

# Parafoveal color discrimination: A chromaticity locus of enhanced discrimination

**Marina V. Danilova**

**J. D. Mollon**

Laboratory of Visual Physiology,  
I.P. Pavlov Institute of Physiology,  
St. Petersburg, Russia, &  
Department of Experimental Psychology,  
University of Cambridge, Cambridge, UK



Department of Experimental Psychology,  
University of Cambridge, Cambridge, UK



Are boundaries between color categories associated with enhanced discrimination? In the present experiments, chromatic thresholds were obtained for discriminations along lines orthogonal to the yellow-blue axis of color space. The targets were parafoveal and thresholds were measured with a spatial two-alternative forced choice. In interleaved experimental runs, we also obtained empirical estimates of the subjective yellow-blue line by asking observers to categorize colors as reddish or greenish. Both types of measurement were made in the presence of a steady background that was metameric to equal-energy white. In a limited region from desaturated yellow to desaturated blue, an enhanced discrimination is found near the subjective transition between reddish and greenish hues. This line of optimal discrimination is not aligned with either of the cardinal axes of color space: In a MacLeod–Boynton chromaticity diagram, it runs obliquely with negative slope.

**Keywords:** color discrimination, linguistic color category, unique hue, parafovea, red-green channel

**Citation:** Danilova, M. V., & Mollon, J. D. (2010). Parafoveal color discrimination: A chromaticity locus of enhanced discrimination. *Journal of Vision*, 10(1):4, 1–9, <http://journalofvision.org/10/1/4/>, doi:10.1167/10.1.4.

## Introduction

What is the relationship between color categories and color discrimination? Is discrimination better across a category boundary (e.g. between green and blue) than it is within a category? Alternatively, is discrimination particularly good at a unique hue, e.g. at a transition between two binary hues, such as that between reddish blues and greenish blues?

Although these questions are celebrated ones, there is only a little empirical evidence that discrimination is enhanced at the boundaries of color categories. Winawer et al. (2007) using a series of blue stimuli, have shown that native Russian speakers respond more rapidly when the discriminanda lie on opposite sides of the boundary between *goluboy* and *signyi*. For a Russian speaker, these two categories differ in hue and lightness and there is no general word for ‘blue’. Native English speakers—for whom blue is a single category—did not exhibit an analogous advantage at the boundary between ‘light blue’ and ‘dark blue’. Similarly, Witzel, Hansen, and Gegenfurtner (2009) have reported shortened reaction times for transitional colors between green and blue when the stimuli had previously been equated for discriminability in a threshold task.

Here we ask whether discriminability itself, measured by two-alternative forced choice thresholds and expressed in terms of cone excitation ratios, exhibits a relationship to

the phenomenological transition between two binary hues. We have been led to the present experiment by an indirect route. We had previously studied the human ability to discriminate the chromaticities of brief, parafoveal stimuli that were spatially separated by up to 10 degrees of visual angle (Danilova & Mollon, 2006a, 2006b). If discrimination depended on local difference signals arising at the edge between the stimuli and extracted early in the visual system (Whittle, 2003), then we might expect performance to deteriorate with increasing spatial separation of the targets; and secondly we might expect discrimination to be best when the two discriminanda fell close to the equilibrium point of a distal color channel—as set by the current background (Krauskopf & Gegenfurtner, 1992; Miyahara, Smith, & Pokorny, 1993). Conversely, if discrimination depended on the comparison of two abstract codes transmitted over a ‘cerebral bus’ (Danilova & Mollon, 2003), then we might expect no deterioration with spatial separation, and it is possible that categories might influence discrimination: for example, discrimination might be better at the transition between reddish blues and greenish blues than it is between two reddish blues.

In fact, discrimination thresholds turn out to be similar for juxtaposed and for well-separated stimuli (Danilova & Mollon, 2006a, 2006b)—a result suggesting that discrimination depends on the central comparison of two separate color signals. This surprising finding let us to ask whether, under the conditions of our experiments, discrimination

would exhibit category effects. Specifically, we asked whether colors would be better discriminated when they straddled a unique hue—when, for example, they fell at the transition between reddish blue and greenish blue.

In the experiment described here, the spatial separation of the edges of the stimuli was held constant at 1.7 deg, since this is the separation that we have previously found to be optimum (Danilova & Mollon, 2006b). As before, the stimuli were parafoveal and the pair of discriminanda could fall anywhere on an imaginary circle that had a radius of 5 deg and was centered on the fixation point (Figure 1).

To study the question of whether color discrimination is enhanced at category boundaries, it is necessary to have an independent metric for the discriminanda. To use an arbitrary series of stimuli (as in the study of Winawer et al., 2007) would be unsatisfactory for our purpose; and it would be circular to use stimuli that were separated by equal units in CIE  $L^*a^*b^*$  space or in CIE  $L^*u^*v^*$  space or in the Munsell system, since the units of these spaces are themselves derived from discrimination experiments. In the present study, we use ratios of cone excitations as an independent metric.

We constructed our stimulus set in an analogue of the chromaticity diagram of MacLeod and Boynton (1979). Since our stimuli were parafoveal, we used the 10-deg cone fundamentals of Stockman and Sharpe (2000), but we retained the relative scaling of L and M cone

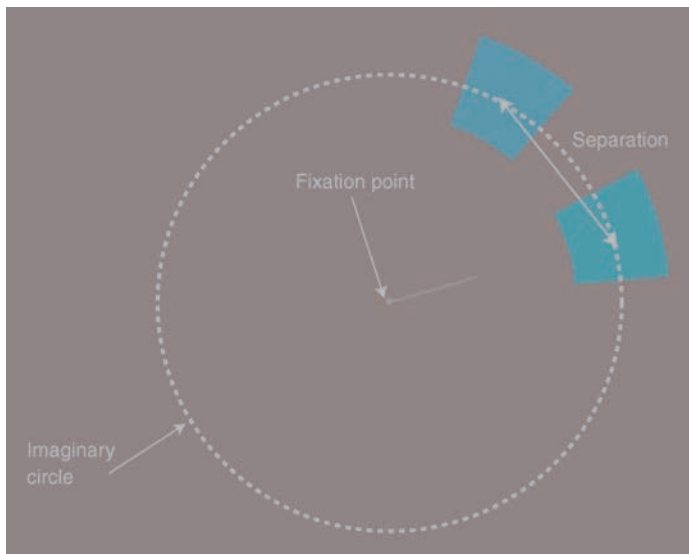


Figure 1. An example of the stimuli used in the discrimination measurements. The centers of the two targets fell on an imaginary circle (radius 5 deg) that was centered on the fixation point. The position on the imaginary circle of the midpoint between the two target patches was randomized from trial to trial, but the spatial separation of the two targets was constant. A thin white bar indicated which was the more clockwise target. For judgments of unique hues, only one target was present, but its position was randomized as for the discrimination measurements.

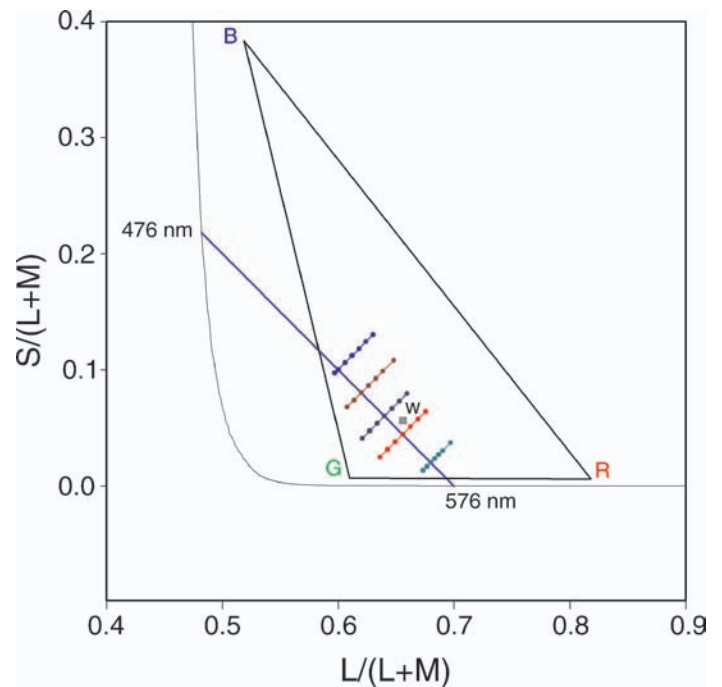


Figure 2. A section of a MacLeod–Boynton chromaticity diagram showing the locations of the reference stimuli used in the discrimination measurements. The triangle RGB represents the gamut of chromaticities that could be produced with the three phosphors of the monitor. A portion of the spectrum locus is shown, together with the line that runs from approximately unique yellow (576 nm) to approximately unique blue (476 nm). Our referent stimuli lay on lines that intersected the 476–576 nm line at 90 degrees and are shown by the solid points; the color used here for each set of referents is also used for the corresponding referents in Figures 3 and 4, to assist comparison. The single gray square represents the monitor background, which was metameric to equal energy white. This diagram is a modified form of the standard MacLeod–Boynton diagram in that it is based on the cone fundamentals of Stockman and Sharpe (2000) and the vertical ordinate has been scaled so that the 476–576 nm line has a slope of  $-45$  deg (see text).

sensitivities from the original diagram (Figure 2). We wished to probe discrimination thresholds along lines that were orthogonal to the ‘yellow-blue line’ that separates reddish and greenish colors. As a preliminary approximation to this line, we took the line that runs between 576 nm and 476 nm, wavelengths that are close to typical estimates of unique blue and unique yellow respectively (Burns, Elsner, Pokorny, & Smith, 1984; Dimmick & Hubbard, 1939; Jordan & Mollon, 1997; Nerger, Volbrecht, & Ayde, 1995; Purdy, 1931; Webster et al., 2002). We scaled our chromaticity diagram so that this line had a slope of  $-45$  deg in the diagram, and we then calculated a series of lines with a slope of  $+45$  deg, which intersected the yellow-blue line at an angle of 90 deg (see Figure 2). We measured discrimination thresholds at a series of points along each of the  $+45$  deg lines.

The 576–476 nm line served only as a preliminary estimate of the yellow-blue axis of color space. Most estimates of unique hues have been obtained with a dark background whereas the present measurements were made in the presence of a white field metameric to equal-energy white. In blocks of trials interleaved with the discrimination measurements, we therefore obtained our own phenomenological estimates of the yellow-blue line: Observers were asked to judge stimuli as ‘reddish’ or ‘greenish’ as chromaticity was varied along +45 deg lines in our rescaled MacLeod–Boynton diagram. Thus the 476–576 nm ‘yellow-blue’ line was used only to bootstrap the experiment, in guiding the initial choice of conditions.

## Methods

### Subjects

All three observers had normal color vision as tested by the Cambridge Colour Test (Regan, Reffin, & Mollon, 1994) and all had extensive training on color discriminations. JM is male, MD and IK female. IK was naïve to the purpose of the experiment. MD and IK are native Russian speakers.

### Apparatus and stimuli

Stimuli were presented on a calibrated color monitor using a Cambridge Research Systems VSG graphics board, allowing a precision of 15 bits per gun. Observer JM was tested in Cambridge with a VSG 2/3 board and a Mitsubishi Diamond Pro 2070 monitor; MD and IK were tested in St. Petersburg using a VSG 2/5 board and a Sony GDM-F500 monitor.

The CRT screen was viewed binocularly from a distance of 57 cm. A steady background field was always present and had a chromaticity metameric to equal energy white. The discriminanda were sectors of an annulus, and their centers lay on an imaginary circle that had a radius of 5 degrees of visual angle (see Figure 1), centered on a continuously present white fixation point. The radial length of each target sector, and its width at its midpoint, were 2 deg. The separation of the midpoints of the sectors was 3.7 deg. On any trial, the midpoint of the two patches lay on a radius that had a random angle chosen in steps of 5°, starting from 12 o’clock. (Randomization of target position serves to discourage observers from moving their eyes in the direction of an expected parafoveal target.) The duration of the stimulus patches was 100 ms, a duration chosen to be too short to allow eye movements towards them.

As an analogue of Judd<sub>(1951)</sub> luminance, we took the sum of the long-wave and middle-wave signals (L + M). The luminance of the background was set to have a value

of 10 cd.m<sup>-2</sup>. The target sectors had a mean luminance that was 30% greater than that of the background when expressed in the (L + M) units of our space; but to ensure that subjects could not discriminate the stimuli on the basis of differences in sensation luminance, we jittered independently the (L + M) value of each target in the range ±5% of the mean value.

### Procedure

Chromatic discrimination thresholds were measured by the spatial forced choice method used in our earlier experiments. In any given experimental session, we tested discrimination along one of the five 45-deg lines shown in different colors in Figure 2. We chose 7 ‘reference stimuli’ placed at different positions along the line. The reference stimuli were never themselves presented, but any given pair of discriminanda lay on the same line in chromaticity space, straddling a particular reference stimulus; and their chromatic separation was increased or decreased symmetrically around the reference chromaticity according to the accuracy of the subject’s performance. The observer’s task was to indicate by pushbuttons whether the more clockwise or the less clockwise stimulus was the ‘redder’ (or ‘less green’). Since the subjective appearance of the stimuli varied greatly at different positions along a 45-deg line and since we wished to minimize any central tendencies within the set of 7 reference stimuli, we tested only one reference stimulus in a given block of trials and we gave auditory feedback to indicate correctness of response. A single staircase was used, which terminated after 15 reversals; the last 10 reversal points were averaged to give a threshold. The staircase tracked 79.4% correct (Wetherill & Levitt, 1965). The reference and test chromaticities were expressed in terms of the abscissa of the chromaticity diagram (i.e. their L/(L + M) or *l* coordinate), and the corresponding S/(L + M) coordinate was then calculated so that they lay on the same 45-deg line. At any one point on the staircase, one of the discriminanda had an *l* coordinate *l*<sub>1</sub> and the other had an *l* coordinate *l*<sub>2</sub>, where *l*<sub>1</sub> was equivalent to the reference coordinate *l*<sub>r</sub> multiplied by a factor *a*, and *l*<sub>2</sub> was equivalent to *l*<sub>r</sub> divided by *a*. After 3 correct responses, the value (*a* – 1) was reduced by 10% and after each incorrect response it was increased by 10%.

Each of the different 45-deg lines was tested in a different experimental session; and at least five repetitions were performed for each 45-deg line. The order of testing referent points on a single line, and the order of testing different lines, were both randomized.

In interleaved experimental sessions, we measured the observer’s transition point between red and green as chromaticity was varied along lines of 45-deg slope. Five of these lines corresponded to those used for the performance measurements of discrimination (see above);

and in order to obtain an extended estimate of the empirical locus of unique hues, we added 2 further lines in the case of MD and IK, and 1 in the case of JM (who was limited by the monitor gamut). A single target was presented for 100 ms with the same spatial properties as in the discrimination trials. The observer was asked to indicate by pushbuttons whether this single stimulus was reddish or greenish; the equivalent Russian terms were unambiguous for our Russian-speaking observers. To avoid sequential effects in these phenomenological measurements, four randomly interleaved staircases were used to track the point of subjective equality, two starting on each side of the expected match (Jordan & Mollon, 1995). Each staircase terminated after 15 reversals. The last 10 reversals of each of the 4 staircases were pooled to give an estimate of the unique hue for a given experimental run. The estimates plotted in Figure 6 are based on a minimum of 5 independent experimental sessions. All the 45-deg lines were tested in a given session, in a different random order in different sessions.

Neither of our two tasks was speeded, in that we did not ask our observers to respond as quickly as possible. However, we routinely recorded the response time on each trial.

The experimental procedures at both sites were approved by the Cambridge University Psychology Ethics Committee.

## Results

Figure 3 offers the most direct representation of the results for one observer: Each pair of data points, linked by a short line, represents a pair of chromaticities that were discriminable on 79.4% of trials. Along each 45-deg line, there is a variation in the separation of the paired targets, with the minimal separation (and highest discrimination) usually in the middle of the range.

The range of threshold variation can be judged from Figure 4. Here, each set of data fitted with a solid line corresponds to the thresholds measured at different points along one particular 45-deg line (Each data set is identified by symbols of the same color in Figures 2–4.) Each threshold is plotted against the  $L/(L + M)$  or  $l$  coordinate of its corresponding reference stimulus. The ordinate corresponds to the factor  $a$  by which each of the two discriminanda differs from the reference chromaticity (see Methods) and so the threshold values are approximately half the values of the conventional Weber fraction. The solid lines fitted to each data set are 3rd-order inverse polynomials: They are used to estimate the minima plotted in Figure 6 but do not have theoretical significance.

Very similar patterns of results are seen for the three subjects. Each of the five data sets, corresponding to the five 45-deg lines probed in the experiment, shows a minimum. This is most marked for the three central lines,

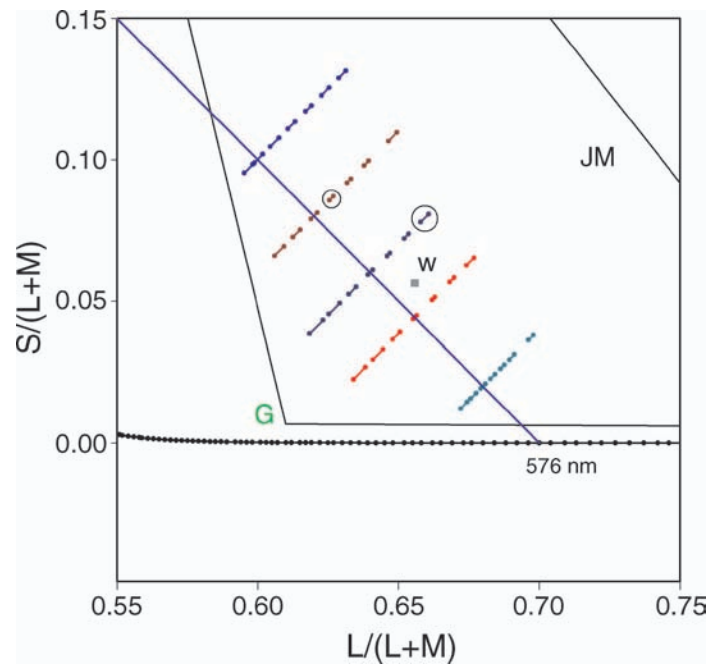


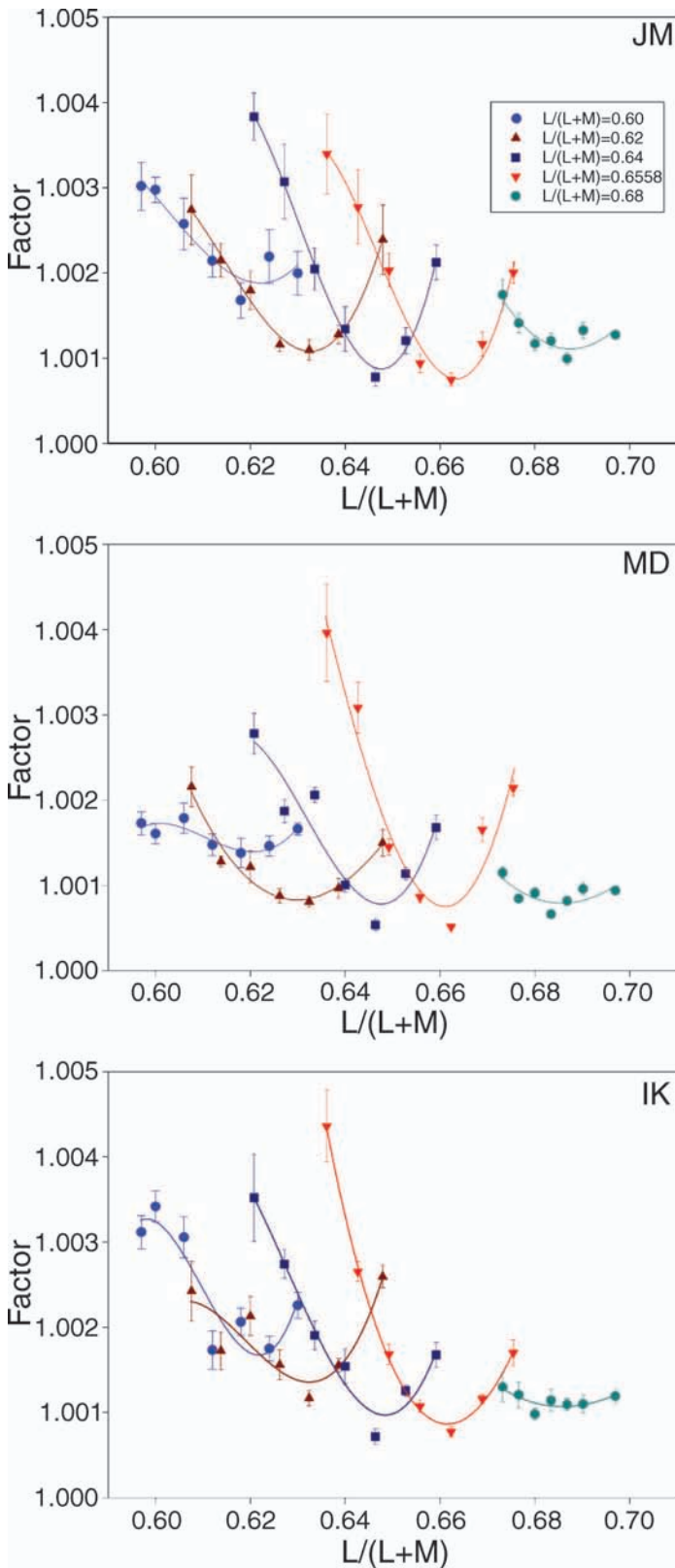
Figure 3. A section of the modified MacLeod–Boynton chromaticity diagram showing directly the separation of our stimuli at threshold. Observer: JM. Each connected pair of points represents targets that could be discriminated with 79.4% accuracy by the observer. Two particular thresholds are identified by circles: notice that the threshold around the reference chromaticity 0.632, 0.093 is lower than that around the reference chromaticity 0.659, 0.079, even though the latter is closer to the adapting chromaticity. For reference, the 476–576 nm line is shown in blue.

which intersect the 476–576 nm line at  $l$  values of 0.62, 0.64 and 0.656; the minima become less clear as the target sets move closer to the long-wave or short-wave spectrum locus. At the minimum, the absolute values of the thresholds are small: The value of the factor  $a$  is of the order of 1.001. It is yet to be determined what neural signal is the basis for the observer’s judgment under these conditions (see Discussion), but if the observer did rely on a signal corresponding to  $L/(L + M)$ , then the threshold change in the signal would be approximately 0.2%.

In Figure 5, we plot for each subject and every condition the average response time against the corresponding average threshold. Although the three observers differ in the absolute values of their response times, all show a strong positive correlation between response time and threshold: Pearson’s product moment coefficients are 0.816, 0.742 and 0.736 for JM, MD and IK respectively ( $p < 0.001$  in all cases). So it is clear that our observers do not achieve precision at the expense of speed: On the contrary, the finest discriminations are the ones that are made most quickly.

In the chromaticity diagram of Figure 6, we plot (blue points) the positions of the red–green transitions as estimated from phenomenological judgments (see Methods) made in interleaved experimental sessions. Expressed in terms of

the  $l$  coordinate, the average SEMs for these settings were .00050 (JDM), .00038 (MK), .00079 (IK): these values, based on between-session variance, suggest that the observers made the judgments with good repeatability.



We also plot in Figure 6 (as red points) the positions of optimum discrimination, derived from the inverse polynomial fits of Figure 4. The estimates of unique hue and of minimal threshold run roughly parallel but do not exactly coincide. In the case of JM and MD, the chromaticities of the unique hues and the chromaticities of minimal threshold fall rather close together for the three central data sets, i.e. for the cases where the +45 deg line intersects the 476–576 nm line at  $l$  values of 0.62, 0.64 and 0.656. Outside this range the two functions diverge. These are regions (*v.* Figure 4) where the minimum of threshold is much less marked (and where estimates of the minimum are less secure). In the case of IK, the unique hues and minimal thresholds coincide very closely at the three highest  $l$  values, but diverge in the region of saturated blues.

## Discussion

### Chromatic channels

In a region of the chromaticity diagram that—under neural adaptation—corresponds to desaturated yellows and desaturated blues, we find a furrow of low thresholds. The enhanced discrimination in this region is also reflected in shorter response times. However, the furrow of low thresholds is not aligned with either of the axes of the MacLeod–Boynton diagram. The latter axes are the ‘cardinal directions’ of Krauskopf, Williams, and Heeley (1982) and are thought to correspond to two chromatic channels in the early visual system, one of which draws opposed signals from L- and M-cones and the other of which draws opposed signals from the S-cones on the one hand and from the L- and M-cones on the other (Derrington, Krauskopf, & Lennie, 1984). The L vs. M signal is thought to be carried by midget ganglion cells in the retina and by parvocellular units in the lateral geniculate nucleus, whereas an S vs. (L + M) signal is thought to be carried by the small bistratified ganglion cells that project to koniocellular layers 3 and 4 of the LGN (Dacey, 2003; Dacey & Lee, 1994).

Figure 4. Thresholds for all three observers plotted against the  $L/(L + M)$  values of the referent stimuli. The color used to identify each set of referents corresponds to the color used in Figures 2 and 3, and the inset key records the  $L/(L + M)$  value at which the 45-deg line of each of these stimulus sets intersects the original yellow-blue line of Figure 2. The ordinate corresponds to the factor by which each of the two targets differed from the reference chromaticity in terms of  $L/(L + M)$ ; see Methods. The fitted lines are inverse third-order polynomials; they do not have theoretical significance but were used to estimate the chromaticities of minimal thresholds plotted in Figure 6.

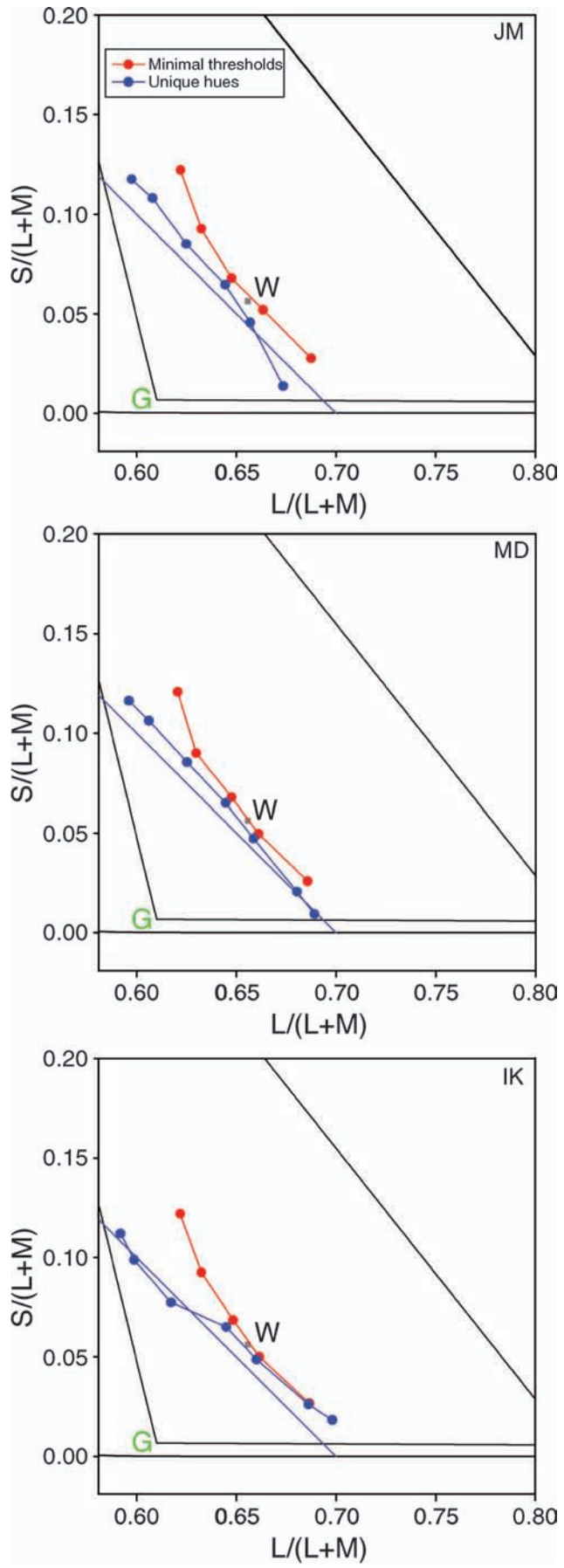
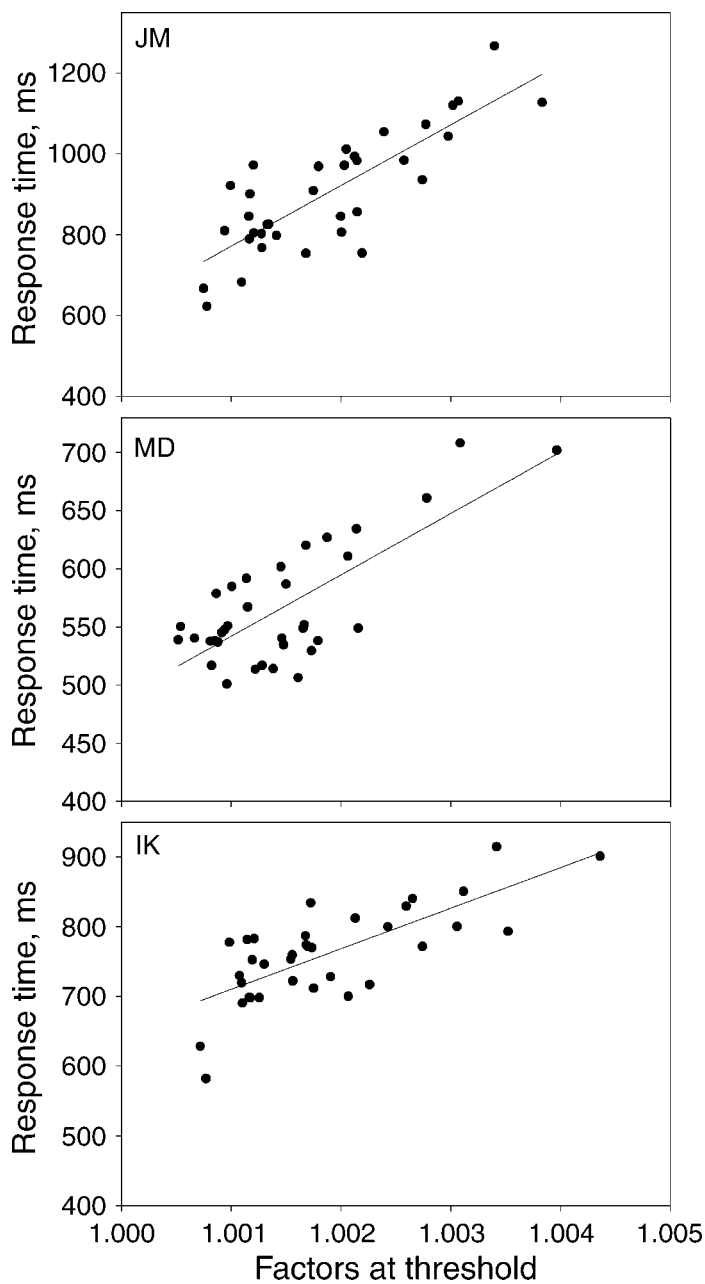


Figure 5. Mean response times for each observer plotted against the corresponding mean thresholds for every condition. The task was not a speeded one, but response times were routinely recorded. Thresholds are expressed as the factor by which each of the two targets differed from the reference chromaticity in terms of  $L/(L + M)$ ; see [Methods](#). Different observers exhibit different absolute response times (note ordinal scales), but each observer shows a strong positive relationship between the two measures: Higher thresholds are associated with longer response times.

When color discrimination has been probed at different positions along an  $L/M$  axis, thresholds have been found to be lowest at the chromaticity to which the observer is adapted (Krauskopf & Gegenfurtner, 1992; Miyahara et al., 1993). The theoretical interpretation has been that neural channels have a limited, and compressive, operating

response, so that sensitivity is highest at the equilibrium point of the channel (Pugh & Mollon, 1979; Polden & Mollon, 1980). If discriminations in the present experiment were determined by a conventional L/M channel and if the adaptive state of this channel were independent of that of any other channel, then we should expect to find minimal thresholds where each of our 45-deg lines transected the tritan line passing through the chromaticity of the white background used in our experiment. For by definition this is a line along which there is a constant ratio of L- and M-cone excitations. Instead, our minima move to lower ratios of L- to M-cone excitation as the level of S-cone excitation increases. Conversely, if discrimination depended only on a channel that extracted the ratio  $S/(L + M)$ , the minima should always occur where our 45-deg lines intersected a horizontal line passing through the white point.

Consideration of Figure 3 also makes clear that our results cannot be summarized by the rule: Thresholds are lower the closer the discriminanda are to the adapting chromaticity and thus to the equilibrium points of the two classical chromatic channels. For example, the threshold around the reference chromaticity 0.632, 0.093 is lower than that around the reference chromaticity 0.659, 0.079, but the latter is closer to the adapting chromaticity. (These two referents are identified by circles in Figure 3.)

So our results might provide evidence for a neural channel that is distinct from the channels thought to correspond to the two axes of the MacLeod–Boynton diagram. This channel would oppose an M-cone signal to a combination of L- and S-cone signals. In the recent study of S-OFF LGN cells by Tailby, Solomon, and Lennie (2008), S-cone signals were most commonly found to be synergistic with M-cone signals; but in the earlier literature there are examples of retinal and LGN cells that are excited by M-cones and inhibited by S- and L-cones (de Monasterio, Gouras, & Tolhurst, 1975; Valberg, Lee, & Tigwell, 1986). If we postulate a channel that draws opposed inputs from M cones on the one hand and from S and L cones on the other, then the chromaticities at which we find minimum thresholds may be chromaticities at which the proposed channel is in equilibrium. They would be chromaticities that produced a constant ratio of the M-cone signal to some combination of the S- and L-cone signals.

A channel of the kind we postulate would be compatible with two earlier measurements of discrimination ellipses. Boynton, Nagy, and Olson (1983) measured a discrimination ellipse centered on a bluish white and found that thresholds were lowest along a +45 deg axis. Krauskopf and Gegenfurtner (1992) recorded two ellipses that lay on

---

Figure 6. Comparison of unique hue judgments and threshold measurements. The blue points show the chromaticities that the observer subjectively judged to be neither reddish nor greenish. The red points show the chromaticities of minimal thresholds measured by two-alternative spatial forced choice, and are derived from the polynomial fits of Figure 4.

either side of the white adapting point approximately on a yellow-blue line: in both these cases, the axis had a long axis that pointed along the yellow-blue line towards the white point, i.e. discrimination was best in a +45-deg direction. Although they did not formally identify the position of the yellow-blue line in their conditions, Krauskopf and Gegenfurtner explicitly remarked: ‘This makes it attractive to think that discriminations can also be made by using mechanisms sensitive to the “redness” and “greenness” of stimuli.’ Also relevant may be the report of Beer, Dinca, and MacLeod (2006), who found that subjects’ settings were maximally scattered along a blue-yellow axis when they were asked to set a field to white in a dark surround.

Some further explanation would be needed to account for the attenuation of the threshold minima in regions closer to the spectrum locus. The restricted region of enhanced red-green discrimination is not entirely unexpected. For this is the region where ‘Tyndall’s Paradox’ occurs: Wavelength discrimination for monochromatic blue lights is not impaired, and even improves, if more than 60% of the monochromatic light is replaced by a bluish white desaturant that is common to both sides of a bipartite stimulus (Mollon & Estévez, 1988; Tyndall, 1933). Tyndall’s result is paradoxical because discrimination improves even though the triplets of cone quantum catches on the two sides of the bipartite field become more similar. Replicating Tyndall’s paradox with a performance measure, Mollon and Estévez wrote: ‘The reader may wonder what the targets looked like. At 100% purity they are a glaring blue and vary little in appearance as the wavelength is changed. At 20% purity 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.’ However, it must be said that Tyndall’s Paradox is clearest when wavelength discrimination is essentially along a tritan line—as it is at 465 nm. Further work will be needed to establish whether there is a relationship between Tyndall’s Paradox and the present phenomenon.

As set out in the Introduction, our earlier parafoveal studies of comparison at a distance led us to carry out these experiments at an eccentricity of 5 degrees. However, preliminary results suggest that a similar phenomenon can be observed for discriminanda presented within the fovea (Danilova & Mollon, 2009).

## Relationship to the phenomenological yellow-blue line

We began these experiments by asking whether there was a relationship between color categories and color discrimination. We find a furrow of low thresholds that runs obliquely across the MacLeod–Boynton chromaticity diagram, approximately in the direction of the yellow-blue line. The latter is the line that marks the transition from

reddish to greenish sensations, as independently estimated for our observers. Do our discrimination results offer a performance correlate of a phenomenological transition between two binary hues? Is there a common physiological basis for the performance and subjective measures? The line of minimal threshold and the phenomenological yellow-blue line run close to each other only over a limited region—the region of desaturated blues and yellows; but this is the limited region where the deep minimum is seen in the discrimination thresholds. Even within this region, a complete coincidence of our two types of measurement could hardly be expected. On the one hand, the minima in the threshold depend on the fit of an arbitrary function to discrete data points. On the other hand, the estimates of unique hue (though statistically reliable) are dependent on the observer's subjective criterion, and in particular on the strategy the observer adopts when uncertain about the category to which to assign stimuli falling close to the transition between binary hues. It sounds straightforward to ask observers to press one button if the target appears greenish and the other if the target appears reddish, but all our observers in fact reported that the 100-ms flashes seldom looked spatially uniform in hue: Near the transition point, greenish and reddish tinges might be concurrently present in different regions of the 2-deg target.

Although we find enhanced discrimination for stimuli close to a unique hue, i.e. stimuli falling close to the transition between reddish and greenish colors, the effect occurs—as we noted above—only for a limited range of relatively desaturated colors. Unique yellow and unique blue are most commonly measured with monochromatic stimuli rather than with the non-spectral stimuli used in the present case. However, a number of previous studies have assessed unique hues in the interior of color space (e.g. Burns et al., 1984; Mizokami, Werner, Crognale, & Webster, 2006); and this indeed may be the more appropriate approach if it proves to be the case that unique hues are determined by real-world stimuli rather than by the wiring of the visual system (Mollon & Jordan, 1997). In this context, it may be significant that the region where we find minimal thresholds corresponds roughly to the 'caerulean line', the locus of the natural illuminants formed by mixtures of sunlight and daylight (Mollon, 2006).

It may be worth noting that the subjective category boundary in question is not of the type most often considered in discussions of the relationship between color categories and color discrimination. More commonly, authors have asked whether there is enhanced discrimination at the boundary between two hues, say green and blue. Here we have asked whether there is enhanced discrimination at the center of a category, at a unique hue, where a transition occurs between two binary hues. The categorical structure of color space is in this sense more complicated than that of speech sounds. In the case of speech sounds, such as the voiced stops *b*, *d* and *g*, listeners perceive little variation within a category

(Liberman, Harris, Hoffman, & Griffith, 1957): We do not speak of hearing *d* sounds that are *b*-ish or *g*-ish. Enhanced discrimination is found at the transition between one category and a second, at the abrupt transition from, say, *b* to *d*.

## Acknowledgments

Supported by the Wellcome Trust grant 082378/Z/07/Z.

Commercial relationships: none.

Corresponding author: Marina V. Danilova.

Email: mvd1000@cam.ac.uk.

Address: I.P. Pavlov Institute of Physiology, Nab. Makarova, 6, 199034 St. Petersburg, Russia.

## References

- Beer, R. D., Dinca, A., & MacLeod, D. I. A. (2006). Ideal white can be yellowish or bluish, but not reddish or greenish [Abstract]. *Journal of Vision*, 6(6):417, 417a, <http://journalofvision.org/6/6/417/>, doi:10.1167/6.6.417.
- Boynton, R. M., Nagy, A. L., & Olson, C. (1983). A flaw in equations for predicting chromatic difference. *Color Research and Application*, 8, 69–74.
- Burns, S. A., Elsner, A. E., Pokorny, J., & Smith, V. C. (1984). The Abney effect: Chromaticity coordinates of unique and other constant hues. *Vision Research*, 24, 479–489. [PubMed]
- Dacey, D. M. (2003). Colour coding in the primate retina: Diverse cell types and cone-specific circuitry. *Current Opinion in Neurobiology*, 13, 421–427. [PubMed]
- Dacey, D. M., & Lee, B. B. (1994). The 'blue-on' opponent pathway in primate retina originates from a distinct bistratified ganglion cell type. *Nature*, 367, 731–735. [PubMed]
- Danilova, M. V., & Mollon, J. D. (2003). Comparison at a distance. *Perception*, 32, 395–414. [PubMed]
- Danilova, M. V., & Mollon, J. D. (2006a). The comparison of spatially separated colours. *Vision Research*, 46, 823–836. [PubMed] [Article]
- Danilova, M. V., & Mollon, J. D. (2006b). The gap effect is exaggerated in the parafovea. *Visual Neuroscience*, 23, 509–517. [PubMed] [Article]
- Danilova, M. V., & Mollon, J. D. (2009). Enhanced colour discrimination at a category boundary. *Perception*, 38, 14–15.
- de Monasterio, F. M., Gouras, P., & Tolhurst, D. J. (1975). Trichromatic colour opponency in ganglion cells of the rhesus monkey retina. *The Journal of Physiology*, 251, 197–216. [PubMed] [Article]



- Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *The Journal of Physiology*, *357*, 241–265. [[PubMed](#)] [[Article](#)]
- Dimmick, F. L., & Hubbard, M. R. (1939). The spectral location of psychologically unique yellow, green, and blue. *American Journal of Psychology*, *52*, 242–254.
- Jordan, G., & Mollon, J. D. (1995). Rayleigh matches and unique green. *Vision Research*, *35*, 613–620. [[PubMed](#)]
- Jordan, G., & Mollon, J. D. (1997). Unique hues in heterozygotes for protan and deutan deficiencies. *Colour Vision Deficiencies Xiii*, *59*, 67–76.
- Krauskopf, J., & Gegenfurtner, K. (1992). Color discrimination and adaptation. *Vision Research*, *32*, 2165–2175. [[PubMed](#)]
- Krauskopf, J., Williams, D. R., & Heeley, D. W. (1982). Cardinal directions of color space. *Vision Research*, *22*, 1123–1131. [[PubMed](#)]
- Liberman, A. M., Harris, K. S., Hoffman, H. S., & Griffith, B. C. (1957). The discrimination of speech sounds within and across phoneme boundaries. *Journal of Experimental Psychology*, *54*, 358–368. [[PubMed](#)]
- MacLeod, D. I. A., & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America*, *69*, 1183–1186. [[PubMed](#)]
- Miyahara, E., Smith, V. C., & Pokorny, J. (1993). How surrounds affect chromaticity discrimination. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, *10*, 545–553. [[PubMed](#)]
- Mizokami, Y., Werner, J. S., Crognale, M. A., & Webster, M. A. (2006). Nonlinearities in color coding: Compensating color appearance for the eye's spectral sensitivity. *Journal of Vision*, *6*(9):12, 996–1007, <http://journalofvision.org/6/9/12/>, doi:10.1167/6.9.12. [[PubMed](#)] [[Article](#)]
- Mollon, J. D. (2006). Monge—The Verriest Lecture, Lyon, July 2005. *Visual Neuroscience*, *23*, 297–309. [[PubMed](#)]
- Mollon, J. D., & Estévez, O. (1988). Tyndall's paradox of hue discrimination. *Journal of the Optical Society of America*, *5*, 151–159. [[PubMed](#)]
- Mollon, J. D., & Jordan, G. (1997). On the nature of unique hues. In C. Dickinson, I. Murray, & D. Carden (Eds.), *John Dalton's colour vision legacy* (pp. 381–392). London: Taylor & Francis.
- Nerger, J. L., Volbrecht, V. J., & Ayde, C. J. (1995). Unique hue judgments as a function of test size in the fovea and at 20-deg temporal eccentricity. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, *12*, 1225–1232. [[PubMed](#)]
- Polden, P. G., & Mollon, J. D. (1980). Reversed effect of adapting stimuli on visual sensitivity. *Proceedings of the Royal Society of London B: Biological Sciences*, *210*, 235–272. [[PubMed](#)]
- Pugh, E. N. J., & Mollon, J. D. (1979). A theory of the  $\pi_1$  and  $\pi_3$  color mechanisms of Stiles. *Vision Research*, *19*, 293–312. [[PubMed](#)]
- Purdy, D. M. (1931). Spectral hues as a function of intensity. *American Journal of Psychology*, *43*, 541–559.
- Regan, B. C., Reffin, J. P., & Mollon, J. D. (1994). Luminance noise and the rapid determination of discrimination ellipses in colour deficiency. *Vision Research*, *34*, 1279–1299.
- Stockman, A., & Sharpe, L. T. (2000). The spectral sensitivities of the middle- and long-wavelength-sensitive cones derived from measurements in observers of known genotype. *Vision Research*, *40*, 1711–1737. [[PubMed](#)]
- Tailby, C., Solomon, S. G., & Lennie, P. (2008). Functional asymmetries in visual pathways carrying S-cone signals in macaque. *Journal of Neuroscience*, *28*, 4078–4087. [[PubMed](#)] [[Article](#)]
- Tyndall, E. P. T. (1933). Chromaticity sensibility to wavelength difference as a function of purity. *Journal of the Optical Society of America*, *23*, 15–24.
- Valberg, A., Lee, B. B., & Tigwell, D. A. (1986). Neurones with strong inhibitory S-cone inputs in the macaque lateral geniculate nucleus. *Vision Research*, *26*, 1061. [[PubMed](#)]
- Webster, M. A., Webster, S. M., Bharadwaj, S., Verma, R., Jaikumar, J., Madan, G., et al. (2002). Variations in normal color vision: III. Unique hues in Indian and United States observers. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, *19*, 1951–1962. [[PubMed](#)]
- Wetherill, G. B., & Levitt, H. (1965). Sequential estimation of points on a psychometric function. *British Journal of Mathematical and Statistical Psychology*, *18*, 1–10. [[PubMed](#)]
- Whittle, P. (2003). Contrast colours. In R. Mausfeld & D. Heyer (Eds.), *Colour perception* (pp. 115–138). Oxford: Oxford University Press.
- Winawer, J., Witthoft, N., Frank, M. C., Wu, L., Wade, A. R., & Boroditsky, L. (2007). Russian blues reveal effects of language on color discrimination. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 7780–7785. [[PubMed](#)] [[Article](#)]
- Witzel, C., Hansen, T., & Gegenfurtner, K. R. (2009). Categorical reaction times for equally discriminable colours. *Perception*, *38*, 14.