# Direct psychophysical estimates of the cone-pigment absorption spectra

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The absorption spectra of the long- and medium-wavelength-sensitive cone photopigments were derived by determining the spectra that best accounted for either the individual differences in the Stiles–Burch 10° color matches [Opt. Acta 6, 1 (1959)] or the changes in color matches at high light levels due to photopigment bleaching [Vision Res. 20, 23 (1980)]. The estimates were made by finding the best-fitting coefficients for an 11th-order polynomial function of wavelength, with no requirement that the resulting sensitivities be consistent with the color-matching functions. The estimates are independent of the scaling effects of any inert screening filters and therefore directly reflect the photopigment sensitivities. The spectra implied by the differences in the matches are similar to the absorption spectra of Smith *et al.* [Vision Res. 16, 1087 (1976)], which were used as initial estimates. However, the peak sensitivity of the required long-wavelength-sensitive pigment is shifted toward slightly longer wavelengths.

## INTRODUCTION

In the preceding paper[1] we used a factor analysis of the Stiles–Burch[2] 10° field color matches to examine the sources of individual differences in the color matches made by normal observers. Among the factors we found to influence the matches were three representing individual variation in the photoreceptors, which we identified with interobserver differences in the wavelength of peak absorption of the long-, medium-, and short-wavelength-sensitive cones (L, M, and S, respectively). In this paper we use the differences in the matches due to the individual differences in $\lambda_{max}$ to estimate the absorption spectra of the photopigments by calculating the absorption spectra for which spectral shifts best reproduce the observed differences in the matches. We also derive similar estimates from independent data on the differences in color matches made at low and high light levels, which presumably differ because of changes in the optical densities of the photopigments at the two light levels.[3]

Because of the way in which we derive them, these estimates are comparatively independent of the effects of any passive screening filters on the calculated sensitivities; they depend directly on the absorption spectra of whatever mechanisms are changing between the different color matches. In contrast, previous psychophysical measures have inferred the sensitivities of the underlying pigments indirectly, by correcting for the presumed influence of known intervening filters. Typically this involves correcting the observed sensitivities for the assumed light losses due to the lens and the macular pigment.[3,4] However, the mean density of these pigments varies widely among observers,[1] and the exact absorption characteristics of the pigments are still not clearly defined.[5] Moreover, other factors, such as possible waveguide effects of the receptors, may also alter the effective radiances of the lights, and since these are poorly understood at best, it is difficult to know how to compensate for them appropriately.

To obtain direct estimates of the absorption spectra (ones that are in principle independent of prior wavelength-dependent filtering or waveguiding), we have calculated the spectra implied by individual variation in the logarithms of color-matching functions. Random interobserver variation in the peak of the absorption spectrum for a given visual pigment (preserving, approximately, the shape of the absorption spectrum) produces correlated changes in the color matches for different test wavelengths and primaries. The pattern of these correlations depends on the particular absorption spectrum that is jittered in this way, and thus the spectrum can be identified by finding the one that best accounts for the observed correlation matrix. Since several such individually varying factors cooperate to determine an individual's color-matching functions, we have used factor analysis to isolate the contribution of each factor. From the factor loadings, we can determine the variance produced by each factor in the logarithm of each primary energy at each wavelength. Any arbitrary filtering by the lens or the macular pigment (or any other potential inert filter) reduces the primary and test radiances at the site of absorption in the visual pigment in proportion to the transmittance of the filter at the wavelength in question. It thereby changes the primary radiance required for a match by a factor equal to the ratio of the transmittances of the filter at the primary and test wavelengths. This factor is the same for any two observers who have different visual pigments (but the same inert filters) and so make different color matches. Thus the inert filters, whatever they may be, may affect the mean color matches, and the absolute differences between them, but have no effect at all on the difference between the *logarithms* of the primary radiances in the two matches; and any change in the visual pigment absorption spectra generates a

change in the log radiances that is unaffected by the inert filters. Because of this, a model that assumes a particular statistical population of absorption spectra can be evaluated through its predictions concerning the observed distribution of the logarithms of the color-matching functions, or primary radiances, without invoking any assumptions about the nature and effects of any prior wavelength-dependent filtering.

In this paper we consider which visual pigment absorption spectra best reproduce the variances in the logs of the color-matching functions that are empirically generated by the factors that we have associated with slight shifts in those spectra. Although they are based on data from intact eyes, the resulting estimates of the visual pigment absorption spectra are therefore direct in the foregoing sense.[6]

## METHODS

In order to calculate the pigment sensitivities implied by the individual differences in photopigment $\lambda_{max}$, we first need to know how the $\lambda_{max}$ variations contribute to the observed variability in the Stiles–Burch matches. As we noted, this information is given by the factor loadings for the $\lambda_{max}$ factors, which we derived and discussed in detail in the preceding paper.[1] For our analysis, the squared factor loadings represent the percentage of the observer variance in each of the three primary settings (matched to each test light) that is due to variations in a given factor. To determine the identity of the three presumed photoreceptor factors, we compared the pattern of loadings associated with them with the loadings predicted by spectral shifts in the photopigment sensitivity estimates of Smith et al.[4] As shown in Figs. 5(a)–5(c) of Ref. 1, there is a close correspondence between the predicted and observed loadings, strongly arguing that $\lambda_{max}$ differences are in fact the basis of these observed factors. Conversely, the close agreement also suggests that the absorption spectra of Smith et al. must be reasonably similar to the sensitivities required by the loadings, for an incorrect sensitivity would generally fail to reproduce the observed pattern of variability in the matches.

Nevertheless, there are some discrepancies between the observed and predicted loadings for $\lambda_{max}$ variations, particularly for the L pigment [shown in Fig. 5(a) of Ref. 1]. At the long wavelengths these could largely reflect rounding errors in the assumed pigment sensitivities (which in our calculations could be as large as 1/20,000th of the peak, a significant quantity at the ends of the spectrum). However, there are also systematic disagreements in the midspectral region where this is not a problem. A variety of tests (discussed in the preceding paper[1]) suggested to us that the observed factor loadings were largely correct, so we were led to examine the possibility that the discrepancies were due instead to errors in the predicted loadings. In fact, if we assume that the observed loadings accurately reflect the effect of simple shifts in the photopigment spectral sensitivities, then it should be possible to determine exactly what set of sensitivities they imply. To do this, we examined whether modifications in the initial sensitivity estimates that we used would lead to more-accurate predictions.

To permit more-or-less arbitrary modifications of the sensitivities of Smith et al., we revised them by multiplying them by an 11th-order polynomial in wave number, including the large number of terms to ensure adequate flexibility in changing the pigment shape. The terms were built up from the Chebyshev–Hermite series[7] and were defined as functions of wave number, $\nu$ (in inverse centimeters), rescaled according to

$$\nu' = (\nu - 18500)/(1500),$$

so that the M- and L-pigment spectra were roughly centered at zero and of unit variance. This assists convergence by making the Chebyshev–Hermite polynomials roughly orthogonal when weighted by the pigment spectra, allowing the modifications produced by each term to be independent. Using the IMSL subroutine ZXSSQ,[8] coefficients for the 11 terms were then selected to define a new pigment whose spectral shift along the wave-number axis (without a change in shape) minimized the sum of squared errors between the observed and predicted loadings. (The calculation of the predicted loadings is outlined in Ref. 1.) The predicted standard deviation in $\lambda_{max}$ for the population of observers was also varied to provide the best fit to the observed loadings. The only constraint on the resultant pigment shape was the requirement that it produce appropriate variability in the logs of the predicted color matches; it was not constrained to be a linear combination of the mean observed color matches or to be consistent with them in any way.

Because of the large number of free parameters, the program sometimes became trapped in solutions representing local minima in the residual sum of squares. To prevent this, for each test wavelength we added a conservatism component to the residual error that was minimized by the fitting program. This component was defined by

$$e_\lambda = [w(s_{\lambda(new)} - s_{\lambda(old)})/s_{\lambda(old)}]^2,$$

where $s_{\lambda(old)}$ is the sensitivity at the sampled wavelength $\lambda$ found by Smith et al. and $s_{\lambda(new)}$ is the modified sensitivity. A large value for $w$ was initially chosen so that the new pigment was forced to stay fairly close to the original pigment. The resulting coefficients were then entered as starting estimates for the next fit, with the weight gradually reduced on each successive run, until with zero weight the pigment was in no way constrained to resemble the initial estimates of Smith et al. (negative values and comblike, multiply peaked spectra being among the permitted possibilities).

## RESULTS

### Pigment Estimates Based on Fits to Factor Loadings

In Fig. 1(a) we have plotted the revised estimates of the L-pigment sensitivity obtained by modifying the L pigment of Smith et al. (dashed curve) to fit the observed loadings for the appropriate factor. The open circles represent the sensitivity of the pigment that best fit the initial $\lambda_{max(L)}$ factor shown in Fig. 5(a) of the preceding paper.[1] In this case the modification was based only on fits to the R and G primary items, as the B loadings are less diagnostic. The crosses show the result of fitting all the observed loadings of the corresponding $\lambda_{max(L)}$ factor from a separate analysis, which included a set of variables designed on theoretical grounds to produce zero loadings for particular types of factor. These zero-loading items were added to a subset of the original
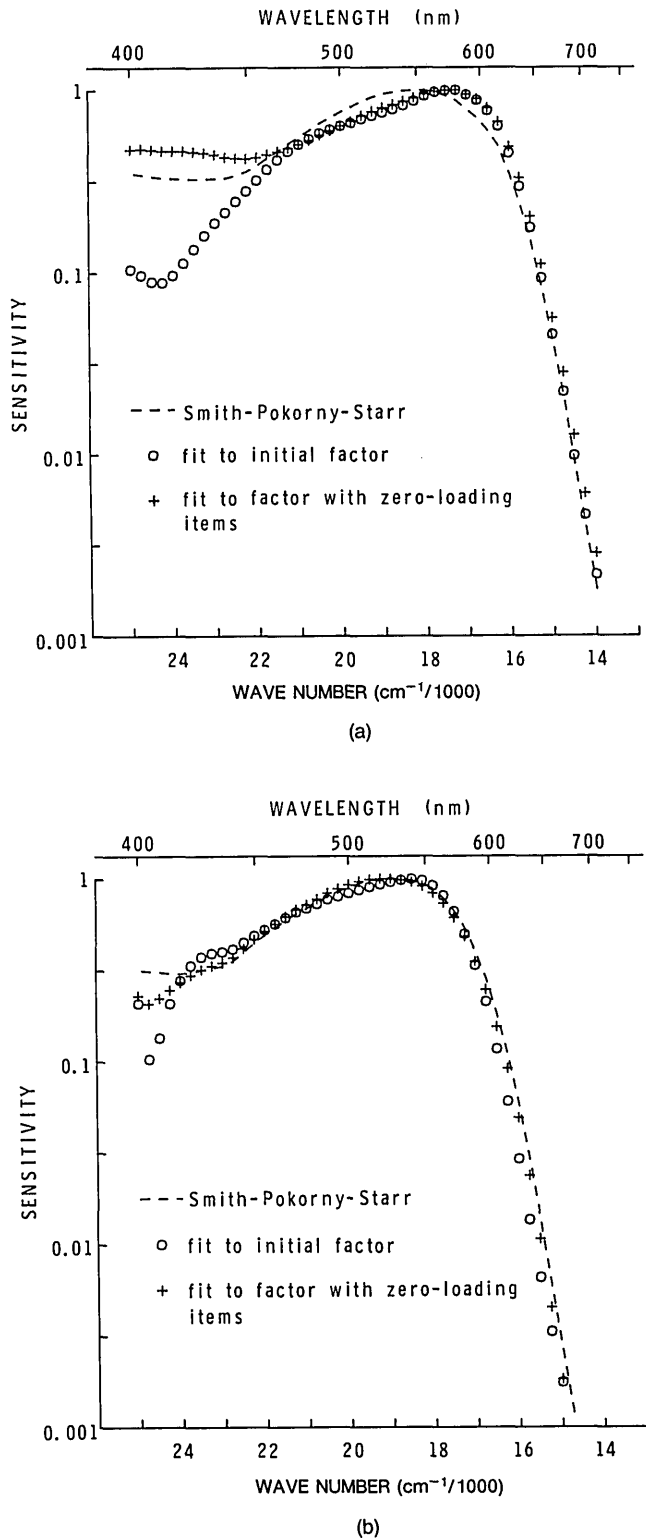
Fig. 1. (a) Estimates of the L-pigment absorption spectrum obtained by modifying the L pigment of Smith et al. (dashed curve) to fit the observed loadings for the $\lambda_{\max(L)}$ factor from an initial analysis of the Stiles–Burch color-matching data (open circles) and from a similar analysis that included a set of theoretically zero-loading items (crosses). The two estimates are similar and differ from the pigment of Smith et al. in having peaks shifted toward slightly longer wavelengths. (b) Same as (a) for the M pigment. The two revised estimates do not differ substantially from the initial M pigment of Smith et al.

variables as part of an attempt to improve the observed loadings for the different factors and were used in the theoretically guided factor rotation discussed in the preceding paper. However, the loadings for the common items remained similar for the two analyses, strongly suggesting that the observed pattern of loadings for both factors accurately reflects the physiological variations to which they correspond.[9] In fitting both factors the unmodified S and M pigments of Smith et al. were used along with the new L pigment to calculate the predicted color matches.

Except at short wavelengths, where the required loadings are not well constrained, the two pigment estimates are similar and indeed remain remarkably similar to the original estimate of Smith et al. (in view of the great latitude allowed by the polynomial description of the spectra). However, both deviate from the original pigment in having a maximum sensitivity shifted toward slightly longer wavelengths, with a peak at roughly 576 nm, compared with 556 nm for the unmodified pigment. Based on the two new pigment estimates, the standard deviation of the $\lambda_{\max}$ variation (in wave numbers) was calculated to be either 34.7 or 39.0 cm$^{-1}$ for the factor without or with the theoretically zero loading items, respectively.

Despite the fact that the sensitivity of Smith et al. already provided a reasonably close fit to the loadings for the factors, these revisions nevertheless substantially improved the predictions. For the initial $\lambda_{\max(L)}$ factor the rms error in the predicted loadings dropped from 0.184 to 0.095, while for the factor with the a priori zero-loading items the rms error also reached a value of 0.095 for the revised pigment. The improvement can be seen in Fig. 2, where we have plotted for the red and green primary items the difference between the observed loadings for the initial $\lambda_{\max(L)}$ factor and the predicted loadings based on either the Smith et al. or revised L pigment [shown as filled triangles or open circles, respectively. For the blue primary both the observed and predicted loadings are close to zero across most of the spectrum; see Fig. 5(a) of Ref. 1]. One of the main effects of the new L pigment is to increase the predicted loadings (and thus bring them into close correspondence with the observed loadings) for the red primary items matched to green test lights, a result that is due to the steeper gradient of the revised absorption spectrum in that region. It was a somewhat similar discrepancy between the predictions of the spectra of Smith et al. and the observed variability in the Stiles–Burch 2° field color matches[10] that led Smith et al. to postulate variation in an inert spectral filter differentially screening the L cones.[4]

As we noted, the predictions for $\lambda_{\max}$ variations were based on shifting the pigment spectra along the wave-number axis without changing their shape. However, this may not be the appropriate axis for shape-invariant translations of the sensitivities. For instance, Barlow has observed that pigments with different peak sensitivities have similar bandwidths when plotted against the fourth root of wavelength.[11] To test whether the choice of axis was critical, we repeated the pigment-modification procedure by shifting the revised pigment estimate along a log wave-number axis (a procedure similar in effect to Barlow's) rather than the linear axis previously used. The resultant estimate of the visual pigment-absorption spectrum was essentially the same as the

estimates of Fig. 1(a) (see Fig. 4 of Ref. 6), showing that the axis along which the translation is presumed to occur has little effect on the predictions.

As we showed in Figs. 4(a)–4(c) of the preceding paper,[1] the observed pattern of loadings for the photoreceptor factors is poorly fitted by the predictions for individual differences in the optical densities of the spectra of Smith et al. We nevertheless examined whether a modified L pigment could account for the observed factor loadings on the basis of density variations, to see whether the factor could possibly represent variations in the density of some pigment. However, the revised L sensitivity actually became negative at some wavelengths, and the fit of the predicted loadings remained poor.

We also tried modifying the M pigment of Smith et al. to fit the factor that we identified with $\lambda_{max}$ variation of the midspectral pigment. However, not only did the new estimates remain similar to the old sensitivity but the rms error was only marginally reduced. The modified pigments are shown in Fig. 1(b), where the dashed curve is again the sensitivity of Smith et al. and the open circles and crosses are the estimates based on fits to the observed loadings with and without the derived zero-loading items, respectively. While the peak of the pigment fitted to the initial factor shifted slightly toward a longer $\lambda_{max}$, the other estimate moved toward a shorter peak. The standard deviations of

the $\lambda_{max}$ variation in the new estimates were 25.9 and 29.9 $cm^{-1}$. Because the variation in the matches made to short wavelengths is dominated by prereceptoral factors, we did not pursue estimates of the S-pigment sensitivity.

## Pigment Estimates Based on Fits to Changes in the Color Matches with Bleaching

To obtain an independent direct estimate of the pigment-absorption spectra implied by differences in color matches, we turned to the color-matching data of Wyszecki and Stiles.[3] In their study matches were made at either 1000 or 100,000 Td, and the resulting differences were modeled by assuming that the densities of the photopigments were reduced at the higher intensity because of pigment bleaching. The pigment spectra and densities consistent with this explanation were then calculated, under the assumption that the psychophysical sensitivities differ from the cone absorption spectra only through the influence of the independently estimated filtering effects of macular pigment and lens absorption. We similarly derived a set of pigments to account for their data on the basis of density differences. However, rather than fitting the absolute differences in the color matches, we fitted the differences in the logs of the matches. As we noted above, this leads to predictions that are independent of assumptions about the absorption spectra of the inert screening pigments in the lens and the macula and
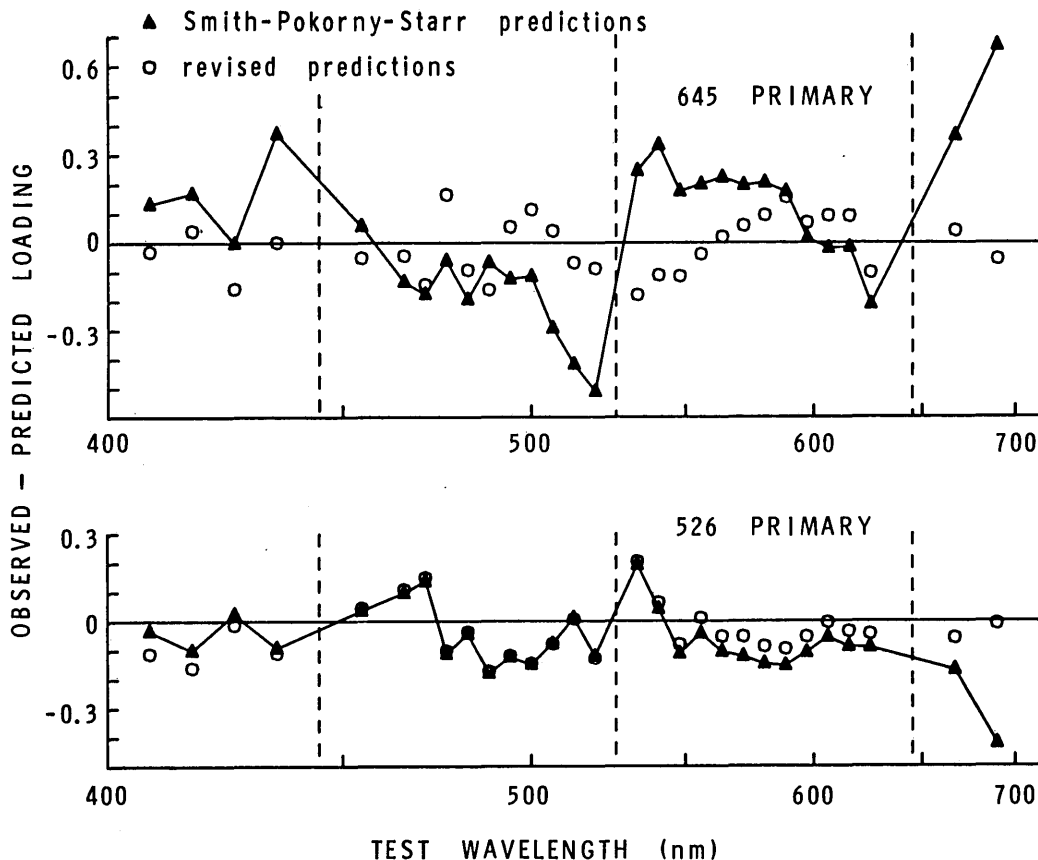


Fig. 2. Difference between the observed loadings for the initial $\lambda_{max(L)}$ factor and the predicted loadings based on either the L-pigment sensitivity of Smith et al. (filled, connected triangles) or the revised sensitivity derived from fits to the observed loadings (open, unconnected circles). The top figure shows the error of prediction for items representing the red primary; the bottom, the green primary. Note the substantial improvement in the predicted loadings for the red primary matched to green test lights as a result of the pigment modifications.

therefore provides direct estimates of the photopigment spectra. In contrast, the sensitivities obtained by Wyszecki and Stiles, as well as those obtained by Smith *et al.*, were derived indirectly by correcting for the presumed influence of the ocular media.

To account for this new set of data, the predicted differences in the color matches were calculated for high and low densities of the photopigments, again starting with the absorption spectra of Smith *et al.* The shapes and densities of the L and M pigments were then varied to obtain the closest fit to the observed differences in the logarithms of the matching primary energies. The shapes of the spectra were modified by using an 11th-order Chebychev–Hermite polynomial as before, while the sensitivities for different densities were calculated as described in the preceding paper. Once again, the absorption spectra were not constrained to have any particular shape or to be consistent with the color-matching functions (as was the estimate derived by Wyszecki and Stiles). Yet, as the crosses in Fig. 3(a) show, the resulting L pigment is similar to the sensitivity estimated from the factor loadings (open circles) and still more similar to the sensitivity that Wyszecki and Stiles originally derived from their data (indicated by the solid curve). The rms error in the prediction of the change in log matching radiance dropped from 0.303 for the pigment of Smith *et al.* to 0.074 for the new estimate. The required densities for the M and modified L pigment at 1000 Td were 0.34 and 0.46, respectively, which are also close to the values calculated by Wyszecki and Stiles.

The results for the M pigment are plotted in Fig. 3(b) along with the Wyszecki–Stiles and Smith *et al.* sensitivities. As we found in fitting the M-pigment factor, little revision was called for in the shape of the M pigment of Smith *et al.*, and only a slight improvement was obtained in the predictions. [With no conservatism the fitted M pigment took on negative values at the shortest wavelengths. The plotted value is thus from the lowest conservatism ($w = 0.1$), yielding positive values throughout the spectrum.]

**Pigment Estimates Based on Fits to the Correlation Matrix**
Surprisingly, when the factor loadings based on the revised M- and L-photopigment sensitivities were used to predict the correlation matrix for the Stiles–Burch color matches (from which the observed $\lambda_{max}$ factors were derived), they turned out to do no better than the original sensitivities of Smith *et al.* The failure of the pigments based on the observed loadings collectively to improve the predictions for the item correlations could be partly due to the fact that the pigments were modified only to fit the loadings for a single $\lambda_{max}$ factor and were thus not constrained to generate loadings conforming closely to other factors. Given this, we were led also to try modifying the pigment sensitivities in order to fit the correlations directly rather than the factor loadings. In the preceding paper we showed how the observed matrix of correlations can be fitted by varying the standard deviations in each of the predicted factors that we used (macular-pigment density, lens-pigment density, independent $\lambda_{max}$ variations in the three cone types, and a single optical density variation common to all three cones). In this case the L- and M-pigment absorption spectra were simultaneously modified along with the standard deviations for the
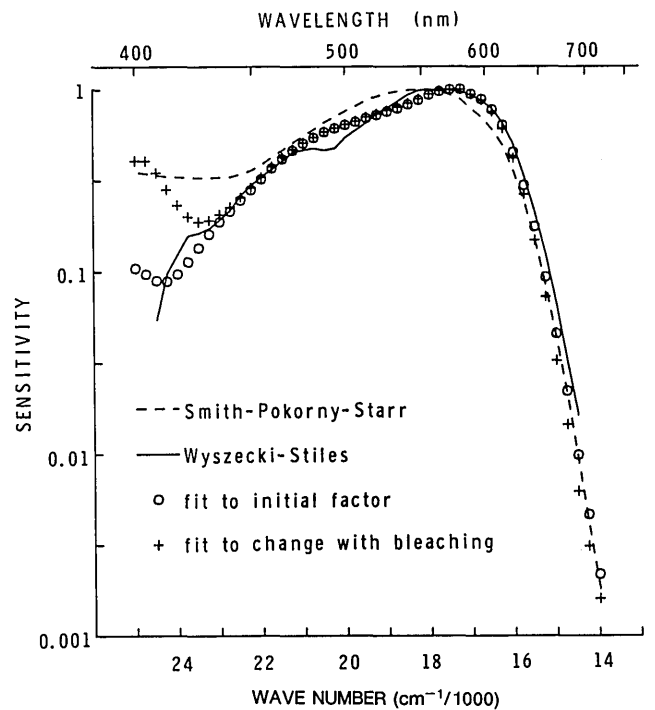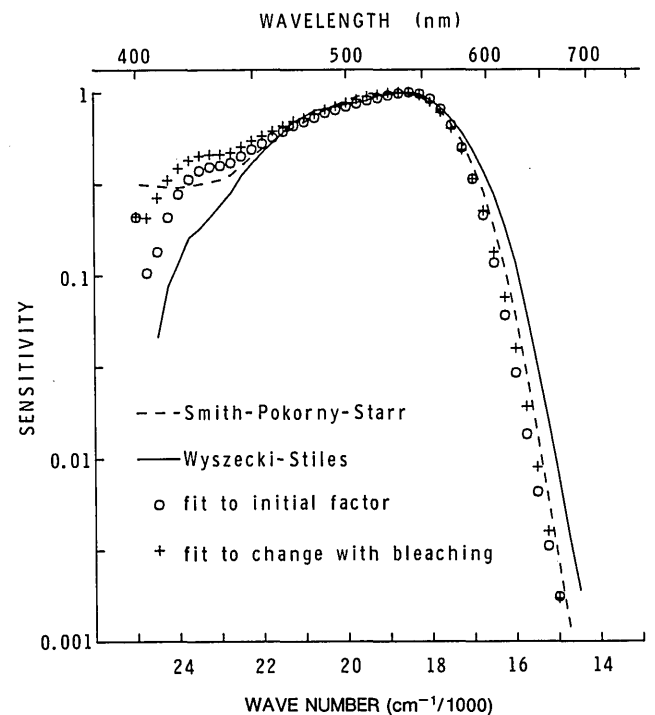


Fig. 3. (a) Estimate of the L-pigment absorption spectrum obtained by modifying the L pigment of Smith *et al.* (dashed curve) to fit the data of Wyszecki and Stiles on the changes in color matches with bleaching. The revised sensitivity (crosses) is similar to the pigment derived from fits to the factor loadings (circles) and also to the L-pigment spectrum that Wyszecki and Stiles calculated from their data (solid curve). (b) Same as (a) for the M pigment. The new estimate (crosses) and Wyszecki and Stiles's own estimate (solid curve) are close to the M pigment of Smith *et al.* (dashed curve).

four predicted photoreceptor factors. (The standard deviations for the lens and the macular pigment were fixed at the best previous estimates.)

The obtained estimates of the sensitivities are shown in Figs. 4(a) and 4(b) for the L and M pigments, respectively. [These results were obtained with a low ($w = 0.5$) conservatism constraint on the pigment sensitivities; with less constraint the L and M spectra became negative at short wavelengths, while the predicted correlations were only negligibly improved.] This time the L pigment (plotted as crosses) remains much closer to the sensitivity of Smith *et al.* Nevertheless, there is still a moderate shift in the peak sensitivity toward longer wavelengths, resulting in a slight improvement in the predictions. As before, the fitted M pigment remained similar to that of Smith *et al.*

The calculated standard deviations in $\lambda_{max}$ for the various pigment estimates are shown in Table 1. The first two rows of numbers indicate the estimates based on fits of the Smith *et al.* or modified pigments to the initial set of factor loadings. In the subsequent rows the standard deviations of all of the factors used to predict the correlation matrix are listed for the sensitivities of Smith *et al.*, the pigments modified to fit the initial factor loadings, or the pigment estimates derived from directly fitting the correlation matrix. For each of the pigments fitted to the correlations we calculated two sets of predictions, depending on whether the variation in $\lambda_{max}$ was allowed to vary independently for the three different cone types. (The standard deviations for the lens and macular-pigment factors do not depend on the choice of photopigments but are included for comparison with the values obtained from fitting the correlations.) In general, the inferred interobserver variability in $\lambda_{max}$ is similar for the different sets of sensitivities, with the standard deviation in the M pigment somewhat smaller than for the L and S pigments.

## DISCUSSION

As we noted above, the fact that the photopigment sensitivity estimates of Smith *et al.* lead to predictions that are in close agreement with the set of observed loadings for our $\lambda_{max}$ factors indicates that these estimates are close to the sensitivities required by the loadings. Thus, not surprisingly, the modifications necessary to improve the predictions were slight, and the revised estimates remained more similar to the spectra of Smith *et al.* than to many other candidate sensitivities. No clear change was called for in the shape of the M pigment of Smith *et al.* However, a slight shift in the peak of the L pigment spectrum toward longer wavelengths was found substantially to improve the fit to the loadings for the $\lambda_{max(L)}$ factor. A similar sensitivity was obtained from predicting the independent data of Wyszecki and Stiles on the basis of changes in self-screening. Further, a shift to longer wavelengths was also called for in modifying the L pigment to fit the correlation matrix for the Stiles–Burch data, though in this case the required change was smaller.

Once again, because these fits were in each case based on the differences in the logs of the color matches, they are independent of the scaling effects of other factors (such as screening pigments) on the color-matching functions and in this sense represent direct estimates of the visual pigment
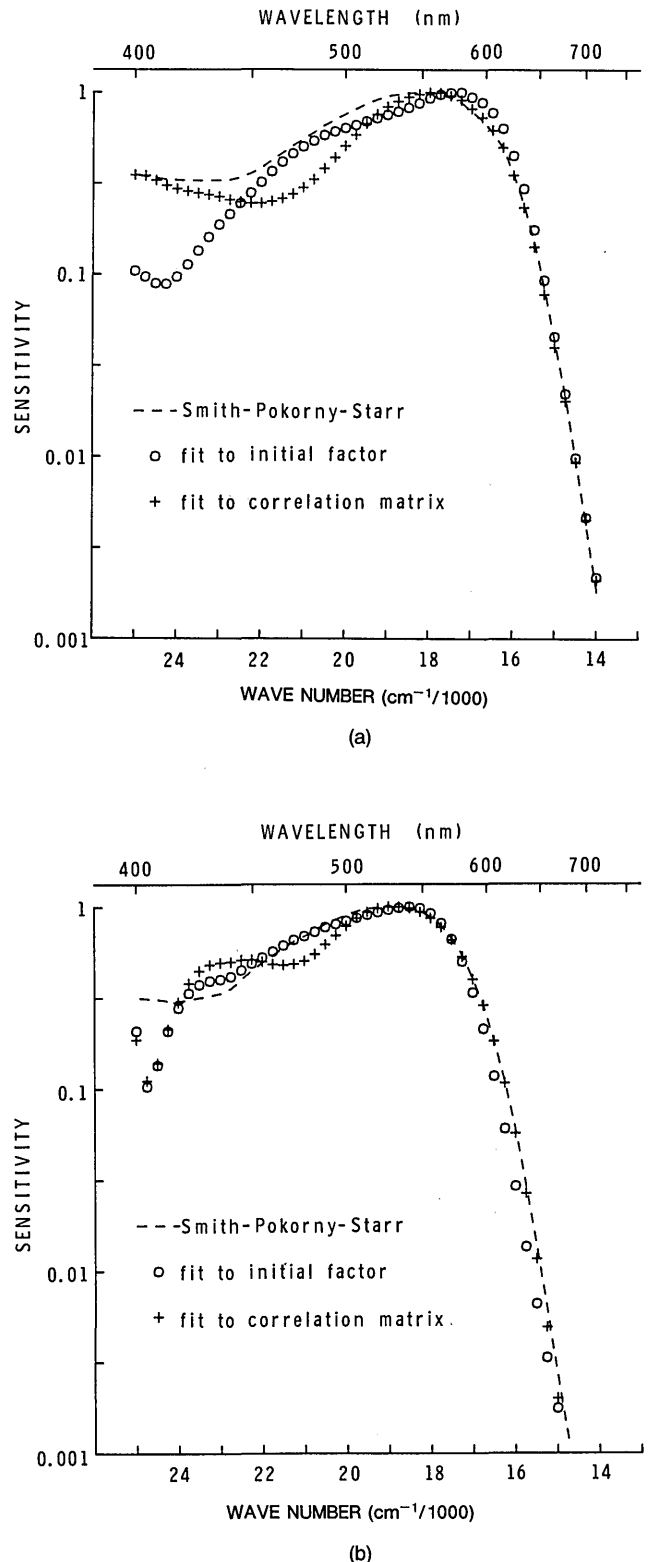


Fig. 4. (a) Estimate of the L-pigment absorption spectrum obtained by modifying the L pigment of Smith *et al.* (dashed curve) to fit the correlation matrix for the Stiles–Burch data. The revised estimate (crosses) is again shifted to longer wavelengths relative to the pigment of Smith *et al.* but does not agree exactly with the L pigment derived from fits to the factor loadings (open circles). (b) Same as (a) for the M pigment. Again the new sensitivity (crosses) remains roughly similar to the M pigment of Smith *et al.* (dashed line).

**Table 1. Estimated Interobserver Standard Deviations in Prereceptoral and Photopigment Density and in Photopigment $\lambda_{max}$ (Wave Number)**

|  | Macular | Lens | $\lambda_L$ | $\lambda_M$ | $\lambda_S$ | Density |
|---|---|---|---|---|---|---|
| From fits to factor loadings | | | | | | |
| For best fits using pigments of Smith *et al.* | | | | | | |
|  | 0.12 | 0.18 | 50.3 | 31.9 | 45.3 | 0.045 |
| For best fits using pigments modified to fit factors | | | | | | |
|  | 0.12 | 0.18 | 34.7 | 25.9 | NE[a] | NE[a] |
| From fits to correlation matrix | | | | | | |
| For best fits using pigments of Smith *et al.* | | | | | | |
| Independent $\lambda_{max}$ | 0.120 | 0.156 | 42.2 | 18.1 | 40.5 | 0.0458 |
| Equal $\lambda_{max}$ | 0.121 | 0.153 | 32.6 | 32.6 | 32.6 | 0.0420 |
| For best fits using pigments modified to fit $\lambda_{max}$ factors | | | | | | |
| Independent $\lambda_{max}$ | 0.122 | 0.171 | 38.5 | 19.2 | 38.5 | 0.0370 |
| Equal $\lambda_{max}$ | 0.123 | 0.173 | 29.5 | 29.5 | 29.5 | 0.0345 |
| For best fits using pigments modified to fit correlation matrix | | | | | | |
| Independent $\lambda_{max}$ | 0.121[b] | 0.153[b] | 44.7 | 20.4 | 41.1 | 0.0453 |
| Equal $\lambda_{max}$ | 0.121[b] | 0.153[b] | 37.4 | 37.4 | 37.4 | 0.0457 |

[a] Not estimated.
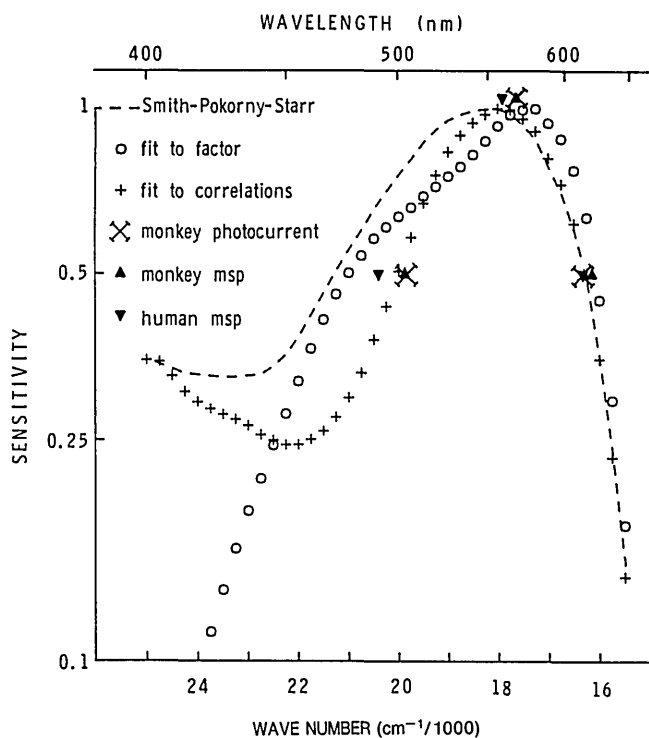
[b] Fixed on the basis of previous estimates.



Fig. 5. Estimated L-pigment sensitivities based on fits to the correlation matrix (crosses) or initial factor loadings (open circles), compared with electrophysiological (photocurrent) or microspectrophotometric (msp) measures of the peak and half-amplitude wavelengths for L sensitivity in human[13] and monkey.[12,15] Note that the vertical scale here spans only one log unit. Both the revised pigments and the physiological measures show a similar deviation from the spectrum of Smith *et al.* (dashed curve).

sensitivities. Direct physiological estimates of the photopigment absorption spectra, obtained by transverse measurements of the pigments, tend to show a similar deviation from the indirect estimates made by Smith *et al.* by correcting dichromatic spectral sensitivities for prereceptoral screening by lens and macular pigment. This can be seen in

Fig. 5, where we have replotted the top 1.0 log units of the curves of Fig. 3(a) and included the peak and half-amplitude estimates of the L-pigment sensitivity based both on the recordings of monkey outer segment photocurrent by Baylor *et al.*[12] and the results of microspectrophotometry for both human[13] and monkey[14] cones. (The various curves have not been equated for pigment density.) The discrepancy between the actual absorption spectra and the cone sensitivities of Smith *et al.* could in part be due to random sampling error for the population of dichromats in the latter estimate. Alternatively, the difference could reflect the influence of an unknown factor, such as waveguiding by the receptors, or the relation between the absorption spectrum and the *in situ* spectral sensitivity. Our own estimates would be independent of these factors so long as any variation in them is independent of the variation in $\lambda_{max}$ (or in photopigment bleaching for the fits to the Wyszecki–Stiles data). The set of observed factors from our analysis of the Stiles–Burch 10° color matches was examined for evidence of interobserver variation in such an influence, but none was identified. However, a potentially related factor was obtained in an analysis of the Stiles–Burch 2° data.[1]

If the differences between our derived absorption spectra and the effective corneal sensitivities were due only to the light losses from the lens and the macular pigment, then it should be possible to reintroduce these factors in order to reproduce the average primary radiances for the Stiles–Burch matches (which should be a linear combination of the corneal sensitivities[15]). In fact, Baylor *et al.*[12] showed that their physiologically derived cone pigments for monkeys, modified by lens and macular absorption, come close to predicting these data (though some systematic discrepancies remain; see their Fig. 4). To examine this for our sensitivity estimates, we calculated the densities of the photopigments and of the lens and macular pigment that provided a least-squares fit to the average matches (transformed to an equal quantum spectrum), using the macular and lens spectra tabulated by Wyszecki and Stiles.[5] Because our estimated M-pigment sensitivity did not consistently differ from that of the Smith *et al.* M pigment, the M and S sensitivities of *Smith et al.* were used along with our various estimates of the L pigment. In each case the required macular-pigment density was between 0.17 and 0.21 (at 460 nm), while the best-fitting lens density ranged from 1.26 to 1.66 (at 400 nm).

The sensitivities of Smith *et al.*, which were in part derived from a linear transformation of a different set of color matches (Judd's revised CIE functions[16]), closely fit the Stiles–Burch data (with a rms error of 0.04). A marginally better fit was obtained by pairing the S and M pigment of Smith *et al.* with our L pigment modified to fit the correlation matrix for the matches (rms error 0.035). However, our other estimates of the L pigment produced larger errors in the predicted matches, ranging from 0.073 for the sensitivity estimated from the loadings or the $\lambda_{max}$ factor with theoretically zero-loading items to 0.10 for the pigment derived from the Wyszecki–Stiles pigment-bleaching data. The largest discrepancies were in the values of the red and green primaries matched to the test wavelengths in the red–green range and are roughly similar to those found by Baylor *et al.* for their pigments. In this spectral region the estimates of the pigment-absorption spectra are relatively well defined, and

possible errors in the lens and macular absorption should have little effect. Thus, if these direct estimates accurately reflect the underlying pigment-absorption spectra, then the poorer fit that they give to the average psychophysical color-matching functions could suggest that an additional unknown intervening factor modifies the effective cone sensitivities.

## ACKNOWLEDGMENT

## REFERENCES AND NOTES

1. M. A. Webster and D. I. A. MacLeod, "Factors underlying individual differences in the color matches of normal observers," J. Opt. Soc. Am. A 5, 1722–1735 (1988).
2. W. S. Stiles and J. M. Burch, "N.P.L. colour matching investigation: final report (1958)," Opt. Acta 6, 1–26 (1959).
3. G. Wyszecki and W. S. Stiles, "High-level trichromatic color matching and the pigment-bleaching hypothesis," Vision Res. 20, 23–37 (1980).
4. V. C. Smith, J. Pokorny, and S. J. Starr, "Variability of color mixture data—I. Interobserver variability in the unit coordinates," Vision Res. 16, 1087–1094 (1976).
5. G. Wyszecki and W. S. Stiles, Color Science (Wiley, New York, 1967).
6. A preliminary account of this work appeared in D. I. A. MacLeod and M. A. Webster, "Factors influencing the color matches of normal observers," in Colour Vision Physiology and Psychophysics, J. D. Mollon and T. L. Sharpe, eds. (Academic, London, 1983), pp. 81–92.
7. M. G. Kendall and A. Stuart, Advanced Theory of Statistics, 3rd. ed., Vol. 1, Distribution Theory (Griffin, London, 1969).
8. IMSL Library (IMSL, Houston, Tex., 1984).
9. The L pigment was fitted to the initial Varimax factor with a priori zero-loadings items, and not to the loadings based on the guided rotation of that factor, simply because the two estimates were so similar. See Ref. 1.
10. W. S. Stiles and J. M. Burch, "Interim report to the Commission Internationale de l'Eclairage, Zurich, 1955, on the National Physical Laboratory's investigation of colour-matching," Opt. Acta 4, 168–181 (1955).
11. H. B. Barlow, "What causes trichromacy? A theroetical analysis using comb-filtered spectra," Vision Res. 22, 636–644 (1982).
12. D. A. Baylor, B. J. Nunn, and J. L. Schnapf, "Spectral sensitivity of cones of the monkey Macaca fascicularis," J. Physiol. 390, 145–160 (1987).
13. H. J. A. Dartnall, J. K. Bowmaker, and J. D. Mollon, "Microspectrophotometry of human photoreceptors," in Colour Vision Physiology and Psychophysics, J. D. Mollon and T. L. Sharpe, eds. (Academic, London, 1983), pp. 69–80.
14. J. K. Bowmaker, J. D. Mollon, and G. H. Jacobs, "Microspectrophotometric results for old and new world primates," in Colour Vision Physiology and Psychophysics, J. D. Mollon and T. L. Sharpe, eds. (Academic, London, 1983), pp. 57–68.
15. J. C. Maxwell, "Experiments on colour, as perceived by the eye, with remarks on colour-blindness," Trans. R. Soc. Edinburgh 21, 275–298 (1855); T. N. Cornsweet, Visual Perception (Academic, New York, 1970).
16. D. B. Judd and CIE Technical Committee No. 7, "Report of the U. S. Secretariat Committee on Colorimetry and Artificial Daylight," in Proceedings of the 12th Session of the CIE (Commission International de l'Eclairage, Paris, 1951, Paris, Vol. 1).