 2025, figure 5a).

6. ARE THERE ADDITIONAL CHROMATIC CHANNELS IN THE EARLY VISUAL SYSTEM?

In Section 5, we showed that several results argue against an account of color discrimination in terms of two independent cardinal channels. One solution would be to postulate an additional channel in the early visual system, a channel that draws signals of the same sign—excitatory or inhibitory—from long- and short-wave cones and signals of the opposite sign from middle-wave cones (Danilova & Mollon 2010). Effectively, such a channel would be signaling redness and greenness, and we might imagine that it would be in its equilibrium state, and at its most sensitive, in the region of the phenomenological yellow-blue locus.

In the early literature, there were occasional reports of chromatically opponent neurons in the primate retina and LGN that behaved as if they did draw synergistic signals from long- and short-wave cones on the one hand and from middle-wave cones on the other (e.g., de Monasterio et al. 1975, Valberg et al. 1986). Very recently, combining calcium imaging with adaptive optics, Godat et al. (2024) confirmed the existence in *Macaca fascicularis* of retinal ganglion cells of both possible noncardinal types: L versus M + S and M versus L + S.

Recent connectomic reconstructions from electron micrographs (Kim & Dacey 2026) suggest that there are several routes by which S-cone signals might interact selectively with either M- or L-cones:

1. Human S-cones, unlike those of macaques or marmosets, show direct cone–cone (telodendritic) contacts to M- and L-cones (Kim et al. 2023). So, the primate retina may not be an exact model for the human retina.
2. As in the case of macaques but not marmosets, OFF midget ganglion cells may draw an input from S-cones via a flat midget bipolar (Kim et al. 2023, Patterson et al. 2019).
3. A subset (10–15%) of ON midget ganglion cells are postsynaptic to S-cone bipolar cells (Kim et al. 2024).
4. The relatively rare “large bistratified” ganglion cells are postsynaptic to excitatory S-cone bipolar cells but also draw inputs from both ON and OFF midget bipolars (Kim et al. 2024).

That firm framework of the late twentieth century has gone.

7. CONCLUSIONS

Since discrimination thresholds are labile, varying with adaptation, with target properties, and with the observer’s task, it will never be possible to offer a single representation in which colors are uniformly spaced in discriminability, even for an average observer. In principle, a comprehensive physiological model of color discrimination would do the job, but such a model is not yet available. And, remarkably, there is still no set of empirical measurements that sample color discrimination throughout the chromaticity diagram under conditions of adaptation to a standard illuminant. Perley G. Nutting Jr. died in South Pasadena, Florida, in 2001. We need a worthy successor.

SUMMARY POINTS

1. Historically, the discrimination of colors has been studied in three distinct experimental strands: the König tradition of wavelength discrimination, the MacAdam tradition of discrimination ellipses obtained from color matches made at different points within the interior of color space, and the Stiles tradition of increment thresholds for detecting monochromatic flashes.

2. A fundamental finding from all these traditions is that discrimination is optimal at the chromaticity to which the observer is currently adapted.
3. Discriminations are impaired at high colorimetric purities (i.e., when colors are subjectively saturated).
4. A reduction in the size of the target disproportionately impairs discriminations that depend on short-wave cones.
5. In the twentieth century, the discrimination ellipses obtained by MacAdam were widely used to estimate the total number of discernable colors and to derive a uniform color space, a diagram in which equal distances would represent equally noticeable color differences. However, these uses of the ellipses are invalid, since MacAdam's primary observer would have been in a different state of adaptation for each of the chromaticities at which he made color matches.
6. A second problem with such uses of discrimination ellipses is that a sensation of difference is not the same as a difference of sensation. When observers are asked to discriminate two abutting fields, they may—under some experimental conditions—use signals originating in a spatially differencing channel that responds to the edge between the fields. If this is the case, then the data cannot be used to estimate the discriminability of isolated, spatially separated colors.
7. In the latter part of the twentieth century, chromatic discrimination was typically explained in terms of two “cardinal” neural channels: One channel differenced the signals of long- and middle-wave cones, and the second extracted the signal of short-wave cones scaled by the sum of the long- and middle-wave cone signals.
8. In this century, accumulating evidence—from psychophysics, physiology, and histology—has suggested that color discrimination cannot be explained simply in terms of two cardinal channels.

FUTURE ISSUES

1. Are there noncardinal channels in the visual system that are used for color discrimination? In particular, is there a neural channel that differences the signals of middle-wave cones against the combined signals of long-wave and short-wave cones? Does this channel correspond to the phenomenological axis of redness and greenness?
2. Are there conditions where chromatic discrimination depends on difference signals that arise at the edge between adjacent areas of color? If so, does discrimination deteriorate when the stimuli are separated in space?
3. Are there important individual differences in color discrimination? Are there observers who inherit three normal types of cone, but lack a particular differencing channel that is present in other observers?
4. If the color discrimination of anomalous trichromats is plotted in a standard chromaticity diagram, then the measurements are necessarily device dependent, since stimuli that are metamers for normal trichromats may not be metamers for anomalous trichromats, and vice versa. However, if data for anomalous trichromats are expressed in a chromaticity

diagram appropriate for their own cone sensitivities, will their chromatic discrimination exhibit the same features as that of normal trichromats?

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