

Flicker photometric study of chromatic adaptation: selective suppression of cone inputs by colored backgrounds

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Flicker photometric equivalence is both additive and transitive when the test and standard are alternated upon a relatively more intense colored background. When the balance of red versus green cone excitation from the background is unequal, the contribution of one cone type to flicker photometric spectral sensitivity may be depressed in relation to that of the other by at least 1 order of magnitude more than Weber's law predicts. The resultant spectral sensitivity is determined predominantly by only one class of cone. The cone spectral sensitivities of normals are then seen to be the same as those of dichromats, although there is some individual variation. A model is developed to explain this surprising phenomenon.

To investigate a single class of cone receptors, test stimuli are often presented as increments superimposed upon colored backgrounds that are designed to desensitize the other types of cone. Unfortunately, a measure of the response of solely one cone type across large spectral ranges is not thought to be generally possible with this technique. Rushton¹ wrote:

How in the living eye can we determine the spectral sensitivity of one class of cone pigment since vision is the resultant of the output of different kinds of cones interacting in an unknown manner? A common practice is to "isolate" one type of cone by using a strong colored background to which rival cones are more sensitive, in the hope that in this way the rival cone output will be reduced to zero, or to ineffectiveness. There is not much *a priori* ground to substantiate this hope, nor a *posteriori* ground to believe it true. Most who use this method find it sufficient to assert that they have "isolated" a single pigment without any justification whatever of that assertion.

Stiles² resorted to an indirect approach and employed a field sensitivity method, measuring the effectiveness of different spectral background fields in reducing sensitivity for a test of fixed wavelength. He concluded that there are a number of parallel mechanisms, which he termed π mechanisms, each permitting detection of the stimulus with a sensitivity that depends on its own level of excitation but not on that of the other mechanisms. Stiles cautiously did not equate any π mechanism with any one class of cone.

The neural signals that are initiated in the cones, and ultimately are responsible for the psychophysical expression of π mechanisms, must of course be transmitted through postreceptoral pathways. For a variety of reasons,³⁻⁵ the postreceptoral neural organization is usually held to consist of separate channels or functional systems of neurons for representing luminance and color. There appear to be two chromatically opponent systems, red-green and yellow-blue, with excitation and inhibition from different types of cone, and one "achromatic" or "luminance" system that adds the different cone outputs. The sensitivity of one of Stiles's seven π mechanisms, π_1 , has been shown convincingly to depend on

postreceptoral chromatically opponent interactions as well as on the quantum catch of the blue cones alone.^{6,7}

Restricting detection of a stimulus to only one postreceptoral system should minimize any changes in sensitivity that could result from shifting the burden of detection from one system to another. By measuring sensitivity through but one channel, it may to some extent be possible to factor out the effects of postreceptoral processing, thus facilitating the study of more peripheral mechanisms.

For such an approach to be useful, there must be one such channel that can be examined across large spectral ranges, if not the entire visible spectrum. The luminance system may fulfill this requirement. Although the physiological substrate of the luminance system is not currently well defined, operationally there are several methods of isolating and measuring its sensitivity. The most widely used method has been heterochromatic flicker photometry, in which two differently colored spatially coincident stimuli are alternated with each other and the radiance of one stimulus is adjusted so as to minimize an observer's subjective impression of flicker. At suitably high flicker frequencies the flicker can be abolished, leaving no perception of color changes. Presumably only the color-blind luminance system, and not the chromatically opponent systems that signal color, can follow this rapid flicker. On this view, the flicker photometric null corresponds to a condition in which the alternating stimuli are equal in their effect on the luminance system.

Besides eliminating participation of the chromatic systems, flicker photometry has other advantages. First, the settings can be made with ease and high reliability. Second, there is evidence, discussed below, that the luminance channel sums linearly the signals from red and green cones. This facilitates estimation of the cone sensitivities.

The combination of flicker photometry and chromatic adaptation holds promise for the study not only of the response properties of different cone types but of receptor level adaptation, which has been demonstrated to occur physiologically.^{8,9} But this approach has not been much exploited. An exception is the work of DeVries,¹⁰ who presented flicker photometric stimuli as increments upon larger red, blue, or

green steady backgrounds. DeVries found that for normal observers, the ratio of test sensitivities at 550 and 654 nm obtained in the presence of sufficiently intense red or blue backgrounds coincided with the ratios from protanopes or deuteranopes, respectively: a simple result but, it is argued below, a surprising one.

We combined flicker photometry and chromatic adaptation and have shown that the properties of heterochromatic additivity and transitivity, commonly ascribed to flicker photometry, could be extended to more general conditions of light adaptation. We also demonstrated a previously unsuspected interaction between red and green cones unique to the luminance channel, which resulted in flicker photometric sensitivity (FPS) being determined almost exclusively by either the red or the green cones alone when the test stimuli are presented upon greenish or reddish backgrounds, respectively.

METHOD

Apparatus

The apparatus was a three-channel Maxwellian view system. We used a G.E. Quartzline lamp rated at 120 V, 200 W, but run at 100 V. The beam supplying the test stimulus passed through a Bausch & Lomb grating monochromator with a bandwidth of 7 nm. Interference filters from Ealing and Baird Atomic were used in both the background and the standard channels along with Kodak Inconel and Ealing neutral density filters. The standard and test were modulated sinusoidally out of phase by means of a rotating polarizer spinning between two out-of-phase polarizers and the light source. The subject could adjust the radiance of the test by means of a servopot connected to a Kodak 2.0-log-unit neutral density Inconel wedge. Observers used dental impressions to ensure a stable position of the beams in the pupil.

Calibration

Precise calibration was imperative.

The monochromator was calibrated against a mercury-cadmium lamp with a precision better than 0.5 nm. We verified that there was no significant stray light of inappropriate spectral composition.

The wedge was calibrated at 20° intervals by using a 555-nm test by a *P-I-N* 10 DP silicon photodetector from United Detector technology connected to a low noise amplifier that was connected in turn to a digital voltmeter. The system was checked for linearity. Graphical interpolation with a smooth curve fitted by eye through the measured points was used to infer wedge density at intermediate points. To minimize stray radiation, the test beam passed through blackened cardboard tubing, an iris diaphragm, three pieces of heat-absorbing glass, and a filter that roughly matched the sensitivity of the cell to that of the eye (the "photopic filter"), before incidence on the photocell, which was located behind the wedge. Insertion of long-wavelength-passing filters verified that infrared radiation was not measurably present at the photocell. The wedge was checked for spectral neutrality every 80° by using representative wavelengths, and small corrections up to 0.02 log unit were made. Calibration was verified by insertion of a precisely calibrated Ealing 1.0 neutral density filter into the test beam, which ensured that several

positions determined to differ in density by 1.0 did in fact differ by that amount.

To determine the relative energy output for the different wavelength tests at the pupil, we used a nulling method. We positioned an EG&G Radiometer/Photometer (model 450-1) at the common focus of the test and standard beams, with the calibrated (see below) photopic filter in place to eliminate infrared. The test and standard were alternated at 15 Hz, and the neutral density wedge was adjusted so as to eliminate the 15-Hz component in the photocell output, monitored by using a General Radio 1900 wave analyzer. This was done for wavelengths of 500–650 nm in 10-nm steps on three separate occasions. Wedge position and transmittance of the photopic filter were used to infer relative energy output of the test beam as a function of wavelength. The spectral sensitivity of the cell was compared with the spectral sensitivities of three radiometric detectors, including the *P-I-N* 10 DP. The spectral sensitivity of the *P-I-N* 10 DP had been calibrated with a claimed tolerance of 2% in relative sensitivity by Optronics Laboratories of Silver Spring, Maryland. All four cells agreed to within their specified tolerances, so the *P-I-N* 10 DP, which had the smallest tolerance, was used as a standard for calibrating the EG&G cell. The photopic filter was itself calibrated in the system using the *P-I-N* 10 DP.

Procedure

The subject fixated a 1.5° test spot centered upon a 7° spectrally colored adapting background field. A 589-nm standard, with a peak luminance typically about 8–17% that of the background, was flickered at 15 Hz in sinusoidal counterphase with a variable test light whose radiance was adjusted by the subject to eliminate or minimize subjective flicker, thus by definition making the standard and test flicker photometrically equivalent. The 15-Hz flicker rate was sufficiently high to eliminate subjective color fluctuations. For each background wavelength μ , we measured sensitivity [i.e., the reciprocal of the test radiance (energy units) required for a flicker null] at a number of test wavelengths λ at 10-nm intervals from 500 to 650 nm when possible. The subject made four settings at each test wavelength and thus generated a flicker photometric sensitivity function $[FPS_{\mu}(\lambda)]$.

Subjects

Seven adults aged 19–28 served as observers: three males with normal color vision, AE, RM, and JW; three females with normal color vision, MH, LF, and HO; and one female deutan carrier, CT. One observer, AE, served as a subject for all experiments to be reported, and unless noted otherwise the results refer to his data. His dark-adapted flicker photometric sensitivity is very nearly equal to the CIE V_{λ} for $\lambda \geq 520$ nm. (See Table 1.) His foveal unique yellow is 578 ± 1 nm.

RESULTS AND DISCUSSION

Not unexpectedly, the backgrounds change relative flicker photometric sensitivity (see for instance, Fig. 3, discussed below). However, the following observations show that $FPS_{\mu}(\lambda)$ is dependent only on the background and not on the spectral composition or the radiance of the standard (within limits), and so a flicker photometric equivalence relation and $FPS_{\mu}(\lambda)$ can be unambiguously defined. That is to say, flicker photometric equivalence (for a given background) is transitive and invariant with intensity.

Table 1. The Ratio w_{G_μ}/w_{R_μ} for Different Backgrounds, Where $FPS_\mu(\lambda)$ is Modeled by $w_{R_\mu}R(\lambda) + w_{G_\mu}G(\lambda)$ with Vos and Walraven's $R(\lambda)$ and $G(\lambda)$, Normalized to Reflect the Relative Contributions to the CIE Standard Luminosity Function^a

No.	μ	td	w_{G_μ}/w_{R_μ}	rms	λ_L	Runs	$R(\mu)/G(\mu)$	$\frac{w_{G_\mu}/w_{R_\mu}}{R(\mu)/G(\mu)}$
1	457	400	0.17	0.008	650	1	1.39	0.122
2	500	700	0.21	0.013	650	4	0.928	0.226
3	500	2820	0.10	0.011	640	1	0.928	0.108
4	541	530	0.42	0.006	650	2	1.45	0.290
5	563	520	1.20	0.013	650	1	1.80	0.667
6	574	460	1.68	0.005	650	4	2.19	0.767
7	574	1820	2.50	0.009	610	1	2.19	1.14
8	584	430	1.96	0.011	650	1	2.62	0.748
9	601	600	4.86	0.008	640	1	4.18	1.16
10	601	2410	≈ 25.00	0.015	600	1	4.18	5.98
11	619	850	8.60	0.009	650	1	7.43	1.16
12	619	3500	≈ 100.00	0.010	600	3	7.43	13.50
13	656	780	15.75	0.006	640	4	21.10	0.746
14	656	3260	≈ 60.00	0.009	620	1	21.10	2.84
15	681	410	15.10	0.008	640	1	25.30	0.597
16	NB ^b	0	0.95	0.013	650	1	—	—

^a The rms column shows the rms deviations, in log units, of the data from the additive model using the entries in the w_{G_μ}/w_{R_μ} column. Test wavelengths ranged from 520 nm to λ_L in 10-nm steps for each background. Runs column shows the number of sessions used in computing $FPS_\mu(\lambda)$. $R(\mu)/G(\mu)$ shows the ratio of the cone sensitivities at the background wavelength. Final column tests Eq. (1) (see text), which predicts constant values.

^b NB, no background.

Transitivity

Transitivity was verified by using standards of 541 and 589 nm and a third metameric with a spectral light of 678 nm. These were presented upon three backgrounds: 500 nm at 700 trolands (td), 574 nm at 460 td, and 619 nm at 3500 td. The standard luminance was 8–17% of the background luminance. The test wavelength λ ranged from 500 to 650 nm and from 510 to 600 nm for the 500- and 619-nm backgrounds, respectively (in 10-nm steps), and was 530, 580, or 630 nm for $\mu = 574$ nm. Figure 1 shows the deviations of each $FPS_\mu(\lambda)$ from the values found by using a 589-nm standard. The root-mean-square (rms) deviations from transitivity were small, ranging from 0.007 to 0.013 log unit for the five spectral traverses shown. The irrelevance of the spectral composition of the standard is bolstered by other observations¹¹ that $FPS_\mu(\lambda)$ was essentially the same as the spectral sensitivity for detection of 15-Hz sinusoidal flicker of a single test stimulus upon backgrounds of 500 nm at 700 td, 574 nm at 640 td, and 619 nm at 3500 td.

Heterochromatic Additivity

We next tested to see whether heterochromatic additivity could be extended from dark- to light-adapted conditions.

Heterochromatic additivity can be defined as follows. Two conditions must be satisfied. The first is Abney's law. For any three test lights A, B, and C, $A \leftrightarrow_\mu B$ (that is, A is flicker photometrically equivalent to B upon a background of wavelength μ) if and only if $A \oplus C \leftrightarrow_\mu B \oplus C$, where $A \oplus B$ refers to the superposition of lights A and B. The second condition is that of invariance. $A \leftrightarrow_\mu B$ if and only if $t \cdot A \leftrightarrow_\mu t \cdot B$. That is, two test lights that are flicker photometrically equivalent remain so if they are either increased or decreased in radiance by the same factor.

To verify the invariance property, we measured $FPS_\mu(\lambda)$ for backgrounds of 500 nm at 700 td, 574 nm at 460 td, and 656

nm at 780 td, using standards of 150 td and 75 td. The differences between the values obtained with the two standard luminances as a function of λ are shown in Fig. 2. Since the usual standards were generally about 0.8 log unit above flicker threshold, by extrapolating downward there is a range of at least 1.1 log units, or a factor of 12 or more, over which the standard radiance can change without altering flicker photometric equivalence. (The equivalence could hardly hold for relatively high test radiances, for the tests would then function as adapting stimuli themselves.) The extrapolation down to threshold is supported by the observation that $FPS_\mu(\lambda)$ was essentially the same as the spectral sensitivity

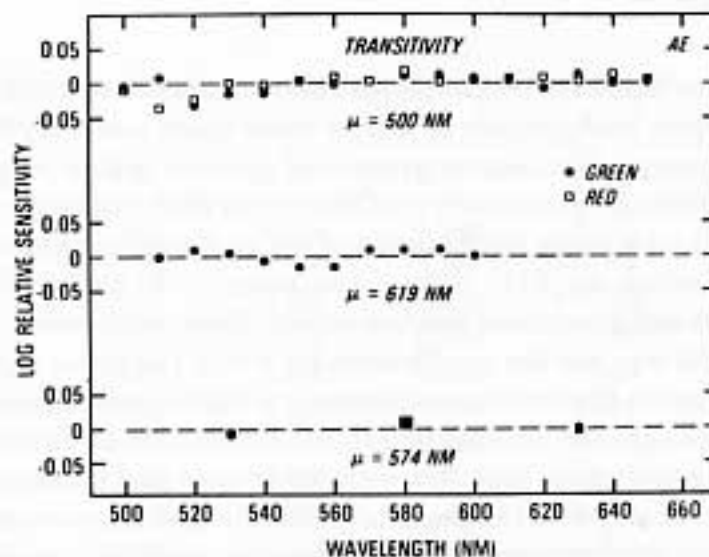


Fig. 1. Ratio of flicker photometric spectral sensitivity obtained by using a 678-nm standard (open squares) or a 541-nm standard (solid circles) to flicker photometric spectral sensitivity obtained by using the usual 589-nm standards. The standard luminance was 75 td for $\mu = 500$ nm (at 700 td) and for $\mu = 574$ nm (at 460 td); it was 300 td for $\mu = 619$ nm (at 3500 td). The data have been vertically translated so that the average deviation is zero.

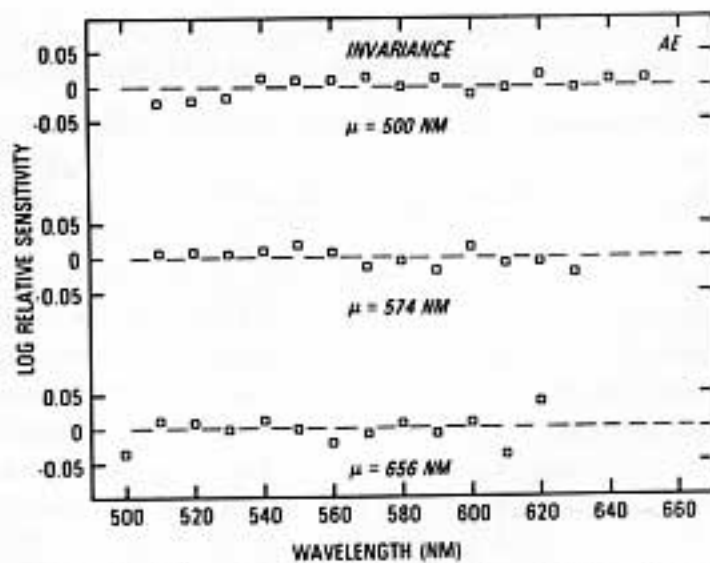


Fig. 2. Ratio of flicker photometric spectral sensitivity obtained with a standard of twice the usual radiance to flicker photometric spectral sensitivity obtained by using the usual 589-nm standards (75 td for $\mu = 656$ nm). The rms deviations from invariance are 0.016 log unit for the 500-nm background, 0.014 log unit for the 574-nm background, and 0.013 log unit for the 656-nm background.

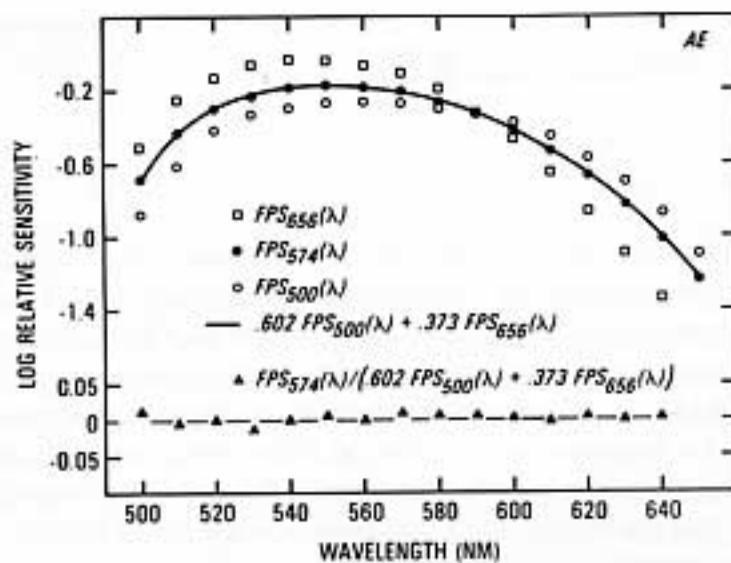


Fig. 3. Top: $FPS_{\mu}(\lambda)$ for $\mu = 500$ nm at 700 td (open circles), for $\mu = 574$ nm at 460 td (solid circles), and for $\mu = 656$ nm at 780 td (open squares) along with the additive combination of $FPS_{500}(\lambda)$ and $FPS_{574}(\lambda)$ constrained to coincide with $FPS_{574}(\lambda)$ at $\lambda = 540$ and 630 nm. Here and elsewhere, sensitivities are computed on an energy basis. Bottom: Deviation of additive combination of $FPS_{500}(\lambda)$ and $FPS_{656}(\lambda)$ from $FPS_{574}(\lambda)$.

for detection of a single 15-Hz sinusoidally alternating test spot upon backgrounds of any of these three wavelengths.¹¹

Apparatus limitations prevented a direct test of Abney's law. Instead, we verified it indirectly by demonstrating that $FPS_{\mu}(\lambda)$ is a linear combination of red and green cone spectral sensitivities, $w_R R(\lambda) + w_G G(\lambda)$, where $R(\lambda)$ and $G(\lambda)$ are the red and green cone spectral sensitivities, respectively, and w_R and w_G are the coefficients by which the input of each cone type to the luminance channel is weighted in the presence of a background of wavelength μ . Given this additivity of cone sensitivities, together with invariance and transitivity, and assuming also the physical principle that the cone quantum catches [represented by the intensity-sensitivity products $R(\lambda_A)I_A$, etc.] from any two incoherent stimuli are simply added when the stimuli are superimposed, it follows that $A \oplus C \rightarrow B \oplus C$ if and only if

$$w_R[R(\lambda_A)I_A + R(\lambda_C)I_C] + w_G[G(\lambda_A)I_A + G(\lambda_C)I_C] \\ = w_R[R(\lambda_B)I_B + R(\lambda_C)I_C] + w_G[G(\lambda_B)I_B + G(\lambda_C)I_C].$$

By subtracting the terms pertaining to C from both sides, we see that this condition is satisfied if and only if $A \rightarrow B$. Thus the additivity of cone sensitivities implies Abney's law.

We took two approaches in order to verify that $FPS_{\mu}(\lambda) = w_R R(\lambda) + w_G G(\lambda)$.

The first combined two observations. First, the invariance property alone implies that $FPS_{\mu}(\lambda) = [K_1 R^{n_{\mu}}(\lambda) + K_2 G^{n_{\mu}}(\lambda)]^{1/n_{\mu}}$; n_{μ} is an exponent that depends on the background μ . Otherwise, the shape of $FPS_{\mu}(\lambda)$ would have to change with test radiance.¹² When $n_{\mu} = 1$, $FPS_{\mu}(\lambda)$ is a linear combination of red and green cone spectral sensitivities. Second, experiments described below show that sensitivities obtained with different backgrounds are linearly related: i.e., for any μ , $FPS_{\mu}(\lambda)$ can be represented as a linear combination of $FPS_{\mu_1}(\lambda)$ and $FPS_{\mu_2}(\lambda)$ for some given μ_1 and μ_2 . We call this property of $FPS_{\mu}(\lambda)$ mutual linear dependence. Together with invariance, this means that there exist a_{μ} and b_{μ} such that

$$FPS_{\mu}(\lambda) = [w_R R^p(\lambda) + w_G G^p(\lambda)]^{1/p} \\ = a_{\mu} [w_{R_{\mu_1}} R^n(\lambda) + w_{G_{\mu_1}} G^n(\lambda)]^{1/n} \\ + b_{\mu} [w_{R_{\mu_2}} R^m(\lambda) + w_{G_{\mu_2}} G^m(\lambda)]^{1/m}$$

for any background μ . This implies (see Appendix 1 of Chap. 2 in Ref. 11 for a proof) that $n = m = p = 1$, so that $FPS_{\mu}(\lambda) = w_R R(\lambda) + w_G G(\lambda)$.

To see whether $FPS_{\mu}(\lambda)$ could be represented as a linear combination of $FPS_{\mu_1}(\lambda)$ and $FPS_{\mu_2}(\lambda)$, we chose for observer AE representative backgrounds $\mu_1 = 574$ nm at 460 td, $\mu_2 = 500$ nm at 700 td, and $\mu_3 = 656$ nm at 780 td. For observer RM, the luminances were reduced to 350 td at 500 nm and 390 td at 656 nm. Both observers produced four sets of data, which were then averaged for each background. The rms deviation from mutual linear dependence across all test wavelengths $\lambda = 500$ –640 nm was less than 0.006 log unit for AE (see bottom of Fig. 3) and less than 0.012 log unit for RM. AE's sensitivities exhibited no systematic deviation from mutual linear dependence; they apparently reflect only random error. In fact, his average standard errors of the mean (SEM) based on between-session variation are as large as, or larger than, the deviations from mutual linear dependence; they are 0.0067, 0.0057, and 0.0065 log unit for the three different backgrounds.¹³ RM may have very slight deviations (easily within experimental error) from mutual linear dependence, which (with one exception) were less than 0.02 log unit at all wavelengths. Abney's law therefore survives this test rather well.¹⁴

Our second check on whether $FPS_{\mu}(\lambda)$ is a linear combination of red and green cone sensitivities was to see if it could be described by a weighted sum of Vos and Walraven's¹⁵ particular estimates of those sensitivities, $R(\lambda)$ and $G(\lambda)$. Here and throughout this paper we use italic R and G for the (unknown) true sensitivities and roman R and G for Vos and Walraven's estimates of them. We argue below that the estimates are quite accurate, at least for observer AE.

From Table 1 we can see that all AE's data, using backgrounds from $\mu = 457$ nm through $\mu = 681$ nm as well as zero background, can be modeled by weighted sums of $R(\lambda)$ and $G(\lambda)$ for $\lambda \geq 520$ nm (Ref. 16), where individual differences in preretinal absorption are relatively small. Even if $R(\lambda)$ and $G(\lambda)$ do not themselves represent AE's cone spectral sensitivities, this result implies mutual linear dependence among all $FPS_{\mu}(\lambda)$.

The mean data for a 574-nm background at 460 td are displayed in Fig. 4 along with the additive fit. If we attempt to model $FPS_{574}(\lambda)$, $\lambda \geq 520$ nm, by $[K_1 R^n(\lambda) + K_2 G^n(\lambda)]^{1/n}$, then the smallest rms deviation occurs at $n = 1.0$, when n is adjusted in increments of 0.1.¹⁷ The only systematic deviation from additivity of more than 0.01 log unit in Table 1 is an excess sensitivity of about 0.02 log unit at $\lambda = 520$ with both 500-nm backgrounds.

Similarly, we might expect that RM's data be expressible as weighted sums of $R(\lambda)$ and $G(\lambda)$ to the extent that his $FPS_{574}(\lambda) = K_1 FPS_{500}(\lambda) + K_2 FPS_{656}(\lambda)$. But they cannot. For instance, if the additive prediction based on $R(\lambda)$ and $G(\lambda)$ is fitted to the data at $\lambda = 540$ nm and $\lambda = 620$ nm for $FPS_{574}(\lambda)$, then it systematically errs by up to 0.04 log unit at intermediate test wavelengths. Likewise, $FPS_{500}(\lambda)$ cannot be modeled without similar systematic errors. This can be reconciled with the finding of mutual linear dependence by supposing that at least one of RM's cone spectral sensitivities is not itself a linear combination of $R(\lambda)$ and $G(\lambda)$. We will present corroborative evidence in the section on red cone isolation below.

Even though FPS is additive, other measures of sensitivity may not be. Figure 5 shows spectral sensitivity for detection of a steady 1.5° test spot upon the usual 574-nm background. Clearly, additivity fails for this measure of sensitivity.

Isolation of Response from One Class of Cone

DeVries¹⁰ measured flicker photometric sensitivity for $\lambda = 550$ and $\lambda = 654$ nm. With a blue background (8000 td) and a red background (10,000 td), normal observers showed the same ratio of sensitivities as deuteranopes and protanopes, respectively. We have found, as these data of DeVries might suggest, that appropriately colored steady backgrounds of only several thousands, or even hundreds, of trolands can isolate or nearly isolate the response from only one class of cone.

Red Cone Isolation

On the basis of convergent evidence presented below, it appears that practically complete red cone isolation for $\lambda \geq 520$ nm could be obtained in six of seven individuals by use of a steady 500-nm background of no more than 1000 td; the sev-

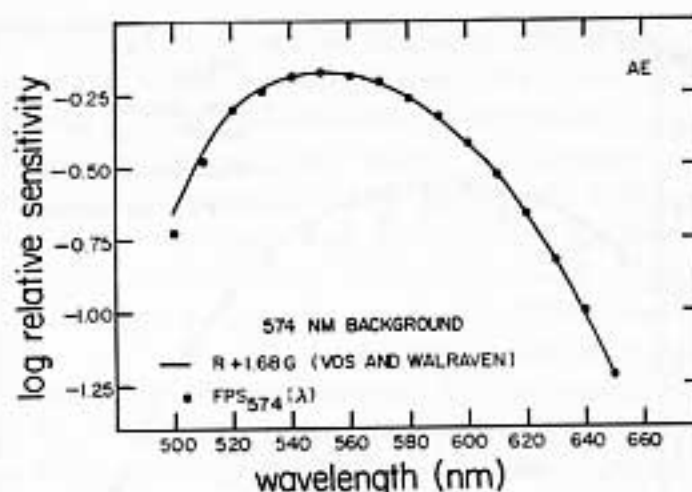


Fig. 4. Flicker photometric spectral sensitivity for a 574-nm, 460-td background [$FPS_{574}(\lambda)$] along with linear combination of Vos and Walraven's $R(\lambda)$ and $G(\lambda)$ constrained to coincide at $\lambda = 540$ and 620 nm.

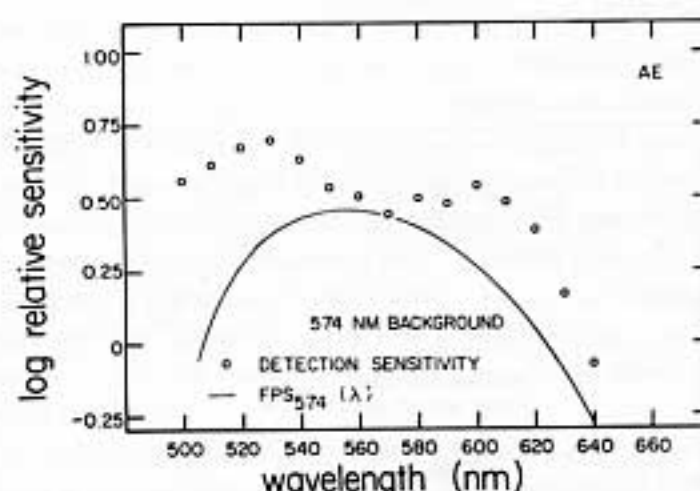


Fig. 5. Spectral sensitivity for detection of a steady 1.5° test spot upon a 574-nm, 460-td background, compared with $FPS_{574}(\lambda)$.

enth (AE) required somewhat higher background levels. Individual differences in preretinal absorption make it difficult to ascertain isolation for $\lambda \leq 520$ nm with a curve-fitting approach.

Mean data from each of these seven individuals are tabulated in Table 2 and are plotted in Fig. 6. Unexpectedly, the

Table 2. Flicker Photometric Spectral Sensitivity for All Seven Observers with a 500-nm Background [$FPS_{500}(\lambda)$]^a

λ	AE	MH	LF	HO	CT	Mean	S.D.	$R(\lambda)$	RM	JW	Mean
520	0.322	0.348	0.259	0.326	0.306	0.314	0.030	0.279	0.260	0.265	0.263
530	0.386	0.389	0.368	0.397	0.385	0.386	0.011	0.377	0.324	0.324	0.324
540	0.429	0.424	0.421	0.443	0.428	0.430	0.007	0.436	0.366	0.342	0.354
550	0.467	0.467	0.474	0.476	0.466	0.470	0.005	0.469	0.400	0.400	0.400
560	0.485	0.480	0.482	0.479	0.484	0.482	0.007	0.487	0.406	0.418	0.412
570	0.480	0.475	0.472	0.476	0.494	0.479	0.009	0.489	0.410	0.419	0.415
580	0.457	0.452	0.449	0.457	0.466	0.456	0.006	0.474	0.394	0.395	0.395
590	0.437	0.436	0.424	0.409	0.426	0.426	0.011	0.441	0.372	0.375	0.374
600	0.383	0.372	0.385	0.379	0.387	0.381	0.006	0.390	0.338	0.346	0.342
610	0.316	0.311	0.323	0.307	0.319	0.315	0.006	0.316	0.277	0.274	0.276
620	0.211	0.217	0.223	0.208	0.218	0.215	0.006	0.214	0.189	0.184	0.187
630	0.078	0.081	0.100	0.082	0.064	0.081	0.013	0.070	0.070	0.076	0.073
640	-0.092	-0.081	-0.070	-0.088	-0.094	-0.088	0.010	-0.102	-0.110	-0.084	-0.097
650	-0.317	-0.303	-0.285	-0.305	-	-0.303	0.013	-0.310	-0.307	-0.301	-0.303

^a Background was 350 td for MH, LF, and RM; 600 td for JW and CT; 990 td for HO; and 2820 td for AE. Data are divided by subjects into two clusters. $FPS_{500}(\lambda)$ is equated for the two clusters at $\lambda = 650$ nm. S.D. is standard deviation between observers. All entries are in log units.

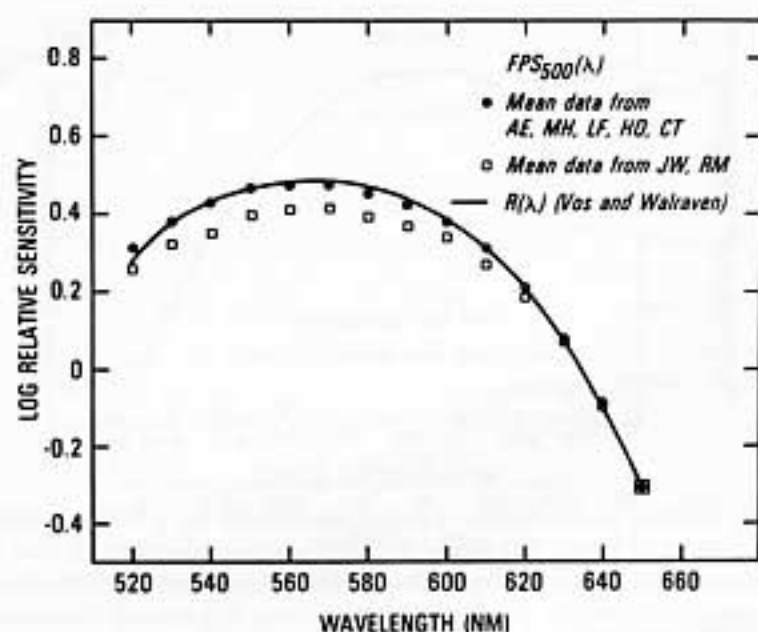


Fig. 6. $FPS_{500}(\lambda)$. The mean data for each group of observers are given. The modal cluster (solid circles) is compared with Vos and Walraven's $R(\lambda)$ (curve).

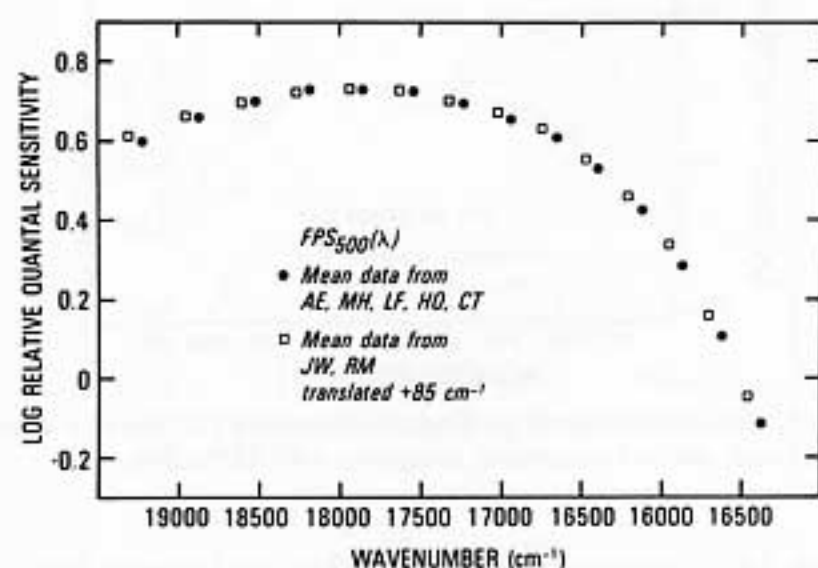


Fig. 7. Same as Fig. 8, but plotted as log quantal sensitivity versus wave number. Open squares have been translated $+85 \text{ cm}^{-1}$. No correction for preretinal absorption has been made.

data fall into two discrete clusters with different wavelengths of peak sensitivity.¹⁸ Data from the four females and one male (AE) comprise one cluster; data from the remaining two males (JW and RM) comprise the other. The data within each class are extraordinarily alike. If results for each person were individually plotted, few would lie outside the size of the data points of Fig. 6 (with the exception of $\lambda = 520 \text{ nm}$, for which individual differences in preretinal absorption are almost certainly greatest). Such interobserver agreement suggests that something fundamental is being measured. Vos and Walraven's $R(\lambda)$ fits the average data from the larger cluster very well (rms deviation of 0.012 log unit), suggesting that the combination of flicker photometry and chromatic adaptation to modest backgrounds can quite effectively isolate the response from the red cones alone.

Data for the remaining two observers cannot be fitted by $R(\lambda)$; nor can they be fitted by any linear combination of $R(\lambda)$ and $G(\lambda)$. However, cone spectral sensitivities of different individuals appear to differ by a transposition on the wave-number axis,¹⁹ and this could be the reason for the individual variation in these results. Figure 7 shows both sets of data

after the small cluster has been shifted 85 cm^{-1} to higher wave numbers. Except for a small discrepancy at the highest wave numbers that may be due to individual differences in density of macular pigment,²⁰ the transposed data are in good agreement. This is consistent with the notion that the cone spectral sensitivities differ only in λ_{max} when plotted as quantal sensitivity versus wave number.²¹ On the other hand, the individual variation could conceivably be due to differences in relative green cone contribution to $FPS_{500}(\lambda)$. However, anomaloscope Rayleigh matches made by one observer from each class (AE and JW) were markedly different, a finding that implies differences in cone spectral sensitivities.²² The measured difference in the matches was in excellent quantitative agreement with the difference predicted by assuming that each observer has green cones with the same spectral sensitivity $G(\lambda)$ (see below) but red cones with different spectral sensitivities, $R(\lambda)$ for AE and $R'(\lambda)$ for JW, where $R'(\lambda)$ is the spectral sensitivity resulting from a transformation of $R(\lambda)$ incorporating the 85-cm^{-1} shift. AE's red-green ratio required for a color match was 0.071 log unit higher than JW's. The predicted difference assuming the 85-cm^{-1} shift was 0.066 log unit. Furthermore, recall that for RM, $FPS_{574}(\lambda)$ could not be represented as a linear combination of $R(\lambda)$ and $G(\lambda)$ despite the fact that his data satisfied a stringent condition for additivity; it can, however, be represented as a linear combination of $R'(\lambda)$ and $G(\lambda)$ (rms deviation = 0.009 log unit).

One of the normal females, LF, appears to be very "red-rich,"²² for even against a yellow background her $FPS(\lambda)$ is very similar to $FPS_{500}(\lambda)$ for herself and the four other observers in her class (rms deviation of 0.02 log unit). Since a yellow background depresses the relative red cone contribution and a blue-green background enhances the relative red cone contribution, it seems clear that the 500-nm background would have isolated the red cones of this observer. Since her $FPS_{500}(\lambda)$ is virtually the same as everyone else's, the suggestion is that isolation was achieved for the other observers, too.

A number of investigators²³⁻²⁵ have proposed that π_5 could represent the red cone spectral sensitivity. Figure 8 shows $FPS_{500}(\lambda)$ for the red-rich observer, LF, compared with $R(\lambda)$ (solid line) and Stiles's π_5 (dashed line). If it is assumed that the red cone response is isolated for $\lambda \geq 610 \text{ nm}$ (see below), it follows that π_5 deviates by more than 0.05 log unit from red cone sensitivity at 610 nm if the two are equated at 650 nm. This deviation is well outside the range of error. Deviations

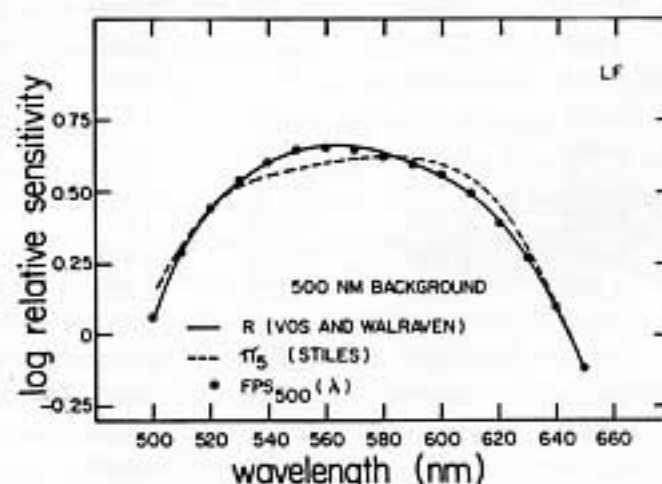


Fig. 8. $FPS_{500}(\lambda)$ for red-rich observer, compared with Stiles's π_5 and with Vos and Walraven's $R(\lambda)$.

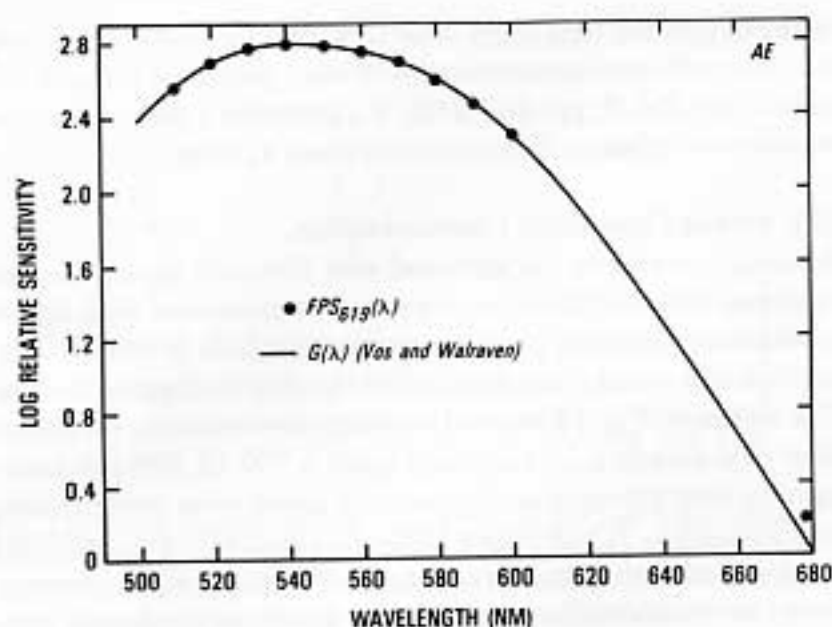


Fig. 9. $FPS_{619}(\lambda)$ compared with Vos and Walraven's $G(\lambda)$. The background luminance is 3500 td.

from π_5 using the other cluster of data (Fig. 6) would be even greater.

The color-matching experiment showed that the 500-nm backgrounds described above did produce a state of monochromacy to test increments of wavelength λ for $\lambda > 610$ nm. The apparatus was modified by inserting razor blades into the test channels to create a 1.5° bipartite field, which was centrally superimposed upon the 7° background field. The standard side of the field was deep red (Wratten 70 filter). The subject's task was to adjust the radiance of randomly presented test wavelengths on the variable side of the bipartite field in an attempt to match the standard in brightness and color if possible. The test wavelengths employed were from 595 to 630 nm in 5-nm steps. Failure to call the stimuli different in all four of four trials was the criterion of monochromacy. Two observers were employed. One, LF, was rendered monochromatic for $\lambda \geq 605$ nm against a 500-nm, 350-td background. The other, AE, was rendered monochromatic for $\lambda \geq 615$ nm against a 700-td background. Vos and Walraven's $R(\lambda)$ is in perfect agreement with $FPS_{500}(\lambda)$ across the range of monochromacy; π_5 is not.

Green Cone Isolation

Can green cones be isolated? The answer is a qualified yes. DeVries¹⁰ apparently isolated them by using deep red backgrounds of 10,000 td inasmuch as his spectral sensitivities agreed with those of protanopes. Our apparatus would not permit us to use such high background luminances. We found for observer AE that a red 656-nm background of 3260 td appeared nearly to isolate the green cones for wavelengths as long as 620 nm, where red cones ordinarily predominate; the contribution of $R(\lambda)$ to $FPS_{656}(620)$ was only about 8% of the green cone contribution [if we assume that Vos and Walraven's $G(\lambda)$ represents green cone spectral sensitivity (see below)]. More unexpectedly, we found that an orange background of 619 nm at 3500 td also appeared effectively to isolate the green cone contribution, or effectively to eliminate the red cone contribution, for $\lambda \leq 600$ nm (see Fig. 9). The rms deviation from $G(\lambda)$ was 0.011 log unit. Unfortunately, light limitations prevented us from determining $FPS_{619}(\lambda)$ for longer wavelengths in a straightforward manner.

We therefore employed the following method to determine $FPS_{619}(\lambda)$ for a long-wavelength test. We substituted a deep red Wratten 70 filter for the 589-nm interference filter ordinarily used in the standard beam. In our apparatus, the Wratten 70 transmitted red light metameric with a spectral light of about 678 nm. Test lights of 600 nm were flicker photometrically equated to this red standard. The relative sensitivity in the red, as compared with 600 nm, was found to be 0.64 ± 0.015 log unit greater with a 500-nm background than with a 619-nm background. The sensitivity in the far red in Fig. 9, $FPS_{619}(678)$, was derived by fixing it 0.64 log unit below $FPS_{500}(678)$ [= $R(678)$], with the two curves arranged to cross at 600 nm.

The far-red sensitivity can then be seen slightly to exceed that of the green cones alone, but only by about 0.14 log unit—this together with additivity allows us to deduce that in the presence of the orange background, the red cone contribution to FPS is depressed by a factor of more than 60 across the entire spectrum.²⁶

However, these orange backgrounds, especially at this intensity, may not in general depress the red cone contribution by so large a factor for all observers. Another normal observer, JW, required an 11,900-td background in order to show evidence of isolation across his measurable spectrum. Another inexperienced observer, HO, failed to produce reliable settings using a 2450-td background. However, a red 656-nm background of 2280 td apparently isolated her green cone response ($\lambda \leq 590$ nm). Data for both these observers are plotted in Fig. 10.

The convergence of the three sets of data is neither so complete nor so compelling as the convergence of $FPS_{500}(\lambda)$ upon $R(\lambda)$. We therefore felt it necessary to estimate green cone sensitivity by using an independent method, Brindley's artificial dichromacy technique.²⁷

The observer (AE) adapted to a 656-nm bleaching field of roughly 25,000 td for 1 min. During the period of green cone monochromacy immediately thereafter (in the spectral region where blue cone sensitivity is negligible), he viewed a bipartite 1.5° field consisting of a test (550- or 610-nm) and a 20-td 589-nm standard. The experimenter adjusted the radiance of the test before each trial haphazardly in a discrete series, and the subject responded that the test was either brighter or

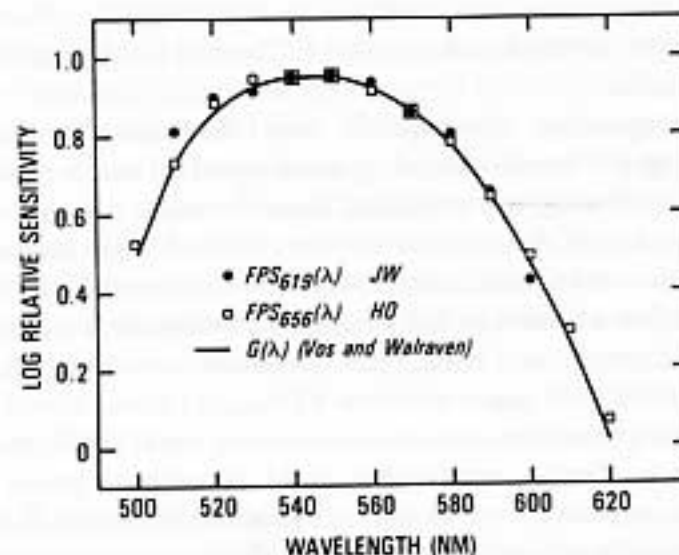


Fig. 10. $FPS_{619}(\lambda)$ at 11,900 td for observer JW and $FPS_{656}(\lambda)$ at 2280 td for observer HO compared with Vos and Walraven's $G(\lambda)$.

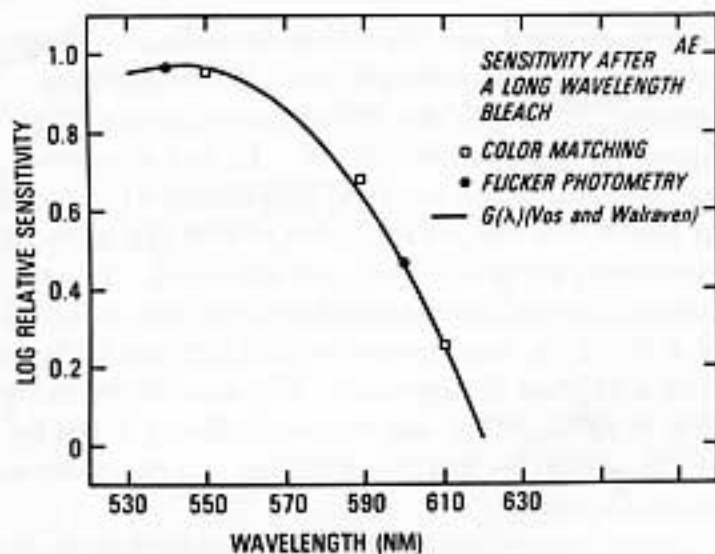


Fig. 11. Green cone sensitivity during artificial protanopia after bleaching with a 656-nm 25,000-td stimulus. Open squares are the sensitivity measured with color-matching data, and solid circles are that measured with flicker photometry; the curve is Vos and Walraven's $G(\lambda)$.

dimmer than the standard. Monochromacy was defined by the observer's subjective inability to detect any chromatic difference between the test and the standard at roughly equal luminance. The subject repeated the bleaching exposure at irregular intervals as necessary to obtain sufficient data. Sensitivity was determined by computing by linear interpolation the reciprocal of the radiance for which the subject would have responded "brighter" as often as "dimmer." Sensitivity was also determined at a third wavelength, $\lambda = 589$ nm, by requiring the subject to adjust the radiance of the 589-nm test to match it physically to the standard. The three sensitivities at $\lambda = 550, 589$, and 610 nm, which by the criterion of monochromacy can be identified with pure green cone sensitivities, are plotted as squares in Fig. 11. Self-screening corrections of about perhaps 0.006 log unit (Ref. 16) have been neglected.

A second check on green cone isolation was a flicker photometric version of Brindley's²⁷ technique. We measured FPS (without any background) using a 300-td 589-nm standard, after extinction of the bleaching stimulus during the period of verified monochromacy. The subject made a null setting within 10 sec of the termination of the bleaching stimulus. Each bleaching stimulus was presented at least 10 min after the presentation of the previous one. This was done four times for each of the two test wavelengths, 540 and 600 nm. Sensitivities are shown as dots in Fig. 11. Standard errors were 0.005–0.008 log unit. Clearly, $G(\lambda)$ provides an excellent fit.

An important observation was that long-wavelength bleaching produced a much greater spectral range of monochromacy, for a given standard, than the steady backgrounds did. In view of this greater efficacy of the bleach in eliciting green cone monochromacy, the convergence of $FPS(\lambda)$ obtained after a bleach with $FPS_{619}(\lambda)$ obtained in the presence of a background can only mean that isolation was practically complete in both cases and that $FPS_{619}(\lambda)$ does indeed coincide with green cone spectral sensitivity for $\lambda \leq 600$ nm.

It seems fairly certain that $G(\lambda)$ represents green cone spectral sensitivity quite well at least for $520 \text{ nm} \leq \lambda \leq 600$ nm. Stiles's π_4 cannot represent the green cone spectral sensitivity of any of the three observers, AE, JW, and HO, for it is too broad. If π_4 and $G(\lambda)$ are equated at 540 nm, then π_4

is about 0.07 log unit more sensitive than $G(\lambda)$ at 600 nm and 0.31 log unit more sensitive at 678 nm. As Stiles himself has noted (see Ref. 2, pp. 240–242), π_4 provides a more plausible estimate of green cone sensitivity than π_4 does.

FPS versus Chromatic Discrimination

Although a steady background can virtually eliminate the response of one or the other cone type as measured with flicker photometry (see the previous section), it fails to do so for detection of a steady test spot or for chromatic discrimination. For instance, Fig. 12 shows the spectral sensitivity for detection of a steady 1.5° test spot upon a 700-td 500-nm background that strongly suppresses the green cone contribution to $FPS_{500}(\lambda)$. It exhibits a hump at about 600 nm, implying a significant inhibitory green-cone-mediated effect on sensitivity at wavelengths at which the green cones do not contribute at all to FPS. Similarly, observers can distinguish a 678-nm red test light by hue from one of 600 nm when both are presented in a bipartite field upon the same 500-nm background that appears to suppress green cone contribution to FPS at both these wavelengths completely. Such chromatic discrimination implies that two cone types are functional.

Color appearance, too, seems at odds with FPS. For instance, a 656-nm test spot appears redder than the background when superimposed upon the same 619-nm background that so depresses the red cone contribution to FPS. Since the green cone contribution to $FPS_{619}(656)$ is more than three times the red cone contribution, we might have expected that the 656-nm test would have appeared greenish, or at least yellower, not redder, than the background. With these and other apparent contradictions in mind, we undertook the following experiment.

We determined the extent to which a steady background of either 656 nm at 3260 td or 619 nm at 3500 td rendered an observer dichromatic in a color discrimination task. The subject viewed a bipartite test field presented upon the background; the standard half was 563 nm and was either 150 or 300 td (the same luminance as the standard in the comparable flicker photometry experiment). The experimenter presented test stimuli of different wavelengths in random order in 5-nm steps, and the subject adjusted the radiance of the test half of the bipartite field in an attempt to match the standard in both color and brightness. The test was called different if and only if this was impossible. The results are shown in Fig. 13. The discrimination at long test wavelengths

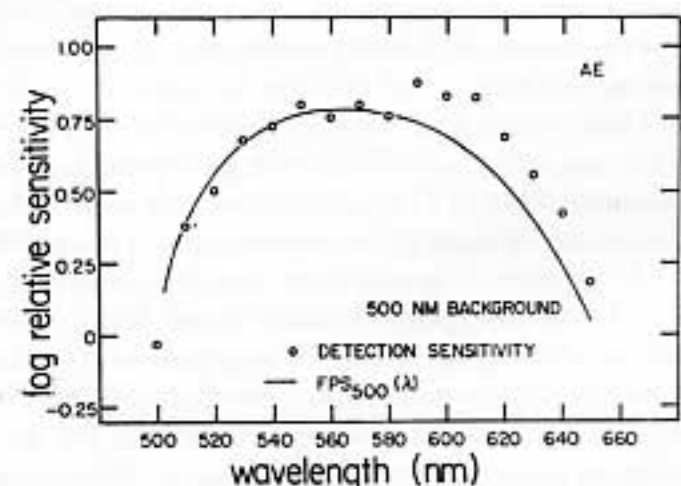


Fig. 12. Spectral sensitivity for detection of a steady 1.5° test spot upon a 500-nm 700-td background, compared with $FPS_{500}(\lambda)$.

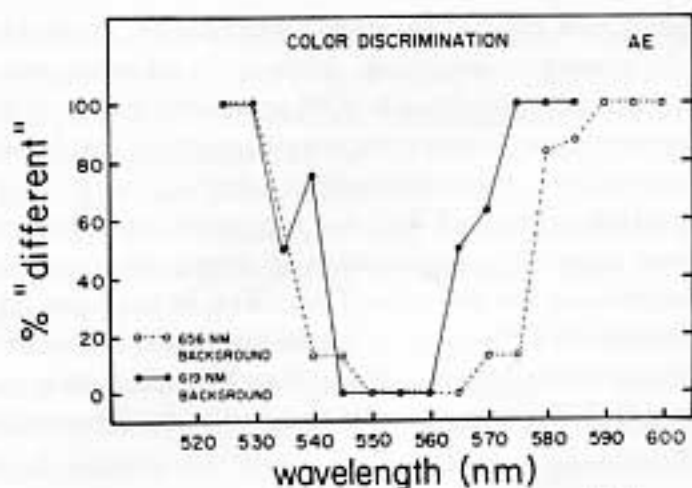


Fig. 13. Color discrimination: a 1.5° bipartite test field upon a 7° background field of either 619 nm at 3500 td (solid lines) or 656 nm at 3260 td (dashed line). The ordinate represents the percentage of times a randomly presented variable test was called "different" from a 563-nm standard at a minimally distinct border setting. Mean of two runs.

is of primary interest, since the discrimination at short wavelengths is almost certainly due to blue cone activation. Clearly, the 656-nm background was more effective in reducing the red cone contribution to chromatic discrimination than the 619-nm background was. However, Table 1 shows that the 619-nm background was at least as effective as the 656-nm background in reducing the red cone contribution to FPS. Thus the two criteria (FPS and color matching) apparently tap different processes of selective adaptation.

WHY IS THERE ISOLATION?

Chromatic backgrounds of quite modest luminance drastically reduce and may even effectively eliminate the contribution of the red or the green cones to $FPS_\mu(\lambda)$. For instance, a 500-nm background of less than 1000 td, by entirely eliminating any measurable green cone contribution to $FPS_{500}(\lambda)$, can completely isolate the red cone response. However, when other indices of cone sensitivity are employed, such as chromatic discrimination, there is no evidence of such complete isolation. *How can steady-state adaptation to a colored background so drastically bias the contribution of one cone type or the other to FPS while not doing so for most other measures of sensitivity?* Attempts to deal with this question constitute the remainder of this paper.

The problematic observation that adaptation to a steady chromatic background may eliminate the contribution of one cone type to FPS can be expressed by stating that if $FPS_\mu(\lambda) = w_{R_\mu}R(\lambda) + w_{G_\mu}G(\lambda)$, then either $w_{R_\mu}/w_{G_\mu} \rightarrow 0$ or $w_{G_\mu}/w_{R_\mu} \rightarrow 0$, depending on the background wavelength. As Rushton¹ has written, such a result would not be expected *a priori*. Our next step is to clarify what the *a priori* expectation might be, and why, in order to define more clearly the novel aspect of the results.

A Plausible but Inadequate Model

We can arrive at one set of predictions for w_{G_μ}/w_{R_μ} from a model involving four explicit assumptions, the first three of which have physiological and/or psychophysical support.

The first two assumptions concern the behavior of the red and green cone signals individually, before their combination into a luminance signal. Assumption (1) is that Weber's law

is satisfied, and assumption (2) is that small-signal linearity holds, so that a flickering test of radiance ΔI_λ against a background of radiance I_μ evokes a signal of amplitude proportional directly to sensitivity at the test wavelength and inversely to sensitivity at the background wavelength. Thus the signal amplitude for the green cones ΔV_G will be given by

$$\Delta V_G \propto [\Delta I_\lambda G(\lambda)]/[I_\mu G(\mu)],$$

and similarly for the red cones.

The remaining assumptions concern the manner in which the cone signals combine. Assumption (3) is that the flicker photometric value of a test light is given by the (weighted) sum of the signals from the red and green cones, that is, by

$$(\Delta I_\lambda/I_\mu)[k_G G(\lambda)/G(\mu) + k_R R(\lambda)/R(\mu)],$$

where the weighting factors k_G and k_R can incorporate postreceptoral factors, such as the numbers of the red and green cones and the gain of the neural pathways from each cone type. The measure of relative flicker photometric sensitivity is the reciprocal of the value of ΔI_λ required to keep this constant; thus, for a constant background wavelength,

$$FPS_\mu(\lambda) = w_{G_\mu}G(\lambda) + w_{R_\mu}R(\lambda),$$

where $w_{G_\mu} = k_G/G(\mu)$, and similarly for w_{R_μ} . This leads to the simple prediction

$$w_{G_\mu}/w_{R_\mu} = (k_G/k_R)[R(\mu)/G(\mu)]. \quad (1)$$

The final assumption, (4), is simply that k_G/k_R , the ratio of the weights applied to the cone signals, is fixed at a value independent of μ , in other words, that the only effect of the background is exerted through the operation of Weber's law within each cone system. With this assumption, Eq. (1) states that the two cone types contribute to $FPS_\mu(\lambda)$ in inverse proportion to their sensitivity to the background.

When compared with the observed values of w_{G_μ}/w_{R_μ} (Table 1), the predictions of Eq. (1) are in error by as much as 2 orders of magnitude. The selective suppression of red cone input by red backgrounds, or of green cone input by green backgrounds, is far greater than predicted. For example, in going from a 500-nm background to a 619-nm background, the relative weighting of the green cones is predicted to increase by a factor of 8:

$$\frac{w_{G_{500}}/w_{R_{500}}}{w_{G_{619}}/w_{R_{619}}} = \frac{R(500)/G(500)}{R(619)/G(619)} \approx 8.$$

But as Table 1 (column 4) shows, the observed increase in green cone weighting (for sufficiently intense backgrounds) is by a factor of about 1000. Comparison of these two backgrounds with an intermediate background, say 574 nm, shows that there is 1 order of magnitude too much isolation in each of the red and green directions. In general, Eq. (1) predicts that the values in the final column of Table 1 should be the same (for sufficiently intense backgrounds), an assumption that is clearly not fulfilled.

Finding the Flaw

Cone Spectral Sensitivities?

The weights given in Table 1 apply to the Vos-Walraven estimates of the red and green cone spectral sensitivities, and other estimates would lead to different weights. However,

no reasonable estimate of these spectral sensitivities can render the data consistent with the model of Eq. (1). Eisner¹¹ proved this by using the data for 500- and 619-nm backgrounds to derive hypothetical cone sensitivities that would be consistent with Eq. (1). The analysis was generalized so that k_G/k_R need not equal 1 from an analysis applied by Walraven *et al.*²⁸ to the case of colored preadaptation. The derived green cone sensitivity became negative in the red, which is clearly impossible. Moreover, sensitivities chosen to predict properly for some particular pair of backgrounds yield incorrect predictions for other backgrounds. These failures substantiate the impression that $FPS_\mu(\lambda)$ can indeed approach the sensitivity of one or the other cone type, rather than being a combination of the two with weights prescribed by Weber's law.

Weber's Law?

At least one of the four assumptions that led to Eq. (1) must be false. The assumption of fixed relative weights, (4), is the most suspect, since it alone has no experimental support. But before indicting it as the faulty assumption, we must consider whether modifying any of the other three assumptions could be sufficient to save the model. Assumption (1), Weber's law, is easily dealt with. Measurements of flicker threshold (at 15 Hz) as a function of background intensity¹¹ show that on the basis of Stiles's displacement rules, backgrounds numbered 3, 7, 10, 11, 12, and 14 in Table 1 were intense enough for Weber's law to be a good approximation for both the red- and the green-sensitive cone mechanisms. Besides, the known failure of Weber's law at low intensities is the wrong direction to improve the fit of the model! We have noted above that other indices of sensitivity under chromatic adaptation, namely, color discrimination, color appearance, and detection thresholds, qualitatively support the assumption of Weber's law for each cone mechanism.

Nonlinear Summation?

Assumption (2), that cone response is linear with incremental test radiance, is not likely to be much in error, since additivity seems to hold very well. Furthermore, if there were deviations from linearity taking the form of $\Delta V = c_0(\Delta I)^n$ (the form required by invariance of FPS with changing standard intensity; see the section on heterochromatic additivity), then the equation for flicker photometric sensitivity takes the form

$$FPS_\mu(\lambda) = [w_R R^n(\lambda) + w_G G^n(\lambda)]^{1/n}.$$

A high value of n reduces the effects of cooperation between different cone types and could lead to $FPS_\mu(\lambda)$ being close to $G(\lambda)$ in the spectral range where $w_G G^n(\lambda)$ exceeds $w_R R^n(\lambda)$. But by the same token, $FPS_\mu(\lambda)$ would then approximate $R(\lambda)$ in the rest of the spectral range. The results sharply

contradict this prediction from nonlinearity. Consider, for example, green cone isolation. Unless the inherent green cone and red cone contributions to FPS are vastly different in favor of the green cones, there exists a wavelength λ_0 (probably close to μ , the background wavelength) such that the red and green cone contributions to $FPS_\mu(\lambda_0)$ are equal, and nonlinearity could not create the appearance of green cone isolation for wavelengths on the red side of λ_0 . Yet, in fact, the red cone contribution to $FPS_{619}(678)$ is still appreciably less than the green cone contribution, even though in this case the test wavelength is far more extreme than the background wavelength.

Phase Effects?

What if the red and green cones responded with different phase lags to the flickering stimuli? Then $FPS_\mu(\lambda)$ would reflect a vectorial sum of red and green cone response rather than a linear sum. Presumably, any phase differences present would be frequency dependent, yet $FPS_\mu(\lambda)$ appeared to be independent of the frequency of alternation. For $FPS_{500}(\lambda)$ at 700 td with 20-Hz flicker and at 2820 td with 5-Hz flicker, there were nonsystematic rms deviations from the 15-Hz data of 0.012 and 0.019 log unit, respectively, no greater than the measured random error at these frequencies, and for $FPS_{619}(\lambda)$ at 3500 td ($\lambda = 540\text{--}610$ nm), data obtained during the same session using flicker frequencies of 15 and 5 Hz differed from each other by only 0.002 log unit rms.

We also measured the stimulus phase difference at 15 Hz required to minimize perceptible flicker, by enabling the observer to adjust the phase angle of a half-wave retarder in the standard beam as well as the radiance of the test beam. The stimulus phase difference required for least flicker, $\Delta\psi$, was not significantly different from zero for 500- or 650-nm tests on a 574-nm 460-td background. This indicates that the response phase difference $\Delta\psi$ was near zero as well. With reddish or greenish backgrounds, however, small phase adjustments were called for (Table 3). It is not clear how to translate these stimulus phase differences into response phase differences, because it is not clear what model of FPS to use in the analysis. By using the model that led to Eq. (1), the difference between the phase lags of the two cone types implied by the data of Table 3 was found to be usually less than 10° , in a direction depending on the background wavelength. The largest calculated phase difference, 23° , perturbs $FPS_\mu(\lambda)$ by less than 0.01 log unit and hence cannot contribute importantly to the deviations from Eq. (1).

The spectral variation of those deviations also provides further evidence that they are not due to phase differences. Consider again green cone isolation. The red cone contribution to $FPS_{619}(678)$ is only about one-third of the green cone contribution as determined empirically. But the We-

Table 3. Mean Stimulus Phase Shift $\Delta\psi$ Required by AE in Adjusting Both Test Intensity and Temporal Phase Difference between Test and 589-nm Standard in Order to Eliminate Subjective Flicker^a

Background Test	500 nm, 700 td	574 nm, 460 td	619 nm, 870 td	619 nm, 3500 td	656 nm, 780 td
500	$4^\circ \pm 1.3^\circ$	$1^\circ \pm 1^\circ$	$-4^\circ \pm 1.6^\circ$	$-3^\circ \pm 0.3^\circ$	$0^\circ \pm 0.4^\circ$
620	—	—	—	$6^\circ \pm 1.3^\circ$	—
650	$-2^\circ \pm 1.2^\circ$	$0^\circ \pm 1.6^\circ$	$4^\circ \pm 1.9^\circ$	—	$-3^\circ \pm 0.6^\circ$

^a SEM are computed from intrasession data. There were four observations for each background except for $\mu = 500$ nm, for which there were eight. Flicker rate was 15 Hz.

ber's law prediction with vectorial summation yields a function in which the red cone contribution dominates, whatever the phase relations. This would preclude green cone isolation at $\lambda = 678$ nm. Chapter 3 of Ref. 11 elaborates this and other arguments against the importance of phase. These include the observation of transitivity and the similarity of flicker threshold to flicker photometric or minimally distinct border sensitivities.

Rejection of the Fixed Weights Assumption

Presumably, there must be something wrong with assumption (4), which asserts that the cones feed their signals with fixed relative weights into a luminance system. That is, although it is true that $FPS_\mu(\lambda) = w_{R_\mu}R(\lambda) + w_{G_\mu}G(\lambda)$, the estimates for w_{G_μ}/w_{R_μ} prescribed by Weber's law only are incorrect, implying that some additional factor reduces the relative contribution from one cone type. Since other measures of cone sensitivity against large steady backgrounds never deviate (in the required direction) from Weber's law predictions, presumably the reason why these predictions are so much in error for FPS lies in the relation between the signals of the two cone types and the luminance system specifically. The colored backgrounds must change the ability of one cone type or the other or both to influence the luminance system, by some process additional to the known adaptational effects expressed in Weber's law. The actual existence of a luminance system is not called into question. Rather, the unique behavior and additivity associated with FPS strongly argue for its existence. In the discussion that follows, we begin by considering how the model of the luminance channel implicit in Eq. (1) must be modified.

GENERAL DISCUSSION

Model for Luminance-Specific Selective Suppression

The results imply that colored backgrounds exert a practically complete bias against one cone type at the input to the luminance system, a result seemingly sharply at variance with Weber's law. We have argued that this bias beyond that which is due to known adaptational effects is due to some sensitivity-modifying process associated solely with the luminance system, a conclusion implying that the chromatic pathways are already segregated from those of the luminance system at the unknown site where the additional suppression takes place.

A second aspect of the results that places an important constraint on models is the fact that what gets selectively suppressed (or escapes suppression) appears always to be simply the red or green cone signal, with no obvious contamination by the other cone type. This tendency toward isolation of one or the other cone signal in pure form by the steady colored backgrounds suggests that these cone signals are kept separate up to the site of the suppression. Since this site appears to follow the splitting of the afferent pathway into chromatic and luminance channels, and in this sense belongs to the luminance system, presumably the cone signals feed into that system without previous interaction. In particular, there is probably no significant previous color opponency, since negative weights were never needed in the description of FPS.

A third and final constraint on possible models is that the additional suppression is caused mainly by responses to the

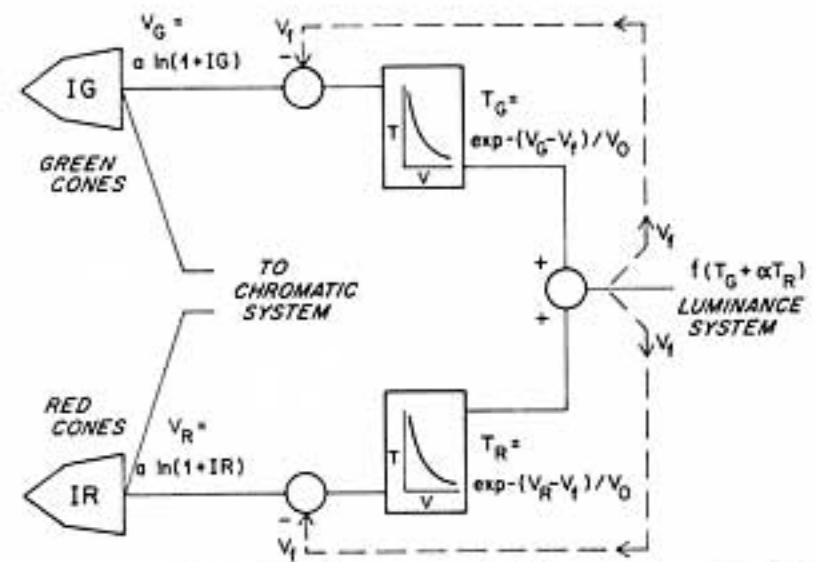


Fig. 14. A model for selective suppression of one cone type by colored backgrounds. The luminance signal is formed at the right by additive combination of signals originating in the green and red sensitive cones (upper and lower triangles at left).

steady background stimulation rather than by responses to the flickering test, for, otherwise, transitivity and additivity would have failed. More importantly, it seems clear that the suppression depends not only on the background level of excitation of the suppressed cones (cone-cone independence) but also on the balance of excitation between the two cone types. The reason for this is that the hypothesis of cone-cone independence provides no way to reconcile the validity of Weber's law, as background intensity varies with its failure for changes of background color, where, according to Table 1, the relative contribution of the suppressed cones in the presence of orange, red, or green backgrounds is reduced by factors that are at least the second or third power of the Weber's law predictions. Although this peculiarly strong influence of background color suggests that the suppression of the separate cone inputs might depend on some spectrally opponent response, there are two reasons why that response can hardly be the subjectively defined red-green opponent response of classical opponent-colors theory. First, if it were, we might perhaps expect that two tritanopic metamers, which excite the red and green cones in equal proportion, would produce different degrees of suppression of green cone input to the luminance channel, with a greenish 500-nm background suppressing green cone input more than its reddish 435-nm counterpart. But when this experiment was tried, we found that the 435-nm background was equally effective in suppressing green cones, giving practically the same spectral sensitivity as the 500-nm background [rms deviations from Vos and Walraven's $R(\lambda)$ were 0.017 log unit for the 435-nm background and 0.020 log unit for the 500-nm background; each background was about 1400 td]. Second, the neutral background, i.e., that background that leaves $FPS(\lambda)$ the same as with no background, lies (for AE) between $\mu_1 = 541$ nm and $\mu_2 = 563$ nm (see Table 1), by interpolation at about 555 nm. Lights of 555 nm would induce approximately equal quantum catches in red and green cones, if we assume equal peak densities. By comparison, with a subjectively pure yellow background (578 nm for AE), there was at least a threefold depression in the relative red cone contribution to FPS.

Figure 14 shows one scheme that meets all three requirements for models mentioned above. First, a logarithmic transformation of the red and green cone signals provides for

independent variation of their incremental sensitivities in accordance with Weber's law; the log transform is an inexact idealization of actual cone behavior, but it should suffice for illustrating the qualitative behavior of the model. Second, the afferent pathway from each cone type is split into parallel channels, one of which serves the luminance system and the other the chromatic systems. Figure 14 traces the further course of the luminance pathway only and shows how the luminance-specific selective suppression is imposed by a later compressive nonlinearity before the signals from red and green cones are finally added together. Overloading of this second nonlinear stage, which would result in deviations from Weber's law as background intensity changes, is prevented by an antagonistic signal at its input. As was noted above, the regulatory signal must include for each cone type a contribution from the other cone type. In Fig. 14, it is derived by feedback of the summed luminance signal. Models making a different assumption²⁹ would have difficulty in accounting for the observation that $FPS_{\mu}(\lambda)$ does not depend on the flicker frequency to any obvious extent.

Physiological identification of the elements of Fig. 14 can only be speculative. To preserve the needed separation of the cone inputs, one might locate the suppression at the cone synaptic membrane, with chromatic and luminance pathways leaving the receptors separately, perhaps via the flat and invaginating bipolars with their different synaptic connections. A quantitative formulation of the behavior of the second site is suggested by the exponential nonlinearity of transmitter release.³⁰ If this is characteristic of the retina, the rate of transmitter release from a cone would be proportional to

$$T = \exp(-V/V_0),$$

where V is the cone membrane hyperpolarization that is due to light and V_0 is a voltage scaling constant. Following Werblin,³⁰ we assume that feedback (from horizontal cells) subtracts a voltage V_f from the cone hyperpolarization. Thus the net hyperpolarization of the red cones becomes

$$V_R - V_f = a \ln \{1 + [I_{\mu}R(\mu) + I_{\lambda}R(\lambda)]/i\} - V_f,$$

where I_{μ} and I_{λ} are the corresponding intensities and i is an intensity scaling factor equal to the background excitation (or intensity-sensitivity product) required to reduce incremental sensitivity to one half. The rate of transmitter release (in arbitrary units) then becomes

$$T_R = \{1 + [I_{\mu}R(\mu) + I_{\lambda}R(\lambda)]/i\}^{-a/V_0} \exp(V_f/V_0). \quad (2)$$

The transmitter release from green cones, T_G , is described by a similar equation, with $G(\lambda)$ and $G(\mu)$ substituted for the red cone sensitivities. If $G(\lambda)$ and $R(\lambda)$ are scaled for equal sensitivity at peak, the final combination of the different cone inputs to form the luminance signal has to be weighted in favor of the red cones by a factor α in order to predict the dark-adapted luminosity curve correctly. As to the value of V_f , the simplest assumption is that the feedback loop adjusts this to hold the luminance output ($T_G + \alpha T_R$) practically constant in the steady state; this does not preclude sensitivity to the transients produced by a flickering test (or by fixational eye movements in normal circumstances). For small incremental test intensities, the influence of the test stimulus on V_f will be negligible, and V_f will satisfy

$$\exp(V_f/V_0) = \{[1 + I_{\mu}G(\mu)/i]^{-a/V_0} + \alpha[1 + I_{\mu}R(\mu)/i]^{-a/V_0}\}^{-1},$$

and the rate of transmitter release can be found by substituting for this in Eq. (2).

If later nonlinearities are neglected, the contribution of the green cones to the incremental sensitivity of the luminance system will be given by the value of dT_G/dI_{λ} for $I_{\lambda} = 0$. By differentiating Eq. (2) and simplifying, it can be shown that at high background intensities [$I_{\mu}G(\mu) \gg i$] this derivative is asymptotically inversely proportional to I_{μ} for any μ , a behavior consistent with Weber's law. The reason why Weber's law holds here for the whole system is that with variation of background intensity (whatever the background color) the net membrane potentials of both cone types are held approximately constant by the feedback loop. Such is not the case when background color changes, for then the hyperpolarization of the more stimulated cones will be too great (and that of the other cones too small) to be canceled by the feedback. For the more stimulated cones, then, the second nonlinear stage may be overloaded (the transmitter cut off) by the sustained response to the background, causing a blocking of their response to incremental inputs over and above the loss of sensitivity implied by Weber's law. A theoretical prediction for $[w_G G(\lambda)/w_R R(\lambda)]$, the relative contribution of the two cone types to luminance at wavelength λ , is given by the ratio of the derivatives of T_G and αT_R with respect to I_{λ} . This yields

$$w_G/w_R = (1/\alpha) \{ [1 + I_{\mu}R(\mu)/i] / [1 + I_{\mu}G(\mu)/i] \}^{1+a/V_0}.$$

As I_{μ} becomes large in relation to i , the ratio of the weights becomes highly sensitive to background color, being asymptotically proportional to $[R(\mu)/G(\mu)]^{1+a/V_0}$ or to the Weber's law prediction [Eq. (1)] raised to a power greater than 1. The high-intensity data of Table 1 suggest an exponent of about 3, which would suggest $a \approx 2V_0$. This is not unreasonable in the light of physiological evidence suggesting that both parameters should be of the order of a few millivolts.^{9,30} In view of the model's simplified character (with neglect of, for instance, membrane nonlinearities), there is no reason to expect that quantitative predictions would be accurate. Indeed, it completely fails to reproduce an important aspect of the results of Table 1: the fact that isolation is approached only at high background levels, with lower levels satisfying Weber's law. Nevertheless, the model does illustrate one plausible structural basis for the paradoxical coexistence of Weber's law with isolation of one cone type by colored backgrounds, and it shows how the isolation, though perhaps of no functional benefit itself, might be a consequence of a functionally desirable regulatory process designed to allow maximal use of the available response range.

Relation to Other Studies

The transitivity and additivity properties of FPS remain unaltered or perhaps hold even more exactly when the test and the standard are superimposed upon colored backgrounds. Ives³¹ found in 1912 that the color of the standard was irrelevant to the shape of the dark-adapted FPS curve, though Piéron³² reported (but did not document) failures of transitivity. Our study verifies transitivity for the light-adapted case. Tufts³³ verified a stronger generalization of Abney's law, and this has been verified several times since for the dark-adapted case.³⁴⁻³⁸ Invariance with the luminance of the standard was examined by DeVries,¹⁰ who found it to hold as long as the luminance was between 5 and 50 td. At greater intensities, more of the red test than the green was required

for a match, an effect also noted by Ives,³⁹ who named it the reversed Purkinje shift. Ingling *et al.*⁴⁰ found the reversed Purkinje shift for tests as low as 30 td. If, as seems likely, the reversed Purkinje shift reflects self-adaptation to the test, departures from invariance (and from additivity in general) would be reduced in the presence of a relatively more intense adapting background. Our results confirm that expectation: the nonsystematic deviations in our data are generally smaller than the systematic deviations of about 0.019 log unit in relative sensitivity to red and green found by Ingling *et al.* on doubling test intensities. The reversed Purkinje effect may therefore reflect adaptational sensitivity changes only and does not imply that signals from different cone types combine nonadditively in the luminance channel.

The results provide more evidence for the parallel processing of color and luminance,³⁻⁵ because we find excessive suppression of the signals originating in one class of cone only when using psychophysical procedures that are thought to tap the luminance channel. Other measures of sensitivity, such as chromatic discrimination and detection of a steady test spot, which appear to tap other channels, fail to manifest excessive suppression.

In fact, our results when viewed in this framework support Wald's⁴¹ claim of isolating cones using 40-msec test flashes upon intense colored backgrounds, for King-Smith and Carden⁴ have shown that the luminance channel enjoys an advantage over the chromatic channels in detecting brief test flashes. Thus Wald may have measured sensitivity through the luminance channel only, thereby aiding isolation of single classes of cones.

In retrospect, the complete suppression of the contribution of a cone type to FPS may be seen in the results of Ikeda *et al.*⁴² (their Fig. 5) and Ikeda and Urakubo⁴³ (their Fig. 7) as well as in the work of DeVries¹⁰ mentioned in the introduction.

The cone spectral sensitivities suggested by our data are almost identical with Vos and Walraven's¹⁵ and Smith and Pokorny's,⁴⁴ at least for $\lambda \geq 520$ nm, where these two sets agree. Actually, our data show individual variation with a suggestion of clustering of red cone spectral sensitivities, but the modal cluster has about the same spectral sensitivity as these estimates derived from a pigment loss model of dichromacy.

The field sensitivity method of Stiles² yields sensitivities defined by the intensities of various spectral backgrounds that produce the same visibility of a constant test. With the exception of π_4 (a green mechanism) and π_3 (a blue mechanism), the field sensitivities differ slightly from dichromat spectral sensitivities. Differences also appear when flickering tests, rather than flashes, are used.⁴⁵ Brindley's artificial monochromacy technique,²⁷ which measures test sensitivities after exposure to intense lights that render the observer monochromatic for the spectral range tested, yields sensitivities that are in agreement with those derived from dichromats and also with those derived here (Fig. 11). King-Smith and Webb⁴⁶ also combined chromatic adaptation with a test-sensitivity method and found agreement with dichromat sensitivities. They measured sensitivity using test flashes presented upon background flashes that transiently overloaded the competing cone mechanisms.

Certain test-sensitivity methods therefore yield spectral sensitivities that agree with dichromat data, whereas field sensitivities may generally not agree. The method described

in this paper is a test-sensitivity method that uses steady rather than very bright or flashed backgrounds. Its advantages are (a) precision, (b) elimination of the assumption of adaptive independence, and (c) the fact that the lights employed are not intense enough possibly to harm the eye.

Rushton,¹ as quoted in the introduction, wrote that "most who use [chromatic adaptation] find it sufficient to assert that they have 'isolated' a single pigment without any justification whatever of that assertion." We have made the assertion; we hope that we have convinced the reader of its justification.

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13. For any given background the sensitivities from each session were multiplied by a normalizing factor before the between-sessions SEM were computed. This translation minimizes the small, but almost inevitable, changes in sensitivity that are due to changes in the apparatus and in the subject's position between sessions. The remaining variance after translation is therefore a more accurate measure of any variation in relative spectral sensitivity.
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17. Suitable coefficients for fitting the data by using different values of n were found by constraining the fits to be exact at $\lambda = 540$ nm and $\lambda = 620$ nm. Subject to this constraint, the least-squares value of n was calculated as the value for which the sum of the deviations of log sensitivity from prediction, each weighted by its derivative with respect to n , was zero; this gave $n = 1.03$. From the rms errors of prediction, the probability of the observed data could be derived as a function of n . The resulting 95% limits for n were 0.92 and 1.18. It should be stressed that, whereas this implies that the summed time-varying signals from each cone type are nearly linear with test stimulus intensity, the data place no strong constraint on the extent of nonlinearity as a function of total intensity, since the test increments were always small in relation to the steady background.
 18. Despite the small number of observers, the evidence for clustering is statistically significant. In the larger cluster of five observers, relative sensitivity to red and green is so uniform that even if all the observed variation between observers were due to variation in the wavelength of peak absorption in the red cones, the rms interobserver variation in that wavelength would be only 0.3 nm. A good estimate of the standard deviation of peak absorption wavelength between observers in a population of deuteranopes is 2.8 nm [based on the data of M. Alpern and T. Wake, "Cone pigments in human deutan vision defects," *J. Physiol.* **266**, 595-612 (1977) and Alpern and Pugh (Ref. 19)]. Reference to the chi-square distribution for 4 degrees of freedom shows that the probability of a standard deviation of 0.3 nm or less in a sample of five from a population standard deviation of 2.8 nm is only 0.03%; the probability that at least one group of five in a sample of seven will be as uniform is only 0.6%. The agreement between the remaining two observers is equally striking.
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