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Reanalysis of λ_{\max} variations in the Stiles–Burch 10° color-matching functions

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Individual differences in the color matches made by normal observers can be attributed in part to small interobserver variations in the spectral peaks (λ_{\max}) of the cone sensitivities. I compared two different analyses of these λ_{\max} variations that were both based on the Stiles–Burch 10° color-matching functions [Opt. Acta **6**, 1 (1959)]: one that suggested that the λ_{\max} values for individual cone classes fall into discrete subgroups [J. Neitz and G. H. Jacobs, in *Colour Vision Deficiencies IX*, B. Drum and G. Verriest, eds. (Kluwer Academic, Dordrecht, The Netherlands, 1989)] and one that failed to find discrete clustering [J. Opt. Soc. Am. A **5**, 1722 (1988)]. I conclude that there is not strong evidence for discrete λ_{\max} variations in the Stiles–Burch matches.

A number of studies have suggested that individual differences in the color vision of normal observers are due in part to small variations in the spectral peaks (λ_{\max}) of the cone photopigments (reviewed in Refs. 1 and 2). However, the specific form of these sensitivity differences remains unclear. In particular, studies have differed concerning the extent to which the implied distribution of λ_{\max} can be considered discrete. In the present analysis I reexamined whether discrete variations are evident in the 10° field color matches of Stiles and Burch.³ These data are the most comprehensive measurements available of color matching in a normal population. Previously MacLeod and Webster^{1,4} obtained estimates of λ_{\max} variations for the 49 Stiles–Burch observers as part of a factor analysis of the color matches. Among the factors identified were three that corresponded closely to predictions for independent variations in the spectral peaks of the long-, medium-, and short-wavelength (L, M, and S) cone pigments. Thus values for individual subjects on these factors (or factor scores) were assumed to represent the relative value of each subject's λ_{\max} for each cone pigment. These factor scores are plotted in Fig. 8 of Ref. 1. For either males or females the factor scores did not show clear evidence of clustering and thus did not reveal discrete subpopulations of the photopigments. In contrast, Neitz and Jacobs⁵ more recently analyzed a subset of the same data and concluded that the color matches of male subjects did fall into discrete groups. From this they concluded that the Stiles–Burch data do reflect discrete λ_{\max} variations in the X-chromosome-linked L and M photopigments. In the present Communication I compare the results of these two studies to try to resolve this discrepancy concerning the Stiles–Burch data.

The specific matches examined by Neitz and Jacobs⁵ were the intensities of the 526-nm (G) and the 645-nm (R) primaries required to match five test wavelengths ranging from 571 to 606 nm. Individual differences in these set-

tings should be affected relatively little by differences in either prereceptoral absorption or the S cones and should therefore reflect primarily variations in the L and the M cones. These wavelengths are also similar to the wavelengths used in Rayleigh matches. Waaler⁶ and Neitz and Jacobs^{2,7} reported evidence for discrete differences in the Rayleigh matches of normal male observers, although other studies have failed to find significantly bimodal distributions (e.g., Refs. 8 and 9). In Neitz and Jacobs's analysis of the Stiles–Burch data, individual values for R and G were first normalized and then were expressed as the ratio of R/(R + G) for each of the five test wavelengths. The ratios for the five tests were then averaged for each subject. In Fig. 1(a) the distribution of the average ratios that they obtained for male subjects (Fig. 2 of Ref. 5) is replotted. (The fourth subject at 0.47 represents a thirty-fourth male who was apparently identified as a female in their analysis.) Values for the 15 female observers are also plotted for comparison.¹⁰ The distribution for males suggests the possibility of discrete subgroups.⁵ In particular, the male values appear to fall into two main clusters, with no value falling within the bin centered on the population mean. However, this gap is narrow relative to the width of the histogram bins, for it is largely masked if the boundaries between the bins are shifted by half the bin width [Fig. 1(b)].

To test whether the observed values differ significantly from a unimodal distribution, Neitz and Jacobs⁵ used Kruskal's bimodality test (described in Ref. 11). In this test the density of the values between two suspected maxima in a distribution is compared with the overall spread in the data. The test is based on the actual values rather than the binned values. Neitz and Jacobs reported that this test indicated a probability of less than 0.05 that the observed values could result from a distribution with a single peak. However, if the test is applied to the set of male values on which Fig. 1 is based, it suggests that

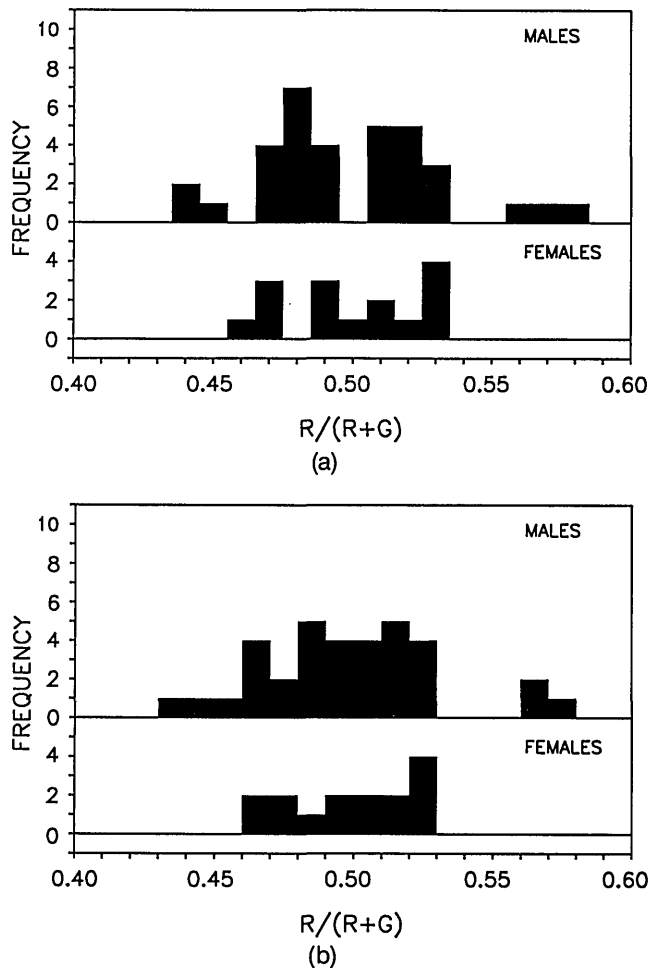


Fig. 1. (a) Distribution of mean matching ratios for male observers, as calculated by Neitz and Jacobs.⁵ Values for female observers are also shown. (b) The same values regrouped after the boundaries between the same bin widths (0.01) were shifted by half the bin width (0.005).

there is a greater than 0.50 probability that the values are unimodally distributed ($n = 34$; dip intensity¹¹ is 1.62).¹² The bimodality hypothesis fails largely because of the spread of the values near the extremes of the distribution. Neitz and Jacobs suggested that these outliers may reflect still further subgroups in the male population, and they therefore excluded extreme values before applying the bimodality test (as they did in Ref. 2). Yet there is no independent basis for grouping or excluding these observers, and thus the bimodality is not appropriately assessed by this procedure.¹³ It remains possible that the Stiles-Burch data reflect a distribution with more than two modes,^{2,7} for which the Kruskal test may have low power,¹¹ but a different test would be required to demonstrate this.

I next examined the relationship between the distribution of factor scores obtained by MacLeod and Webster^{1,4} and the distribution of matching ratios calculated by Neitz and Jacobs.⁵ If the λ_{\max} variations implied by the factor scores are in error, then they may fail to predict individual differences in the matching ratios. To calculate predicted matching ratios, I estimated pigment sensitivities for each subject by using the L and the M factor scores to shift the sensitivities of Smith *et al.*¹⁴ along the wave-

number axis. Values intermediate to the tabulated sensitivities of Smith *et al.* were interpolated with a cubic spline. These sensitivities were then used to calculate the average value of $R/(R + G)$ for the five test wavelengths, as defined above. The factor scores are constrained to have mean 0 and variance 1 and thus do not indicate the absolute position or variance of the λ_{\max} distribution. The standard deviations of the L and the M shifts were therefore varied to obtain a least-squares fit of the predicted-to-observed ratios.

Figures 2(a) and 2(b) show scatterplots of the predicted versus the observed matching ratios for males and females, respectively. The correlation between the two sets of values is 0.975 for males and 0.984 for females. Thus the variations in the factor scores of these two factors alone are sufficient to predict at least 95% of the variance in the observed matching ratios, although the predictions do fail to resolve the narrow central gap between the male values in the observed measurements. The best-

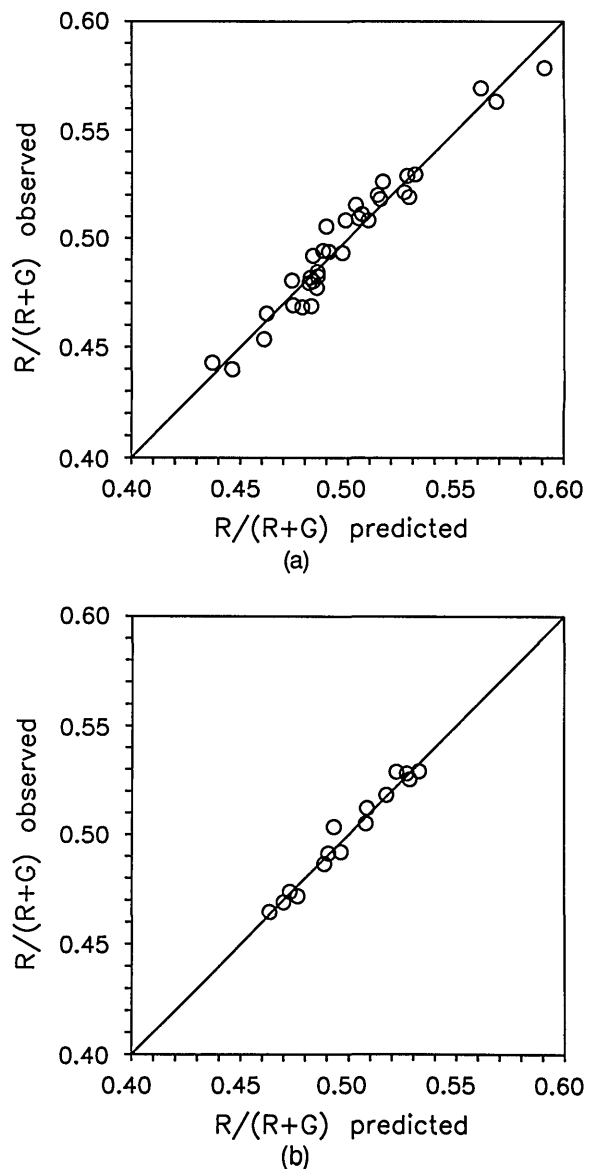


Fig. 2. Comparison of predicted and observed mean matching ratios for (a) males and (b) females. The rms error in the predictions for all subjects is 0.0066. The diagonal is the line of slope 1.

fitting standard deviations in λ_{\max} were 59 cm^{-1} (L) and 32 cm^{-1} (M) or $\sim 1.8 \text{ nm}$ (L) and $\sim 1.0 \text{ nm}$ (M) near the wavelengths of peak sensitivity.¹⁵ Neitz and Jacobs showed that, for the matches that they considered, the effects of varying either the L or the M pigment were similar and thus suggested that λ_{\max} variations in the two pigments could be confounded for individual observers in the factor scores. Thus the observed matching ratios can be predicted almost as well if the presumed L pigment factor scores are used to define the predicted M pigment and vice versa. However, the factor scores were not derived from the individual differences in selected matches but rather from the pattern of variation (or correlations) across the full set of color matches, and λ_{\max} variations in the L and the M pigments produce clearly different effects on these correlations; if they did not then a factor analysis could not resolve them as separate components. In fact the factor loadings are sufficiently unique to constrain strongly the estimates of the average absorption spectra of the pigments.¹⁶ Similarly, the specific matches considered here can be fitted well by assuming that the factor scores for these two factors correspond to variations in the optical density of the photopigments rather than to λ_{\max} . Yet the pattern of factor loadings for these factors is inconsistent with density differences as the basis of the variation in these factors.¹

Discrete variations in photopigment sensitivities have been implied by a variety of studies (see Refs. 1 and 2) and have suggested a polymorphism of the genes encoding the photopigments. Supporting this, recent evidence suggests that a single amino acid substitution at position 180 of the L and possibly the M pigment proteins alters the pigments' absorption spectra^{17,18} and correlates with individual differences in Rayleigh matches^{19,20} [although the size of the λ_{\max} shift (4–7 nm) in the pigment is larger than the variation implied by the Rayleigh matches¹⁹ or the Stiles–Burch matches]. However, the present analysis suggests that these discrete variations are not conclusively evident in the color-matching data of Stiles and Burch.

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13. Even with the three highest and the three lowest male values excluded the Kruskal test does not yield a dip intensity with a probability less than 0.05 (dip intensity 2.90; $p < 0.10$), although a $p < 0.05$ is indicated by the original, incorrect interpolation formula.¹¹
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